Influence of Soil Temperature on the Expression of Yellows and Wilt of Crucifers by *Fusarium oxysporum*

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ABSTRACT

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The effect of soil temperature (10–24 C) on disease expression by five pathotypes of *Fusarium oxysporum*, the incitant of yellows and wilt on crucifers, was investigated in soil temperature tanks. Various cabbage cultivars were also tested in a coastal California field naturally infested with *F. o.* f. sp. *conglutinans* race 2. For all pathotypes, virulence on their respective susceptible hosts was influenced strongly by soil temperature, with disease severity increasing as soil temperatures increased. With two pathotypes, *F. o.* f. sp. *conglutinans* race 2 and *F. o.* f. sp. *raphani*, susceptibility was observed on their respective susceptible hosts, cabbage cultivar Golden Acre and radish cultivar White Icicle, at 10 C. In cabbage, monogenic dominant (type A) resistance was highly effective against *F. o.* f. sp. *conglutinans* race 1, but was progressively less effective against *F. o.* f. sp. *conglutinans* race 2 as soil temperatures were increased from 14 to 20 C, and was ineffective at 22 and 24 C. The polygenic (type B) resistance in cabbage was highly effective against *F. o.* f. sp. *conglutinans* race 1 at 20 C and below, but was only effective against *F. o.* f. sp. *conglutinans* race 2 at 10 and 12 C. In the field test, resistance in cabbage cultivars with either type A or type B resistance was expressed under cool coastal California conditions during the summer months.

An early example of the successful uses of temperature-conditional genes in breeding for disease resistance has been the control of cabbage yellows, caused by *Fusarium oxysporum* Schlecht. f. sp. *conglutinans* (Wr.) Snyd. & Hans. race 1 (8). Walker and colleagues (1,6,7,9) studied the effect of soil temperature on disease development and the inheritance of resistance in cabbage. They described two types of resistance, a monogenic dominant (type A) and a polygenic (type B) resistance (8). The type A resistance was found to be stable at soil temperatures up to 28 C, whereas type B resistance became ineffective at soil temperatures above 22 C. They also observed that soil temperatures at or below 18 C were below the minimum for disease development in susceptible cabbage cultivars. Type A and B resistance have been deployed for over 70 years in many economically important cabbage cultivars. They are still effective in most cabbage growing areas, including Wisconsin where they were first introduced. In California in 1985, a new pathotype of cabbage yellows was found that was pathogenic to cultivars with type A resistance. This pathotype was originally designated *Fusarium oxysporum* f. sp. *conglutinans* race 5 (5), but under a proposed reclassification of the strains of *Fusarium oxysporum* on crucifers it has been designated *F. oxysporum* f. sp. *conglutinans* race 2, reflecting its closer relationship to the other cabbage strain and differentiating it from the pathotypes on radish and *Matthiola* (4). Yellows-susceptible cabbage and other cole crops can be successfully grown in many areas of California because soil temperatures during the growing season are generally too low for disease development. However, a preliminary study (3) of the effect of soil temperature on disease expression by *F. o.* f. sp. *conglutinans* race 1 and race 2 indicated that *F. o.* f. sp. *conglutinans* race 2, the new California isolate, was virulent at 14 C, whereas *F. o.* f. sp. *conglutinans* race 1 was avirulent at this temperature. It seemed appropriate, therefore, to further investigate the

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virulence patterns of the five known pathotypes of *F. oxysporum* from crucifers over a range of soil temperatures.

MATERIALS AND METHODS

Temperature tank test. Isolates used in this study were representative of the five known pathotypes from crucifers and have been accessioned at the American Type Culture Collection (Rockville, MD). Accession numbers and corresponding subspecific designations are: *F. o.* f. sp. *conglutinans* race 1, 52557; *F. o.* f. sp. *conglutinans* race 2, 58385; *F. o.* f. sp. *raphani*, 58110; *F. o.* f. sp. *matthioli* race 1, 16602; and *F. o.* f. sp. *matthioli* race 2, 16603. The cultivars used in the differential set were chosen for their ability to distinguish among the isolates of the five known pathotypes. Wisconsin Golden Acre cabbage, Golden Acre cabbage, and White Icicle radish seed were supplied by Alf. Christianson Seed Co., Mt. Vernon, WA. Scarlet Knight radish seed, lot 39321-A5028, was supplied by the Northrup King Co., Woodland, CA, and had a >99% proportion of resistant individuals. The *Matthiola incana* cultivars Giant Imperial Purple and Pacific Pink were provided by Ferry-Morse Seed Co., Mountain View, CA, and Petoseed Co., Inc., Saticoy, CA, respectively. The roots of 7-day-old seedlings of each cultivar grown in silica sand were washed and dipped into a concentration of 1×10^6 spores and mycelial pieces per milliliter of each specific isolate (10). At least 20 seedlings of each differential cultivar were transplanted to each pan containing 1 Jiffy-Mix:1 silica sand (by volume). Only one pathotype was present in each pan. The differential cultivars were randomized within each of two pans, and the pans were placed in separate Wisconsin soil temperature tanks, continuously illuminated at 250 $\mu mol \cdot s^{-1} \cdot m^{-2}$, and watered daily with one-half strength Hoagland's solution. The temperature tanks were situated in an air-conditioned greenhouse maintained at 24 ± 3 C, with shading to keep direct sunlight from reaching the test pans. Soil temperatures were 10, 12, 14, 16, 18, 20, 22, and 24 C. The soil temperature for the duration of each pathogenicity test had a maximum fluctuation of ±0.5 C. Temperatures were randomly assigned to the soil temperature tanks and two soil temperature tanks were set at the same temperature. Each temperature tank represented a block providing a randomized complete block design for statistical analysis. The experiment was repeated.

After 14 days, plants were evaluated for disease symptoms on a 0–9 scale (10), where 0 = no symptoms in tops or roots (as in uninoculated controls); 1 = darkening of roots, no stunting or symptoms in tops; 3 = darkening of roots, slight top stunting, no chlorosis; 5 = dark stunted roots, tops stunted, slight chlorosis; 7 = severe stunting of roots and tops, severe chlorosis; and 9 = death. The even numbers were used to assess intermediate responses. A disease severity index (DSI) for each host-pathotype tested was calculated by multiplying the number in each symptom class by the symptom rating and dividing the sum of all classes by the total number of plants.

Field test. A summer (June–August) field trial of yellows resistant and susceptible cabbage cultivars was conducted near Arroyo Grande, CA. The field had been determined to be infested naturally with *F. oxysporum* f. sp. *conglutinans* race 2 (R. H. Morrison, *unpublished*). Cultivars tested were Golden Acre and Headstart (susceptible), Wisconsin Hollander No. 8 and Rio Verde (type B resistance), and Wisconsin Golden Acre, Tastie, and Greenboy (type A resistance). Golden Acre, Wisconsin Hollander No. 8, and Wisconsin Golden Acre are open-pollinated cultivars, whereas Headstart, Rio Verde, Greenboy, and Tastie are hybrids. Seedlings were started in a greenhouse and transplanted into the field at 3 wk of age. The test was done in a randomized complete block design with three replications with 15 plants per cultivar per replication. Plants were spaced 30 cm apart within a row. Cultural practices were those used by the grower for commercial fresh market cabbage production.

At fresh market stage, 90-day-old plants were harvested and rated for yellows based on a 0–9 scale, where 0 =

Table 1. Disease severity indices of a differential set of crucifer cultivars inoculated with isolates representing the five different pathotypes of *Fusarium oxysporum* f. sp. *conglutinans, F. o.* f. sp. *raphani*, and *F. o.* f. sp. *matthioli* at eight different soil temperatures

Cultivar	Soil temperatures 10 C	12 C	14 C	16 C	18 C	20 C	22 C	24 C
***F. o.* f. sp. *conglutinans* race 1 (ATCC 52557)[y]**								
Radish								
Scarlet Knight	1.0[z]	1.0	1.0	1.0	1.3	1.0	1.2	1.0
	(0.0)	(0.0)	(0.0)	(0.0)	(1.3)	(0.0)	(1.1)	(0.0)
White Icicle	1.0	1.4	1.0	1.0	1.5	2.3	4.0	3.2
	(0.0)	(0.5)	(0.0)	(0.0)	(0.9)	(1.1)	(3.6)	(3.2)
Cabbage								
Wisconsin Golden Acre	1.0	1.0	1.2	1.0	1.5	1.4	1.7	1.4
	(0.0)	(0.0)	(1.6)	(0.0)	(1.5)	(1.4)	(2.0)	(2.6)
Wisconsin Hollander No. 8	1.0	1.0	1.4	1.0	1.5	1.2	2.7	5.3
	(0.0)	(0.0)	(0.8)	(0.0)	(1.4)	(0.7)	(2.0)	(3.6)
Golden Acre	1.0	1.3	1.6	1.4	1.6	6.3	6.9	8.9
	(0.4)	(0.0)	(1.5)	(1.4)	(1.4)	(2.7)	(2.5)	(0.6)
Matthiola								
Pacific Pink	0.0	0.6	1.9	2.6	0.0	0.0	0.3	2.0
	(1.0)	(1.3)	(2.8)	(1.1)	(0.0)	(0.0)	(0.7)	(3.4)
Giant Imperial Purple	0.0	0.7	1.3	4.6	0.9	0.2	0.5	2.1
	(0.3)	(0.6)	(1.9)	(2.9)	(1.7)	(0.7)	(0.4)	(3.5)
***F. o.* f. sp. *conglutinans* race 2 (ATCC 58385)**								
Radish								
Scarlet Knight	1.0	1.0	1.0	1.1	1.3	1.3	1.8	1.5
	(0.0)	(0.0)	(0.1)	(0.7)	(1.2)	(1.6)	(1.6)	(1.7)
White Icicle	2.0	2.7	4.3	4.9	5.7	6.5	8.3	8.2
	(1.2)	(1.8)	(2.3)	(2.7)	(3.0)	(2.3)	(1.8)	(2.3)
Cabbage								
Wisconsin Golden Acre	1.5	1.9	2.0	2.4	4.0	3.7	7.2	7.6
	(0.8)	(1.8)	(2.0)	(2.2)	(3.1)	(3.0)	(1.4)	(2.3)
Wisconsin Hollander No. 8	1.8	2.0	3.2	4.1	3.8	3.5	7.0	7.4
	(1.8)	(2.0)	(2.5)	(3.1)	(2.6)	(1.8)	(1.4)	(2.5)
Golden Acre	3.2	4.4	6.0	7.3	6.9	8.8	8.8	8.9
	(2.0)	(1.9)	(1.8)	(2.1)	(1.7)	(0.6)	(0.6)	(0.4)
Matthiola								
Pacific Pink	1.8	2.1	3.1	4.3	3.7	5.5	5.8	4.9
	(2.4)	(1.8)	(3.3)	(2.8)	(1.9)	(3.3)	(2.1)	(3.3)
Giant Imperial Purple	0.8	1.3	3.6	5.0	3.6	5.0	5.2	6.2
	(2.0)	(1.0)	(3.2)	(2.3)	(3.2)	(2.7)	(3.5)	(3.5)
***F. o.* f. sp. *raphani* (ATCC 58110)**								
Radish								
Scarlet Knight	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
White Icicle	3.0	4.7	5.2	7.9	8.9	8.8	9.0	9.0
	(1.6)	(1.4)	(1.4)	(0.7)	(0.4)	(0.7)	(0.0)	(0.0)

(*continued on next page*)

[y] American Type Culture Collection (ATCC) (Rockville, MD) identification number.

[z] Mean and standard deviation (in parentheses below mean) of disease severity indices were calculated with two replicates of 20 plants. Disease symptoms were assayed 14 days after inoculation on a scale of 0–9, where 0 = no evidence and 9 = death.

no evidence of disease; 1 = slight discoloration of roots, no vascular discoloration or top symptoms; 3 = slight discoloration of roots, slight vascular discoloration in lower stem, no top symptoms; 5 = moderate root discoloration and vascular discoloration, plant slightly stunted, lower leaves mildly chlorotic; 7 = severe root and vascular discoloration, plant stunted, lower and middle leaves chlorotic; and 9 = death. Data were analyzed by one-way analysis of variance, and differences in disease means were evaluated using Tukey's procedure ($P = 0.05$).

RESULTS

Disease expression data collected revealed that *F. o.* f. sp. *conglutinans* race 2 and *F. o.* f. sp. *raphani* were virulent on their respective susceptible hosts at all temperatures examined (Table 1). At 18 C or below, *F. o.* f. sp. *conglutinans* race 1 and *F. o.* f. sp. *matthioli* race 1 and race 2 were avirulent. *Fusarium oxysporum* f. sp. *conglutinans* race 1 was highly virulent on the susceptible cabbage Golden Acre at 20, 22, and 24 C. *Fusarium oxysporum* f. sp. *conglutinans* race 1 was slightly virulent on Wisconsin Hollander No. 8 with type B resistance (DSI = 2.7) at 22 C and was moderately virulent (DSI = 5.3) at 24 C. *Fusarium oxysporum* f. sp. *conglutinans* race 1 was avirulent on Wisconsin Golden Acre with type A resistance at all temperatures examined.

When Golden Acre was the host, *F. o.* f. sp. *conglutinans* race 2 was virulent at all temperatures examined. However, *F. o.* f. sp. *conglutinans* race 2 was avirulent on Type B resistance (Wisconsin Hollander No. 8) at 10 and 12 C, having DSIs of 1.8 and 2.0, respectively. At 14, 16, 18, and 20 C, *F. o.* f. sp. *conglutinans* race 2 was moderately virulent on type B resistance, with DSIs of 3.2, 4.1, 3.8, and 3.5, respectively. At 22 and 24 C, *F. o.* f. sp. *conglutinans* race 2 was virulent on both type A and type B resistance. *Fusarium oxysporum* f. sp. *conglutinans* race 2 was avirulent on the host containing Type A resistance at 10 (DSI = 1.5), 12 (DSI = 1.9), 14 (DSI = 2.0), and 16 C (DSI = 2.4). *Fusarium oxysporum* f. sp. *conglutinans* race 2 had a moderate virulence at 18 (DSI = 4.0) and 20 C (DSI = 3.7), and was highly virulent at 22 (DSI = 7.2) and 24 C (DSI = 7.6).

The radish pathotype, *F. o.* f. sp. *raphani*, was highly virulent on White Icicle, the susceptible host, but was avirulent to Scarlet Knight and the three cabbage cultivars. *Fusarium oxysporum* f. sp. *raphani* expressed moderate to high virulence to the *Matthiola incana* cultivars at all temperatures examined.

The pathotype from *Matthiola incana*, *F. o.* f. sp. *matthioli* race 1, was virulent only at 22 and 24 C to both the susceptible cultivar Pacific Pink and the *Matthiola* resistant cultivar Giant Imperial Purple. *Fusarium oxysporum* f. sp. *matthioli* race 2 was avirulent on Giant Imperial Purple at all temperatures and virulent on Pacific Pink only at 22 and 24 C.

Under coastal California field conditions during the summer months, cabbage cultivars with either type A or type B resistance were protected from *F. o.* f. sp. *conglutinans* race 2 (Table 2). In contrast, cabbage cultivars without type A or type B resistance were severely diseased.

Table 1. (*continued from preceding page*)

Cultivar	Soil temperatures							
	10 C	12 C	14 C	16 C	18 C	20 C	22 C	24 C
Cabbage								
Wisconsin Golden Acre	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)
Wisconsin Hollander No. 8	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)
Golden Acre	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)
Matthiola								
Pacific Pink	0.6 (1.0)	1.0 (1.0)	1.1 (1.4)	2.3 (0.8)	3.0 (1.9)	1.8 (1.0)	3.9 (2.7)	3.0 (1.5)
Giant Imperial Purple	0.8 (0.9)	0.9 (1.0)	0.8 (1.6)	3.0 (1.4)	2.1 (2.5)	3.3 (3.9)	1.2 (0.6)	2.6 (2.5)
***F. o.* f. sp. *matthioli* race 1 (ATCC 16602)**								
Radish								
Scarlet Knight	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	2.0 (2.4)	1.2 (0.5)
White Icicle	1.0 (0.6)	1.0 (0.0)	1.0 (0.2)	1.3 (0.8)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	2.7 (2.4)
Cabbage								
Wisconsin Golden Acre	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.3 (0.7)
Wisconsin Hollander No. 8	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.2 (0.6)
Golden Acre	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.2 (0.6)
Matthiola								
Pacific Pink	1.0 (1.6)	1.3 (1.3)	1.8 (1.0)	1.5 (1.3)	1.4 (0.9)	1.8 (1.5)	6.1 (1.7)	7.1 (3.0)
Giant Imperial Purple	1.4 (1.7)	1.4 (1.4)	1.3 (1.8)	1.9 (1.7)	1.5 (0.9)	2.8 (2.3)	6.0 (3.0)	8.4 (1.2)
***F. o.* f. sp. *matthioli* race 2 (ATCC 16603)**								
Radish								
Scarlet Knight	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)
White Icicle	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)
Cabbage								
Wisconsin Golden Acre	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)
Wisconsin Hollander No. 8	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)
Golden Acre	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.5 (1.3)
Matthiola								
Pacific Pink	0.8 (1.3)	0.7 (0.9)	1.4 (0.4)	1.7 (3.0)	1.5 (2.0)	2.7 (2.7)	6.0 (3.2)	8.9 (0.4)
Giant Imperial Purple	1.0 (1.2)	0.8 (1.6)	2.3 (2.0)	2.0 (3.0)	1.5 (2.3)	2.8 (2.3)	1.2 (0.6)	2.5 (1.4)

DISCUSSION

The effects of soil temperature on disease expression were evident when the disease severity indices were viewed across temperatures in soil temperature tank studies. The virulence profile in Table 1 indicates an ecotypic variation between *F. o.* f. sp. *conglutinans* race 1 and *F. o.* f. sp. *conglutinans* race 2, with *F. o.* f. sp. *conglutinans* race 2 having the ability to cause disease below 14 C, whereas *F. o.* f. sp. *conglutinans* race 1 was avirulent at 18 C and lower. For the plant breeder, the presence of two pathotypes in an area, *F. o.* f. sp. *conglutinans* race 2 and *F. o.* f. sp. *raphani*, will mean that a crop must have resistance even when soil temperatures are cool.

When the virulence of *F. o.* f. sp. *conglutinans* race 2 on Wisconsin Golden Acre (type A resistant cultivar) and Golden Acre (susceptible cultivar) is examined over the range of temperatures, a resistance that is conditional on soil temperature was evident. This is

Table 2. Reaction of various cabbage cultivars in a California field naturally infested with *Fusarium oxysporum* f. sp. *conglutinans* race 2

Cultivar	Disease severity index[u]	Plants[v]		Response[w]	
		Resistant (%)	Susceptible (%)	Disease reaction	Type of resistance
Headstart	8.7 a[x]	0	100	S[y]	None[z]
Golden Acre	6.5 b	7	93	S	None
Wisconsin Hollander No. 8	2.1 c	87	13	R	B
Rio Verde	1.2 c	91	9	R	B
Wisconsin Golden Acre	2.1 c	95	5	R	A
Tastie	2.2 c	91	9	R	A
Greenboy	1.0 c	100	0	R	A

[u] Disease severity index based on a scale of 0–9, where 0 = no evidence of disease and 9 = death.
[v] Plants rated 0–3 were considered resistant and those rated 4–9 were considered susceptible.
[w] Response to *F. o.* f. sp. *conglutinans* race 1.
[x] Within column, cultivars with the same letter are not significantly different at the 5% level with Tukey's method.
[y] S = susceptible and R = resistant, based on established reactions to *F. o.* f. sp. *conglutinans* race 1.
[z] A = monogenic dominant resistance and B = polygenic resistance.

demonstrated when the DSIs are compared at 24 and 14 C (Table 1). Wisconsin Golden Acre had a DSI of 7.6 and 2.0, and Golden Acre a DSI of 8.9 and 6.0 at 24 and 14 C, respectively. The type B resistant cultivar Wisconsin Hollander No. 8 also gave a reaction dependent on soil temperature, but was somewhat more susceptible at temperatures of 14–16 C.

There was also no evidence for a differential interaction of *F. o.* f. sp. *conglutinans* race 1 and *F. o.* f. sp. *conglutinans* race 2 and type A and B resistance.

It is interesting to note that the two pathotypes that are virulent at lower soil temperatures, *F. o.* f. sp. *conglutinans* race 2 and *F. o.* f. sp. *raphani*, also grow more vigorously on agar than *F. o.* f. sp. *conglutinans* race 1 (2). On the agar medium, *F. o.* f. sp. *conglutinans* race 1 and *F. o.* f. sp. *conglutinans* race 2 differed significantly in growth rate at all temperatures examined, except 12 C, with race 2 growing faster than race 1 (2). The lack of evidence for a differential interaction among the cabbage hosts having type A or B resistance suggests that genes in the pathogen for aggressiveness are important for the increased expression of disease at lower temperatures.

Field tests done in 3 consecutive years in the same field in coastal California have given similar results to those reported here for cabbage. Broccoli and cauliflower cultivars were also evaluated in some of these field tests, and none of these showed susceptibility under the field conditions (R. H. Morrison, *unpublished*). However, in California, cauliflower has been identified as having been infected by *F. o.* f. sp. *conglutinans* race 2 (P. W. Bosland, *unpublished*).

Both soil temperature tank and field tests suggest that type A and type B resistance can give protection at cooler temperatures. These resistances will continue to be useful to plant breeders in the development of cultivars that will be grown in relatively cool soils and exposed to *F. o.* f. sp. *conglutinans* race 2. Type A resistance in cabbage, which has been temperature stable, is now apparently temperature dependent against isolates of *F. o.* f. sp. *conglutinans* race 2.

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