Horizontal Resistance of Red Rustproof Oats to Crown Rust

H. H. Luke, W. H. Chapman, and R. D. Barnett

Research Plant Pathologist, Plant Science Research Division, ARS, USDA, Plant Pathology Department, University of Florida, Gainesville 32601; Chairman and Assistant Agronomist, respectively, Agricultural Research and Education Center, Quincy, Florida 32351.

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ABSTRACT

Some cultivars of Red Rustproof (RRP) oats (*Avena byzantina*) exhibit a specific (necrotic) reaction to a few races of crown rust (*Puccinia coronata* f. sp. *avenae*), but their principal defense against this pathogen is through horizontal resistance (late-rusting and slow-rusting).

A late-rusting cultivar is one that exhibits crown rust symptoms 10-14 days later than susceptible cultivars. When symptoms develop, late-rusting cultivars exhibit a susceptible reaction. Late-rusting has been observed only under natural field conditions, and is not associated with any stage of plant growth (age of the host). Late-rusting seems to be dependent upon environment or upon spore concentration.

A slow-rusting cultivar is one on which the percentage of crown rust infection increases more slowly than it does on a susceptible cultivar. Slow-rusting cultivars usually exhibit a lower percentage of infection than susceptible cultivars throughout the growing season. Slow-rusting can be reproduced under artificial conditions. Apparently, a different mechanism is involved from that responsible for late-rusting. Both, however, seem related to the maturity dates of specific cultivars, because late-maturing cultivars exhibit pronounced slow-rusting and late-rusting, whereas early-maturing RRP cultivars do not.

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Red Rustproof (RRP) oats, *Avena byzantina* K. Koch, were introduced into the southern United States during the 1860's (5). The first observation on the reaction of RRP oats to *Puccinia coronata* f. sp. *avenae* Fraser & Led. indicated that they were absolutely rustproof in all cases (7); hence the name "Rustproof". Stanton pointed out that Rustproof is a misnomer because RRP cultivars are not actually immune (5). He indicated that rust develops later in the life of the plant than it does on susceptible cultivars. This characteristic was referred to as "late-rusting" (5). In addition to late-rusting, we observed a low percentage of infection on certain RRP cultivars. Caldwell (1) and Hooker (3) referred to this characteristic as "slow-rusting".

In 1958, we initiated studies to determine why RRP cultivars escape severe crown rust damage. This paper is concerned with various aspects of the horizontal (6) or generalized (1) resistance of RRP oats to crown rust. Late-rusting and slow-rusting are considered herein as forms of this type of resistance.

MATERIALS AND METHODS.—*Field tests.*—Stanton reported that all RRP cultivars are not late-rusting (5). We observed 17 cultivars under field conditions for 2 years. During this time we confirmed Stanton's report, and observed that late-maturing cultivars exhibit late-rusting, but early-maturing cultivars do not. We made panicle selections of early-maturing Fulghum (C.I. 708) and Alabama Red Rustproof 43A (C.I. 3934); intermediate-maturing Burt (C.I. 824) and Brunker (C.I. 2054); and late-maturing Red Rustproof 14 (C.I. 4876) and Buck Selection (C.I. 7037) cultivars. Seed of the selections was increased and planted at monthly intervals, beginning in mid-October and terminating in mid-January. Planting dates were staggered so that all cultivars would be at several stages of development in the spring when crown rust occurs naturally. A susceptible cultivar (Fulgrain, C.I. 3253) was planted adjacent to each test cultivar. Percentage of infection was recorded at 10-day intervals following the first observation of natural infection. In this report, "percentage of infection" refers to an estimate of the percentage of crown rust coverage of the most severely infected leaves.

Growth chamber tests.—Field observations indicated that RRP 14 did not show signs of rust infection in early March, but had a low percentage of infection (10-30%) in mid-April. These observations were used to study the effects of environment on late-rusting (expression of symptoms 10-14 days later than susceptible cultivars) and slow-rusting (low percentage of infection throughout the growing season).

A growth chamber was programmed to reproduce the average night and day temperatures (9 and 24 C, respectively) at Gainesville, Fla., for the week of 8 March. Another growth chamber was programmed to reproduce the average night and day temperatures (12 and 28 C, respectively) for the week of 12 April. Day-lengths for these periods are 12 and 13 hr, respectively. Plants were grown under these conditions in 4-inch clay pots filled with a soil-peat mixture. Each pot contained 10 seedlings of RRP 14, Alabama RRP 43A, or Fulghum. Three replications of each cultivar were used in most experiments.

Seedlings 8 to 10 days old were inoculated with crown rust race 327 (4). Foliage was sprayed with water prior to inoculation. Inoculum (1 mg spores/50 mg talc) was dusted onto the plants in each pot. Plants were placed in a horizontal position and rotated during inoculation to distribute spores uniformly over the foliage. The interior of clear plastic bags was sprayed with water, and the bags were placed over plants and pots. Bags were secured with rubber bands, and the pots returned to the

TABLE 1. Percentage of crown rust infection[a] observed at 10-day intervals[b] on Red Rustproof oats having different maturity dates

Maturity characteristic and cultivar	Crown rust reading dates[b]								
	1960[c]			1961[c]			1962[c]		
	1	2	3	1	2	3	1	2	3
Late-maturing									
Red Rustproof 14	0	0	0	0	4	14	0	16	18
Buck Selection	0	0	0	0	2	8	0	14	22
Intermediate-maturing									
Burt	0	10	32	38	74	90	50	82	88
Brunker	0	0	20	40	65	75	45	82	90
Early-maturing									
Alabama RRP 43A	2	12	48	85	92	95	55	85	92
Fulghum	12	32	82	80	92	95	70	92	95

[a] Percentage of infection is an average calculated from four replications. Minimum differences for significance: 5% = 17; 1% = 23.

[b] Rust readings were taken at 10-day intervals from 20 March to mid-April.

[c] Data were collected during spring of 1960, 1961, 1962.

respective growth chambers for 20 hr. Plastic bags were then removed, and the plants were maintained in the growth chambers for 10 days.

RESULTS.—*Field experiments.*—Late-maturing cultivars expressed signs of crown rust infection about 15 days later than early-maturing cultivars (Table 1). There was, however, no relationship between the stage of growth of a specific cultivar and the percentage of crown rust infection. For example, plantings of RRP 14 in the juvenile and heading phases of growth had about the same percentage of infection throughout several growing seasons (H. H. Luke, *unpublished data*). Therefore, data from the four planting dates were composited and statistically analyzed.

Under field conditions, late-maturing cultivars (RRP 14, Buck Selection) exhibited late-rusting and slow-rusting; intermediate-maturing cultivars (Burt, Brunker) exhibited distinct slow-rusting and some late-rusting; but early-maturing cultivars (Fulghum, Alabama RRP 43A) did not exhibit either characteristic. When rust infection was not severe, late-maturing cultivars did not exhibit crown rust symptoms (Table 1, 1960). The differences between intermediate- and early-maturing cultivars could not be evaluated until the latter part of the growing season. When rust infection was moderate (1961), late-maturing cultivars had a significantly lower percentage of infection than did the intermediate- and early-maturing cultivars. This difference persisted throughout the growing season; but the intermediate- and early-maturing cultivars showed a significant difference in percentage of infection only at the first reading date. In 1962, when rust was severe, the late-maturing cultivars showed a significantly lower percentage of infection than did the intermediate- and early-maturing cultivars. However, there was no significant difference in the percentage of infection on intermediate- and early-maturing cultivars. Regardless of the severity of infection, late-maturing cultivars exhibited a lower percentage of infection than did the intermediate- and early-maturing cultivars.

Highest percentages of infection were recorded on three cultivars over an 11-year period (Table 2). In 3 of 11 years (1960, 1967, 1969), the cultivar that exhibited the highest degree of horizontal resistance (RRP 14) was virtually free of infection, and had more than 40% infection only in 1 year (1965). The severe infection that occurred on RRP 14 in 1965 was influenced by the heavily infected susceptible cultivars planted adjacent to each test cultivar. Under normal field conditions, the percentage of infection in 1965 would probably have been less than 90%. When environmental conditions are not favorable for crown rust development, the intermediate-maturing cultivars react like slow-rusting cultivars (Table 2; Burt, 1960, 1967, 1969). If rust appears early and reaches epiphytotic proportions, the

TABLE 2. Maximum percentages[a] of crown rust infection observed on three Red Rustproof cultivars[b] over an 11-year period under field conditions

Year	Red Rustproof 14	Burt	Fulghum
1960	0	30	85
1961	20	90	95
1962	35	95	95
1963	40	90	95
1964	30	80	90
1965	90	95	95
1966	25	70	95
1967	5	50	90
1968	20	90	90
1969	0	10	80
1970	30	90	95

[a] Percentage of leaf coverage of the most severely infected leaves.

[b] Red Rustproof 14, Burt, and Fulghum are late-, intermediate-, and early-rusting cultivars, respectively.

intermediate-maturing cultivars become heavily infected during the latter part of April (Table 2; 1962, 1963, 1965). But they do not become as heavily infected as the early-maturing cultivars during March and early April.

Growth chamber experiments.—These tests were designed to determine environmental conditions that influence the late-rusting and slow-rusting reactions of RRP oats. Six experiments were completed using plants in the first-leaf stage. On two occasions, uredial formation was 2 to 3 days later on RRP 14 than on Fulghum. Four tests were completed using plants in the third-leaf stage (about 25 days old). In one of these tests, a slight delay (2 days) in uredial formation was observed on RRP 14. This delay occurred only under conditions of the week of 8 March.

Although we did not reproduce the late-rusting phenomenon, a lower percentage of infection (slow-rusting) occurred on RRP 14 than on Fulghum. When 0.5 mg of urediospores was used to inoculate 10 plants, the average number of pustules per leaf (calculated from three replications of five leaves/replication) on RRP 14 and Fulghum was 11 and 23, respectively. In another test using 1 mg of spores, the average number of pustules observed on RRP 14 and Fulghum was 16 and 53, respectively. The slow-rusting of RRP 14 was more pronounced under conditions of the week of 8 March. However, under conditions of the week of 12 April, fewer pustules were observed on RRP 14 than on Fulghum. This occurred at most of the spore concentrations used (0.25 – 2 mg/10 plants). The slow-rusting reaction was observed on plants in both the first- and third-leaf stages of growth.

DISCUSSION.—Van der Plank visualized horizontal resistance as a type that slows down the epidemic after it has started (6). From this viewpoint, the slow-rusting of certain RRP cultivars may be considered a form of horizontal resistance. Late-rusting, however, delays the start of an epidemic, and may be erroneously classified as vertical resistance. We think that late-rusting is a unique form of horizontal resistance because RRP cultivars have exhibited late-rusting to all races of crown rust that have occurred in north Florida during the past 12 years. The latter viewpoint is compatible with Caldwell's concept of generalized resistance (1).

We have purposely avoided the term "RRP resistance" because most crown rust races induce a susceptible reaction on RRP cultivars; yet these cultivars exhibit a very effective defense mechanism against this pathogen. The capacity of RRP cultivars to withstand the crown rust disease is manifested in their ability to exhibit signs of infection later than other cultivars (late-rusting), and to develop a low percentage of infection during the growing season (slow-rusting). These two factors comprise the essence of the horizontal resistance of RRP oats to crown rust.

Some may argue that there is no real difference between late-rusting and slow-rusting. There are two forms of evidence which indicate that slow-rusting and late-rusting are separate phenomena: (i) Under field conditions, the intermediate-maturing cultivars (Burt and Brunker) exhibit slow-rusting, but not late-rusting (Table 1); (ii) in growth chamber experiments, we reproduced slow-rusting but not late-rusting.

We do not know why certain RRP cultivars are late-rusting, but assume that density of inoculum plays a major role. Two observations contribute to this assumption. (i) Application of spores (without talc or moisture) on late-rusting cultivars under field conditions results in infection and symptom expression. Infection can be obtained by this method at a time (March) when RRP 14 shows no crown rust symptoms under natural conditions. (ii) When moist chambers are used, infection occurs even at low spore concentrations (0.5 mg spores/10 plants) (H. H. Luke, *unpublished data*). Infection at low spore concentrations may be explained by the assumption that a volatile compound, which triggers a susceptible response in the host, is trapped in the moist chamber. This agrees with a recent report indicating that ethylene induces a susceptible reaction to leaf rust of wheat (2). We suggest that a similar mechanism may explain the late-rusting phenomenon in oats. This idea is based on the assumption that a higher spore concentration is required to induce the susceptible reaction in late-rusting cultivars than is required for cultivars that do not have the late-rusting characteristic. A mechanism of this type would explain why late-rusting cultivars always become infected when moist chambers are used, and would also explain why RRP 14 can be infected in the field with heavy spore concentrations at a time (early March) when natural infection cannot be observed. Moreover, late-rusting cultivars become infected later in the season than do susceptible cultivars because the natural spore concentration must reach a certain point before the susceptible mechanism is activated.

Our data preclude a conclusion concerning the mechanism(s) that controls slow-rusting. Caldwell (1) and Hooker (3), however, suggested that slow-rusting may involve exclusion of the parasite, slow growth and development of the parasite, and a reduction of spore production.

Van der Plank (6) and Hooker (3) indicated that late blight of potatoes and rust of corn can be effectively controlled over long periods of time through the use of horizontal or generalized resistance. We have shown that RRP cultivars carry a very effective type of horizontal resistance to crown rust. If this horizontal resistance (late-rusting and slow-rusting) can be effectively transferred to agronomically improved oats, the new cultivars should not be vulnerable to perpetual changes in crown rust races. We have promising F_4 and F_5 selections from crosses involving RRP 14. Preliminary tests indicate that about 80% of the slow-rusting character was recovered in selections that mature 6-8 days earlier than does RRP 14.

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