Physiological Responses to Wind- and Sandblast-Damaged Winter Wheat Plants[1]

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ABSTRACT

Yield depression due to physical damage by wind and windblown soil (sandblast damage) is well known. The objective of this research was to determine if this yield depression was due to physiological changes within the plant or to the loss of viable plant tissue.

Physiological responses of winter wheat (*Triticum aestivum* L. em. Thell) to injury by a 20-minute exposure to wind (13.4 m/sec), wind plus sand (5, 10, and 15 kg), and partial defoliation (removal of the distal 1/4 and 1/2 of each leaf) were evaluated. Net photosynthesis, dark respiration, ribulose-1,5-diphosphate (RUDP) carboxylase activity, total chlorophyll, dry weight, leaf area, and total nonstructural carbohydrates (TNC) were determined 1, 3, and 7 days after treatment.

Dry-weight production and accumulation decreased with increased plant injury. Reduced growth of sandblasted wheat seedlings is caused by loss of viable leaf tissue and physiological changes, which are mainly reduced photosynthesis and increased respiration. It is not clear from this study whether these changes result from partial defoliation, short-term high-intensity moisture stress, or a combination of both.

Additional index words: Net photosynthesis, Dark respiration, RUDP carboxylase, Chlorophyll, Partial Defoliation, TNC.

T HE Soil Conservation Service estimated that from November 1, 1970, to May 31, 1971, 1.8 million ha (4.5 million acres) of cropland in the 10 Great Plains States were damaged by wind erosion (21).

Most duststorms, reportedly 95% (10), occur between November 1 and May 31, the period when winter wheat (*Triticum aestivum* L. em. Thell) is extremely vulnerable to wind-erosion damage.

Wind has been shown to reduce the growth and yield of rape (*Brassica napus* L.) (22, 23), barley (*Hordeum vulgare* L.) (23), and peas (*Pisum sativum* L.) (23). Windblown soil has reduced the yields of cotton (*Gossypium hirsutum* L.) (2, 11), tomatoes (*Lycopersicon* sp.) (4), alfalfa (*Medicago sativa* L.) and grasses (15), greenbeans (*Phaseolus vulgaris* L.) (18), soybeans (*Glycine max* (L.) Merr.) (3), and winter wheat (1, 25) by abrasive injury. Yields of soybeans (8) and corn (*Zea mays* L.) (8) have been reduced by hail simulation.

In all those studies on plant damage by wind, windblown soil, or hail, no attempt was made to assign the dry matter and yield reductions to a physiological change. We investigated the photosynthetic and respiratory responses of wind- and sandblast-injured winter wheat to determine whether yield reductions

are caused by physiological changes or by reductions in viable leaf area.

MATERIALS AND METHODS

Twenty seeds of 'Parker" winter wheat were planted in 18-cm-diameter plastic pots filled with 4 kg of masonry sand, sieved to remove all particles larger than 3.35 mm. Pots were placed in a greenhouse, where daylength was extended to 14 hours by a combination of fluorescent and incandescent lamps. Temperature was maintained between 20 and 35 C. Plants were watered daily with 0.2-strength Hoagland nutrient solution. Three weeks after seeding, the plants were thinned to 10 plants per pot.

Four weeks after planting, the plants (6- to 8-leaf stage) were exposed to wind and sandblast injury in a wind tunnel (26). In all treatments, plants were exposed for 20 minutes to a 13.4 m/sec (30 mph), free-stream wind velocity. The wind velocity was determined in the center of the tunnel (0.3 m upwind of the plants), using a pitot-static tube and incline-gage alcohol manometer. Predetermined amounts of sand (0.420- to 0.297-mm diameter) were placed on a smooth-bottomed, open-ended tray located directly upstream from the plants. After exposure, the plants were returned to the greenhouse.

Exposure treatments were: no wind or sand (check), wind only, wind plus 5 kg of sand, wind plus 10 kg of sand, wind plus 15 kg of sand, removal of the distal 1/4 of each leaf, and removal of the distal 1/2 of each leaf. Treatments were imposed between the hours 0800 and 1000.

Four pots were selected randomly a priori from each exposure treatment 1, 3, and 7 days after treatment. Five plants were removed from each pot for ribulose-1,5-diphosphate carboxylase enzyme assay and chlorophyll determination. The remaining 5 plants were used to determine net photosynthesis rate, dark respiration rate, leaf area, dry weight, and total nonstructural carbohydrates.

Net carbon exchange in the light and dark was determined using a closed system and an infrared gas analyzer (17). The plant chamber, a 30-cm-diameter by 60-cm high plexiglas cylinder, was removable to permit changing experimental plants. Air was circulated upward through the chamber at an average velocity of 2.8 m/sec by a fan in the heat exchanger. Temperature in the chamber was controlled at 25 ± 1 C.

Light at an intensity of 0.47 cal cm^{-2} min^{-1} was supplied to the chamber by four 300-watt, cool-beam, medium spotlights. Net photosynthesis was determined by recording the time required for CO_2 in the chamber to change from 350 to 250 ppm with lights on. The time required for CO_2 to increase to 350 ppm with lights off was taken as dark respiration. All readings were taken between the hours 1000 and 1300.

After carbon dioxide assimilation was measured, the plants were cut off at the sand surface, stripped of leaves, and separated into viable and dead tissues. Areas of viable and dead leaves were measured. Plant parts were combined, dried 48 hours at 70 C, and weighed.

Ribulose-1,5-diphosphate (RUDP) carboxylase (EC 4.1.1.39) was extracted from 1 g of leaf-blade tissue homogenized with 20 ml of cold (2 to 3 C) mixture containing 0.1 mmoles Tris [tris (hydroxymethyl) aminoethane] (pH 8.0), 0.004 mmoles 2-mercaptoethanol, and 0.01 mmoles reduced glutathione per ml. The homogenate was filtered through a fine mesh sieve, and a 0.5-ml aliquot was taken for chlorophyll determination by a modification of the methods of Arnon (6) and MacKinney (16). The remaining homogenate was centrifuged at 20,000 $\times$ g for 15 minutes and the supernatant used for the enzyme assay. The activity of RUDP carboxylase was assayed by a modified method used by Chen, McMahon, and Bogard (9), Kleinkopf, Huffaker, and Matheson (14), and Trown (20) by following the incorporation of NaH$^{14}CO_3$ into acid-stable products at 30 C. Total nonstructural carbohydrates (TNC) were determined by Smith's (19) method.

RESULTS

Final plant dry weights were not reduced significantly by the 5-kg and 10-kg sand treatments, but dry matter accumulation (difference between day 1 and day 7) was reduced by all treatments (Table 1). Re-

Table 1. Total dry-weight production, dry-weight accumulation from 1 to 7 days after treatment, viable leaf area, percent viable leaf area, and total chlorophyll content of winter wheat seedlings after treatment.†

Treatment	Dry wt	Accumulation	Viable leaf area		Chlorophyll
	— g —		dm²	%	mg/gfw‡
Check	1.70a*	0.84 a	3.22a	100a	1.90b
Wind	1.28b	0.46c	2.45bc	99a	1.95b
Wind + 5kg	1.55a	0.68b	2.75b	92b	1.47c
Wind + 10 kg	1.60a	0.50c	2.60b	89b	2.18a
Wind + 15 kg	1.25b	0.46c	2.04cd	74c	2.33a
1/4 leaf area removed	1.08c	0.35c	1.92e	75c	2.16a
1/2 leaf area removed	0.80d	0.48c	1.56e	50d	1.79b

*Means followed by the same letter are not significantly different at the 5% level by Duncan's New Multiple Range Test. †Averages for the three sample dates. ‡gfw=gram fresh weight.

Table 2. Net photosynthesis rate, ribulose-1,5-diphosphate carboxylase activity, dark respiration rate, and percentage of total nonstructural carbohydrates of winter wheat seedlings after treatment.†

Treatment	Photosynthesis, mgCO₂/ pot per hr	RUDP carboxylase, μmoles ¹⁴CO₂/ gfw per hr	Respiration, mgCO₂/ pot per hr	TNC %
Check	87.7a*	7.92b	29.3cd	2.58a
Wind	59.6c	8.36a	28.6cd	1.84b
Wind + 5kg	82.4a	7.39c	36.3b	1.43bc
Wind +10 kg	76.5ab	7.60c	44.1a	1.83b
Wind +15 kg	65.4bc	6.96d	28.8cd	0.86c
1/4 leaf area removed	57.4c	5.90e	33.2bc	1.81b
1/2 leaf area removed	42.1d	5.85e	26.8d	0.93c

*Means followed by the same letter are not significantly different at the 5% level by Duncan's New Multiple Range Test. †Averages for the three sample dates.

moving the distal end of each leaf caused the greatest reduction in dry-weight production, but dry-weight accumulation was equal to that of the wind-only, 10-kg sand, and 15-kg sand treatments. Plants in the wind-only treatment failed to grow as well as plants in other treatments. The reasons for this poor growth could not be determined.

Viable leaf area was reduced significantly by all treatments (Table 1). Only the leaf tips were injured visibly by the wind-only treatments. Leaf tips, edges, and areas across the width of the leaf 2 to 3 cm above the tunnel floor were killed when sand was added to the windstream.

Net photosynthetic rates were reduced significantly by all treatments except 5-kg sand and 10-kg sand (Table 2). Plants subjected to wind-only and leaf-removal treatments had the lowest net photosynthesis.

Ribulose-1,5-diphosphate carboxylase activity was reduced significantly by all treatments except wind-only, which was significantly higher (Table 2). Removing leaf area depressed RUDP carboxylase activity the most.

Total chlorophyll was increased significantly by 10-kg sand, 15-kg-sand, and 1/4-leaf removal treatments and reduced only by the 5-kg-sand treatment (Table 1).

Dark respiration rates were significantly increased by the 5-kg-sand and 10-kg-sand treatments and were unchanged by the other treatments (Table 2).

Total nonstructural carbohydrates were reduced significantly by all treatments (Table 2). The 15-kg-sand and 1/2-leaf-removal treatments had the lowest TNC.

DISCUSSION

The sand amounts used in this study were comparable to Woodruff's (25) low, intermediate, and moderate rates. As single fall exposures, Woodruff's rates reduced grain yields 21 to 31%; as single spring ex-

posures, 37 to 56%. Though grain yields were not obtained in this study, reductions in dry-weight production were similar to Woodruff's.

Dry-weight production and accumulation apparently are closely related to viable leaf area. Loss of equal leaf area by sandblast (15-kg sand) or defoliation (¼-leaf removal) caused the defoliation treatment to accumulate less dry matter. These differences must have resulted from physiological changes within the damaged plants.

Photosynthetic rates per pot were reduced 8 to 52% on damaged plants, but if calculated on live-leaf-area basis the rate increased on all but two treatments (wind only and ½-leaf removal) by 8 to 18%. The increases in photosynthesis rates of the remaining live tissue agree with those of other studies on the effect of partial defoliation (12, 24). However, the activity of RUDP carboxylase did not increase because of the treatments, but chlorophyll increased where 11 to 26% of the leaf area was killed, as has been reported for defoliated corn and bean plants (24).

Dark respiration per pot was increased on three treatments and decreased on three, with no relationship to leaf area lost, but dark respiration per live-leaf area was increased 28 to 90%. This increase in respiration possibly was caused by a short-term moisture stress resulting from the huge demand of plant leaves with broken cells exposed to a high wind velocity. In this regard, leaf-water potentials in soybeans were found to increase for 4 to 24 hours after sandblast damage (5). Increases in respiration rates with moisture stress have been reported by Brix (7) for tomatoes and loblolly pine (*Pinus taeda* L.).

Moisture stress also could account for the decrease in per-pot photosynthesis and the decreased activity of RUDP carboxylase. RUDP carboxylase activity in barley has been shown to be reduced by moisture stresss (13).

The decrease in photosynthesis and the increase in respiration would help account for the reduction in total nonstructural carbohydrates. Under moisture stress, starches may convert more rapidly to sugars, which would thereby become an available source of energy for cell repair or respiration.

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