Correlation of Low Level Wheat Streak Mosaic Virus Resistance in Triumph 64 Wheat with Low Virus Titer

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ABSTRACT

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Wheat streak mosaic virus (WSMV) reduced the yield of Triumph 64 (cultivar having a low level of resistance to virus multiplication) by 18% compared with 40% for the cultivar Centurk. Triumph 64 consistently had a lower virus titer as determined by infectivity assay and enzyme-linked immunosorbent assay (ELISA). As incubation temperature increased from 15 to 30 C, differences in relative titer between cultivars decreased. ELISA values decreased from the tip to the base in expanding leaves but were more uniform from tip to base in fully expanded leaves.

Wheat streak mosaic (WSM) caused by wheat streak mosaic virus (WSMV) is one of the most serious threats to wheat (*Triticum aestivum* L.) production in western Kansas (7,18). High levels of resistance to WSMV have been translocated into common wheat from two *Agropyron* species (14,17). The *Agropyron*-derived resistance has given complete protection from WSMV in mechanically inoculated and naturally infected field trials. However, attempts to incorporate this high level of resistance into agronomically acceptable cultivars have failed because of linkages between WSMV resistance and undesirable agronomic characteristics.

Low-level resistance to WSMV (sometimes referred to as tolerance) has been reported in common wheat cultivars (13,15). Cultivars carrying this level of resistance become infected and develop WSM symptoms, but yield is reduced less than in susceptible cultivars. This type of resistance has not been used extensively in breeding progress because of the difficulty and inaccuracy of the screening process. Selection procedures involve time-consuming replicated trials comparing yield from paired plots of inoculated versus healthy plants. These trials normally have to be repeated for several years to accurately identify the resistant reaction.

Resistance in cereal crops to plant viruses has been associated with reduced virus titer (6,16). Measurement of virus titer has been labor intensive in the past; however, enzyme-linked immunosorbent assay (ELISA) can now be used to quantitate virus concentration (2,4,8,11,16).

In this paper, we summarize 8 yr of data from yield trials mechanically inoculated with WSMV, which demonstrate the effectiveness of resistance in Triumph 64 compared with the susceptible cultivar, Centurk. We have correlated the use of ELISA with infectivity assays in determining relative WSMV titer in both cultivars and established that differences do exist between these cultivars in the field and in the seedling stage in a controlled environment.

MATERIAL AND METHODS

Virus maintenance. Isolate KS-1 of WSMV was used in field studies before 1982; isolate H81 was used in field studies after 1981 and in all other tests reported here. The method of virus maintenance has been described previously (9).

ELISA. Antiserum to WSMV (titer = 1:64 by the microprecipitin test) was provided by J. K. Uyemoto (Kansas State University). ELISA was performed as described by Clark and Adams (3), except that 250-μl volumes were used at each step. Coating and conjugated antibodies (from a 1-mg/ml stock) were used at 1:100 for the dilution curve and ELISA-infectivity correlation experiments and at 1:400 (economy of antibody usage) for all other experiments. Samples were assayed in randomly located triplicate wells. The antibodies were conjugated with alkaline phosphatase (Type VIIS, Sigma Chemical Co., St. Louis, MO) at a 2:1 (enzyme:antibody) ratio (3). After a 30-min incubation at room temperature, substrate reactions were stopped by adding 50 μl of 3 M NaOH per well. Absorbance was measured at 405 nm (ELISA values) using a Titertek Multiskan microelisa plate reader (Flow Laboratories, Inc., McLean, VA).

For all experiments, the reported absorbance is the observed value minus the absorbance of the healthy control for that treatment.

Infectivity assay. Inoculum was prepared by macerating diseased tissues at a 1:300 dilution in 0.02 M potassium phosphate buffer. The method of inoculation used throughout this investigation was reported previously (9).

Inoculated plants were maintained in a greenhouse at 27 ± 3 C for 2 wk, and the number of systemically infected plants was recorded.

Yield loss from WSMV. A split-plot experimental design was used with cultivars as main plots and healthy versus WSMV-inoculated plants as subplots. Each treatment was replicated four times. Subplots consisted of four rows, 3.9 m long with 0.3-m row spacing, seeded at 50 kg/ha. Planting was done in mid- to late September each year. Plants were inoculated 14 days after emergence using an air-blast inoculation technique (10). Incidence of WSMV infection was estimated in late April or early May, when symptoms could easily be observed. Subplots were hand trimmed to 2.4 m just before harvest, in late June to early July. Volume weights and yields were measured and corrected to a 12% moisture basis. Data were combined over years (1973–1975, 1982–1986) for analysis of variance (ANOVA).

Dilution curve. Wheat was seeded in 30-× 50-cm, soil-filled flats and grown in a growth chamber (Warren/Sherer Model E138-15) at 22 C with a 12-hr photoperiod of fluorescent light (approximately 500 $\mu E \cdot sec^{-1} \cdot m^{-2}$). Seedlings were inoculated at the base of the primary leaf 6 days after planting. Third leaves of infected plants were harvested 14 days postinoculation (DPI). Harvested tissue was ground in a mortar and pestle at a 1:2 (w/v) dilution in PBS. Twofold serial dilutions (1:2–1:1,024) were made in PBS. Healthy tissue was treated identically in all cases. Data reported are the means of four replications, with each replication done on different days.

Cultivar virus titer and ELISA-infectivity correlation. Wheat cultivars (Eagle, Centurk, and Triumph 64) were seeded, inoculated, and maintained under the same conditions as the seedlings used in the dilution curve experiments. Control plants, inoculated with buffer and abrasive only, were placed in the same growth chambers. The third leaf of infected plants was harvested from each cultivar when they were fully expanded (14 DPI) in the first two trials. The fourth leaf (half the length of leaf 3) was used in trial 3. The tissue was ground in PBS (1:15, w/v) and applied to microelisa plates. The remaining extract was further diluted to a final dilution of 1:900 and applied to the same plates. The test was repeated three times with four replications of each cultivar in each test. Data from each test were analyzed separately.

Equivalent infected leaves from other test plants in the same planting were harvested for infectivity assay. Infectivity data from all three trials were combined for analysis of variance. Simple correlation coefficients were generated from infectivity data and ELISA values of each test.

Determination of virus titer in field-grown plants. During the spring of 1984, WSMV-inoculated field plots of Centurk and Triumph 64 were sampled to determine relative virus titer with the ELISA. Six flag leaves were harvested from each replication and maintained on ice or in a refrigerator at 5 C until they were ground in a mortar and pestle in PBS (1:20, w/v). Two hours or less elapsed between sample harvest and ELISA processing. A final sample dilution of 1:600 (w/v) was applied to ELISA plates. Four replications of each cultivar were sampled on two dates (8 and 22 May). Flag leaves were about 50% emerged on the first date and fully developed on the second date (5 days postanthesis).

Temperature study. Wheat was seeded into metal flats. Seedlings of Centurk and Triumph 64 were inoculated and kept in 15, 20, 25, and 30 C chambers having the same lighting condition as described previously. Leaf length measurements on 25 plants from each treatment were made every 3 days and on days when samples for ELISA were taken. Six leaves from each treatment were harvested 7, 14, 21, and 28 DPI. Harvested tissue was ground in a mortar and pestle and diluted to 1:600 for ELISA. The 1:600 dilution used for this study against the 1:400 dilution antibody phases was previously determined to be in the linear response range of the ELISA dilution curve for the antiserum used. The experiment was repeated three times. ELISA values of individual leaves of Centurk and Triumph 64, on a given sampling day and temperature, were subjected to ANOVA to determine the statistical reliability of the cultivar differences. A weighted mean (average ELISA value of all leaves present, corrected for fresh weight of each leaf) was calculated for each plant at each sampling time and temperature. This mean was used in ANOVA to determine if significant interactions occurred between cultivar response and incubation temperature.

Asynchronous plant growth effects. The lengths of the third and fourth leaves of systemically infected plants of Centurk and Triumph 64 (14 DPI) were measured. Leaf ratios (length of fourth leaf/length of third leaf) varied from 0.15 to 0.85 within a single replication of a single genotype because of normal asynchronous plant growth. Third leaves from plants that had leaf ratios of 0.25. 0.50, and 0.75 were harvested from each of four replications for each cultivar (six leaves/ratio/cultivar/replication). The tissue was ground in a mortar and pestle and diluted to 1:600 for ELISA. The procedure was repeated twice and data were subjected to ANOVA to determine if differences in virus titer existed between leaf ratio classes within cultivars.

Within-leaf virus distribution. Third leaves of infected Centurk and Triumph 64 seedlings were sampled at 7 DPI (third leaf one-half the length of second leaf) and 14 DPI (third leaf fully expanded and twice the length of fourth leaf). Six leaves, per treatment per replication, were cut into thirds based on leaf length (base, middle, and tip). Tissue was ground in a mortar and pestle and diluted with PBS to 1:600 for ELISA. Data presented are means of four experiments and are compared using an LSD ($P = 0.05$).

RESULTS

Yield loss due to WSMV. WSMV reduced average (8 yr) yield and volume weight of Centurk by 40.7 and 10.6%, respectively, and of Triumph 64 by 18.3 and 2.8%, respectively (Table 1). Loss difference between cultivars was highly significant as indicated by a significant cultivar × inoculation interaction ($P \leq 0.01$). There was no significant year × inoculation × cultivar interaction, indicating consistency in cultivar response to WSMV over the 8 yr. Both cultivars averaged 90% infection in inoculated plots over 8 yr. Healthy plots had from 1 to 5% WSMV-infected plants (average 2%).

Dilution curve. The dilution curve was the most linear from the 1:64 to the 1:1,024 dilutions (Fig. 1). Within this range of dilutions, the ELISA value doubled in response to every doubling of virus concentration. This corresponds to a relative virus concentration of 1.6–0.1, assuming that the initial concentration in the leaves was 100. An ELISA value was considered positive if it was four times greater than the corresponding healthy extract response.

Cultivar virus titer and ELISA-infectivity correlation. Triumph 64 had lower mean ELISA values compared with Eagle and Centurk at the 1:15 sample dilution (Table 2). However, Triumph 64 was significantly lower than Eagle only in trials 1 and 3 and was never significantly lower than Centurk at the 1:15 sample dilution. When samples were diluted to 1:900 (within the linear range of the dilution curve), Triumph 64 was significantly lower than Eagle and Centurk in all trials (Table 2).

The infectivity assay confirmed the ELISA results with the 1:900 dilution. The average percents of infection for the three trials were 75, 66, and 45% for Eagle, Centurk, and Triumph 64, respectively. Triumph 64 was significantly lower than Eagle and Centurk, whereas Eagle and Centurk were not different at $P < 0.05$. Rank correlations between the 1:900 dilution ELISA and the infectivity

TABLE 1. Grain yield and volume weight of WSMV-infected and healthy Centurk and Triumph 64 wheat cultivars over 8 yr at Hays, KS

		Year								
Cultivar	Treatment	1973	1974	1975	1982	1983	1984	1985	1986	Mean
Yield (Kg/ha)										
Centurk	Healthy	3,438	2,560	2,210	4,253	3,860	3,454	4,823	3,952	3,568
Centurk	Inoculated	2,474	1,527	1,068	1,588	2,735	2,266	2,741	2,528	2,116
Triumph 64	Healthy	3,641	2,153	2,324	3,494	3,706	3,525	4,780	3,470	3,386
Triumph 64	Inoculated	3,033	1,799	1,881	2,168	3,515	2,892	3,709	3,145	2,768
									LSD 0.05	170
Volume wt (Kg/m^3)										
Centurk	Healthy	759	750	759	...[a]	766	758	729	762	755
Centurk	Inoculated	710	680	674	...	701	693	618	652	675
Triumph 64	Healthy	808	792	789	...	806	787	793	776	793
Triumph 64	Inoculated	778	783	754	...	790	757	773	768	771
									LSD 0.05	6.4

[a] Volume weights not taken.

assay were 1.0 for all three trials. Simple correlation coefficients between the two assays were 0.995, 0.999, and 0.974 for the three trials.

Virus titer in field-grown plants. The average ELISA value for emerging flag leaves of Triumph 64 on 8 May (0.058) was significantly lower ($P \leq 0.05$) than that for the flag leaf of Centurk (0.115), but a significant difference was not detected on 22 May, with ELISA values of 0.117 and 0.125 for Triumph 64 and Centurk, respectively.

Temperature study. Leaf 1 (the inoculated leaf) did not develop symptoms at any temperature. At 7 DPI, no symptoms were evident in any plant material at 15 C but were present in all leaves, except leaf 2, at 20 C and above. Symptoms were not visible in leaf 2 until 2 wk PI at 20 C and above and not until 3 wk PI at 15 C. At 15 C, leaf 3 had symptoms at 2 wk PI. All leaves of both cultivars at 15 C had symptoms at 21 and 28 DPI. Symptoms appeared identical when like tissue was compared between cultivars. Severity of symptoms increased with leaf age.

WSMV could not be detected at 15 C until 14 DPI. ELISA values continued to increase through 28 DPI for each leaf in both cultivars (Fig. 2). Leaf 2 had reached full length by 7 DPI and maximum fresh weight by 14 DPI, whereas maximum length and fresh weight for leaf 3 occurred at 21 DPI, with leaf 4 still increasing in length and weight at 28 DPI.

ELISA values of plants grown at 20 C decreased to a peak at 14 DPI and declined for leaves 2 and 3 in both cultivars (Fig. 2). The highest ELISA values for leaves 4 and 5 occurred as the leaves were emerging (14 and 21 DPI, respectively). Peaks of ELISA values for leaf 3 coincided with maximum leaf length and weight. In leaf 2, the peak occurred at the same time, but leaf 2 was already fully expanded at 7 DPI. Leaf length and fresh weights were still increasing for leaves 3 and 4 at 28 DPI.

At 25 C, ELISA values for all leaves, in both cultivars, progressively decreased from the first sample to the last (Fig. 2). This decrease occurred in leaves that were fully expanded or still growing. Maximum leaf length and weight for leaf 2 occurred at 7 DPI and for leaf 3 at 14 DPI, whereas leaves 4 and 5 were still increasing in length and weight at the end of this study. Absorbance values decreased with time after 7 DPI in all leaves.

ELISA readings at 30 C for all leaves in both cultivars progressively decreased from 7 to 28 DPI (Fig. 2). Leaf 2 had reached full length and weight by 7 DPI, and leaf 3 was at full length and weight at 21 DPI, with leaves 4 and 5 still increasing in length and weight at 28 DPI. Absorbance values were reduced for all leaves after leaf 2.

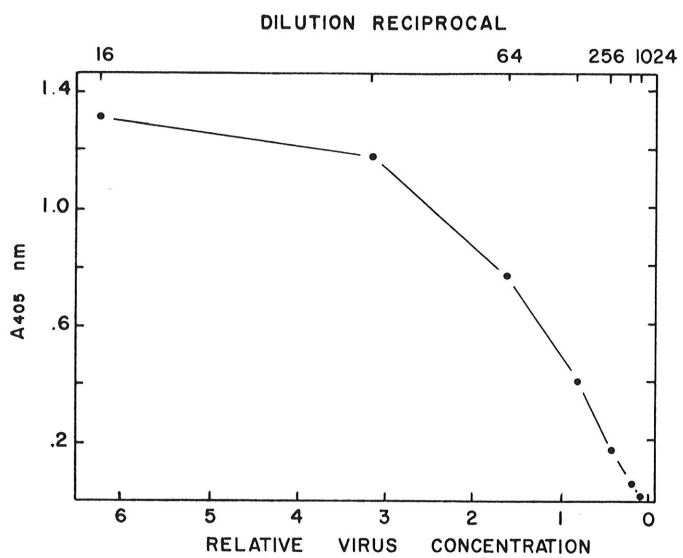

Fig. 1. Dilution curve derived from crude extracts of wheat streak mosaic virus-infected wheat leaves as determined by the enzyme-linked immunosorbent assay. Results are means after correction for the absorbance of healthy controls.

On an individual leaf basis, ELISA values for Centurk were always higher than those for Triumph 64, but the differences were not always significant. ELISA values for Triumph 64 were significantly lower ($P \leq 0.05$) than those of Centurk at 15 C for leaves 3 and 4 and leaves 3 and 5 at 21 and 28 DPI, respectively. At 20 C, in leaf 3, leaf 4, and leaf 5, and leaf 2 at 7, 14, 21, and 28 DPI, respectively. At 25 C, this relationship occurred for leaves 2 and 3, leaf 4, and leaf 2 at 7, 14, and 28 DPI, respectively. At 30 C, ELISA values were different for leaves 2, 3, and 4 at 7, 14, and 21 DPI, respectively. There was a significant interaction ($P \leq 0.05$) between cultivar ELISA values and temperature when weighted average ELISA values for all systemically infected leaves present on a plant were compared across the four temperatures. Triumph 64 averaged 40, 26, 24, and 8% lower than Centurk at 15, 20, 25, and 30 C, respectively.

Asynchronous plant growth effects. Significant differences in absorbance values between the leaf ratio classes present at 14 DPI in either cultivar were not detected. All leaf ratio classes of Centurk were significantly higher than all leaf ratio classes of Triumph 64. Average ELISA values (for both trials) for Centurk were 0.228, 0.228, and 0.234 for the leaf ratio classes 0.25, 0.50, and 0.75, respectively. Average ELISA values for the same leaf ratio classes of Triumph 64 were 0.178, 0.182, and 0.186, respectively. The coefficient of variation and LSD ($P \leq 0.05$) for the combined analysis were 8.0 and 0.025, respectively.

Within-leaf virus distribution. ELISA values increased from the leaf base to leaf tip in both cultivars in the expanding third leaf at 7 DPI (Table 3). A significant difference in ELISA values was not evident in the fully expanded third leaf at 14 DPI.

DISCUSSION

Triumph 64 had reduced levels of virus titer in seedlings (Table 2) and in spring vegetative growth from the field, when compared with Centurk. Triumph, the WSMV-resistant parent of Triumph 64, has been reported to yield less virus in purification trials than other cultivars (1), which agrees with our results. This difference between the two cultivars was not detected during the grain filling stage. Maturity differences and/or temperature effects on WSMV

TABLE 2. Enzyme-linked immunosorbent assay values of different dilutions of extracts from wheat streak mosaic virus-infected wheat leaves

	Trial					
	1[a]		2[a]		3[b]	
	Dilution		Dilution		Dilution	
Cultivar	1:15	1:900	1:15	1:900	1:15	1:900
Eagle	1.395	0.296	0.907	0.242	1.513	0.443
Centurk	1.299	0.265	0.971	0.202	1.498	0.360
Triumph 64	1.237	0.203	0.898	0.159	1.448	0.252
LSD (0.05)	0.090	0.035	0.169	0.024	0.058	0.054

[a] Third leaves (from the crown) were sampled when they were fully expanded and the fourth leaf was one-half the length of the third.
[b] Fourth leaves (from the crown) were sampled when they were one-half the length of the leaf directly below (third leaf).

TABLE 3. Enzyme-linked immunosorbent assay value distribution in different parts of the third leaf of wheat streak mosaic virus-infected plants

		Days postinoculation	
Cultivar	Leaf part	7[a]	14[b]
Centurk	Base	0.072	0.115
	Middle	0.108	0.121
	Tip	0.134	0.122
Triumph 64	Base	0.042	0.080
	Middle	0.097	0.098
	Tip	0.144	0.098
LSD (0.05)		0.017	0.019

[a] Leaf 3 not fully expanded, one-half the length of leaf 2.
[b] Leaf 3 fully expanded and twice the length of leaf 4.

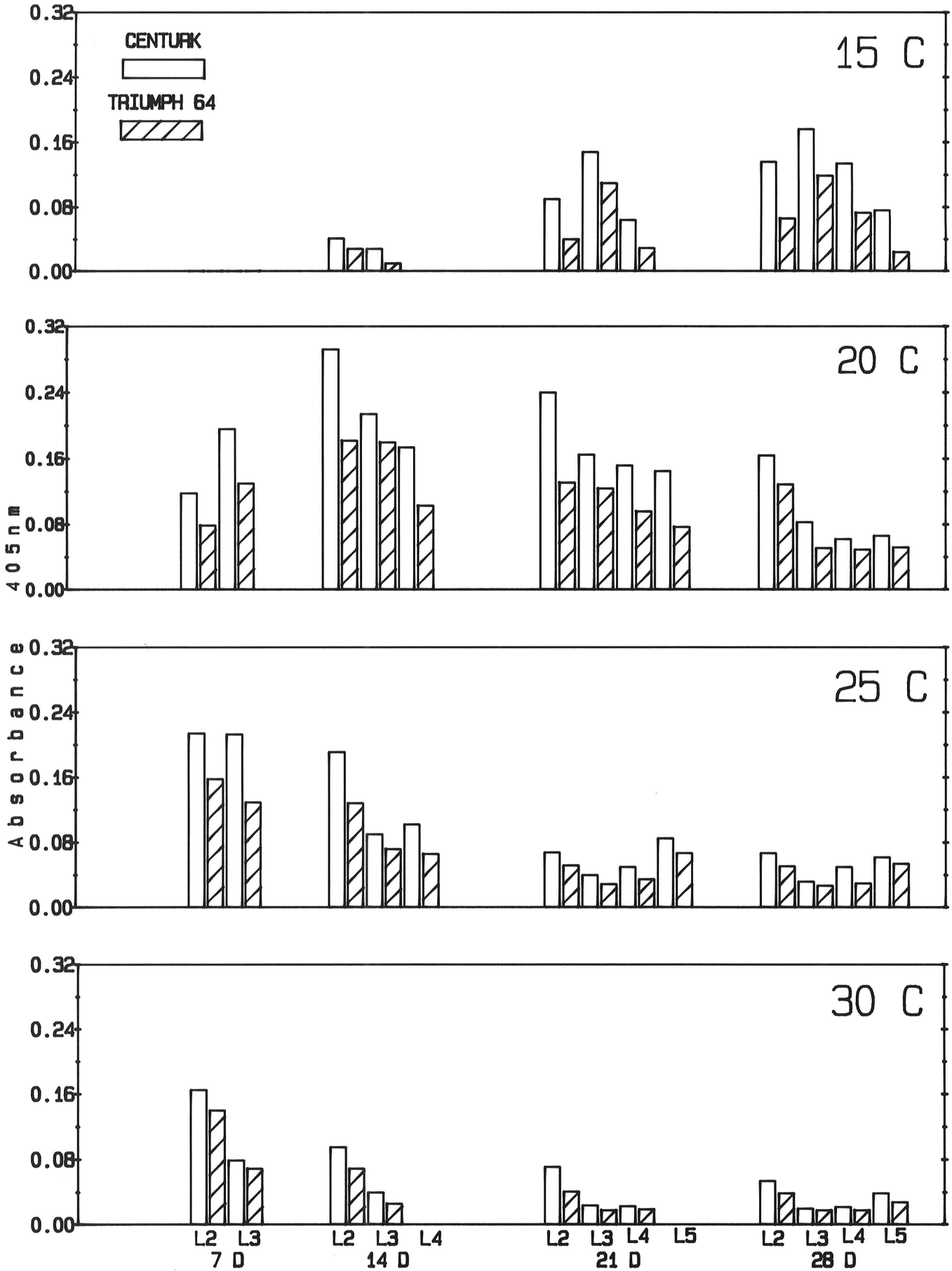

Fig. 2. Enzyme-linked immunosorbent assay values from wheat streak mosaic virus leaves of Centurk and Triumph 64 wheat incubated at 15, 20, 25, and 30 C.

replication may have been involved.

Maturity differences between the two cultivars could have resulted in older tissue being sampled from Triumph 64 than Centurk. Triumph normally heads 5–7 days earlier than Centurk; thus, at the last sampling it was not known if the sampled tissue was the same age from both cultivars.

The smallest difference in ELISA values between Centurk and Triumph 64 occurred at 30 C (Fig. 2). Temperatures during grain filling were much higher than temperatures during early spring growth. Increased temperatures could have also played a role in our inability to detect differences in ELISA values at the late flag leaf sample. Triumph 64's response to WSMV in the field over an 8-yr period was very consistent, but it might be expected to respond less favorably under extended periods of high temperatures. Temperature sensitivity to WSMV has been reported for other cultivars (9,12).

If ELISA is to be used as a screening tool to detect the Triumph level of resistance associated with reduced virus titer, the most effective temperature to separate genotypes and the leaf tissue to be sampled must be determined. All temperatures tested separated the two cultivars, but all leaves did not always give significant differences. Based on the value of P for the difference between the two cultivars at 25 and 30 C, the most consistent differences were in the youngest, not yet fully expanded leaves. At 15 and 20 C, the youngest, fully expanded leaves were more consistent. At all temperatures, except 15 C, the absorbance values decreased to low levels at the later sampling dates, and consistent cultivar differences were less common. Because ELISA values at 28 DPI were low, it might be possible to measure more consistent differences between cultivars at this time by using less dilute samples. Experimental error could have had a very large effect at the low readings, thus, not allowing statistical differences to be measured.

At 15 C (Fig. 2), absorbance values were positive at 14 DPI and continued to increase through 28 DPI. At all three of the higher temperatures, absorbance values peaked and then declined. The higher the temperature, the lower the ELISA values were at 28 DPI. The highest ELISA value occurred at 20 C at 14 DPI, which agrees with published data based on infectivity assay (5,9). The highest ELISA value measured at 25 and 30 C occurred at 7 DPI, but it is possible that the actual peak occurred either earlier than 7 DPI or betwaen 7 and 14 DPI.

Regardless of temperature, if ELISA values were increasing in a leaf, they were increasing in all leaves present on that plant (Fig. 2). If ELISA values were decreasing in a leaf, they were decreasing in all leaves present. Systemically infected leaves on emergence had absorbance values close to or below the value for subtending leaves on the same plant. However, there were sufficient differences among leaves of the same plant to prohibit valid comparisons of cultivars using different leaves. Comparisons among cultivars must be made on the same leaf during seedling growth. The normal variation in leaf size that occurs within a cultivar had no effect on the comparison of these two cultivars. Thus, it is not necessary to compare third leaves of different cultivars whose fourth leaves are exactly the same size.

To minimize grinding time and buffer use, it would be advantageous to assay only part of a leaf when comparing cultivars. A gradient in ELISA values existed in the expanding third leaf (Table 3). Highest values were measured in the leaf tip and the lowest at the base. In the fully expanded leaf, this gradient was not significant. but there was a tendency for the base to be slightly lower in ELISA value. Sampling part of a fully expanded leaf may introduce less error into comparisons than sampling part of an expanding leaf.

Investigations are currently under way to determine if low virus titer in Triumph 64 genetically segregates with the reduced yield reduction caused by WSMV. We are also determining if low levels of resistance to WSMV in other cultivars and experimental lines are associated with reduced virus titer. If enough genetic variation exists in common wheat for this type of resistance, characterized by reduced virus titer, it may be possible to combine different sources of low level resistance to produce a highly effective level. The use of ELISA in a recurrent selection program appears promising. ELISA allows for the screening of relatively large numbers of plants or lines and does not require the destruction of the whole plant. Plants with low virus titer can be crossed with other low titer plants within a population, during the same generation in which virus titer determinations were made. With incorporation of additional sources of resistance and using proper sampling procedures selecting for resistance on a single plant rather than on a population basis may be possible.

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