Nonspecific Resistance to Rust in Pubescent and Glabrous Common Bean Genotypes

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ABSTRACT

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Six pubescent and three glabrous bean genotypes from diverse genetic and geographic origins were inoculated on the primary leaves with uniform amounts of urediniospores. Air turbulence was created in small chambers on each genotype, and amounts of spore production were measured by the secondary infection they produced on the trifoliolate leaves and by counts of infective spore units. The sporulating capacity of the primary and trifoliolate leaves was measured on each genotype. Seven bean genotypes, six of which were pubsescent, showed a moderately susceptible reaction to rust on the primary leaves and reduced uredinia size and density on the upper leaves. Rust on the same bean genotypes had low sporulating capacity on the primary and trifoliolate leaves. These resistance components reduce disease progress and would need to be selected for in the field. Although abaxial long leaf trichomes are associated with nonspecific resistance to bean rust, they are not the only factor involved.

Additional keywords: Phaseolus vulgaris, Uromyces appendiculatus.

Partial resistance or reduced susceptibility to the bean rust pathogen *Uromyces appendiculatus* (Pers.:Pers) Unger has been termed "low receptivity" and is recognized as a component of rust resistance that is race-nonspecific (5). Genotypes of *Phaseolus vulgaris* L. that have long, straight trichomes on the abaxial leaf surface have been reported to have reduced infection intensity to several mixed or individual races under field environments (9–11,16,17). In addition, reduced uredinia size but not density in the upper leaves has been consistently associated with pubescent genotypes under glasshouse environments (M. T. Mmbaga and J. R. Steadman, *unpublished*).

Topographic features of the bean leaf surface (8) that induce appressoria formation by germ tubes of *U. appendiculatus* have been described, and it has been suggested that unfavorable leaf topography could contribute to low receptivity. Although low receptivity has been observed repeatedly in pubescent genotypes, it has been difficult to demonstrate the mechanism of pubescence in rust resistance under glasshouse environments (9). It has been theorized that dense trichomes on the abaxial leaf surface interfere with deposition of urediniospores and therefore prevent germ tubes from reaching the leaf stomates and initiating infection (11,12). Trapping of urediniospores by the trichomes has been observed (M. T. Mmbaga and J. R. Steadman, *unpublished*), but the significance of spore trapping at different levels of leaf expansion and inoculum densities has not been assessed. Zang and J. R. Stavely (*personal communication*) studied the relationship of leaf trichome density and length, stomata density, and stomata ridge height to low rust receptivity in four cultivars under glasshouse conditions. Significant differences occurred among cultivars in density and length of trichomes, and density of abaxial stomata, but these differences were not correlated with receptivity.

Other components of race-nonspecific resistance, such as development of more sparsely sporulating pustules, longer latent period, or lower physiological susceptibility have not been studied in relation to leaf pubescence. A study on Brazilian bean cultivars showed that race-nonspecific resistance was expressed through reduced sporulation of the rust fungus (1). The objective of this study was to assess the sporulation capacity of *U. appendiculatus* on primary and trifoliolate leaves of pubsecent and nearly glabrous genotypes and its epidemiological implications in rust disease development.

MATERIALS AND METHODS

Bean genotypes and inoculum. Nine genotypes were used in this study to represent different genetic and geographic origins and, where possible, pubescent and glabrous lines selected from land races were compared. Alubia 33 (A33-1) derived from an Argentinean land race, Pompadour Checa 83-30 (PC83-30) and Pompadour Q (PQ-5) derived from the Dominican Republic Pompadour land race, Jamaica Red (JR) from a Jamaican land race, 'Kabanima' (Kab-5) a commercial variety from Tanzania, and Diacol Calima (DC) from Colombia were the pubescent genotypes that have long, straight trichomes on the abaxial leaf surface of the upper trifoliate leaves. Glabrous selections of Pompadour Q (PQ-1) and Kabanima (Kab-1), and 'Pinto U.I. 114' (P114) represented genotypes that lack dense abaxial trichomes. Single-pustule rust cultures US86NP10-1 from Nebraska and 87HP2-19 from Honduras were used because they produced large

uredinia on the primary leaves of all nine genotypes. The two rust cultures were mixed in a 1:1 (v/v) ratio to make a spore suspension of 5 mg/150 ml water with 40 μg/L Tween-20.

Plant growth and inoculation. Bean plants were grown in 13-cm clay pots in a soil mixture of 2:2:1:1 (v/v) silty clay loam, peat moss, vermiculite, and sand. Two seeds were sown per pot with four pots per genotype arranged in a completely randomized design. In experiments that required primary and trifoliolate leaves for simultaneous inoculation, planting was done twice at 18-day intervals to generate plants with young primary leaves and plants with three trifoliolate leaves. The primary leaves were inoculated when they were 35–65% expanded, or 6–7 days after planting and the trifoliolate leaves were inoculated when the third trifoliolate leaves were 20–25% expanded, which was 24–25 days after planting. Plants were inoculated with a modified hand sprayer described by Stavely (15), and spore suspensions of 22,000–25,000 spores per milliliter were deposited on the abaxial leaf surfaces as uniformly as possible. The leaf surface was allowed to dry before plants were moved to a large mist chamber at 100% relative humidity and 19 ± 2 C for about 16 h of incubation. All experiments were repeated once.

Measurement of urediniospore. After inoculation and incubation, plants were moved to a glasshouse room set at 24 ± 2 C and 12-h photoperiod, where they were observed daily for uredinia development. When 50% of the uredinia had turned brown, the plants were moved to small growth cages 65 × 65 × 25 cm covered with clear plastic on four sides and a light muslin cloth on two sides, one pot per cage. At 14 days after inoculation, when all the uredinia were fully developed and open, a current of cool air was blown through the leaves by using a hair dryer set at cold air. Preliminary experiments showed that 3 min at medium setting or about 0.6 m/sec speed of airflow (wind speed sensor Met One Inc., Grants Pass, OR) was adequate to release most urediniospores from the plants. The position of the youngest unfolded leaf at the time of spore release was noted in each genotype. The plants were left undisturbed for a minimum of 30 min to allow the spores to settle on the leaf surface before they were moved to the mist chamber for 16 h of incubation at 100% relative humidity and then moved back into their respective cages. The process of spore release was repeated twice at 3-day intervals. Plants were then placed on a glasshouse bench, and disease was allowed to develop fully. The primary leaf infection was recorded 14 days after inoculation following the first spore release, and the trifoliolate leaf infection was recorded 14 days after the last spore release. Uredinia density on each leaf position was measured by the number of uredinia in a 9-cm^2 area, and uredinia size was measured by use of an ocular comparator (Edmundson Scientific, Barrington, NJ). Uredinia were counted on each half leaf of the primary leaves and each leaflet of the trifoliolate leaves to obtain an average number per leaf area.

Secondary infection on the trifoliolate leaves of most genotypes was low except in P114 and PQ-1. To determine whether the low infection was caused by low inoculum level as a result of low spore production, two sets of plantings were done for each genotype. One set consisted of two plants per pot as a pure stand with each genotype in separate pots, and a second set consisted of two plants per pot as a mixed stand with one plant of P114. Each time air turbulence was created in the cages, a spore sample was collected by using a sticky slide kept in a horizontal position at the bottom of each cage. Spores were counted at 100× in 10 fields, picked at random along a transect set across the length of the slide. The relative numbers of spores in each cage was represented by a mean number of infective units per field view. The infective units were either single spores or clusters of spores forming discrete units.

Assessment of sporulating capacity. Plants at the primary leaf and at the third trifoliolate leaf stages were inoculated simultaneously as described above. After incubation, plants were moved to a room at 24 ± 2 C and 12-h photoperiod. Observations were made daily and the number of days for 50% of uredinia to open were noted; this was regarded as the latent period and represented the time taken for the plants to become infectious (14). At 14 days after inoculation, urediniospores produced on each plant were harvested three times at 3-day intervals by tapping the leaves to release spores onto glassine paper. Spores from the four primary leaves in each pot were harvested as one unit. Urediniospores from the three inoculated trifoliolate leaves were also harvested as one unit and were weighed on an analytical balance (Mettler AE100). Disease intensity was rated 14 days after inoculation.

Data from all the experiments were analyzed with Statistical Analysis System (SAS) for general linear model's procedure of Student's *t* test. Sporulating capacity of the primary and trifoliolate leaves within the same genotype was compared by using a split-plot analysis of least significant differences between two main plots and same subplot according to Gomez and Gomez (6).

RESULTS

Primary leaf infection. Large uredinia, 500–800 μm in diameter, were produced on the primary leaves of all genotypes, but some differences were observed. Pubescent A33-1, PC83-30, JR, PQ-5, DC, and Kab-5 with long abaxial hairs on the upper trifoliolate leaves, developed significantly smaller uredinia (500–550 μm) on

TABLE 1. Rust infection on the primary leaves of nine *Phaseolus vulgaris* bean genotypes and secondary infection produced on the trifoliolate leaves as a result of urediniospores released from the primary leaves by air turbulence

Bean[a] genotypes	Abaxial Pub.[b]	Primary leaf infection[c]		Trifoliolate leaf infection[c]							
				Uredinia density[d]				Uredinia size (μm)			
		Uredinia density	Uredinia size (μm)	TR1	TR2	TR3	Mean[e]	TR1	TR2	TR3	Mean[e]
A33-1	5	24 c	550.0 bc	6	9	9	8 d	300.0	312.5	375.0	329 bc
PC83-30	5	34 b	537.5 bc	6	8	1	5 d	200.0	325.0	350.0	291 c
JR	5	41 a	525.0 bc	6	3	1	3 d	300.0	337.5	400.0	345 b
PQ-5	5	36 b	550.0 bc	13	28	1	14 c	300.0	300.0	350.0	316 bc
Kab-5	5	35 b	500.0 b	2	4	6	4 d	300.0	350.0	400.0	350 b
DC	5	25 c	500.0 b	...	6	6	6 d	300.0	312.5	375.0	329 bc
Kab-1	1	28 bc	562.5 c	4	1	1	2 d	225.0	237.5	300.0	254 c
PQ-1	1	33 b	733.3 a	58	29	9	32 b	416.7	550.0	750.0	572 a
P114	1	30 bc	712.5 a	180	169	41.8	130 a	400.0	437.5	700.0	512 a

[a] A33-1 = Alubia 33-1; PC83-30 = Pompadour Checa 83-30; JR = Jamaica Red; PQ-5 = Pompadour Q pubescent selection; Kab-5 = 'Kabanima' pubescent selection; DC = Diacol Calima; Kab-1 = Kabanima glabrous selection; PQ-1 = Pompadour Q glabrous selection; P114 = 'Pinto U.I. 114'.

[b] Abaxial pubescence on the fourth trifoliolate leaves, on a 1–9 scale, where 1 = glabrous and 9 = dense trichomes >1,000 per cm^2 (9).

[c] Mean values of four replicates; means within the same column followed by the same letter are not significantly different at $P = 0.05$ according to the Student's *t* test. TR1-TR3 = trifoliolate leaf 1–3 up the plant.

[d] Number of uredinia in 9 cm^2.

[e] Average of three trifoliolate leaves.

their glabrous primary leaves than the glabrous genotypes PQ-1 and P114, which lack dense abaxial pubescence on any leaves. The glabrous PQ-1 and P114 developed uredinia 700–800 μm in diameter, but a glabrous selection Kab-1 developed smaller uredinia similar to the pubescent selection Kab-5. These observations were consistent in all the experiments. Overall genotypic differences in uredinia size were significant at $P = 0.0001$, but the infection measured by number of uredinia in 9-cm^2 area was similar in all the genotypes except in one experiment, where JR had a significantly larger number of uredinia than the other genotypes and A33-1 and DC had fewer uredinia than other genotypes (Table 1). The latent period for 50% erumpent uredinia was 11.5 days for all genotypes except JR, which was 10 days.

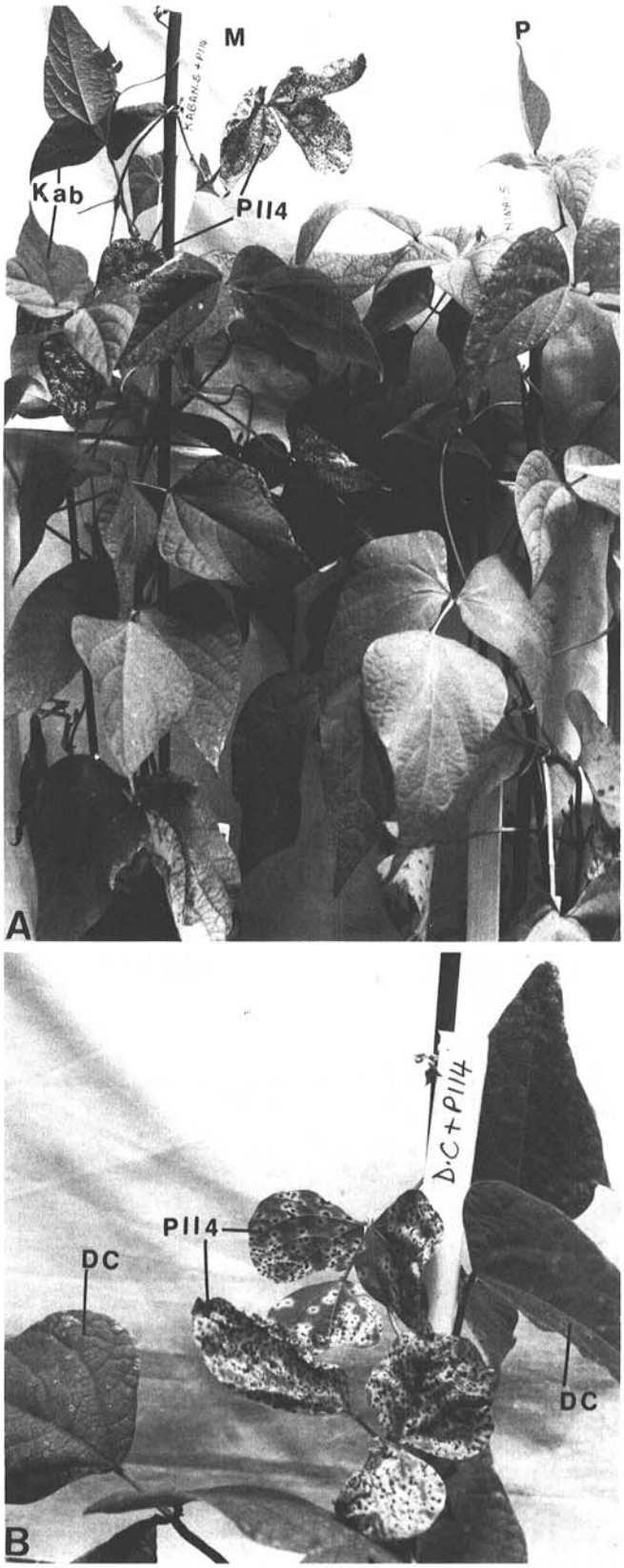

Fig. 1. Rust resistance associated with leaf pubescence shown in, **A,** "Kabanima" (Kab) and, **B,** "Diacol Calima" (DC) grown in a mixed stand (M) with Pinto U.I. 114 (P114) and in pure stand (P).

Urediniospore release. Air turbulence created in the cages released urediniospores into the atmosphere within the individual cages. At the time of the first spore release, the first trifoliolate leaf of all the genotypes was at an early stage, 1–2 days after unfolding. At the second spore release, the first trifoliolate leaves were expanded to about 60% of the full size and the second trifoliolate leaves were at 1–2 days after unfolding. At the third period of spore release, the third trifoliate leaves were at 1–2 days after unfolding and the fourth trifoliolate leaves were in bud stage. The first trifoliolate leaves were exposed to three spore showers, two when the leaf was more than 50% expanded. The second trifoliolate leaves were exposed to two spore showers of secondary inoculum when 25–60% expanded, and the third trifoliolate leaves were exposed to one spore shower when they were 25–30% expanded.

Secondary infection developed on all the three trifoliolate leaves, and there were significant genotypic differences ($P = 0.01$) in density and size of uredinia. Genotypes A33-1, PC83-30, JR, DC, Kab-5, PQ-5, and Kab-1 developed small uredinia in all the trifoliolate leaves (Table 1). The first and second trifoliolate leaves developed very small uredinia 200–350 μm in diameter, whereas the third trifoliolate leaves either did not develop any uredinia or had uredinia 300–400 μm in diameter. The first and second trifoliolate leaves of P114 and PQ-1 developed numerous

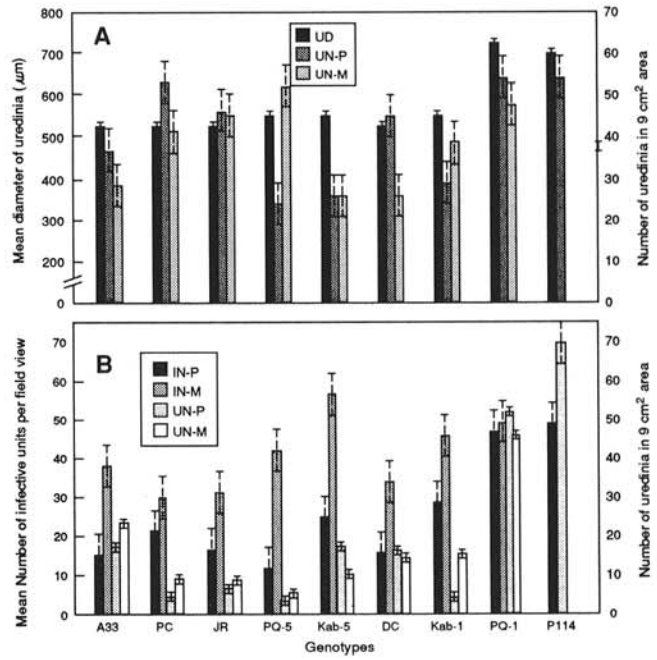

Fig. 2. Urediniospore production on the primary leaves and the density of secondary uredinia they produce on the trifoliolate leaves when bean genotypes are grown in pure stand and in a 1:1 mixed stand with Pinto U.I. 114. **A,** Mean disease intensity on the spore-producing primary leaves. **B,** Number of infective spore units on sticky slides and uredinia density on the trifoliolate leaves. Mean values are from four replicates and error bars represent standard error at $P = 0.05$. UD = Uredinia diameter, UN = Uredinia density; IN-P = Number of infective units from pure genotype stand, IN-M = Number of infective units from mixed genotype stand. UN-P uredinia density from pure genotype stand, UN-M uredinia density from mixed genotype stand. A33 = Alubia 33-1; PC = Pompadour Checa 83-30; JR = Jamaica Red; PQ-5 = Pompadour Q pubescent selection; DC = Diacol Calima; Kab-5 = 'Kabanima' pubescent selection; PQ-1 = Pompadour Q glabrous selection; Kab-1 = Kabamina glabrous selection and P114 = Pinto U.I. 114.

uredinia 400–550 μm in diameter, and the third leaf developed uredinia 700–750 μm in diameter. The glabrous selection Kab-1 had fewer and smaller uredinia than the pubescent selection Kab-5, and it was also significantly different from the other glabrous genotypes P114 and PQ-1. Genotypes JR and Kab-1 had the lowest mean intensity of infection, while PC83-30 and Kab-1 had the smallest mean sizes of uredinia (Table 1). All the pubescent genotypes and glabrous Kab-1 had very low mean uredinia density, about 2–60 times less than P114. The actual intensity of infection when compared to P114 or PQ-1, was much lower than is reflected by the differences in uredinia densities because it is coupled with the smaller uredinia size.

A comparison of pubescent versus glabrous genotypes and primary versus secondary infection showed significant differences at $P = 0.01$ for both uredinia size and number, whether mixed with P114 or in pure culture. The P114 plants had high uredinia density and significantly larger uredinia; the adjacent pubescent plant or Kab-1 within the same pot had almost no infection (Fig. 1). Spore release caused by turbulent air mixing was estimated by using sticky slides, and significant differences ($P = 0.01$) were observed between genotypes. The spore counts in cages with pure stands of PC83-30, Kab-5, DC, and PQ-1, and mixed stands of JR and Kab-5 with P114 were highest in the second spore release ($P = 0.01$) but decreased to the original amount in the third spore release. The spore counts from the remaining cages were statistically similar over time. Spore counts from mixed plant stands were higher than those from pure genotype stands. Mixed stands of A33-1, JR, PQ-5, Kab-5, and DC with P114 produced more than twice the number of urediniospores than the pure genotype stands (Fig. 2). PQ-1 in pure stands and in mixed stands produced amounts of spores similar to P114. Overall, the pubescent genotypes and glabrous Kab-1 in pure stands produced similar levels of urediniospores for secondary inoculum, which were significantly lower than spore counts from the glabrous P114 and PQ-1 (Fig. 2).

Even though rust infection on the primary leaves was similar, there were significant genotypic differences ($P = 0.01$) in spore production (Table 2). Genotypes A33-1, PC83-30, JR, PQ-5, Kab-5, DC, and Kab-1 produced similar spore masses that were significantly smaller ($P = 0.001$) than those produced by P114 or PQ-1. Linear comparisons of spore production over time were highly significant at $P = 0.01$ with decreasing spore production over time. Most genotypes produced no new spores after the third harvest, except P114 and PQ-1, which continued to produce large amounts of spores (Table 2). Spore production on the trifoliolate leaves was lower than on the primary leaves of the sparsely sporulating genotypes, but it was higher in P114 and PQ-1 (Table 2). There was uniform infection density, but P114 and PQ-1 had significantly larger uredinia size, and Kab-1 and Kab-5 had smaller uredinia size than the other genotypes ($P = 0.001$). The overall trend in spore production from the trifoliolate leaves was similar to that of the primary leaves with linear decrease in spore production over time. Most genotypes stopped producing new spores after the second spore harvests, but P114 and PQ-1 continued to produce large spore masses (Table 2).

DISCUSSION

Bean rust disease development depends, in part, on the susceptibility of the host genotype and the amount of secondary inoculum that will be produced within a bean field. The escape of urediniospores of *U. appendiculatus* from a bean field and the development of bean rust epidemics in the field has been studied (2–4). Aylor and Ferrandino (3) indicated that the amount of urediniospores produced within a bean field affects the rate of disease development, and inoculum blown from other fields plays an insignificant role beyond the initial infection. Thus, the epidemiological consequences of a high level of initial infection might be reversed or partially compensated by low production of secondary inoculum. Seven of the nine genotypes in our study had produced significantly smaller spore masses than two genotypes with essentially the same disease density on the primary leaves. These genotypes would drastically reduce disease progress through a combination of several factors that would include reduced uredinia size and number coupled with reduced spore production on the upper leaves compared to P114 and PQ-1. This reduced receptivity functioned when an outside inoculum source was simulated by mixed planting with P114.

Even though mass spore production decreased over time, the amount of urediniospores released as a result of turbulent air mixing and estimated on trap slides did not decrease significantly over time. This indicates that the air turbulence created in the cages did not remove all the spores available, and repeated air turbulence allowed additional inoculum to be released to the atmosphere within the cages. The susceptible P114 and PQ-1 developed very high levels of infection, and the number of uredinia in trifoliolate leaves one and two was so high that availability of infection sites became limiting. Infection intensity of the seven resistant genotypes remained low even when inoculum was available from P114 in mixed planting. The smaller uredinia size in trifoliolate leaf one and two than in the third trifoliolate leaf was in response to the effect of leaf age at the time of inoculation

TABLE 2. Rust intensity and sporulating capacity on primary and trifoliolate leaves of nine *Phaseolus vulgaris* common bean genotypes

Bean[a] genotypes	Abaxial Pub.[b]	Rust intensity: Uredinia density[c] Primary leaves	Rust intensity: Uredinia density[c] Trifoliolate leaves	Rust intensity: Uredinia diam. (μm) Primary	Rust intensity: Uredinia diam. (μm) Trifoliolate[e]	Urediniospores produced per harvest[d] (mg): Primary leaves 1	Primary leaves 2	Primary leaves 3	Primary leaves Mean[f]	Trifoliolate leaves 1	Trifoliolate leaves 2	Trifoliolate leaves 3	Trifoliolate leaves Mean[f]
A33-1	5	33.0 b[g]	15 b	562.5 c	300 c	23.1 c	4.9 c	2.6 c	10.2 c	10.6 b	4.1 b	0 c	4.9 c
PC83-30	5	32.3 b	20 b	537.5 c	283 cd	20.8 c	2.3 c	3.9 c	9.0 c	2.0 b	1.2 b	0 c	1.1 c
JR	5	33.5 b	11 b	525.0 c	285 cd	25.3 c	6.2 c	3.5 c	11.6 c	2.1 b	1.5 b	0 c	1.2 c
PQ-5	5	39.5 b	30 b	537.5 c	283 cd	32.6 b	10.6 c	5.4 c	16.2 c	4.6 b	4.3 b	1.4 c	3.4 c
Kab-5	5	37.0 b	17 b	525.0 c	247 ef	21.0 c	12.1 c	8.2 c	13.7 c	3.5 b	1.9 b	0 c	1.8 c
DC	5	36.3 b	16 b	512.5 c	283 cd	24.3 c	3.5 c	0.3 c	9.4 c	4.9 b	1.1 b	0 c	2.2 c
Kab-1	1	28.8 b	10 b	525.0 c	217 f	19.7 c	4.4 c	1.0 c	8.4 c	1.4 b	0.4 b	0 c	0.6 c
PQ-1	1	85.7 a	60 a	662.5 b	629 a	88.6 a	73.6 a	54.8 a	72.4 a	154.0 a	250.0 a	148.0 a	184.0 a
P114	1	28.5 b	74 a	737.5 a	526 b	36.5 b	32.9 b	37.6 b	35.7 b	118.0 a	229.0 a	55.0 b	97.5 b

[a] A33-1 = Alubia 33-1; PC83-30 = Pompadour Checa 83-30; JR = Jamaica Red; PQ-5 = Pompadour Q pubescent selection; Kab-5 = 'Kabanima' pubescent selection; DC = Diacol Calima; Kab-1 = Kabanima glabrous selection; PQ-1 = Pompadour Q glabrous selection; P114 = 'Pinto U.I. 114'.

[b] Abaxial pubescence on the fourth trifoliolate leaves, on a 1–9 scale, where 1 = glabrous and 9 = dense trichomes >1,000 per cm^2 (9).

[c] Number of uredinia in 9 cm^2.

[d] Values are means of four replicates, two plants per replicate.

[e] Average of three trifoliolate leaves per plant.

[f] Mean from three harvests (1-3) at 3-day intervals.

[g] Mean values followed by the same letter within a column were not significantly different at $P = 0.05$ according to the Student's t test.

documented by Shaik and Steadman (13). These observations indicate that there may be an additional factor that restricts establishment of infection in A33-1, PC83-30, JR, DC, Kab-5, Kab-1, and PQ-5 compared to P114 and PQ-1. This may reduce the effective inoculation, possibly as a result of a shorter period of leaf receptivity.

Our data demonstrate the complexity of the nonspecific resistance observed in the pubescent beans. The reduced infection density in the upper leaves of resistant genotypes was also observed in the upper leaves of P114 in glasshouse experiments (9; M. T. Mmbaga and J. R. Steadman, *unpublished*). This may have been caused by the small leaf area available at inoculation and lack of repeated inoculum for P114 as the leaves expanded and remained receptive for a longer period than the resistant genotypes.

The seven genotypes appear to have several factors that operate together to confer rust resistance in the upper leaves: low sporulating capacity, reduced uredinia size and density, and low receptivity. These characteristics are recognized as components of nonspecific resistance (1,5,7), but more virulence groups would need to be tested before race-nonspecificity can be confirmed. Although these genotypes may show a susceptible reaction in the seedling stage in response to rust cultures with certain virulence patterns, disease progress on the upper leaves would be reduced, and thus the plants might not have high levels of disease at a criticial stage in plant development that would influence yield. Nonspecific rust resistance previously was associated with pubescent genotypes (11,12,16,17), but how leaf trichomes contribute to the resistance has not been shown. The fact that we have found a glabrous selection that expresses the same type of resistance, indicates that although closely linked with pubescence, leaf pubescence is not the only factor in this resistance.

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