# Evaluating Fusiform Rust Symptoms on Greenhouse-Grown Slash Pine Seedlings to Predict Field Resistance

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**ABSTRACT**

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Twenty-two fusiform rust traits (symptoms) were evaluated in greenhouse tests on slash pine seedlings for their usefulness in predicting rust resistance in the field. Seeds from five to 20 open-pollinated parents of known field rust resistance were mixed to obtain resistant, intermediate, and susceptible seed lots for inoculation. Seedlings from these seed lots were screened in 12 greenhouse tests (4 wk in each of three seasons). Logistic transformation of binomial traits was used to reduce seed lot × week and seed lot × season interactions. After transformation, all traits except medium gall size consistently ranked seed lots among weeks and seasons of inoculation and show promise for inclusion in a quantitative selection index for evaluating resistance in the field. Four traits—short galls, typical gall form, galls and adventitious shoots, and number of adventitious shoots—are the most promising because, in addition to giving consistent rankings, they were linearly related to field progeny test breeding values and could be measured on one gall per seedling.

Resistance of slash pine (*Pinus elliottii* Engelm. var. *elliottii*) and loblolly pine (*P. taeda* L.) to fusiform rust (caused by *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*) may be evaluated by field tests, but these tests are time-consuming and costly. Attempts to find indirect testing methods led to artificial inoculations (9) and the development of the concentrated basidiospore suspension (CBS) technique (11,15, 16,19). The CBS technique is used at the Resistance Screening Center (RSC), established by the USDA Forest Service at Asheville, NC, to screen large numbers of slash and loblolly pine seedlings for rust resistance (1).

Initially, a single greenhouse trait (percentage of galled seedlings) was used at the RSC to evaluate resistance of slash and loblolly pine families to fusiform rust. This trait discriminated resistant from susceptible families but did not identify families that, under field conditions, appeared to have an intermediate level of rust resistance (4). Walkinshaw et al (24) suggested that field resistance to fusiform rust could be predicted more accurately by observing the incidence of "symnos" (purple lesions that did not develop into galls), fat galls, and smooth galls. An index based on regression analysis with these three greenhouse traits explained 62% of the variation in field performance of the families tested. Hubbard (8) reevaluated Walkinshaw et al's data (24) and recommended a new index based on standardized family expression of symnos, rough galls, and short galls; the incidence of healthy seedlings was later added to this index (10).

The currently used index of traits for slash pine was developed using data from a small number of field tests on a few families in a single season. It is possible that variation in seedling growth due to seasonal variation in greenhouse conditions affects expression of traits. Family-by-environment interaction has been demonstrated for fertilization (20), inoculum source (22), and inoculum density (7,14). For optimal prediction of field performance, the greenhouse screening technique should discriminate among families with different levels of resistance across all seasons of inoculation.

Most traits evaluated on fusiform rust-inoculated seedlings in the greenhouse are scored as presence or absence of the trait and are therefore binary on individual seedlings. Thus, the assumptions of normality and homogeneity of variance required for analysis of variance are not met. In addition, the ability to discriminate and/or predict family resistance or susceptibility is greatly reduced when the incidence of a trait is below 30% or above 70% (13). To circumvent this problem, such data are often transformed by the logistic and arcsine functions (3,6,18).

Our ultimate goal is to develop a selection index to predict breeding values for rust resistance of slash pine in the field from measurements of one or more greenhouse traits. The specific objectives of this study were to determine the effects of season and week of inoculation on the expression of symptom traits, to

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evaluate the logistic and arcsine transformations for each binomial trait, to determine which greenhouse traits efficiently discriminate seed lots of known field rust resistance, and to assess the utility of measuring more than one gall per seedling.

## MATERIALS AND METHODS

**Plant material.** Seeds from five to 20 open-pollinated slash pine families from seed orchards in the Florida Cooperative Forest Genetics Research Program were mixed to create six seed lots. Two seed lots each were classified, according to their average predicted field parental breeding values for rust resistance, as susceptible, intermediate, and resistant (Table 1). Seed lots in the same classification were randomly mixed from the same parents and are replications. Parental breeding values were estimated from at least four field tests by best linear prediction (25). Although our ultimate goal requires evaluation of half-sib and full-sib families, this study was based on seed lots (mixtures of families) because of logistic limitations imposed by multiple tests in multiple seasons. In addition, the susceptible and resistant seed lots are standard check lots used operationally at the RSC.

**Table 1.** Composition, classification, and average predicted field breeding value[a] for fusiform rust resistance of six slash pine seed lots inoculated in greenhouse screening tests

| Seed lot | Classification | Number of parents | Breeding value (%)[a,b] |
|---|---|---|---|
| 1 and 2 | Susceptible | 9 | 86 ± 12 |
| 3 and 4 | Intermediate | 20 | 50 ± 16 |
| 5 and 6 | Resistant | 5 | −10 ± 20 |

[a] Parental breeding values were obtained from the Florida Cooperative Forest Genetics Research Program. Each breeding value predicts the average percentage of rust infection in a field environment where unimproved material would incur 50% infection (i.e., 50% of the individuals would have galls). The resistant seed lots have a breeding value of −10% because the methodology places no bounds on the prediction.
[b] Mean ± standard deviation.

**Table 2.** Traits (symptoms) evaluated 6 mo after inoculation of slash pine seed lots with the fusiform rust fungus in the greenhouse

| Trait name | Abbreviation | Description | Reference |
|---|---|---|---|
| Healthy | HEA[a] | Rust symptoms absent | 24 |
| Symno | SYM[a] | Purple discoloration on needle base or stem | 7,24 |
| Proportion galled | PGA[a] | The proportion of seedlings with any type of gall | 24 |
| Fat gall | FR2,[a] FT2[b] | Gall whose diameter is twice that of the stem if it were not galled | 23 |
| Rough gall | ROR,[a] ROU[b] | Gall with an area of discoloration that covers more than 50% of the gall surface, making it rough | 23 |
| Short gall | SHR,[a] SHT[b] | Gall less than 25 mm long | 7,8 |
| Typical gall | TPR,[a] TYP[b] | Gall with swelling around the entire circumference of the stem | 23 |
| Adventitious shoots | ADR,[c] ADV[b] | Number of adventitious shoots emerging at acute angles along the galled portion of the stem | 8,12,23 |
| Gall and adventitious shoots | PAD[a] | Both gall and adventitious shoots present | 12 |
| Number of galls | GAL | Number of galls per seedling | New |
| Medium gall | MED[a] | Gall whose diameter is more than one-third greater but less than twice the diameter of the stem if it were not galled | New |
| Thin gall | THN[a] | Gall whose diameter is not one-third or more greater than the diameter of the stem if it were not galled | New |
| Gall size | FAR,[c] FAT[b] | Gall scored as 1 (fat), 0.5 (medium), or 0 (thin) | New |
| Entry | ENT | Seedling scored as 2.5 (healthy), 2 (symno), 1 (one gall), 0.5 (two galls), or 0 (more than two galls) | New composite |
| Postentry | PEN | Seedling scored as the sum of 0.5 (if no adventitious shoots), 1 (if gall is short), 1 (if gall is not fat), and 1 (if not typical), and as 0 otherwise | New composite |
| Current RSC[d] traits | CRT | Seedling scored as 0 (gall long and not rough), 0.25 (gall short and not rough), 0.5 (gall rough and long), 1 (gall rough and short), 2 (symno only), or 3 (healthy) | New composite |

[a] Binomial trait evaluated as presence (1) or absence (0) of the symptom.
[b] Trait evaluated on all galls on each seedling.
[c] Trait evaluated on a single gall on each seedling.
[d] Rust Screening Center.

**Greenhouse tests.** Twelve tests were conducted at the RSC using their standard techniques (2,10). Briefly, seeds were stratified and sown in trays measuring 10 × 15 × 5 cm; germinated seeds were transplanted into Ray Leach tubes 3 wk after sowing; and seedlings were inoculated 5 wk after transplantation with a concentrated suspension (20,000 spores per milliliter of water) of basidiospores obtained from red oak (*Quercus rubra* L.) inoculated with aeciospores collected in five slash pine-growing areas, incubated in a chamber for 24 hr (at approximately 20 C and 97% humidity), grown in the greenhouse (at approximately 20 C with a 12-hr photoperiod), and evaluated for symptom expression 6 mo after inoculation.

The 12 tests were initiated in four consecutive weeks during three seasons: winter (9 November 1987), summer (11 April 1988), and fall (18 July 1988). The winter season was characterized by the lowest ambient (outside) temperatures and the shortest days during sowing, transplanting, and inoculation, with seedlings growing under increasing ambient temperature and day length until the beginning of the summer. Artificial light and heat were required for the first 6 mo of the winter season. The summer season was characterized by low ambient temperatures during sowing and transplanting and higher temperatures and the longest days during inoculation. The seedlings grew under increasing ambient temperature and day length until winter. Artificial light and heat were required for the 3 mo preceding evaluation. The fall season was characterized by higher ambient temperatures during sowing, transplanting, and inoculation, with the seedlings growing under low ambient temperatures and short days. Artificial light and heat were required for 6 mo following inoculation.

For each of the four tests (weeks) within a season, 120 seedlings of each of the six seed lots were inoculated. The 120 seedlings were divided into six plots of 20 seedlings each and were inoculated in two "runs" (three plots each) 1 day apart. The inoculated seedlings were placed in a humid chamber for 24 hr and were then randomly placed in the greenhouse in six blocks (one plot per block). Each week in each season, 720 seedlings (20 seedlings × six blocks × six seed lots) were inoculated, for a total of 8,640 seedlings. Symptoms were evaluated 6 mo after inoculation.

**Trait selection and evaluation.** Twenty-two symptom traits were selected for evaluation (Table 2). Nine of the traits (HEA, SYM, PGA, FR2, ROR, SHR, TPR, ADR, and PAD) have been used by the RSC and/or by others to evaluate fusiform rust resistance in slash pine (7,8,12,23,24). The other 13 traits are new or new combinations: MED and THN are individual gall traits; GAL, FT2, FAT, ROU, SHT, TYP, and ADV are evaluated on all galls on a seedling (normally, the RSC evaluates only the most prominent gall); and FAR, ENT, PEN, and CRT combine several traits into one quantitative score. Traits evaluated only as present or absent yield binomial data, whereas GAL, ADR, ADV, FAR, FAT, ENT, PEN, and CRT yielded continuous data. The traits SYM, SHR, and ROR have been associated with resistance (7,23).

**Data analysis.** Analysis of variance (Table 3) was conducted on plot means for each symptom trait. The binomial traits HEA, SYM, PGA, FR2, MED, THN, ROR, SHR, TPR, and PAD were analyzed as the untransformed proportion of seedlings displaying the symptom (the untransformed plot mean) and as the logistic (3) and arcsine (21) transformations of the plot means. For traits based on all galls on a seedling (FT2, FAT, ROU, SHT, TYP, and ADV), plot means were obtained by first averaging the galls on each seedling and then averaging all seedlings in a plot. *F* tests were calculated for all effects. Satterthwaite's approximate *F* test (17) was used for effects with no exact test (i.e., season and weeks nested in season). All tests of significance were at $P = 0.05$.

To determine whether differences among seed lots in symptom expression reflected differences in the level of field resistance or were the result of sampling error (replications within resistance level) within a seed lot, the sum of squares among the six seed lots was partitioned into that due to differences among the three levels of resistance, with two degrees of freedom (df), and that due to replications within levels of resistance, with 3 df. The mean square for the interaction between seed lots and season of inoculation, with 10 df, was the denominator for the *F* tests.

To investigate the pattern of variation for each trait across the three levels of resistance, the sum of squares due to level of resistance, with 2 df, was partitioned into two orthogonal contrasts (linear and quadratic), with 1 df each.

The sum of squares due to the interaction between seed lots and season was partitioned into that due to the interaction between level of resistance and season, with 4 df, and that due to the interaction between replications nested in level of resistance and season, with 6 df. The mean square due to the interaction between seed lots and weeks nested in season, with 45 df, was the denominator for the *F* tests.

## RESULTS AND DISCUSSION

**Test means and transformations.** The test mean for PGA (proportion of seedlings galled), averaged over all seed lots, seasons, weeks, and blocks, was 0.83 (Table 4), indicating successful inoculations. The resistant seed lots had higher mean values for HEA, SYM, THN, ROU, ROR, SHT, SHR, ENT, PEN, and CRT and lower mean values for the other traits than the susceptible and intermediate seed lots. These results agree with those of others (7,23) suggesting that SYM, SHT, SHR, ROU, and ROR indicate resistance, whereas TYP and TPR indicate susceptibility, and with the results of Layton (12) indicating that adventitious shoots (ADV, ADR, and PAD in this experiment) are susceptible reactions.

When we analyzed untransformed plot means of the 22 traits, statistically significant interactions occurred for level of resistance × season (nine traits), replication within level × season (two traits), and seed lot × week within season of inoculation (12 traits). These significant interactions could result from a change in rank of the seed lots across seasons or weeks, a response that reduces the usefulness of the trait for predicting field performance, or they could arise from scale effects (i.e., changes in relative differences among seed lot means among tests) with no changes in rank. Interactions resulting from scale effects often can be eliminated by appropriate transformation (5).

**Table 3.** Analysis of variance, expected mean squares, and partition of seed lot and seed lot × season sum of squares for the 432 plot means (six blocks × six seed lots × 4 wk × three seasons) for each trait in the greenhouse evaluation of fusiform rust resistance in slash pine

| Source of variation | df | Expected mean squares |
|---|---|---|
| Season | 2 | $\sigma_e^2 + 6\sigma_{cw}^2 + 24\sigma_{sc}^2 + 6\sigma_b^2 + 36\sigma_w^2 + 144\sigma_s^2$ |
| Week (season) | 9 | $\sigma_e^2 + 6\sigma_{cw}^2 + 6\sigma_b^2 + 36\sigma_w^2$ |
| Block (week, season) | 60 | $\sigma_e^2 + 6\sigma_b^2$ |
| Seed lots | 5 | $\sigma_e^2 + 6\sigma_{cw}^2 + 24\sigma_{sc}^2 + Q$ (seed lots) |
| Level of resistance | 2 | |
| Linear contrast | 1 | |
| Quadratic contrast | 1 | |
| Replication (level) | 3 | |
| Seed lot × season | 10 | $\sigma_e^2 + 6\sigma_{cw}^2 + 24\sigma_{sc}^2$ |
| Level × season | 4 | |
| Replication (level) × season | 6 | |
| Seed lot × week (season) | 45 | $\sigma_e^2 + 6\sigma_{cw}^2$ |
| Seed lot × block (week, season) | 300 | $\sigma_e^2$ |

**Table 4.** Overall test means and means for susceptible, intermediate, and field-resistant slash pine seed lots for the 22 traits evaluated 6 mo after artificial inoculation with the fusiform rust fungus in the greenhouse

| Trait[a] | Test mean[b] | Seed lot level of field resistance[c] | | |
|---|---|---|---|---|
| | | Susceptible | Intermediate | Resistant |
| HEA | 0.065 | 0.041 | 0.040 | 0.114 |
| SYM | 0.105 | 0.051 | 0.058 | 0.205 |
| GAL | 1.119 | 1.223 | 1.275 | 0.859 |
| PGA | 0.830 | 0.908 | 0.901 | 0.682 |
| All galls evaluated | | | | |
| ADV | 1.646 | 2.062 | 1.567 | 1.309 |
| FAT | 0.557 | 0.628 | 0.601 | 0.443 |
| FT2 | 0.292 | 0.348 | 0.335 | 0.193 |
| ROU | 0.545 | 0.473 | 0.556 | 0.606 |
| SHT | 0.194 | 0.119 | 0.172 | 0.291 |
| TYP | 0.710 | 0.814 | 0.737 | 0.579 |
| Single gall evaluated | | | | |
| ADR | 1.759 | 2.200 | 1.701 | 1.374 |
| PAD | 0.666 | 0.757 | 0.681 | 0.540 |
| FAR | 0.590 | 0.660 | 0.643 | 0.467 |
| FR2 | 0.323 | 0.383 | 0.377 | 0.209 |
| THN | 0.144 | 0.064 | 0.092 | 0.275 |
| MED | 0.533 | 0.554 | 0.530 | 0.516 |
| ROR | 0.573 | 0.502 | 0.593 | 0.624 |
| SHR | 0.123 | 0.051 | 0.085 | 0.235 |
| TPR | 0.786 | 0.895 | 0.831 | 0.632 |
| ENT | 1.063 | 0.960 | 0.940 | 1.287 |
| PEN | 1.184 | 0.894 | 1.036 | 1.623 |
| CRT | 0.677 | 0.471 | 0.533 | 1.028 |

[a] For trait definitions, see Table 2.
[b] Averaged across seed lots, seasons, weeks, and blocks.
[c] Averaged across replications within level of resistance, seasons, weeks, and blocks. Differences among levels of resistance were significant ($P$=0.05) for all traits except MED.

The logistic and arcsine transformations were evaluated for their utility in inducing additivity of main effects (eliminating interactions due to scale effects) for the 10 binomial traits. The logistic transformation benefits eight of the 10 binomial traits by eliminating interactions for level × season (HEA, SYM, PGA, PAD, SHR, and TPR) or for seed lot × week within season (SYM, ROR, THN, and TPR). Two binomial traits (FR2 and MED) had no significant interaction for either untransformed or transformed data. The logistic transformation was chosen instead of arcsine because it reduced or eliminated interactions for more traits.

**Two-way interactions.** Among the 22 traits (10 binomial traits on the logistic scale and 12 untransformed plot means), the level of resistance × season interaction was statistically significant only for GAL, FT2, and ENT. Graphic analyses showed that these interactions did not result from rank changes. For all traits, the screening procedure ranked seed lots with different levels of resistance consistently among seasons.

Interaction between replication within level and season was significant for two traits (HEA and ENT). These significant interactions may be attributed to scale effects and also to minor changes in rank between the two replications within the same level of resistance (an example for ENT is shown in Fig. 1). These two traits did not discriminate susceptible from intermediate seed lots, and some rank change occurred among the four means (two susceptible and two intermediate seed lots) from season to season.

To investigate the interaction between seed lot and week within a season, we conducted analyses of variance for all traits for each season of inoculation. The sum of squares due to seed lots × week was partitioned into the portion due to level of resistance × week (6 df) and that due to replication within level × week (9 df). The level of resistance × week interaction was statistically significant in two (ADV and SHT, winter) of the 66 possible cases (22 traits × three seasons). These significant interactions, like those previously discussed, are attributed to scale effects and not to rank changes. The interaction between replication within level and week of inoculation was statistically significant for one, two, and four traits (out of 22 possibilities in each season) for the first, second, and third season, respectively. Because these interactions occurred randomly and never occurred for the same trait in more than one season, they were considered unimportant.

In general, all interactions were of minimal biological importance; that is, they did not result from change in rank among seed lots with different levels of resistance among seasons or weeks within a season. However, scale effect interactions do exist. Thus, to rank seed lots screened in different seasons or in different weeks of the same season, the seed lot means should be adjusted first by expressing them as deviations from the overall test mean and second by accounting for different variances among tests.

**Main effects.** Differences among weeks were significant for five traits for the first season, nine for the second, and six for the third. In general, differences in trait means among weeks of inoculation occurred randomly; that is, no traits varied significantly among weeks for all seasons. For the season main effect, the means differed from season to season for all traits except HEA, PGA, FAR, and THN (Table 5). Although the greenhouse conditions were controlled, large fluctuations in outside ambient conditions (e.g., temperature, day length, and light intensity) may have affected growing conditions and thereby trait expression. For example, seedlings inoculated in the winter varied more in height, were smaller in diameter, and had higher means for all symptom traits expressing susceptibility than seedlings inoculated in the other two seasons. To compare results from different weeks or seasons, the family means must be adjusted for scale effects.

Means for seed lots with different levels of field rust resistance differed for all traits except MED (Table 5). This trait might include galls that stop growing as well as those that later become fat galls. The trait MED adds no information to discriminate among families with different levels of rust resistance and holds little promise for future investigation.

Significant differences for both linear and quadratic contrasts were observed for SYM, GAL, PGA, ADV, FAT, FAR, FR2, THN, ROR, ENT, PEN, and CRT (Table 5). Even though the quadratic response was significant, the sum of squares for the linear contrast accounted for more than 90% of the level of resistance sum of squares for all traits except GAL, FR2, ROR, and ENT. For all traits except ROR, the quadratic effect occurred because the means for the intermediate seed lots (Table 4) were closer to those of the susceptible seed lots than was predicted by the linear regression on field breeding values. For these traits, the greenhouse test discriminated well between resistant and

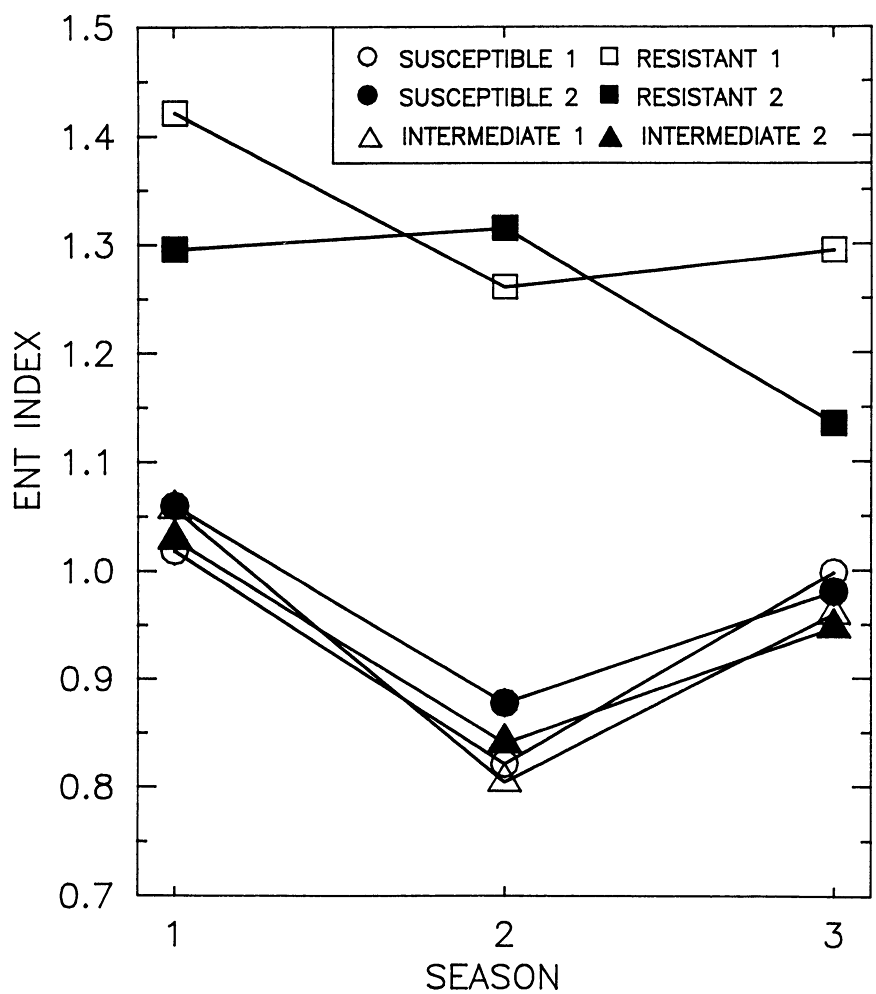


**Fig. 1.** Effect of season (1 = winter, 2 = summer, 3 = fall) on the entry (ENT) index (seedling scored as 2.5 [healthy], 2 [symno], 1 [one gall], 0.5 [two galls], or 0 [more than two galls]) of slash pine seed lots inoculated with *Cronartium quercuum* f. sp. *fusiforme*. Levels of rust resistance (susceptible, intermediate, and resistant) were determined from field progeny tests.

**Table 5.** Summary of analysis of variance for the 22 symptom traits measured 6 mo after artificial inoculation with the fusiform rust fungus on slash pine seed lots with different levels of field rust resistance

| | Mean squares[b] | | | | | |
|---|---|---|---|---|---|---|
| | Level of field resistance | | | | | Level × |
| Trait[a] | Total | Linear | Quadratic | $R^{2c}$ | Season | season |
| HEA[d] | 30.974** | 55.395** | 6.553 | 0.89 | 7.005 | 1.324 |
| SYM[d] | 85.289** | 156.069** | 14.500** | 0.91 | 6.116* | 1.184 |
| GAL | 7.392** | 11.460** | 3.323** | 0.78 | 3.999* | 0.547** |
| PGA[d] | 104.392** | 190.802** | 17.830** | 0.91 | 7.119 | 0.438 |
| All galls evaluated | | | | | | |
| ADV | 21.107** | 37.969** | 4.245* | 0.90 | 86.499** | 0.977 |
| FAT | 1.432** | 2.696** | 0.169* | 0.94 | 0.374* | 0.023 |
| FT2 | 1.073** | 1.951** | 0.194 | 0.91 | 1.389** | 0.068* |
| ROU | 0.652** | 1.199** | 0.106 | 0.92 | 6.536** | 0.054 |
| SHT | 1.122** | 2.231** | 0.013 | 0.99 | 0.933** | 0.025 |
| TYP | 2.049** | 4.088** | 0.011 | 0.99 | 0.707* | 0.047 |
| Single gall evaluated | | | | | | |
| ADR | 24.955** | 46.507** | 3.402 | 0.93 | 87.959** | 0.966 |
| PAD | 43.348** | 86.682** | 0.013 | 0.99 | 56.640** | 1.052 |
| FAR | 1.638** | 2.989** | 0.287** | 0.91 | 0.223 | 0.022 |
| FR2[d] | 31.725** | 54.961** | 8.488* | 0.87 | 40.660** | 1.209 |
| THN[d] | 109.487** | 206.664** | 12.309** | 0.94 | 6.317 | 0.728 |
| MED[d] | 1.589 | 2.901** | 0.277 | 0.91 | 32.098** | 1.757 |
| ROR | 13.614* | 21.359** | 5.868* | 0.78 | 149.239** | 1.697 |
| SHR[d] | 93.023** | 181.315** | 4.730 | 0.97 | 1.595** | 1.930 |
| TPR[d] | 95.870** | 190.475** | 1.264 | 0.99 | 28.271* | 0.524 |
| ENT | 5.491** | 9.067** | 1.915 | 0.83 | 0.932* | 0.184** |
| PEN | 21.528** | 41.423** | 1.633* | 0.96 | 6.780** | 0.232 |
| CRT | 13.428** | 24.847** | 2.009** | 0.93 | 3.798** | 0.082 |

[a] For trait definitions, see Table 2.
[b] Asterisks indicate statistical significance at $P = 0.01$ (**) and 0.05 (*). Data in these columns without asterisks are not significant.
[c] $R^2$ expresses the portion of the total variability among the three levels of resistance that is accounted for by the linear relationship between trait expression and field level of resistance.
[d] Binomial trait evaluated on logistic scale.

other seed lots, but not between intermediate and susceptible seed lots (Fig. 2B). For ROR only, the intermediate seed lots were closer to the resistant ones than predicted by linear regression on breeding values. ROR may be useful for identifying highly susceptible families, while GAL, FR2, and ENT may be useful for identifying resistant families.

Linear response (but not quadratic) was significant for HEA, FT2, ROU, SHT, TYP, ADR, PAD, SHR, and TPR (Table 5). We expected traits with a linear response to discriminate adequately among a broad range of field resistance. This was true for SHT, TYP, ADR, PAD, SHR, and TPR (e.g., TPR in Fig. 2A). However, HEA, FT2, and ROU did not fit this profile since they did not discriminate either susceptible and intermediate seed lots (HEA and FT2) or intermediate and resistant seed lots (ROU). The lack of significant quadratic contrast for HEA, FT2, and ROU was probably the result of lack of power of the $F$ test resulting from the use of a larger seed lot × season interaction as the error term.

**Promising traits for predicting field rust resistance.** A trait is considered promising for predicting field performance when it satisfies at least two of the following conditions: 1) it ranks seed lots consistently among weeks and seasons; 2) it discriminates among seed lots with different levels of field rust resistance; 3) it is relatively easy to evaluate. Traits related to disease resistance mechanisms could be most meaningful; unfortunately, there is little information on this relation.

All traits except MED ranked susceptible, intermediate, and field-resistant seed lots consistently among weeks and seasons. The traits SHT, SHR, TYP, TPR, ADR, and PAD also satisfied the second condition, as they were linearly related to seed lot field resistance level and efficiently discriminated among susceptible, intermediate, and resistant seed lots. For all gall traits, evaluation of a single gall per seedling yielded information as reliable as evaluation of all galls on a seedling. Therefore, the traits SHR, TPR, PAD, and ADR best met our criteria for the most promising traits for predicting field resistance (i.e., they satisfied all three conditions). In addition, the traits HEA, SYM, PGA, THN, FAR, FR2, GAL, ENT, PEN, and CRT, which satisfied the first and third conditions, should be considered when the goal is to discriminate between intermediate and resistant seed lots. The relative importance of these traits may be adjusted in the future as our understanding of disease mechanisms increases or for tests involving primarily resistant seed lots.

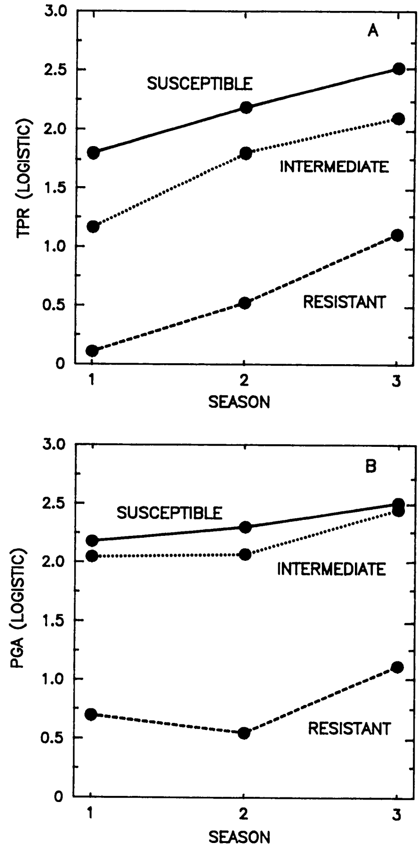


**Fig. 2.** Effect of season (1 = winter, 2 = summer, 3 = fall) on **(A)** the incidence of typical galls (TPR) and **(B)** the proportion of seedlings galled (PGA) on slash pine seed lots inoculated with *Cronartium quercuum* f. sp. *fusiforme*. Levels of rust resistance (susceptible, intermediate, and resistant) were determined from field progeny tests. A significant quadratic effect occurred for PGA (but not for TPR) because susceptible and intermediate seed lots were more similar than the field progeny tests predicted.

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