# Seedling Age and Fertilization Affect Susceptibility of Loblolly Pine to Fusiform Rust

S. J. Rowan and Klaus Steinbeck

Principal Research Plant Pathologist, U. S. Department of Agriculture, Southeastern Forest Experiment Station, Forestry Sciences Laboratory, Carlton Street, Athens, GA 30602; and Associate Professor, School of Forest Resources, University of Georgia, Athens, GA 30602.

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## ABSTRACT

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The susceptibility of *Pinus taeda* seedlings to infection by *Cronartium fusiforme* increased with seedling age at the time of artificial inoculation. Fertilization with N and with P also influenced the infection rate, as did all possible interactions between seedling age at inoculation and the N and P treatments. Potassium supply had no direct effect on seedling susceptibility. Foliar levels of P, K, Mg, Mn, and Zn were not related to infection rate. Gall length, seedling susceptibility to the disease, and the number of lateral branches were correlated with seedling growth rate. Seedlings grew best when 300 μg/ml of N and 75 μg/ml of P were supplied in nutrient solution. Symptoms of the disease developed earliest on seedlings supplied with the optimum amount of N and P and inoculated at 8 wk of age.

*Additional key words:* tree disease, seedling growth rate, disease development.

Fusiform rust (which is caused by *Cronartium fusiforme* Hedgc. & Hunt ex Cumm.) is a serious disease of loblolly pine (*Pinus taeda* L.). The effects of various cultural practices on the susceptibility of pine to fusiform rust are not understood fully, but factors that increase pine growth appear to increase disease incidence. Cultivation, fertilization (3, 4, 5, 6, 9, 12, 20), fire (21), overstory density (19), site preparation (15, 17), site drainage (12, 15), stand density, and stand age (10, 18, 22, 23) have been reported to increase the incidence of the disease.

Although fertilization has been reported to increase the susceptibility of pines to fusiform rust, the effects of individual nutrients upon rust incidence have not been tested adequately. The effects of nitrogen (N), phosphorus (P), and potassium (K) were reported to affect the susceptibility of slash pine seedlings to rust if they were inoculated 2 wk after fertilization (20). The present paper describes the results of a greenhouse sand culture study in which the effects of seedling age at the time of inoculation and the effects of N, P, and K upon the susceptibility of loblolly pine to fusiform rust were tested. Seedling development, disease development, and the relationship of foliar levels of five nutrient elements to disease susceptibility also were studied.

## MATERIALS AND METHODS

Seeds collected from open-pollinated loblolly pine were stratified 30 days and planted in flats of common builder's sand (99.6% sand, 0.4% silt, and a trace of clay). Seedlings were transplanted to plastic flats (33 × 13 × 11 cm) filled with builder's sand that had been washed with tap water. Seed stratification, planting, and seedling transplanting were scheduled so that on the day of inoculation with *C. fusiforme*, groups of seedlings were obtained that were 4, 8, and 12 weeks of age, from emergence. Only seedlings that had emerged during a 4-day period were transplanted in each age group. Thirty seedlings were transplanted into each flat.

The effects of N, P, and K fertilization and seedling age variables were tested at three levels in a 3×3×3×3 factorial experiment, using a randomized complete block design with 10 replications. The basic nutrient solution applied to all seedlings contained 80.000 μg/ml Ca as $CaCl_2$, 24.000 μg/ml Mg as $MgSO_4$, 0.001 μg/ml Mo as $Na_2MoO_4$, 0.006 μg/ml Cu as $CuSO_4$, 0.090 μg/ml B as $H_3BO_3$, 0.100 μg/ml Zn as $ZnSO_4$, and 0.700 μg/ml Mn as $MnCl_2$, 5.5 μg/ml Fe as Sequestrene-330 Fe (sodium ferric diethylenetriamine pentaacetate). The concentrations of the three nutrients were 0, 100, and 300 μg/ml N as $NH_4NO_3$, 0, 75, and 150 μg/ml P as $Na_2HPO_4$, and 0, 100, and 300 μg/ml K as KCl. All nutrient solutions were prepared, and the pH was adjusted to 5.5, on the day of application. The flats were irrigated with tap water as needed during the first 14 days. For 18 consecutive weeks, 400 ml of nutrient solution was applied weekly to each flat after it had been flushed with approximately 500 ml of tap water. Three biweekly applications were made during the 6 wk following the above 18-wk period and montly applications were made during each of the subsequent 4 mo. Any additional irrigation needed prior to the inoculation date was applied in a manner that prevented drainage and leaching of nutrients.

At the time of inoculation, 10 seedlings in each flat were selected at random, cut off at the root-collar, dried at 75

C, and weighed. Four replicates were selected at random for chemical analyses. The needles were ground in a Wiley mill to pass a 841-μm screen. Foliar-K, -Mg, -Mn, and -Zn were analyzed by atomic absorption spectroscopy (2). Foliar P was analyzed colorimetrically by the molybdate-elon reagent method (11). Foliar Ca also was analyzed but, because of erratic results, these data are omitted.

Aeciospores collected from galls on loblolly pine in Green County, Georgia, in 1971 (source 1-71) were used to infect northern red oak (*Quercus rubra* L.) seedlings. Basidiospores were collected from the oak leaves, and suspensions containing 100,000 basidiospores per milliliter (14) were sprayed onto pine seedlings.

Numbers of seedlings with stem galls were recorded at 3 and 12 mo after inoculation. Tree height, number of lateral branches, and gall length were recorded for each seedling 12 mo after inoculation. The percentage of trees infected and indices related to stimulation of branching and rate of symptom expression were generated from these data. The indices were: (i) the ratio of branches per diseased tree to branches per healthy tree, and (ii) the ratio of seedlings with stem lesions or galls 3 mo after inoculation to those with galls after 12 mo, multiplied by the average gall length 12 mo after inoculation. The percentage of variation attributable to each source of

TABLE 1. Effect of fertilization and seedling age at inoculation on loblolly pine seedling susceptibility to fusiform rust

| Source of variation | Percent infection | Gall length | Symptom expression rate[c] |
|---|---|---|---|
| Age (A)[a] | 21.1**[b] | 7.0** | NS |
| Nitrogen (N) | 19.1** | 49.3** | 53.2** |
| Phosphorus (P) | 26.4** | 34.7** | 29.3** |
| Potassium (K) | NS | NS | NS |
| A×N | 8.8** | 0.4** | NS |
| A×P | 6.8** | 1.2** | 3.1** |
| A×K | NS | NS | NS |
| N×P | 5.0** | 6.0** | 4.9** |
| N×K | NS | NS | NS |
| P×K | 0.9* | NS | NS |
| A×N×P | 0.7* | NS | 1.3* |
| A×N×K | NS | NS | NS |
| A×P×K | NS | NS | NS |
| N×P×K | NS | NS | NS |
| A×N×P×K | NS | NS | NS |

[a]Seedling age at inoculation (4, 8, or 12 wk from emergence).
[b]Significance $P = 0.01$ is indicated by **, at $P = 0.05$ by *, and nonsignificance by NS as determined by Fisher's F-test. The numbers represent the percentage of the total variation accounted for by each significant source of variation (source mean square divided by the sum of all mean squares, the quantity multiplied by 100).
[c]Symptom expression rate = infection percentage at 3 mo divided by the infection percentage at 12 mo, the quantity multiplied by the average gall length.

TABLE 2. Effect of fertilization and seedling age at inoculation on loblolly pine seedling growth

| Source of variation | Seedling height (mm) | Number of lateral branches | Branch formation rate[c] |
|---|---|---|---|
| Age (A)[a] | 15.6**[b] | 7.0** | 7.7** |
| Nitrogen (N) | 42.9** | 53.0** | 59.8** |
| Phosphorus (P) | 33.4** | 29.8** | 14.4** |
| Potassium (K) | NS | NS | NS |
| A×N | 0.8** | 1.1** | 1.9** |
| A×P | 0.7** | 0.9** | 1.4* |
| A×K | NS | NS | NS |
| N×P | 6.0** | 7.6** | 6.9** |
| N×K | NS | NS | NS |
| P×K | NS | NS | NS |
| A×N×P | 0.2** | 0.2** | 1.8** |
| A×N×K | NS | NS | NS |
| A×P×K | NS | NS | NS |
| N×P×K | 0.1* | NS | NS |
| A×N×P×K | NS | NS | NS |

[a]Seedling age at inoculation (4, 8, or 12 wk from emergence).
[b]Significance $P = 0.01$ is indicated by **, at $P = 0.05$ by *, and nonsignificance by NS as determined by Fisher's F-test. The numbers represent the percentage of the total variation accounted for by each significant source of variation (source mean square divided by the sum of all mean squares, the quantity multiplied by 100).
[c]Branch formation rate = number branches on diseased seedlings divided by the number branches on healthy seedlings.

TABLE 3. The effects of seedling age at inoculation upon seedling development, susceptility to infection by *Cronartium fusiforme*,

| Observation | Seedling age at inoculation | | |
|---|---|---|---|
| | 4-wk | 8-wk | 12-wk |
| Seedlings infected (%) | 25.5 A[a] | 37.5 B | 39.9 B |
| Gall length per seedlings (mm) | 87.3 A | 97.1 B | 111.9 C |
| Symptom expression rate[b] | 49.0 A | 51.2 A | 47.1 A |
| Lateral branches per seedling (no.) | 1.8 A | 2.5 B | 3.1 C |
| Branch formation rate[c] | 8.4 A | 5.7 B | 5.2 B |
| Seedling height (mm) | 147.4 A | 189.0 B | 215.1 C |
| Foliar P (%) | 0.33 A | 0.21 B | 0.22 B |
| Foliar K (%) | 0.74 A | 0.49 B | 0.54 C |
| Foliar Mg (%) | 0.15 A | 0.15 A | 0.20 B |
| Foliar Mn (μg/g) | 295.8 A | 386.6 B | 423.2 C |
| Foliar Zn (μg/g) | 64.7 A | 45.2 B | 33.5 C |

[a]Treatment means in each horizontal row followed by a common letter are not significantly different, $P = 0.05$, by Duncan's multiple range test.
[b]Symptom expression rate = infection percentage at 3 mo divided by infection percentage at 12 mo multiplied by average gall length.
[c]Branch formation rate = number branches on diseased seedlings divided by number branches on healthy seedlings.

variation was calculated from the ratio of the mean square for each source of variation to the sum of all mean squares in the analysis of variance table.

Statistical significance of data was determined by analysis of variance methods and differences between means were determined by Duncan's new multiple range test.

## RESULTS

**Susceptibility to fusiform rust.**—Seedling age (A) at time of inoculation, fertilization with N, fertilization with P, and the interactions A×N, A×P, N×P, P×K, and A×N×P all significantly affected the percentage of seedlings infected (Tables 1, 3, 4, 5). Incidence of infection was not affected by seedling age if neither N nor P was supplied in nutrient solution. Increasing the level of N or P in the nutrient solution resulted in a larger percentage of seedlings infected at the age of 8 and 12 wk, but not at 4 wk. Fertilization had not affected growth, and consequently susceptibility, of the 4-wk-old seedlings.

Percentages of seedlings infected were significantly correlated with seedling heights (r = 0.94) and seedling top weights (r = 0.97). Fertilization with potassium did not affect seedling susceptibility to the disease at any age.

Seedling age, N, P, and their interactions accounted for 87.9% of the total variation associated with percentage of seedlings infected (Table 1) and are the important variables contributing to the susceptibility of seedlings to fusiform rust.

**Gall length.**—The average length of galls on seedlings 12 mo after inoculation was significantly correlated with seedling height (r = 0.98) and was affected by the same variables that affected seedling susceptibility to infection (Tables 1, 3, 4, 5). Gall growth, therefore, is proportional to seedling growth and is increased by treatments that increase seedling growth.

Fertilization with N, P, and the interaction between

TABLE 4. The effects of fertilization with nitrogen upon susceptibility of loblolly pine seedlings to infection by *Cronartium fusiforme;* disease development, seedling development, and foliar levels of five nutrient elements

| Observation | Nitrogen level in nutrient solution | | |
|---|---|---|---|
| | 0 μg/ml | 100 μg/ml | 300 μg/ml |
| Seedlings infected (%) | 26.5 A[a] | 35.3 B | 41.1 C |
| Gall length per seedlings (mm) | 62.4 A | 107.5 B | 126.5 C |
| Sympton expression rate[b] | 26.6 A | 53.8 B | 67.1 C |
| Lateral branches per seedlings (no.) | 0.5 A | 2.6 B | 4.2 C |
| Branch formation rate[c] | 11.8 A | 4.6 B | 3.0 B |
| Seedling height (mm) | 120.3 A | 202.1 B | 229.2 C |
| Foliar P (%) | 0.24 A | 0.25 AB | 0.26 B |
| Foliar K (%) | 0.68 A | 0.56 B | 0.53 B |
| Foliar Mg(%) | 0.18 A | 0.17 B | 0.15 C |
| Foliar Mn (μg/g) | 402.3 A | 365.5 B | 337.9 C |
| Foliar Zn (μg/g) | 43.4 A | 48.8 AB | 51.2 B |

[a]Treatment means in each horizontal row followed by a common letter are not significantly different, $P = 0.05$, by Duncan's multiple range test.

[b]Symptom expression rate = infection percentage at 3 mo divided by infection percentage at 12 mo multiplied by average gall length.

[c]Branch formation rate = number branches on diseased seedlings divided by number branches on healthy seedlings.

TABLE 5. The effects of fertilization with phosphorus on the susceptibility of loblolly pine seedlings to infection by *Cronartium fusiforme*, disease development, seedling development, and foliar levels of five nutrient elements

| Observation | Phosphorus level in nutrient solution | | |
|---|---|---|---|
| | 0 μg/ml | 75 μg/ml | 150 μg/ml |
| Seedlings infected (%) | 24.4 A[a] | 40.1 B | 38.5 B |
| Gall length per seedling (mm) | 66.9 A | 113.6 B | 115.8 B |
| Symptom expression rate[b] | 31.4 A | 58.1 B | 57.9 B |
| Lateral branches per seedling (no.) | 0.9 A | 3.2 B | 3.2 B |
| Branch formation rate[c] | 9.1 A | 5.3 B | 4.9 B |
| Seedling height (mm) | 126.1 A | 213.0 B | 212.5 B |
| Foliar P (%) | 0.15 A | 0.30 B | 0.31 B |
| Foliar K (%) | 0.61 A | 0.57 A | 0.60 A |
| Foliar Mg (%) | 0.17 A | 0.17 A | 0.17 A |
| Foliar Mn (μg/g) | 363.8 A | 365.2 A | 376.7 A |
| Foliar Zn (μg/g) | 42.6 A | 48.8 B | 51.9 B |

[a]Treatment means in each horizontal row followed by a common letter are not significantly different, $P = 0.05$, by Duncan's multiple range test.

[b]Symptom expression rate = infection percentage at 3 mo divided by infection percentage at 12 mo multiplied by average gall length.

[c]Branch formation rate = number branches or diseased seedlings divided by number branches on healthy seedlings.

these two elements accounted for 90.0% of the total variation associated with gall length (Table 1). Seedling age and the interactions A×P and A×N accounted for an additional 8.6% of the variation associated with gall length.

**Symptom expression rate.**—Fertilization with N, fertilization with P, and the interactions A×P, N×P, and A×N×P all affected the rate at which disease symptoms developed (Tables 1, 3, 4, 5). Although the rate of symptom development did not increase with seedling age at inoculation, gall length increased with seedling age (Table 3). Fertilization with N and P and their interaction accounted for 87.4% of the variation attributed to the rate of symptom development (Table 1).

**Seedling height.**—Seedling age at inoculation, fertilization with N, fertilization with P, and the interactions A×N, A×P, N×P, A×N×P, and N×P×K significantly affected seedling height 12 mo after inoculation (Table 1). Although fusiform rust may reduce seedling height growth, the greater incidence of infection in seedlings fertilized with higher levels of N and P did not cause a loss of growth superiority during the first 12 mo after inoculation.

Fertilization with N and P and their interactions accounted for 82.3% of the variation associated with tree height and appear to be more important factors affecting tree height growth than seedling age at inoculation (Table 1). Seedling height growth was apparently near optimal at 300 μg/ml N and 75 μg/ml P (Tables 4, 5). Potassium fertilization did not significantly affect tree height.

**Rate of branch formation and number of lateral branches.**—The rate of branch formation and number of branches 12 mo after inoculation were affected by seedling age, fertilization with N, fertilization with P, and by the interactions A×N, A×P, N×P, A×N×P (Tables 2, 3, 4, 5). The number of branches increased with increasing age, N, and P and, therefore, is closely associated with increased rates of seedling growth. Fertilization with N and P and the interaction between these two nutrients accounted for 90.4% of the variation attributed to number of seedling branches (Table 2).

The rate of branch formation measured the relative increase in number of branches formed on diseased seedlings compared to the number on healthy ones—the larger the number, the greater the increase in branches caused by *C. fusiforme*. Fertilization with N and P, and the interaction between these two nutrient elements, accounted for 81.1% of the variation attributed to the branch formation rate. The largest increase in the rate of branch formation occurred on trees inoculated at 4 wk of age (Table 3) and fertilized with the low rate of N and P (Tables 4, 5). These same treatments (age 4, low N, and low P) produced trees with the fewest lateral branches.

**Foliar levels of five nutrient elements.**—Seedling age and fertilization with N significantly affected the amount of P, K, Mg, Mn, and Zn in foliage tissue (Tables 3, 4). Foliar P also was affected by P fertilization (Table 5) and the interactions A×N, A×P, N×P, and N×K. Foliar K was affected by K fertilization and the interactions A×N and A×P; foliar Mg by K fertilization; foliar Mn by the A×N and A×P interactions; and foliar Zn by P fertilization and the A/N interaction.

Susceptibility of loblolly pine seedlings to fusiform rust was not correlated with foliar levels of either of the five elements P, K, Mg, Mn, or Zn. Although the percentages of seedlings infected increased along with foliar levels of P (Tables 4, 5), Mg (Table 3), Mn (Table 3), and Zn (Tables 4, 5), the percentages of seedlings infected also increased as the amount of these same four elements decreased in foliage (Tables 3, 4). Foliar K was not related to seedling susceptibility because foliar K increased with increasing supply of K while the percentage of seedlings infected remained unchanged.

## DISCUSSION

Seedling age at time of inoculation and fertilization with N and P significantly affected gall length, seedling height, number of lateral branches, the rate of branch formation on infected seedlings, and number of seedlings infected with fusiform rust. Seedling age at inoculation did not affect the rate of disease symptom development, but N and P fertilization did. In general, the most pronounced effects on any measured parameter were those caused by seedling age at inoculation, fertilization with N and P, and the interaction between these three variables.

If the relative rate of gall growth is a measure of compatibility, the fungus and the pine host are most compatible when seedlings are fertilizaed with optimum rates of N and P. Since gall growth was greater on seedlings inoculated at 12 wk of age than on seedlings inoculated at 4 or 8 wk, the rate of gall growth may depend on the number of meristematic cells available for invasion as well as on the rate of host growth.

The disease apparently can be diagnosed earliest on seedlings inoculated at 8 wk of age and fertilized with 300 μg/ml of N and 75 μg/ml of P. Because seedlings that received low levels of N and P were significantly less infected than those that received intermediate or high levels, fertilization of seedlings prior to inoculation should provide a better assessment of disease response than fertilization applied after inoculation. Hosts which are most efficient in using nutrients would grow faster and be more susceptible than less efficient hosts if grown under fertile conditions, but their growth rate and degree of susceptibility may be nearly identical when grown under nonoptimal fertility conditions. Both fertilized and nonfertilized seedlings may be desired if tests indicate significant interactions exist between fertilization and host genotype, inoculum genotype, or inoculum density. These data suggest that tests for fusiform rust resistance among seedling progenies in the Fusiform Rust Testing Center should be made by inoculating both fertilized and nonfertilized seedlings at 8 wk of age. Inoculations at the Rust Testing Center presently are made 6 wk after emergence and seedlings are grown in a topsoil medium in which fertility is not rigidly controlled.

Susceptibility of loblolly pine seedlings appears to depend largely upon the amount of susceptible tissue exposed because: (i) percentage of seedlings infected was significantly correlated with seedling height (r = 0.94) or seedling top weight (r = 0.97); and (ii) susceptibility of seedlings that were supplied with adequate amounts of N and P increased with increasing age (and size) at time of inoculation and increased as N and P supply increased the growth of 8- and 12-wk-old seedlings. The number of lateral branches was proportional to seedling growth ($r = 0.98$) and they may serve as additional infection courts. Although rust infections caused an increase in the number of lateral branches formed on certain seedlings, rate of branch formation was promoted more by N and P fertilization than by the fungus. The promotion of branch formation by the fungus in poorly fertilized seedlings may not be biologically significant, but their formation increases the amount of susceptible tissue for subsequent infection. The susceptibility of tissue on rapidly growing seedlings apparently is not correlated with foliar levels of P, K, Mg, Mn, or Zn.

Previous nutritional studies of loblolly (1, 8) and slash (7, 12, 13, 16) pine have shown that the growth of both species is significantly increased by fertilization with N and P and that the effect of either element is dependent upon the presence of an adequate supply of the other. Data in this study confirm these previous observations and illustrate that the increased growth attributed to N and P supply is significantly correlated with susceptibility to fusiform rust.

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