Differences Among Bean Cultivars in Receptivity to *Uromyces phaseoli* var. *typica*

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Scientific Journal Series Paper 11,374 of the Minnesota Agricultural Experiment Station, St. Paul.
Accepted for publication 7 July 1981.

ABSTRACT

Groth, J. V., and Urs, N. V. R. R. 1982. Differences among bean cultivars in receptivity to *Uromyces phaseoli* var. *typica*. Phytopathology 72:374-378.

Receptivity (number of uredia obtained per propagule applied) to rust (caused by *Uromyces phaseoli* var. *typica*) was measured on unifoliolate and trifoliolate leaves of six cultivars of bean (*Phaseolus vulgaris*). Differences in receptivity among cultivars were observed after precision inoculation of leaves having a range of ages and less precise inoculation of leaves of uniform age. Both methods showed cultivar differences in receptivity. Plants of cultivar Royal Red Kidney, which was least receptive overall, exhibited lower receptivity for both unifoliolate and trifoliolate leaves at every age than did those of the highly receptive cultivar Pinto 111. Differences in receptivity for these two cultivars over all ages were approximately threefold for both leaf types. Method of measuring receptivity influenced the results obtained; those made on leaves of different ages provided sufficient information for fully describing receptivity.

Additional key words: infectibility, infection efficiency, components of resistance, bean rust.

In disease resistance work, receptivity can be defined as the number of visible lesions that form per unit of applied inoculum. Also known as infection frequency, infectibility (10), infection efficiency (6,9), or simply as the number of rust pustules (3), the concept has been studied mainly as a component of resistance (3–7,10). Unlike some of the other terms, the term receptivity most clearly implies a property of the host; therefore, we believe that it is a more precise term for describing host-pathogen interaction in the rust diseases. Receptivity differences among host cultivars have been demonstrated in barley leaf rust caused by *Puccinia hordei* (6); in wheat stem rust and leaf rust, caused by *P. graminis* f. sp. *tritici* (5,7) and *P. recondita* (11), respectively; and in oat stem rust and crown rust caused by *P. graminis* f. sp. *avenae* and *P. coronata* (4), respectively.

The role of low receptivity as a component of partial resistance is poorly understood. In at least one case, it is thought to be one of the most important elements of such resistance (2), but this has never been clearly established. In other instances, low receptivity is thought to be one of several components of resistance whose relative importance is not known (2,6). Accurate measurement of receptivity has been difficult. In particular, the effects of tissue age and disease severity on receptivity have been dealt with only preliminarily (5,6,9). Schein (9) examined the relationship between leaf expansion and receptivity to bean rust (*Uromyces phaseoli* (Pers.) Wint. var. *typica*) in a single cultivar of field bean (*Phaseolus vulgaris* L. 'Pinto 111'). He observed that receptivity in the unifoliolate (primary) leaves rapidly increased, reaching a peak at an expansion of 0.15 of mature area, and gradually decreased thereafter.

The purpose of this study was to measure receptivity to *U. phaseoli* var. *typica* in several cultivars of dry beans and snap beans to determine whether differences in receptivity exist and, if so, their magnitudes.

MATERIALS AND METHODS

All inoculations were made with a single-uredial isolate of *U. phaseoli* var. *typica* designated K9-1. It was collected in 1975 in a commercial field of Royal Red Kidney beans near Hector, MN. Uredial inoculum was increased and maintained on seedlings of susceptible cultivars Pinto 111, Pinto 114, and Pinto 166 in a 24-C greenhouse. The fungus isolate was periodically purified by collecting and increasing uredospores from a single, isolated pustule.

Six bean cultivars that, in previous work (1), appeared to possess high or low receptivity were selected for this study. The cultivars, Bountiful, Gratiot, Mecosta, Pinto 111, Royal Red Kidney, and Seafarer, represented a wide array of bean types. Seeds were sown in vermiculite and germinated in a 24-C greenhouse. Selected, uniform plants of each age were transplanted singly to steamed soil in 10-cm-diameter clay pots.

Fresh uredospores were used in the study. Inoculation was done

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0031-949X/82/04037405/$03.00/0

in two ways. First, established semiquantitative methods (1) were used in inoculating a single leaf of plants of different cultivars that were all of the same chronological age. Because of cultivar differences and variation among seedlings within each cultivar, these plants were not necessarily at the same stage of development. Efforts were made to apply about the same number of spores to each leaf or leaflet by spraying for a standard interval of time from the same distance. The second method involved the use of Schein's (8) quantitative inoculator (QI), that places a precise number of fresh uredospores suspended in 0.25% Bacto agar onto a circle of bean leaf tissue about 1.5 cm in diameter. Each experiment with the QI involved 49 plants of each cultivar, consisting of seven plants at each of seven stages of leaf expansion (from newly opened to 6 days past opening) of the primary or trifoliolate leaf to be studied. Both primary leaves of each plant were inoculated in primary leaf trials, while the terminal leaflet and one of the lateral leaflets of the first trifoliolate leaf were inoculated in trifoliolate leaf trials. After inoculation, plants were placed in a moist chamber for 18–24 hr at 24 C. Pustules were counted about 12 days after inoculation. Diameter of the inoculated circle was measured at this time. Extended-time experiments were made with the cultivars Pinto 111 and Mecosta. In this case, the time interval between successive ages was 3 days rather than 1 day. All cultivars except Upland were used in studies involving the QI.

When equal-aged plants of two different cultivars were inoculated simultaneously by the semiquantitative method, comparable leaves usually differed in degree of expansion. This resulted in dissimilar target areas that needed to be adjusted to give inoculum dosage on a per unit area basis, and in a difference in tissue age, and consequently receptivity per unit area, as determined in an earlier study (9). Since we chose to express receptivity on a per leaf basis, both of these factors were adjusted prior to summarizing and statistically analyzing the data. As an example of how the corrections were made, a Pinto and a Seafarer plant in a pot comprised a pair. Each plant had a single trifoliolate leaf partly expanded at the time of inoculation (primary leaves were not used in this trial). The number of pustules on the Pinto leaf was 28, while that on the Seafarer leaf was 12. To correct for difference in degree of expansion, measurements of leaflet length and width were taken at inoculation and at leaf maturity. For each cultivar, the areas of six primary and six trifoliolate leaves of nearly full expansion were measured with an electronic digitizer, and a coefficient that related length × width of the leaflets to the area was obtained as the mean of the six coefficients for each leaf type and cultivar. For Pinto trifoliolates this coefficient was 0.65, while for Seafarer trifoliolates it was 0.61. Target areas were standardized by multiplying one of the pustule counts (in this case that for Seafarer) by the ratio of leaf areas of the pair at the time of inoculation. In this case, the area of the Pinto leaf was 32 cm^2, while that of the Seafarer leaf was 63 cm^2. The adjusted number on Seafarer was thus (32/63)(12) = 6 pustules.

To correct for the effect of degree of expansion on receptivity (9), the relationship between number of pustules and degree of leaf expansion was first determined for each cultivar and leaf type. Fig. 1 shows an example. This was done as part of the second study

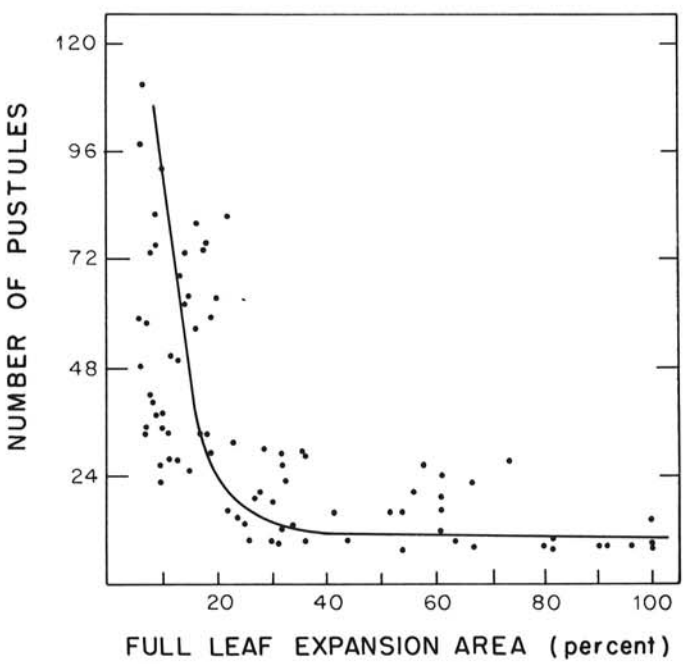

Fig. 1. Receptivity measured as numbers of *Uromyces phaseoli* var. *typica* uredial pustules per leaf, over percentage of leaf expansion for primary leaves of the bean cultivar Mecosta each inoculated with the same number of uredospores. A smooth curve has been empirically drawn through the points.

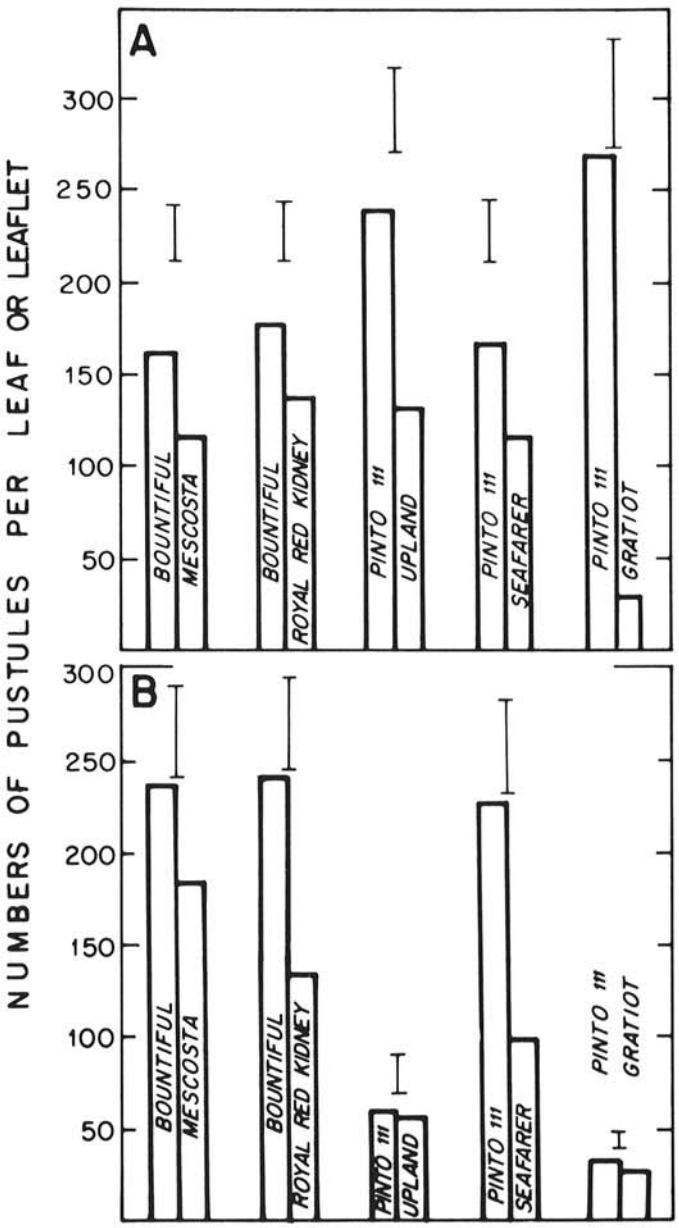

Fig. 2. Mean numbers of uredial pustules of *Uromyces phaseoli* var. *typica* standardized with respect to relative leaf area at the time of inoculation and relative receptivity because of difference in degree of expansion, for five comparisons involving **A,** both unifoliolate leaves, and **B,** the first trifoliolate leaf of seven bean cultivars. Paired plants were grown in the same pot. Only comparisons shown as adjoining bars were made, using a paired *t*-test, with X = 0.05 and a minimum *n* of 40. From previous subjective observations, plants of cultivars Bountiful and Pinto 111 were tentatively identified as being of high receptivity.

reported here using the quantitative inoculator. The area of inoculation and the area of infection were measured for each leaf, and the degree of expansion at inoculation was expressed as the percent of full expansion (area at inoculation divided by area at full expansion multiplied by 100). A smooth curve was empirically drawn through these points. Paired leaves usually differed somewhat in degree of expansion and, consequently, in relative receptivity per unit area at inoculation. For example, in the pair used here, the Pinto leaf was 42% expanded while the Seafarer leaf was 68% expanded. In terms of fully expanded receptivity per unit area for each cultivar this meant that from their respective curves, the Pinto leaf was 2.28 times as receptive as at full expansion, while the Seafarer leaf was only 1.38 times as receptive. The ratio of these receptivities was applied as a correction factor for expansion differences arbitrarily to the raw uredial count of pinto, as $(1.38/2.28)28 = 17$ uredia. While they often resulted in only slight changes, these two adjustments were made on all pairs of leaves. Two-way factorial ANOVAs were used to test for main cultivar effects, main age effects, and cultivar × age interactions in the quantitative inoculation studies. Duncan's new multiple range test was used to compare specific cultivar means. Receptivity was visually represented by plotting pustule numbers over leaf age and drawing a trend line between mean uredial numbers for each leaf age.

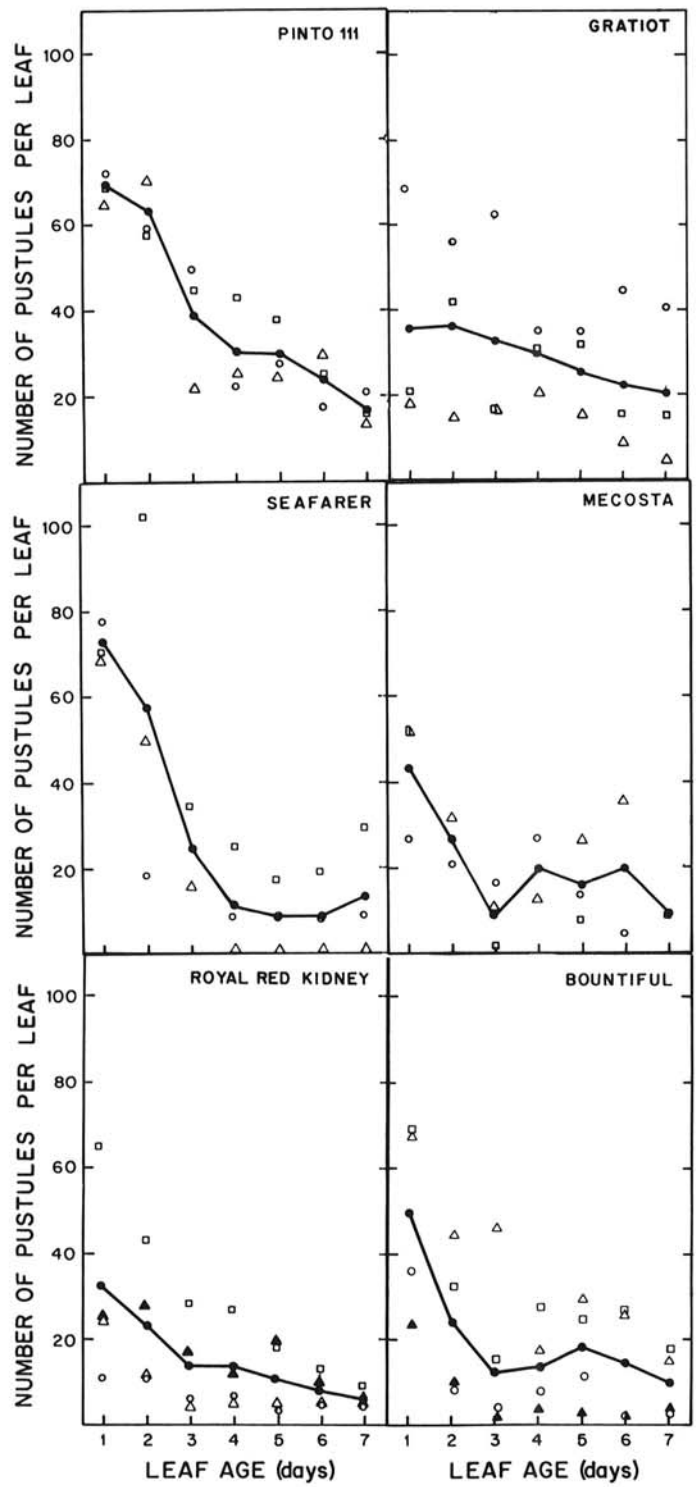

Fig. 3. Numbers of uredial pustules of *Uromyces phaseoli* var. *typica* over leaf age for primary leaves of six bean cultivars. Each point represents the average of seven plants; means of individual trials (shown by open circles, triangles, or squares) are joined to give the overall trend.

RESULTS

The quantitative inoculator delivered a similar number of uredospores to each inoculated leaf. When uredospores were counted on target glass slides or petri plates containing 2% water agar, coefficients of variability ranged from 15 to 20%. Plants contributed most of the variation in pustule counts, for which coefficients ranged from about 50 to 100% in several experiments with Pinto 111. Where petri plates of 2% water agar and primary leaves were alternately "inoculated," 89% of the total variation sums of squares was among-plant variation, while only 11% was due to variation in delivery of spores by the QI. Since uredia were counted on leaves while spores were counted on plates, the among-plant variation could have been contributed to by all stages of pathogenesis.

Mean uredial numbers for leaves inoculated under partially standardized conditions are represented in Fig. 2. Numbers were adjusted for differences in relative leaf size and differences in receptivity due to unequal degree of expansion. Comparisons are only valid within each pair of bars. Differences were significant in all five comparisons of primary leaves (Fig. 2A) and three of the five comparisons of trifoliolate leaves. Differences in numbers of uredia were not significant when Upland and Gratiot were compared with Pinto 111 (Fig. 2B).

The ANOVAs were similar for unifoliolate and trifoliolate leaves in that both leaf types showed significant cultivar ($F = 7.33$ and 18.16 for the two leaf types, respectively) and age ($F = 16.76$ and 7.04, respectively) main effects. There were no significant cultivar × age interactions. Table 1 presents mean uredial numbers over all ages for each cultivar ranked from highest to lowest receptivity on unifoliolate leaves. The representations of receptivity in Figs. 3 and 4 are useful because the areas under these curves give identical ranking of, and proportionally very similar values to, the means present in Table 1. Whereas in Fig. 2, Bountiful vs Mecosta and Bountiful vs Royal Red Kidney showed significant receptivity differences for both primary and trifoliolate leaves, none of these differences was significant, when receptivity was measured over all ages (Table 1). Likewise, both unifoliolate and trifoliolate leaves of Pinto 111 had significantly higher receptivity than those of Seafarer when age was not controlled, whereas only unifoliolate leaves differed significantly over several leaf ages. Results from the two experimental approaches agreed for trifoliolate leaves of Pinto and

TABLE 1. Mean numbers of uredia of *Uromyces phaseoli* var. *typica* per bean leaf or leaflet, averaged over all leaf ages

Cultivar	Mean number of uredia per:	
	Unifoliolate leaf	Trifoliolate leaflet
Pinto 111	38.8 A[a]	73.0 AB
Gratiot	29.9 A	87.4 A
Seafarer	28.3 B	65.9 B
Bountiful	21.3 BC	34.5 C
Mecosta	20.1 BC	40.8 C
Royal Red Kidney	15.0 C	29.4 C

[a] Values in each column followed by the same letter do not differ significantly ($P = 0.05$) according to Duncan's new multiple range test.

Gratiot in that no significant differences were observed. Primary leaves of this comparison had significantly different receptivities in Fig. 2, but not in Table 1. The direction of receptivity differences for pairwise comparisons that were obtained by the two approaches was the same except in the case of Bountiful vs Mecosta trifoliolate and Pinto 111 vs Gratiot trifoliolate leaves.

Another potentially important component of resistance to *U. phaseoli* var. *typica* was noted in this work. Tissue age strongly affects pustule size. Leaves of Pinto 111 that were nearly expanded at inoculation with the quantitative inoculator had uredia that were only 0.16 of the diameter of the uredia on leaves that were inoculated at the youngest age, when the leaf area was about 0.15 the area of the completely expanded leaf.

Although significant cultivar × age interactions were not found, pustule number-leaf age curves of some of the cultivars appeared, on inspection, to differ in slope. Linear regression analysis on two of the curves, those of Pinto 111 and Royal Red Kidney primary leaves, revealed a highly significant difference in their slopes ($F = 14.0$). Shape of curves could not be compared in any simple way.

DISCUSSION

The work presented here indicates that the method employed to study receptivity influences the result. In general, more differences were shown in the paired, single-age studies than when pustule number-leaf age curves were compared. For two cultivars where results of the two methods most strikingly differed, the difference between them in shape of the pustule number-leaf age curves at least partly explains the discrepancy. Pinto 111 vs Gratiot primary leaves and Bountiful vs Royal Red Kidney trifoliolate leaves were inoculated in single-age experiments when leaves were from 0.2 to 0.3 of their full expansion area. This corresponds roughly to the 2-day point on pustule number-leaf age curves (Figs. 3 and 4), a time when differences in receptivity between cultivars were greatest, or nearly so. Generalizing from these examples, it appears that receptivity studies that do not account for age of tissue cannot adequately describe receptivity. If tissue age is carefully controlled within narrow limits, as in the paired studies here, results can be deceptive. If, as with whole-plant receptivity studies, all ages of tissues are included, the age effect will be confounded with other sources of variation, and the rapid and large changes in receptivity with increasing age (whatever the direction of change) can be expected to result in an imprecise estimate of receptivity, at best.

We did not detect an early period of lower receptivity in unifoliolate leaves that was reported for Pinto 111 (9). Receptivity simply decreased as age increased. Trifoliolate leaves may have exhibited such an effect. Decreasing rank order of these leaves, taken over all six cultivars, was 2, 3, 1, 4, 5, 6, and 7 days. Differences between the 2-, 3-, and 1-day-old leaves were not significant according to Duncan's new multiple range test.

Earlier studies on receptivity have clearly shown that it is a difficult variable to precisely or accurately measure. Parlevliet and Kuiper (6) did not use receptivity as a measure in their studies on the inheritance and nature of partial resistance because of the large error variances associated with its measurement relative to that of the parameter that they ultimately chose, latent period. Johnson and Wilcoxson (3) were unable to determine heritability of this (possible) component of slow-rusting because of the large amount of variation associated with it in field studies. Authors of other studies (5,6,10) also explicitly note that large standard deviations were associated with receptivity measurements.

Receptivity over time can be influenced by overall life expectancy of the leaf. It was observed, for instance, that navy (pea) type beans had shorter-lived primary leaves than did the other five cultivars. At 12 days after inoculation, older leaves of the navy types—Seafarer, Gratiot, and Upland—were beginning to senesce, whereas those of the other cultivars were not. This is one reason why we thought age was more appropriate as a measure of leaf development than was degree of expansion. A difference in longevity of trifoliolate leaflets among cultivars was not evident. This may partly explain why Gratiot trifoliolate leaves appeared to be slightly more receptive than those of Pinto 111, while primary leaves of Gratiot appeared slightly less receptive. It suggests that it is important to select the relevant tissues when quantitative characters are being measured with the intent of extrapolating the results to field epidemiology. Clearly, trifoliolate leaves are the proper choice in this case.

Characterization of leaf "demography" is also necessary if detailed information on receptivity is to be used to predict epidemic

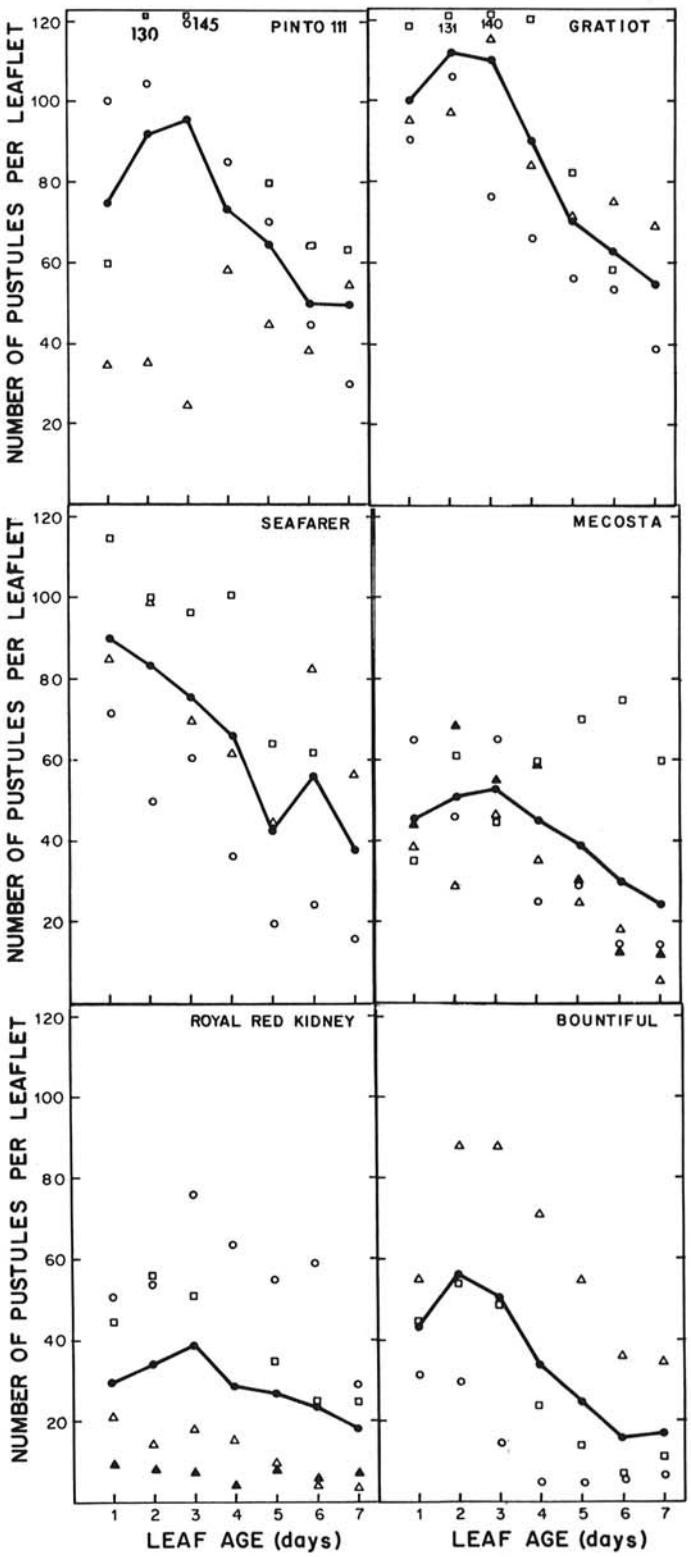

Fig. 4. Numbers of uredial pustules of *Uromyces phaseoli* var. *typica* over leaf age for trifoliolate leaflets of six bean cultivars. Each point represents the average for seven plants; means of individual trials (shown by open circles, triangles, or squares) are joined to give the overall trend.

development in the field. The relative role of partially and fully expanded leaves in a stand in supporting an epidemic is a function of both proportional areas of the various ages and time. Both parameters seem to indicate a greater importance of fully expanded leaves because they are larger and because fully expanded leaves persist longer than the time required for partially expanded leaves to fully expand. This is offset by the larger size of pustules that form on leaves infected when young. Not only are uredospores on such leaves more likely to result in uredia because of increased receptivity, but such uredia will produce many more second-generation uredospores due to their larger size, as compared with those on older leaves.

The germ tubes of uredospores of rust fungi generally enter their host leaves through stomata (12). It is therefore likely that stomatal density influences receptivity. Our data indicate that stomatal density cannot account for all differences in receptivity, either among cultivars or within a cultivar because of age. Counts of stomata on fully expanded trifoliolate leaves showed that Pinto 111 did indeed have the highest density of stomata, being from two to three times those of Bountiful, Mecosta, and Royal Red Kidney. Gratiot and Seafarer had densities of around 75% those of Pinto 111. Figure 1 provides evidence that stomatal density does not wholly explain receptivity. If lower stomatal density fully explained the decrease in receptivity over time, the relationship should be linear. In all cases, however, the relationship was clearly not linear, but instead asymptotic with the *x*-axis. Moreover, with trifoliolate leaves of two cultivars, Pinto 111 and Mecosta, sets of leaves were inoculated with the QI every 3 days, giving a range of 18 days. Full expansion was reached early in this period, yet receptivity of both cultivars continued to decline, albeit slowly, over the entire time. Thus, while stomatal density possibly contributes to changes in receptivity, it is not the sole contributor.

Other parameters that were not dealt with in this study have been shown to influence receptivity. Increasing inoculum density reduced the size of differences among barley cultivars in receptivity to leaf rust (6). Although increasing age in bean leaves led to a decrease in receptivity to rust, barley leaves became more receptive to leaf rust as they matured (6). Temperature was shown to directly influence the absolute and relative values of receptivity of wheat cultivars to stem rust (5). It also appeared that wheat growth stage may affect receptivity to stem rust. Mortensen and Green (5) showed that the magnitude of differences between wheat cultivars with low and high receptivity to stem rust was much greater for adult plants than for seedlings. Their data also suggest that there are modest but significant race × cultivar interactions with respect to receptivity. This might indicate that low receptivity is not a stable form of resistance, but rather is subject to "erosion" as the pathogen adapts to the cultivar possessing low receptivity. All of the above variables would have to be accounted for before a complete quantitative understanding of receptivity is possible.

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