Systemic Movement of Barley Yellow Dwarf Virus in Small Grains

Stanley G. Jensen

Research Plant Pathologist, Plant Science Research Division, ARS, USDA, Northern Grain Insects Research Laboratory, Brookings, South Dakota 57006.

Cooperative investigations of Plant Science Research Division, ARS USDA, and the Plant Science Department, South Dakota State University.

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ABSTRACT

Three cultivars each of wheat, oats, and barley which differed in field susceptibility to barley yellow dwarf virus (BYDV) differed also in the rate of systemic movement of the virus. The more susceptible varieties had the higher rate of systemic movement. In oats, the most rapid movement of BYDV occurred at 21 C with slower movement at higher or lower temperatures. These findings may account for some of the seasonal differences in the expression of BYDV symptoms. Reduced rate of systemic movement of the virus may be one mechanism of resistance genetically controlled in plants.

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Additional key word: resistance.

Over the past 40 years, beginning with the classic work of Samuel (7), plant pathologists have learned a great deal about the systemic movement of viruses in plant tissues. Systemic plant viruses generally spread slowly from cell to cell throughout the mesophyll. When the virus reaches vascular tissue, it spreads rapidly throughout the plant (3). Most studies of systemic movement have been conducted with mechanically transmissible viruses, and nearly all involved viruses which infect both mesophyll and vascular tissue.

Barley yellow dwarf virus (BYDV) is transmissible

only by aphids which carry the virus in a circulative manner. This virus, which is believed to be confined to vascular tissue (1, 2, 5), infects many of the Gramineae and can cause serious economic loss to most small grains. Gill (4) reported that systemic movement of BYDV out of the inoculated leaf can occur as soon as 6 hr after the viruliferous aphid begins to feed. The percentage of plants in which systemic movement has occurred continues to increase up to and beyond 72 hr after the initiation of inoculation feeding. Gill's experiments were carried out using a single aphid feeding on the first leaf blade of 'Rodney' oats (*Avena sativa* L.) or 'Parkland' barley (*Hordeum vulgare* L.).

At this laboratory, we have been studying the nature of resistance to BYDV in small grains and attempting to identify sources of resistance in wheat (*Triticum aestivum* L.) (6). One of the possible mechanisms by which resistance could be manifest is through the retardation of virus movement and establishment of systemic infection throughout the plant. Experiments described in this paper tested the hypothesis that such a mechanism of resistance does exist and can be measured.

MATERIALS AND METHODS.–Three cultivars each of wheat, oats, and barley were used. The cultivars were chosen to represent a high, moderate, and low level of field susceptibility to BYDV. Seedlings were grown in flats of soil in a greenhouse at 18-20 C until the second leaf had elongated to approximately 8-12 cm. Plants were inoculated by placing 10-15 viruliferous *Rhopalosiphum padi* (L.) in a rectangular plastic box-type cage and attaching the cage over the second leaf to within 2-4 cm of the leaf base. The plants were held in a controlled environment chamber at 20 C during the inoculation feeding period. At intervals of 12, 24, and 48 hr after the feeding period began, the infested leaf was cut off approximately 1 cm above the place where it emerged from the whorl. After the leaf had been removed, the plant was enclosed in a tubular polyethylene cage and held in a greenhouse at 15 C for 2 weeks. Occasionally an aphid, particularly a small nymph, would escape from the leaf cage during the inoculation feeding period. The tubular cages prevented them from moving from that plant. During the two weeks of incubation, any plant found with an aphid was discarded.

Since some cultivars developed very poor visible symptoms, it was necessary to recover virus from the plants to determine its presence. Virus was recovered by placing the excised third leaf in a humidified petri dish containing 15-20 nonviruliferous aphids. After 24 hr, the aphids were transferred to C.I. 666 barley seedlings for 2 days of inoculation feeding before being killed with nicotine sulphate spray. These indicator plants were held in the greenhouse at 15 C for 2 weeks before the number of infected plants was determined by symptom expression. Failure to recover the virus was interpreted to mean that the virus had not moved systemically from the inoculated leaf into the remainder of the plant at the time the leaf was removed. Significance of differences between cultivars was determined by chi-square analysis. Each experiment was repeated 6-8 times over a period of months until at least 100 plants had been analyzed under each condition.

TABLE 1. Systemic movement of barley yellow dwarf virus out of inoculated leaves after stated intervals

Cultivar[a]	Hr after inoculation		
	12	24	48
OATS			
Clintland 60	25.00	57.66	86.51
Newton	22.85	53.84	89.77
Ill. 63-1105	5.00**[b]	37.58**	96.93*
BARLEY			
Atlas 57	36.91**	85.10	89.47
Rojo	74.57**	87.27	97.75
Atlas 68	19.61**	48.18**	93.75
WHEAT			
C.I. 13567	47.52**	65.57**	87.91
Chris	26.05**	46.15	88.23
LR64 × Son64	12.61**	54.44	85.00

[a] Cultivars are listed in decreasing order of field susceptibility.

[b] Values indicated with an asterisk are different from the other values in the set at the 95 (*) or 99 (**) percent confidence level.

RESULTS.–*Movement of virus in different cultivars.*–The results of these experiments are shown in Table 1. The rate of systemic movement of BYDV differed significantly from cultivar to cultivar. Systemic movement occurred only one-fourth to one-half as quickly in the tolerant cultivars as it did in the more susceptible cultivars. By extrapolation, it appears that in several cultivars, it is possible for systemic movement to begin immediately after inoculation, while in other cultivars, systemic movement does not begin until 6-8 hr after inoculation.

Effect of temperature on rate of movement.–The rate of systemic movement was also determined for two oat cultivars at four different temperatures; 10, 15.5, 21, and 26.5 ± 0.5 C. At each temperature, the inoculated leaf was removed 24 hr after the aphid feeding began. Incubation and recovery procedures were the same as for the previous experiment. This experiment was repeated until at least 100 plants had been tested at each temperature. The results of these experiments are shown in Fig. 1.

Temperature has a pronounced effect on rate of systemic movement of BYDV. At 10 and 15.5 C, there was some systemic movement 24 hr after inoculation had begun. The percent of the plants in which systemic movement had occurred increased very sharply between 15.5 and 21 C. At 26.5 C, the percent systemic movement decreased. It is possible that different temperatures may have affected the activity and feeding of the aphids; however, by using a large number of aphids per plant, the effect should have been minimized.

DISCUSSION.–Systemic movement beginning at zero time may be possible because the vector feeds in

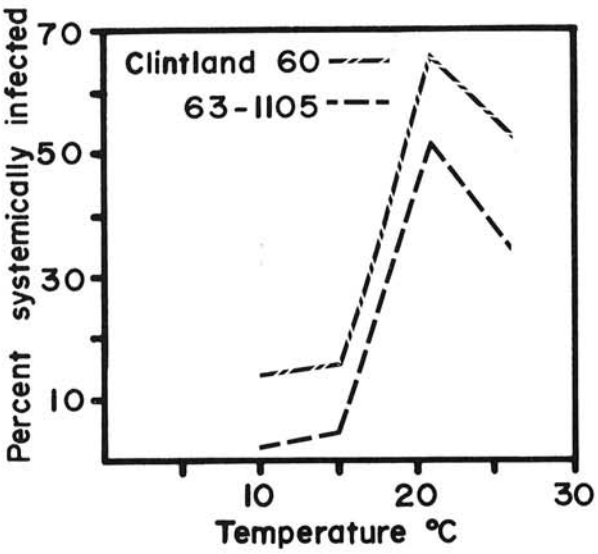

Fig. 1. The effect of temperature on the systemic spread of barley yellow dwarf virus in two cultivars of oats 24 hr after infestation with viruliferous aphids.

phloem tissue and might release virus directly into the sieve elements (1). If this happens and the virus can move systemically without multiplication, susceptible cultivars must differ in their ability to translocate the infectious entity whether it be ribonucleoprotein or nucleic acid.

A delay of 6-8 hr in the onset of systemic movement would be expected if the phloem sieve elements were not capable of being infected directly and it was only second or third generation virus particles which moved systemically. Another possible explanation would be that only free nucleic acid moves systemically, and a period of time must lapse while the protein coat is being stripped from the infectious nucleic acid core.

Systemic infection occurring 24 or 48 hr after first feeding may result directly from feeding and the consequent release of virus into the phloem tissue, or it may result from the release of infectious virus from a previously infected cell. As more and more cells in the phloem tissue become infected, the probability of a second or third generation virus particle moving systemically increases. If a single infected cell releases virus that infects several new cells, the number of cells infected increases geometrically. If this happens, the degree of systemic invasion found in a susceptible plant 7 days after inoculation could be greater than that found in a resistant cultivar by the end of summer.

At high temperatures, the growth rate of healthy plants is very rapid, and tall, spindly plants result. Also, at high temperatures, BYDV symptoms are greatly reduced and may be masked completely in certain cultivars. At 10 C, healthy plants develop slowly into short, sturdy, dark-green plants. Barley yellow dwarf virus symptoms are slow to develop but eventually become very pronounced with much reddening or yellowing of the leaves and severe stunting. Different symptom expressions at high and low temperatures may result from differences in BYDV infection effects on the physiology of the plant, but they also may be due to differences in the degree of systemic invasion of the virus.

When field infection occurs late in the season, losses to BYDV are generally not severe, presumably because the plants were mature enough to complete development even though infected (however, see 8). It is also possible that elevated temperatures of late season reduce the amount of tissue systemically invaded. When plants are infected early in the growing season, the cool nighttime temperatures would reduce growth while daytime temperatures in the order of 20 C would permit the most rapid systemic movement of the virus, and conditions would be ideal for complete systemic invasion of the infected plant.

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