Differential Effects of Barley Yellow Dwarf Virus on the Physiology of Tissues of Hard Red Spring Wheat

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ABSTRACT

Three cultivars of hard red spring wheat which varied in their response to barley yellow dwarf virus infection were grown in the field in the summer of 1969. Plants were infested with viruliferous aphids in the seedling stage. When the plants reached the late milk or early soft-dough stage of maturity, photosynthetic rates, respiratory rates, and the accumulation of dry matter were measured in tissues above the top vegetative node. The most susceptible cultivar contained 42% excess dry weight in the flag leaf blade where there was a 72% reduction in photosynthetic capacity and a 36% stimulation of respiration. Similar tissues of a resistant cultivar showed only 20% excess accumulation of dry weight, 60% reduction in photosynthesis, and a 20% reduction in respiration. Among the tissue classes, the flag leaf blades were severely affected and the leaf sheaths moderately affected, while no significant effect was measured on the culm and spike. We suggest that most of the yield in infected susceptible plants is derived from photosynthesis of the spike.

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The work of several authors (1, 5, 6, 7, 8) has shown that carbohydrates stored in the grains of wheat are derived mostly from photosynthetic action of the flag leaf blade, leaf sheath, spike, and culm immediately below the spike. Estimates of the photosynthate contribution from each type of tissue to the grain have varied, depending upon time and method of analysis and cultivars of wheat involved in the experiment. In general, the lamina (blade) of the flag leaf and glumes of the spike appear to contribute approximately equal amounts to filling of the grain (1).

Barley yellow dwarf virus (BYDV) infection results in reduced photosynthesis, with the greatest reduction occurring in the lower leaves, and the less severe reduction in the upper leaves of barley (2) and wheat (4). Barley yellow dwarf virus-infected plants also have a massive accumulation of soluble carbohydrates and starches in the flag leaf, and to a lesser extent in the leaf sheath, with no significant accumulations in the culm or spike (3).

In measuring the rate of photosynthesis of all tissue above the top vegetative node, we found that photosynthesis per gram of fresh weight of tissue had been reduced by 25% in BYDV-infected plants (4). This paper reports the results of an experiment designed to measure separately the photosynthetic capacity of various tissues of healthy and BYDV-infected field-grown hard red spring wheat.

MATERIALS AND METHODS.–Because of time and equipment limitations, we used only three cultivars in this experiment. Hard red spring wheat, *Triticum aestivum* L. em. Thell., cultivars selected had moderate tolerance (LR64 X Son64), moderate susceptibility (Chris [C.I.13751]), and high susceptibility (C.I.13567 [North Dakota 81 X Conley]) to BYDV infection as measured by yield potential in field trials. Seeds of each cultivar were planted in the field 13 May 1969 in a split-plot design. On 9 June, leaves from BYDV-infected plants carrying a heavy population of *Rhopalosiphum padi* (Linnaeus), the bird cherry oat-aphid, were strewn between plants of the plot to be inoculated. This inoculation technique has been found to be very efficient for rapidly establishing uniform infection. After 5 days, the plants were sprayed with malathion to kill the aphids and prevent further spread of infection. On 2 July, the plots were sprayed with maneb to minimize rust infections.

Physiological measurements were begun on 17 July, when the grain was in the late milk or early soft-dough stage of development. In each plot, we selected several main tillers of average height and spike size, and typical of the cultivar and treatment represented. These tillers were cut off just below the top vegetative node and placed in a flask of water.

Four types of tissue samples were prepared from each cultivar and each treatment. Sample 1 consisted of three intact plant tops; sample 2 consisted of three leaf sheaths with attached flag leaf laminae and enclosed culms; sample 3 consisted of three spikes with attached exposed culm tissue; and sample 4 consisted of the laminae of three flag leaves. To prevent desiccation, excess tissue was left on the base of each sample, and this excess was submerged in a test tube filled with water and sealed in place with a sponge-rubber seal and a parafilm wrapping. At the conclusion of the experiment, we cut off the excess tissue and used only the exposed part for determination of fresh weight and dry weight.

To measure photosynthesis and respiration, each tissue sample was placed in a separate sealed chamber and submerged in a water bath at 23 C. Gas exchange rates were monitored by an infra-red CO_2 gas analyzer under 4,000 ft-c of illumination for photosynthetic rates, and under total darkness for respiratory rates. The apparent rates of photosynthesis were corrected for dark respiration.

Experiments with each tissue type, each treatment, and each cultivar were repeated on 17, 18, 19, 21, and 22 July to give five replications. By taking replications over a 6-day period, there was some maturation of tissue, but statistical analysis of the data did not reveal significant differences between replications. In making physiological measurements, we have always found a greater day-to-day variation in field-grown material than in material reared in a growth chamber under constant conditions. Because of this variation, differences between treatments were analyzed by a paired t-test, and other comparisons were made by using analysis of variance of the data expressed as a per cent of the control.

RESULTS.—Table 1 summarizes the data from the five replications. There are many significant differences between healthy and diseased tissues, among various types of tissue examined, and among the three cultivars tested.

The effects of BYDV were most severe in the highly susceptible cultivar C.I.13567, less pronounced in the moderately susceptible cultivar Chris, and least in the moderately tolerant cultivar LR64 X Son64. This trend is best exemplified by the effects of BYDV on the per cent dry weight and photosynthesis of the combined lamina and sheath of the flag leaf. Expressed as per cent of control, BYDV infection increased dry weight 32.6%, 22.6%, and 12.3%, and

TABLE 1. Effects of barley yellow dwarf virus (BYDV) infection on per cent dry weight, photosynthesis, and respiration of various tissues of cultivars of field-grown hard red spring wheat

		Cultivar and reaction to BYDV								
		C.I. 13567 (highly susceptible)			Chris (moderately susceptible)			LR64 X Son64 (moderately tolerant)		
Tissue analyzed	Quantity measured	Healthy	Diseased	% of control	Healthy	Diseased	% of control	Healthy	Diseased	% of control
Complete plant top	% dw[a]	24.2	26.1	107.9*[b]	25.0	26.8	107.2**	30.3	33.6	110.9**
	Ps/fw	17.6	13.5	76.7*	30.6	20.7	67.6**	16.7	13.9	83.2
	Ps/dw	72.6	51.7	71.2**	122.2	76.8	62.8**	54.9	41.2	75.0
	R/fw	5.6	6.8	121.4*	5.1	7.0	137.3*	6.0	6.1	101.7
	R/dw	23.0	25.8	112.2*	20.5	25.9	126.3	19.8	18.2	91.9
Flag leaf blade and sheath	% dw	23.0	30.5	132.6**	23.9	29.3	122.6**	28.4	31.9	112.3*
	Ps/fw	43.0	15.0	34.9**	65.2	28.0	42.9**	51.9	36.2	69.7**
	Ps/dw	186.6	49.2	26.4**	272.0	95.3	35.0**	182.3	113.4	62.2**
	R/fw	7.8	10.3	132.1*	8.6	9.4	109.3	8.7	8.7	100.0
	R/dw	33.9	33.8	99.7	36.0	31.9	88.6	30.5	27.1	88.9**
Flag leaf blade	% dw	25.3	36.0	142.3**	27.5	36.0	130.9**	34.2	40.8	119.3
	Ps/fw	73.7	20.9	28.4**	118.9	32.2	27.1**	88.2	35.1	39.8**
	Ps/dw	290.8	58.1	20.0**	430.9	89.5	20.8**	258.0	85.9	33.3**
	R/fw	11.2	15.3	136.6*	12.2	14.0	114.8	13.4	10.8	80.6
	R/dw	44.2	42.4	95.9	44.1	38.9	88.2	39.1	26.5	67.8
Culm and spike	% dw	26.6	27.7	104.1	25.8	28.2	109.3	34.3	33.3	97.1
	Ps/fw	17.7	16.0	90.4	19.7	18.0	91.4	12.9	11.8	91.5
	Ps/dw	66.6	57.6	86.5	76.1	63.7	83.7	37.5	35.4	94.4
	R/fw	6.5	6.6	101.5	7.0	6.0	85.7	6.5	5.9	90.8
	R/dw	24.4	23.8	97.5	27.1	21.3	78.6	19.0	17.8	93.7

Summary of analysis of variance of the data expressed as per cent of control

F ratios for:	% dw	Ps/fw	Ps/dw	R/fw	R/dw
Differences between reaction of tissues to BYDV	26.78**	53.56**	75.53**	3.68*	NS
Differences between reaction of cultivars to BYDV	5.83*	5.31*	6.17*	6.83*	NS
Difference in tissue by cultivar reaction to BYDV	NS	NS	NS	NS	NS

[a] R = respiration in μliter CO_2/min. Ps = photosynthesis in μliter CO_2/min. dw = dry weight in g. fw = fresh weight in g.
[b] * = Significantly different from 100% at the .05 confidence level. ** = Significantly different from 100% at the 0.01 confidence level.

reduced photosynthesis 65.1%, 57.1%, and 30.3% for C.I.13567, Chris, and LR64 X Son64, respectively.

When comparing the effects of BYDV infection on various tissues within the same cultivar, the most striking observation is the severity of the effect on the flag leaf blade; there is no significant effect on the culm and head. Photosynthetic capacity per gram fresh weight of the infected flag leaf blade ranges between 27 and 40% of the control. When the leaf sheath is considered together with the blade, this value ranges from 35 to 70% of the control. Since the photosynthetic capacity of the combined tissues is much higher than it is for the blade alone, and the sheath constitutes less than 30% of the combined tissue (3), the inference is that the photosynthetic capacity of the infected leaf sheath is approaching that of the control, at least for the cultivar LR64 X Son64.

The photosynthetic capacity of the infected culm and spike was about 90% of the control for each of the three cultivars. This 10% loss of photosynthesis was not statistically significant at the 5% confidence level because of variation; but there may be some small reduction of photosynthesis in the culm and spike after BYDV infection.

Healthy plants of the three cultivars show large differences in the total photosynthesis, but the proportion of photosynthesis contributed by each of the plant parts to this total is quite similar. The proportion of the total photosynthesis contributed by the culm and spike is about 35%, whereas the contribution from the blade and the sheath is about 55% and 10%, respectively.

Total photosynthesis of the diseased plants is appreciably lower than photosynthesis of the comparable controls. This is due in part to reduced photosynthetic rate, and in part to reduced size of these tissues. Diseased tissues of the three cultivars, unlike their healthy counterparts, had similar rates of total photosynthesis; and again the per cent contribution to this total that was made by each of the plant parts was quite similar for each of the cultivars. However, the drastic effect of BYDV infection on the photosynthetic rate of the flag leaf lamina greatly reduced the importance of this organ in the photosynthetic economy of the plant top. Whereas healthy flag leaf blades conducted over half of the total photosynthesis, diseased flag leaf blades conducted only one quarter. Because of this great decrease in photosynthetic activity in the flag leaf blade, the importance of the photosynthetic activity of the sheath, culm, and spike increased greatly. The proportion of the total photosynthesis conducted by the culm and head increased from 35% in the healthy tissues to 43% in the diseased, and the proportion conducted by the sheath increased from 10% in the healthy to approximately 30% in diseased tissues.

We regularly observed that BYDV infection stimulated the rate of respiration per gram fresh weight of tissue (2, 4) in lower leaves. For the moderate and highly susceptible cultivars, it was true in this experiment also; but the moderately tolerant cultivar LR64 X Son64 showed a consistently reduced rate of respiration in the infected flag leaves, culms, and spikes. Because of variation, differences were not statistically significant at the 5% confidence level. Although differences were not large, in the over-all carbohydrate economy of the plant it would mean that less carbohydrate was being utilized via respiration, and that there was more carbohydrate available for translocation.

DISCUSSION.–Under normal circumstances, a large proportion of the carbohydrates stored in the grain originates from photosynthetic activity of the flag leaves (1, 5, 6, 7, 8). During the early stages of the productive life of the flag leaf, some of the photosynthetic products are utilized in development and expansion of the head (7). Our data show that 55% of the total photosynthetic capacity of a healthy plant top is contained in the flag leaf blade.

In diseased plants, photosynthetic capacity per unit fresh weight is greatly reduced, and so is total size (fresh weight) of the flag leaf lamina. At the same time, there is a massive accumulation of carbohydrates in the leaf tissue (2, 3). This leads to the assumption that little if any photosynthate from the flag leaf blade is translocated to the grain for storage. The physiological balance of the leaf sheath is disturbed by BYDV infection in much the same manner as the leaf blade, but to a lesser extent. In healthy wheat, a relatively insignificant 10% of the total photosynthesis of the plant top is carried on by the sheath. This photosynthetic contribution increases to 30% in BYDV-infected leaf sheaths because, although affected, they retain a large measure of their photosynthetic capacity. It is possible that the photosynthetic production of the sheath is in excess of that utilized or stored in the sheath, and that some carbohydrates are translocated to the grain for storage.

Barley yellow dwarf virus-infected culms and spikes were reduced in size, probably as the result of an insufficient carbohydrate supply during development and expansion, but there was no significant reduction in photosynthesis per gram fresh weight of tissue. In a diseased plant, only 43% of the total photosynthesis of the plant top is conducted by the culm and spike; but this 43% may result in most of the total carbohydrate translocated to the grain.

Most susceptible cultivars of wheat, when infected at the early stage of growth, yield only 20 to 40% as much grain as uninfected plants; and it seems likely that most of the grain fill in infected plants is derived solely from the photosynthesis of the spike.

In cultivars more similar in genetic background and in their response to BYDV infection, we have been unable to identify cultivar effects in the physiology of diseased plants (4). However, the three cultivars examined in this experiment were selected because of their diverse yield response to BYDV infection. All of the cultivars displayed pronounced visual symptoms of BYDV infection, yet the more tolerant cultivars (particularly LR64 X Son64) retained a moderate yield potential. This may be due in part to the photosynthetic capacity of the infected leaf, and particularly of the leaf sheath. Infected tissues of this cultivar accumulated a significant excess of dry weight, but this excess was not nearly so great as was found in the more susceptible cultivars; and it suggests that this cultivar may retain some ability to translocate the products of photosynthesis out of the leaf blade and sheath and into the grain.

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