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Symptomology and Relationships Between *Armillaria* Root Rot Infection Levels, Inoculum Load and Environmental Variables in Northwestern Ontario

A.M. Wiensczyk, M.T. Dumas and R.N. Irwin



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**SYMPTOMOLOGY AND RELATIONSHIPS BETWEEN *ARMILLARIA* ROOT ROT
INFECTION LEVELS, INOCULUM LOAD AND ENVIRONMENTAL VARIABLES
IN NORTHWESTERN ONTARIO**

A. M. Wiensczyk¹, M.T. Dumas^{2,3} and R.N. Irwin³

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¹ General Delivery
Fort St. James, BC V0J 1P0
(604) 996-5200
Fax (604) 996-5290

² Author to whom correspondence should be addressed

³ Natural Resources Canada
Canadian Forest Service—Sault Ste. Marie
Sault Ste. Marie, Ont. P6A 5M7

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ABSTRACT

Eight 5 to 15 year old black spruce (*Picea mariana* [Mill.] B.S.P.) plantations from each of the Northwestern Ontario Forest Ecosystem Classification Treatment Units (TU's) B, C, D, E and F were sampled for *Armillaria* root rot. Data was also collected on stock type, competition index, soil texture, moisture regime, pH, and nutrient status, number and basal area of both infected and non-infected stumps. A significant non-linear relationship was found between tree age and *Armillaria* infection levels. Infection levels were adjusted to a common age of 15 years prior to regression analysis against the environmental variables. The stepwise linear regression procedure was used to select the significant environmental variables for inclusion in the non-linear model. The logistic or logit function was the non-linear model used in the analysis. Significant factors included the dummy variables for Treatment Units B and D, stock type, total Basal Area of all stumps, percent clay in the C-horizon, and the phosphorus level in the A-horizon. The non-linear model had a resultant R^2 of 0.94 and a mean square error of 0.0026. *Armillaria* was found in all of the plantations sampled in this study and ranged from slightly less than 1 to 32 percent. Some differences were observed among FEC Treatment Units but these differences were not statistically significant ($p < 0.05$). Plantations in TU F had the highest average infection level (16.93 percent) while those in TU B had the lowest (7.24 percent). Plantations in TU F had significantly higher cumulative mortality levels than did those in TU B ($p < 0.05$). The average ratio of infected healthy trees to infected dead trees was 3.28:1 across all Treatment Units. The total number and total basal area of all stumps and of all infected stumps were similar across the Treatment Units. Variations did exist in the ratio of conifer to hardwood stumps and reflected the differences in the species composition of the original stands. Infection levels based on aspen (*Populus tremuloides* Michx.) traplogs were not found to be a good indicator of percent infection in the trees. The use of colour and relative shoot growth was only moderately effective in identifying trees infected by *Armillaria*.

RÉSUMÉ

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INTRODUCTION

Mortality of young trees caused by root rot is of concern to foresters managing regeneration programs. *Armillaria* root rot seems to be the most common chronic disease problem in Ontario (Whitney et al. 1974, Whitney 1988). For black spruce (*Picea mariana* [Mill.] B.S.P.) plantations 7 to 20 years old Whitney found that mortality levels, at the time of plot establishment, ranged from 0–13 percent and averaged 5.0 percent. After six years of assessments the accumulated average mortality was 14.6 percent and the mean average annual mortality for juvenile stands of black spruce was 1.5 percent. Livingston (1990) found essentially the same situation prevailing in Maine. *Armillaria* infected trees were found in the majority of the plantations sampled but the level of mortality was low, usually less than 1 percent but mortality levels may not be a true indicator of the level of infection by *Armillaria*. Whitney et al. (1989) found symptomless trees infected with *Armillaria* in plantations with infected dead trees. For black spruce the ratio of infected symptomless trees to infected dead trees was 3:1. Although all infected symptomless trees may not die as a direct result of the disease, the root decay and death caused by this fungus may predispose the trees to windthrow, especially on shallow rocky sites (Whitney 1976, Morrison et al. 1991).

Site characteristics seem to play an important role in the incidence and spread of *Armillaria* both directly, through their effects on the fungus itself, and indirectly, through their effects on the host. Redfern and Filip (1991) discuss several environmental factors, including soil temperature, pH, moisture, organic matter content and nutrient status which may directly affect the growth of *Armillaria* rhizomorphs through the soil. Damage by *Armillaria* root rot is known to increase in severity of attack when trees are stressed either by abiotic or biotic factors (Wargo and Harrington 1991), and certain site characters such as soil texture and moisture regime relate to stress susceptibility. As well, tree vigour and the resistance of the tree to infection may be a function of site. Whitney (1978) found that as the moisture regime increased, the proportion of black spruce trees infected with *Armillaria* decreased. He also found that six times as many black spruce trees were infected by *Armillaria* in plantations on sandy soils than in those on silty soils. Whether these factors are functioning as direct or indirect effects, or are a combination of both, is undetermined.

The Northwestern Ontario Forest Ecosystem Classification (NWO FEC) system was used in this study to identify and classify the various site types. The NWO FEC system utilizes a two stage process in which forest stands are first classified according to the dominant vegetation and may then be further classified according to the dominant soil conditions. Assessment of the vegetation results in stands being classified into one of 38 Vegetation or V-types and 22 Soil or S-types into which the V-types may be further subdivided (Sims et al. 1989). Similar vegetation types may also be grouped together into Treatment Units (TU's), which are defined as "management-oriented aggregations of defined soil and vegetation conditions that possess similar species composition, productivity, macroclimate or ecological properties." (Racey et al. 1989).

The objectives of this study were to survey black spruce plantations growing on sites classified as one of five FEC Treatment Units, determine the levels of *Armillaria* infections, and determine if

Armillaria infection levels could be predicted prior to any regeneration treatments using a combination of measurable environmental variables. This would allow the forest manager to determine if any special site treatments were required prior to planting to reduce the *Armillaria* infection hazard.

METHODS

A list of candidate plantations planted to black spruce in northwestern Ontario, 5–15 years old, was compiled from forest companies and Ontario Ministry of Natural Resources (OMNR) records. The FEC vegetation type was determined for each plantation using Forest Resource Inventory (FRI) maps and further categorized into FEC treatment units. The Treatment Units proposed in the Interpretation Guide (Racey et al. 1989) were used and plantations in TU's B, C, D, E, and F were selected (Figure 1). Treatment Unit B represents aspen hardwood (*Populus tremuloides* Michx.) and mixedwood V-types while V-types in TU C are dominated by white birch (*Betula papyrifera* Marsh.). Treatment Unit D represents balsam fir (*Abies balsamea* L.) or white spruce (*Picea glauca* [Moench] Voss) dominated conifer and mixedwood V-types. Treatment Unit E are upland black spruce–jack pine (*Pinus banksiana* Lamb.)/Feathermoss V-types and TU F are jack pine/feathermoss dominated V-types. Because of insufficient plantations in TU G, plantations with V-type 11 were included in TU B and plantations with V-type 17 and 28 were included in TU F. Eight plantations in each of the five Treatment Units were randomly selected from the list of candidate plantations with an additional ten plantations selected from each Treatment Unit to serve as alternates in case one of the initial eight was inaccessible.

Field Methods

The plantation were located and the FEC vegetation type, Treatment Unit and stock type (paperpot vs bareroot) were confirmed. Figure 2 shows the location of the black spruce plantations sampled. The first transect was located at a randomly selected point between 10–100 m along an azimuth that would lead into the plantation. Five transects were established within each plantation. Subsequent transects were located 100 m from the previous transect along an azimuth that would ensure that the transects remained within the plantation and did not cross previously established transects (Figure 3). In small plantations, shorter distances between strips were used in order to fit the five transects within the plantation.

For each transect a random azimuth was selected and a 4 m wide by 50 m long transect was laid out. Percent slope, slope position and azimuth were determined at the start of each transect. In addition soil samples from the A-horizon and the C-horizon were taken at the start of each transect using a Dutch Soil Auger. The presence of any mottling or gleying in the C-horizon was noted. All samples from the A-horizon were taken back to the lab for texture and nutrient analysis. A-horizon samples were analyzed for nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), iron (Fe), copper (Cu), manganese (Mn), zinc (Zn), aluminum (Al), sodium (Na), pH and cation exchange capacity (CEC). From the first transect, a soil sample of the C-horizon was taken back to the lab for texture analysis only. Samples of the C-horizon from the other transects were not analyzed unless they appeared to be considerably different from the first transect sample. Soil moisture regime was determined based on percent slope, and the soil texture, depth, and mottling or gleying of the C-horizon (Sims et al. 1989).

All black spruce trees within the transect were rated as healthy or symptomatic based on foliage colour and relative growth. Foliage colour was categorized as healthy (code 0), slightly chlorotic (code 1), or very chlorotic (code 2). Relative growth was visually estimated as follows:

$$\text{Relative shoot growth} = \frac{\text{Last complete year of growth (1992 shoot growth)}}{1/2 (1990 + 1991 \text{ shoot growth})} \quad (1)$$

Trees with a relative shoot growth of less than 50 percent of a healthy tree and/or very chlorotic (colour code 2) were considered symptomatic. Whether the tree regenerated naturally or through planting was also noted. A minimum sample size of 40 trees per transect was expected. If fewer than 40 trees were found within the transect, the last tree in the transect was noted and the transect line was extended. The measurement process continued until 40 trees were sampled. All dead trees within the strip were noted and classified as recently killed (i.e. those judged to have died during the present or previous growing season) or dead for a period of >1 year and their roots were examined for signs of *Armillaria*.

Every fifth tree (minimum of 8) and each tree classified as symptomatic were tagged and measured in detail for total height, shoot growth for the 1990, 1991 and 1992 growing seasons, diameter at 10 cm and on trees of sufficient height, at 1.3 m, the 1991 foliage colour, (based on the Munsell colour charts for plant tissues), and competition index (Towill and Archibald 1991). If a naturally regenerated or dead tree was encountered as the fifth tree, it was not measured and the next planted tree was selected. In addition to the 200+ trees in the five transects, the condition of 300 randomly-selected trees, either healthy or symptomatic, was classified in a random survey of the plantation. All of the tagged, symptomatic trees and a selected sample of 30 tagged, healthy trees per plantation were excavated to check the roots for *Armillaria* infection. Samples were taken from all infected trees for culturing in the lab to confirm the presence of the fungus.

For each transect the number of residual stumps from the last harvest were assessed for the following:

- species (if possible) or conifer, hardwood or unknown;
- diameter; and,
- presence of mycelial fans, rhizomorphs and state and type of decay.

Three to four major roots were excavated near the base of the stump to check for signs of infection by *Armillaria*. Samples of infected stump material were taken for culturing in the lab.

Traplogs consisting of healthy trembling aspen sections, 5–10 cm in diameter and 50 cm long, were installed in all plantations during the fall of 1993. The traplogs were sharpened at one end and the bark was scored with a chainsaw, to facilitate infection by *Armillaria*, and driven into the ground at an approximately 45° angle to a depth of 30–40 cm. A total of 25 traplogs were installed in each plantation. The first traplog for each transect was located 5 m from the start of the transect with subsequent logs located at 10 m intervals along the transect lines. They were removed and evaluated for *Armillaria* infection one year later.

Data Analysis

Non-linear regression techniques were used to construct a model of environmental variables to predict *Armillaria* infection levels. The stepwise method for multiple linear regression analysis (Draper and Smith 1966) was used to determine the significant environmental variables to be used in the non-linear model. Table 1 lists the variables assessed. Four dummy variables (D1-D4) with the values of 0 (false condition) and 1 real variable (TU F) with a value of 1 (true condition) were used to represent the five FEC Treatment Units (D1=TU B, D2=TU C, D3=TU D, D4=TU E) and another (D9) was used to represent stock type (1 bareroot, 0 paperpot). For categorical variables such as FEC Treatment Unit and stock type, N-1 dummy variables are used where N=the number of categories. This was done to avoid creating an unsolvable singular matrix in the regression analysis. A similar situation arises with percent sand, silt and clay for the A- and C-horizons, because the sum of the percentages is always 1.00 for each plantation. This also creates an unsolvable singular matrix when all three are included. For this reason, only percent clay and sand were included in the analysis. For nutrient levels, the median value from the five transects for each plantation was used as it was considered a better representative of the plantation's nutrient levels than was the mean.

The logistic or logit function was the non-linear model used in the analysis. The general form of the model is as follows:

$$Y = \frac{e(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots)}{1 + e(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots)} + \varepsilon \quad (2)$$

where,

Y = dependent variable;
 $X_{1\dots}$ = independent variables;
 $\beta_{1\dots}$ = estimated coefficients; and,
 $\varepsilon \equiv (0, \sigma^2)$.

Armillaria infection levels showed a significant positive linear correlation with tree age ($P=0.0218$). As a result it was deemed appropriate to adjust the *Armillaria* infection levels to a common tree age before assessing the effect of the environmental variables. Tree age was calculated by adding the initial age of the planted trees to the plantation age. For plantations planted with bareroot stock 3 years (1 n +1 n or 2+1) was added to the plantation age, while for those plantations planted with paperpot stock (16-18 weeks old), tree age was equal to plantation age. Since the percent infection of *Armillaria* can only range between 0 and 100 percent, the sigmoidal growth function (a nonlinear function) was chosen as the most appropriate model to fit to the data (Payandeh 1983). This model has the form with 0 and 100 as the lower and upper asymptotes, respectively:

$$Y = 100 * (1 - e^{(b_0 * X)^{b_1}}) \quad (3)$$

where,

Y = percent *Armillaria* infection;
X = tree age; and
 b_0 and b_1 are estimated coefficients.

Analysis of variance was used to test for differences between Treatment Units. The distribution of the data was tested for normality using the Shapiro-Wilk statistic and variances were tested for homogeneity using the Bartlett test prior to analysis of variance. If the distribution of the data was non-normal or if the variances were non-homogeneous then the data were transformed. If differences were found to exist between Treatment Units at the 5 percent level of significance then the Student-Newman-Keul test was used to determine where these difference were. All data analysis was done using the SAS® software package.

Lab Methods

Isolations

Isolation of *Armillaria* was attempted from all infected root material on 3 percent malt agar medium amended with the following antibiotics: 500 ppm Streptomycin sulphate, 100 ppm chlortetracycline, 100 ppm neomycin sulphate and 2 ppm Methyl-1-Benzimidazole Carbamate Phosphate (Lignasan®). Cultures were incubated at 25°C in the dark. Pure cultures were subcultured on 3 percent malt agar. Isolates from within each plantation were then mated to determine the number of clones and/or species of *Armillaria* within each plantation (Adams 1974).

Species Determination

All isolates were cultured on Garraway's medium (1.5 percent Agar plus 5.0 g/l D-glucose, 2.0 g/l L-asparagine, 1.75 g/l KH_2PO_4 , 0.75 g/l $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 1.0 mg/l Thiamine-HCL and 500 µg/ml Ethanol) for 3–4 weeks at 25°C in the dark (Garraway 1974). Three 7 mm plugs taken from the edge of each culture were transferred to a liquid medium (Garraway and Weinhold 1967) and incubated at 25°C for 3 weeks. The species of *Armillaria* were determined by analysis of their esterases and total proteins (Lin et al. 1988).

Similar procedures were followed for the traplog and stump isolates. *Armillaria* isolates from stumps within a plantation were also mated with isolates from infected roots from the same plantation to determine if the residual material was the source of infection of the planted trees.

RESULTS

Model Construction

Prior to analysis of the environmental effects the percent infection of *Armillaria* was adjusted to a common tree age of 15 years using the fitted sigmoidal growth function as illustrated in Figure 4. This model gave a highly significant fit ($p > 0.0001$) and an R-square value of 0.7777 (Table 2). A tree age of 15 years was chosen so that all of the infection levels remained positive.

A stepwise regression method for multiple linear regression was then run using the adjusted *Armillaria* infection percentages as the dependent variable. Significant variables were D1, and D3 (the dummy variable for TU's B, and D, respectively), D9 (the dummy variable for stock type (1 for bareroot and 0 for paperpot), percent clay content of the C-horizon as a decimal fraction (15 percent = 0.15), the total basal area of all stumps (m^2/ha), and the phosphorus level (ppm). These variables were then fitted in the non-linear function. The resultant model had an R^2 value of 0.9402

with an Mean Square Error (MSE) of 0.0026 (Table 3). Dropping the phosphorus level from the model resulted in a slight reduction in the R^2 value to 0.9353 and an increase in the MSE to 0.0027 (Table 3).

Trees infected with *Armillaria* were found in all of the plantations sampled. *Armillaria ostoyae* was the dominant species isolated from the tree, traplog and stump samples. Of the 56 stump samples, *Armillaria sinapina* (Bérubé and Dessureault) was isolated from one hardwood and one conifer stump. Infection levels varied amongst the plantations and according to FEC treatment unit but these differences were not statistically significant. Plantations in TU B had the lowest mean level of *Armillaria* infection at 7.24 percent while those in TU F had the highest at 16.93 percent (Table 4). The plantation with the highest level of infection was also in TU F while the plantation with the lowest *Armillaria* infection level was in TU D. There was a high level of variability in the infection levels within Treatment Units as exhibited by large coefficients of variation (CV) which ranged from 35 percent for plantations in TU C to 76 percent for plantations in TU D.

The percentage of trees killed by *Armillaria* varied significantly among Treatment Units (Table 5). Plantations in TU F had the highest average level of cumulative mortality at 5.70 percent while plantations in TU B had the lowest average mortality level at 2.28 percent. The highest overall mortality level, almost 10 percent, occurred in a plantation in TU F. One plantation in TU B had no mortality attributable to *Armillaria*. However, the coefficients of variation were large showing considerable variability among plantations within Treatment Units.

There were no statistically significant differences in the percentage of infected symptomatic trees among the Treatment Units (Table 6). Treatment Unit F had the smallest percentage of infected symptomatic trees while TU C had the largest percentage. As with percent infection and percent mortality, the coefficients of variation were very large indicating high levels of variability within Treatment Units.

The percent of infected traplogs varied significantly among Treatment Units. Treatment Unit C had the largest percentage of infected traplogs at just over 75 percent while TU E had the smallest at just under 50 percent (Table 7). Treatment Units B, C, and D had similar percentages of infected traplogs. There was also wide range in infection levels among plantations within each Treatment Unit although the coefficients of variation were much smaller. Treatment Unit F had the widest range with a low of 16 percent and a high of 96 percent infected traplogs.

The total number of stumps, the total basal area and the basal area of stumps infected with *Armillaria* did not differ significantly among Treatment Units (Table 8). The basal area of infected hardwood stumps similarly did not differ among Treatment Units. However, there were significant differences in the number, basal area and infected basal area of conifer stumps and the number and total basal area of hardwood stumps among Treatment Units. Plantations in TU's E and F had significantly larger average numbers of conifer stumps than plantations in TU's B and C. In addition, plantations in TU's D, E, and F had significantly larger average total basal areas of conifer stumps and significantly larger average basal areas of infected conifer stumps than plantations in TU's B and C. For hardwood stumps, plantations in TU B had a significantly larger average number of stumps and a significantly larger average total basal area than plantations in TU F (Table 8). There was a high level of variability among the plantations within Treatment Units.

A total of 1 344 trees were measured in the 40 plantations. Of the 1 195 trees categorized as healthy, 104 (8.7 percent) were found to be infected with *Armillaria*. Of the 145 symptomatic trees, 71 (49 percent) were infected with *Armillaria*. Of the non-infected symptomatic trees 18 (24 percent) had other problems that were noted in the tree condition codes. Treatment Unit B had the smallest percentage of healthy trees with *Armillaria* (4 percent) while TU's C and F had the largest percentage of infected healthy trees (11.67 and 11.34 percent, respectively). Treatment Unit D had the largest percentage of infected symptomatic trees (77 percent), and TU B had the smallest (33 percent).

Average tree age, height, diameter at 10 cm, and relative shoot growth for healthy and symptomatic trees were generally similar among the Treatment Units (Table 9) and because of the different ages of the plantations, no statistical tests were conducted to compare these attributes. The relative shoot growth of both infected and non-infected symptomatic trees was less than 100 percent for all Treatment Units. There was little difference in the relative shoot growth between infected symptomatic and non-infected symptomatic trees. The relative shoot growth for both infected healthy and non-infected healthy trees exceeded 100 percent for all Treatment Units (Table 9). Non-infected healthy trees had greater relative shoot growth than infected healthy trees for all Treatment Units with the exception of TU E. Symptomatic trees consistently had a larger average colour code than healthy trees. Within the symptomatic trees, those infected with *Armillaria* had a larger average colour code than non-infected symptomatic trees for plantations in all TU's. There were no consistent trends in average colour code between infected and non-infected healthy trees.

DISCUSSION

A significant positive relationship existed between tree age and the level of *Armillaria* infection. The sigmoidal growth function, a non-linear model, was chosen to best fit this relationship. Infection levels only range between 0 and 100 percent and the sigmoidal growth function used takes this into account. A similar relationship was found by Lundquist (1993) in *Pinus elliottii* (Engelm.) plantations in South Africa. Although he used a curvilinear function to fit his data, the same trend was evident. His data showed a gradual increase in infection levels as measured by gap size as tree age increased from 0–17 years. After 17 years of age the data pattern changed dramatically. In this study tree age was used as opposed to plantation age because it had a stronger relationship with *Armillaria* infection level. For all of the plantations in this study the planted stock type and hence initial tree age was known. The bareroot stock planted in the plantations used in this study was either 1 1/2+1 1/2 or 2+1 stock and hence was three years old when planted. The root mass and general size of the three-year old bareroot stock is generally much greater than that of the 16–18 week old paperpot stock planted in some of the plantations. Statistics from one study show an average initial root area index (RAI) of 59.0 cm², shoot length (SL) of 25.2 cm and root collar diameter (RCD) of 4.8 mm for 1+2 bareroot black spruce stock compared to an RAI of 8.0 cm², SL of 9.7 cm and an RCD of 1.8 mm for paperpot seedlings (Mattice 1981). The larger initial root mass of the bareroot stock may lead to a greater probability of infection by *Armillaria* and hence the use of tree age to adjust infection levels would reflect this difference.

Age also showed a significant ($p < 0.05$) positive relationship with soil phosphorus levels and cation exchange capacity and a significant ($p < 0.05$) negative relationship with all of the stump variables. This created severe problems with multicollinearity when age was included as a factor in the stepwise regression process. Multicollinearity problems arise when there are stronger relationships

amongst the independent variables than between the independent variables and the dependent variable or when one or more independent variables can be expressed as a linear combination of some or all of the others. Because of the significant relationship between age and *Armillaria* and because of the multicollinearity problems when age was included as an independent variable it was decided that adjustment of the infection levels to a common age was necessary before testing of the environmental variables began. Infection levels were adjusted along the non-linear age/*Armillaria* curve to a common age of 15 years. This age was chosen because it kept all of the infection levels positive. Negative infection levels would have resulted in errors in the non-linear *Armillaria*/environmental factors model. Although a significant relationship existed between age and the numbers and basal area of the stumps, adjustment of the data using age as a covariate gave erroneous results and was not deemed appropriate. In addition, information on the initial numbers and basal area of stumps and the effect of the differing site characteristics in each of the plantations such as soil texture, moisture regime, and site preparation types on the rate of decomposition of the stumps was not available. Similarly, changes in P levels and CEC over time may be influenced by site factors, such as those affecting soil microbial activity and rate of organic matter decomposition and adjustment of these variables to a common age for all plantations using simple linear regression would be misleading.

Stepwise regression using the adjusted *Armillaria* infection levels resulted in the following significant variables. D1 and D3, the dummy variables for TU's B and D, D9, the dummy variable for stock type (1 for bareroot and 0 for paperpot), percent clay in the C-horizon as a decimal fraction (i.e. 15 percent=0.15), the total basal area of all stumps (m²/ha) and the median P- level in the A-horizon (ppm). These variables were fitted to the non-linear equation (Table 3). This model predicts the *Armillaria* infection level one could expect when the trees in the plantation are 15 years old. Although this model appears to be complicated it is in fact very simple and easy to use. The dummy variables will be either 1 if the condition is true or 0 if it is not. In some cases the model will have as few as four terms in it. For example, TU E planted with paperpot stock will have only the constant, percent clay, total BA of stumps, and the P level terms, as the others will be multiplied by 0. Alpha is same for both the numerator and denominator and is the power to which e, the natural base logarithm, is multiplied. The value $e^{(\alpha)}$ is subtracted from 1 in the denominator.

The parameter estimates for both D1 and D3 (TU's B and D) are both negative indicating that these TU's generally had lower infection levels if all other factors were held constant. This is supported by the mean *Armillaria* infection level by TU which shows that plantations in these two TU's did have the lowest infection levels (Table 4). Plantations in TU B were dominated by aspen stands prior to harvest and planting to spruce while those in TU D were dominated by balsam fir and/or white spruce. It was originally thought that disease severity was greater in conifer stands planted on sites originally dominated by hardwood as compared to those planted on sites originally supporting conifer (Redfern and Filip 1991). Recently, however, increasing numbers of reports have documented high levels of *Armillaria* infection on second generation conifer sites (Redfern and Filip 1991).

The parameter estimate for clay content of the C-horizon was also negative indicating lower levels of *Armillaria* infection as percent clay increased. Whitney (1978) also reported lower *Armillaria* infection levels for black spruce growing on silty soils as opposed to those growing on sites with sandy soils. The decreased incidence of *Armillaria* infection on finer textured soils may be a result

of the effect of soil texture on rhizomorph growth or it may be a result of the better moisture relations in the finer textured soils with respect to the growth of black spruce. However, rhizomorphs are known to be more abundant in the upper soil horizons. Redfern (1973) found that the main concentration of rhizomorphs occurred between 2.5 and 20.0 cm below the surface. He reported that rhizomorphs were rarely found below 30 cm. Morrison (1976) found that on moist sites, rhizomorphs were concentrated in the upper 10 cm of soil, whereas on drier sites they were found deeper in the soil. The soil texture of the A-horizon was generally coarser than that of the C-horizon and was not a significant factor in explaining the severity of the disease. This might suggest that the influence of clay content of the C-horizon may have been related to the growth of the black spruce rather than having a direct effect on the growth of the *Armillaria* rhizomorphs. However, analysis of the total height and diameter at 10cm (corrected for age) of healthy, black spruce trees showed no significant differences among TU's and showed no significant relationship with clay content of the C-horizon or moisture regime. It is possible that trees growing on the finer textured soils were subjected to less moisture stress during dry periods of the growing season than those growing on the drier coarser textured soils and this may not be reflected in differences in tree growth. Another possibility relates to changes in the root form of black spruce planted in different textured soils. On drier, sandy soils black spruce may develop a more fibrous root system with extensive feeder roots in order to increase moisture uptake as opposed to the development of a more compact root system in the finer textured soils. Sutton (1968) found that the total root length of five year old white spruce trees was markedly influenced by soil properties. He found that the mean number and total length of roots (≥ 5 cm) was greater on the sites with sandy soils than on the sites with clay soils. The same pattern existed for the tertiary and higher order roots. A similar pattern could be expected from black spruce (Sutton, personal communication). A more fibrous root system may increase the probability of contact of the tree roots with the rhizomorphs of the fungus and for root grafting thereby increasing the chances of infection. However, only three sites had greater than 50 percent clay content in the C-horizon, two of which had A-horizon clay contents greater than 45 percent. The majority of plantations in this study had less than 20 percent clay content in the C-horizon and less than 10 percent clay content in the A-horizon. More study is needed to define the role of soil texture in the spread and severity of *Armillaria* root rot.

The positive parameter estimate for stock type (D9) indicates that plantations planted with bareroot stock had higher infection levels than those planted with paperpot stock. This is positive even after the age difference of the two stock types is taken into account with the adjustment of the infection levels. Similar results were found by Singh (1975) in a survey of softwood plantations in Newfoundland. He reported that *Armillaria* infection levels were higher in plantations planted with bareroot stock than those planted with container stock or direct seeded. One possible explanation for this is that the bareroot may be subject to more planting stress than container stock. During the outplanting process bareroot stock loses direct contact with the soil and often loses a proportion of its fine roots during lifting from the nursery beds (Tinus 1974, Sutton 1978). Nursery procedures, such as root pruning, undercutting and wrenching, which promote a fibrous root system, and care in lifting, grading, packing and planting can minimize these losses of fine roots (Tinus 1974). Container stock, on the other hand, maintains root contact with the soil and has an external source of moisture and nutrients in addition to its internal supply and this results in reduced planting stress as shown by increased initial survival and growth (Tinus 1974). J-roots and other deformations of the root system may also make the trees more susceptible to infection (Sutton 1969). Both container stock and bareroot stock may exhibit root deformation, the former

as a result of container design and the latter as a result of poor nursery and/or planting practices (Van Eerden 1978).

Positive parameter estimates were also obtained for total BA of stumps per hectare and for the soil P levels indicating that as the total BA of all stumps or P level increased so did the infection level. It is interesting to note that it was the total BA of all stumps and not the BA of infected stumps that showed a significant relationship with infection level. The relationship between the BA of stumps and infection level seems relatively straight forward. As the amount of food base increases so too does the incidence of the disease. Inclusion of stump data separated into conifer and hardwood components did not affect the model.

Morrison (1975) found that growing rhizomorph tips absorbed P and N from the soil and he concluded that nutrients available from the food base may be supplemented by uptake from the soil. Higher P levels may have resulted in increased rhizomorph growth and increased levels of *Armillaria* infection. Phosphorus levels are also known to affect the root development of plants, especially the development of lateral and fibrous rootlets (Brady 1984). The increased lateral and fibrous root development as a result of higher P levels may have increased the probability of root contact with *Armillaria* rhizomorphs or infected stump material and resulted in higher infection levels. Phosphorus level explained only a small proportion of the variance in *Armillaria* infection levels. Omitting P from the model reduced the R^2 value by only 0.5 percent and increased the MSE by 0.0001. Dropping P level from the model may be advisable from the stand point of field practicality and applicability.

Armillaria ostoyae was found in all of the plantations sampled in this study. Infection levels ranged from slightly less than 1 percent to as high as 32 percent with an overall average of 12.75 percent. This included infected healthy, symptomatic and dead trees. These levels were much higher than was expected based on Forest Insect and Disease Survey reports (Biggs et al. 1994). Mortality levels, based on infected dead trees, were also high ranging from 0–6 percent with an average of 3.67 percent across all TU's. These mortality levels were similar to, although slightly below, those found by Whitney (1988) and were greater than those found by Livingston (1990). The average ratio of infected healthy trees to infected dead trees was 3.28:1 across all TU's, which is comparable to the ratio of 3.0:1 for black spruce found by Whitney et al. (1989). Ratios in this study ranged from 12.50:1 for a plantation in TU C, to 0.07:1 for a plantation in TU D. TU C had the largest average ratio of 5.20:1, while TU B had the smallest average ratio of 2.43:1. This ratio of infected healthy trees to infected dead trees is particularly important because it demonstrates that percent mortality due to *Armillaria* is not an accurate measure of infection level and that actual *Armillaria* infection levels may be significantly higher. Although infected healthy trees may not die as a result of infection by *Armillaria*, they will certainly have reduced growth and vigour and may succumb to other forest pests or stresses such as windthrow (Whitney 1976, Morrison et al. 1991).

Some differences in *Armillaria* infection levels were observed among TU's but these differences were not statistically significant. The lack of statistical significance may have been due to an inadequate sample size as a result of the large variability in infection levels between plantations within TU's. There were, however, statistically significant differences among TU's in the percent cumulative mortality due to *Armillaria*. Plantations in TU B had a significantly smaller mean percent mortality than did plantations in TU F. The mean mortality levels for each TU mirrored the

mean levels of *Armillaria* with one exception. Treatment Unit C plantations had a larger mean percent of *Armillaria* than TU E plantations but had a smaller mean percent mortality. This is because plantations in TU C had larger infection levels in the apparently healthy trees than did plantations in TU E, as seen by the large ratio of infected healthy to infected dead discussed earlier. This further demonstrates the need for extreme caution if percent mortality is to be used as the sole indicator of percent infection. In addition the mortality levels reported in this paper may be smaller than the actual cumulative mortality, because mortality was assessed at a specific point in time. In the older plantations sampled it is possible that trees that may have succumbed to the infection by *Armillaria* and died early in the life of the plantation may have already decomposed and therefore would not have been included in the survey. The only way this could have been avoided would have been to begin the assessment of the plantation at the time of establishment.

There were no statistical differences among TU's in the percentages of infected symptomatic trees. The mean percent of infected symptomatic trees by TU did not mirror the mean percent infection or the mean percent mortality. Although plantations in TU F had the largest mean infection level and largest mean percent mortality, they had the smallest mean percent infected symptomatic trees which would seem to indicate that infected trees in TU F died very soon after infection by *Armillaria*. In part, this may be due to the fact that plantations in TU F generally had coarser textured soils and were drier. It is possible that partial loss of the root system was enough to kill the trees under these conditions whereas on more moist sites the trees could survive the loss of several roots before succumbing to this disease.

Infection levels based on traplogs were not found to be a good indicator of percent infection in the trees. No significant relationships were found between percent infection level based on trees and the percent infected traplogs over all TU's combined or within the individual TU's, with the exception of TU F. A significant but inverse relationship existed within TU F with percent infected trees decreasing as percent infected traplogs increased. The overall relationship also showed a slight negative trend as did the relationships within TU's B and C. Site factors, such as soil texture and moisture content, are known to influence rhizomorph production (Redfern 1970, 1973) and may have had an effect on traplog infection levels, although these effects should also have influenced the infection levels in the trees as well.

The total average number, total average basal area and the total average infected basal area of stumps (conifer and hardwood combined) was statistically similar among the five TU's. There were, however, differences in the proportions of average number, total average basal area and average infected basal area of conifer stumps, and average number, and total average basal area of hardwood stumps between TU's. In general, plantations in TU's D, E, and F were dominated by conifer stumps while plantations in TU's B and C were dominated by hardwood stumps. This was expected and reflects the species composition of the original stand.

The use of colour and relative shoot growth were only moderately effective in identifying trees infected by *Armillaria*. Only slightly less than half of the trees identified as symptomatic had the disease, although a quarter of these had other problems which were noted in the tree condition codes. Other factors such as nutrient-poor or extremely shallow soils, flooding, frost damage, insects, and physical damage from other trees, eg. top whipping, as well as undetermined shoot damage, caused trees to display symptoms similar to those of *Armillaria* and resulted in the misdiagnosis.

Although no significant differences were found in *Armillaria* infection levels among TU's, the dummy variables for TU's B and D were significant factors in the model for predicting *Armillaria* infection levels in the plantations sampled. Stock type, the total basal area of stumps, percent clay content of the C-horizon, and P level in the A-horizon were also significant. Because of the limited sample size and the complexity of the relationship between this disease, its hosts and the environment, it is suggested that further studies be conducted to verify these results. As well, further information should be gathered on the relationship between tree age and the incidence of the disease. Ideally, stands should be sampled before harvest to assess infection levels. This should then be followed by monitoring over time of the plantations established on these sites to assess the progression of the disease.

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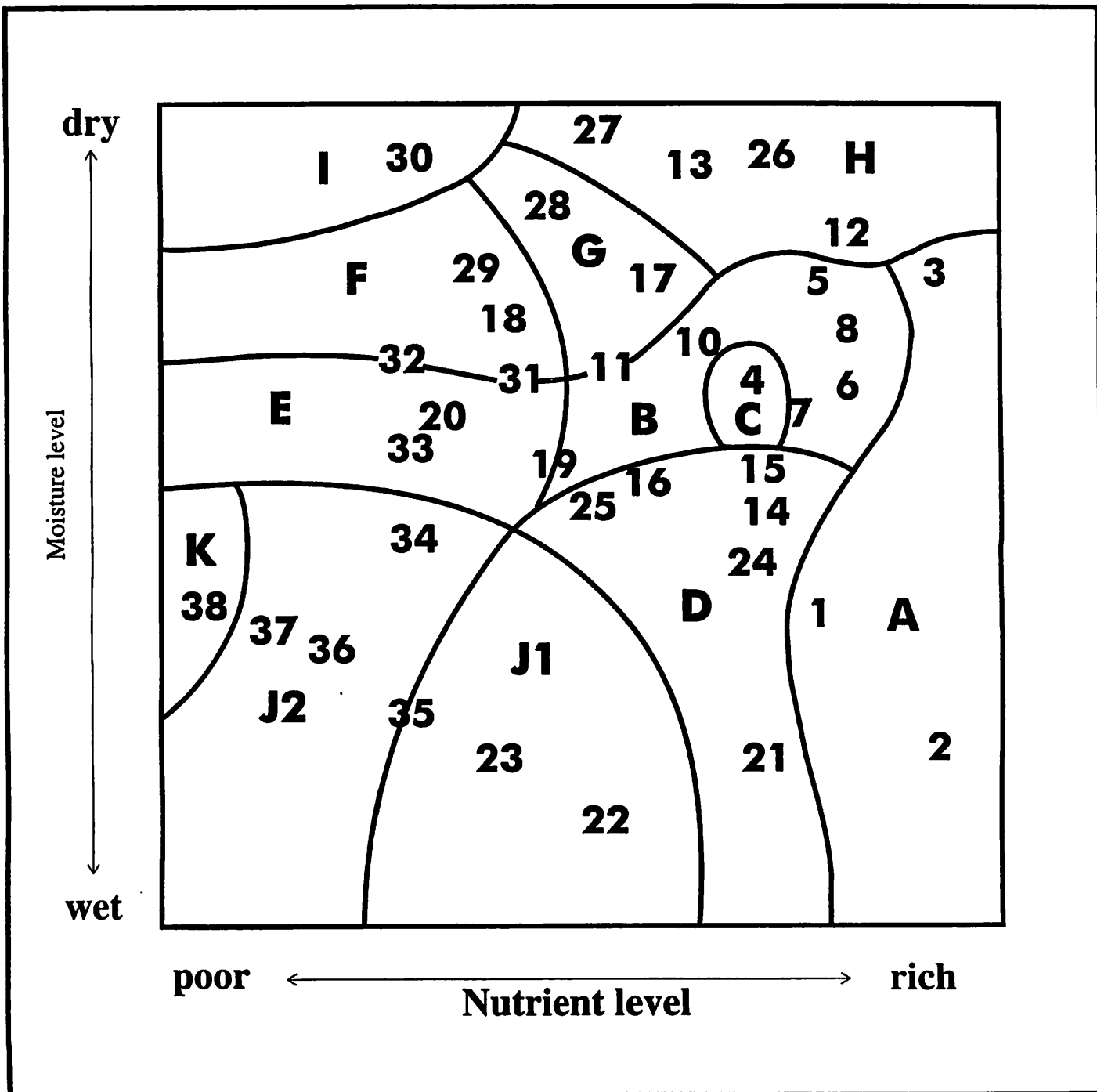


Figure 1. Treatment Unit groupings superimposed upon NWO FEC V-Types (*after* Racey et al. 1989).

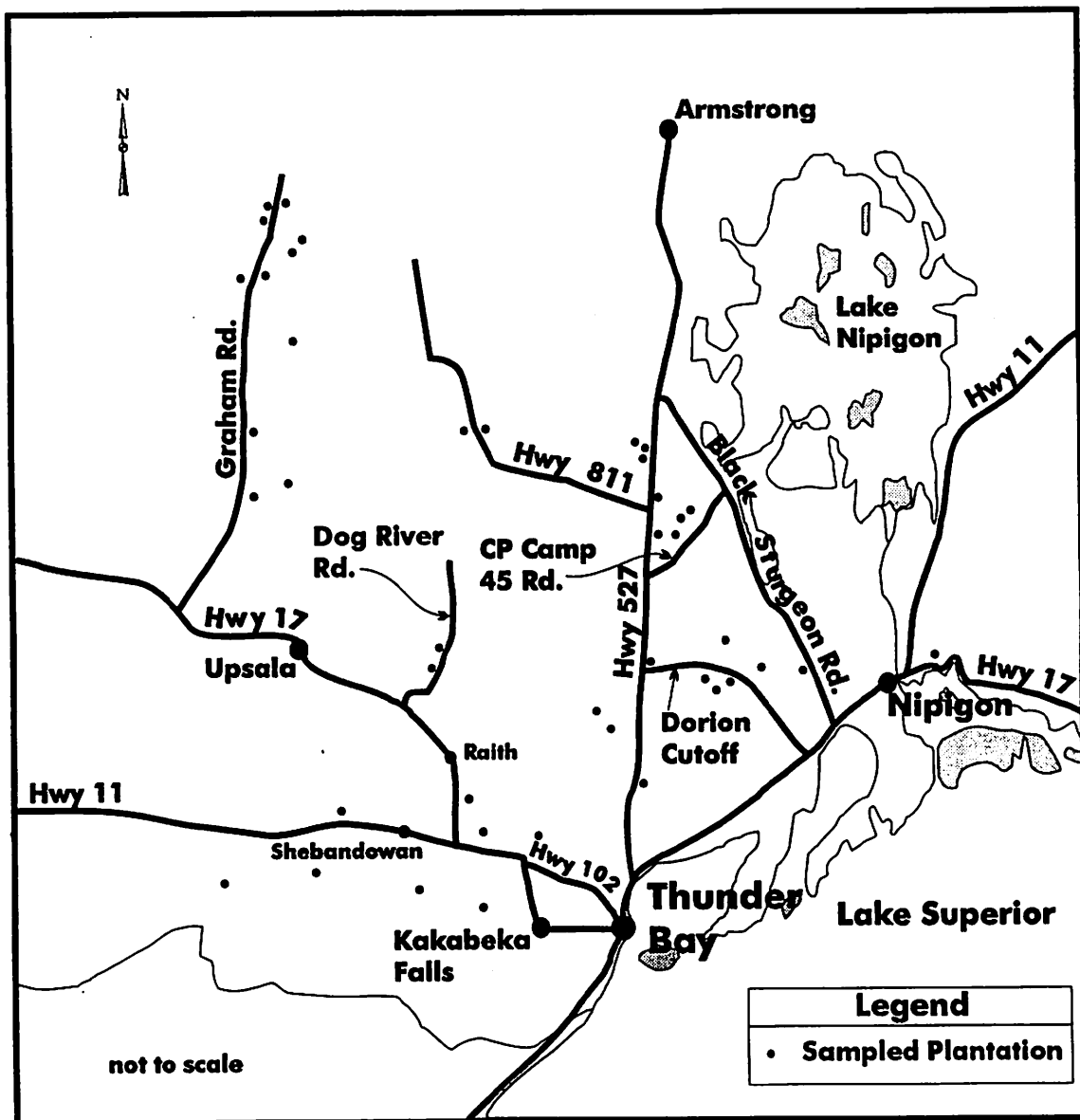


Figure 2. Location of sampled black spruce plantations in northwestern Ontario.

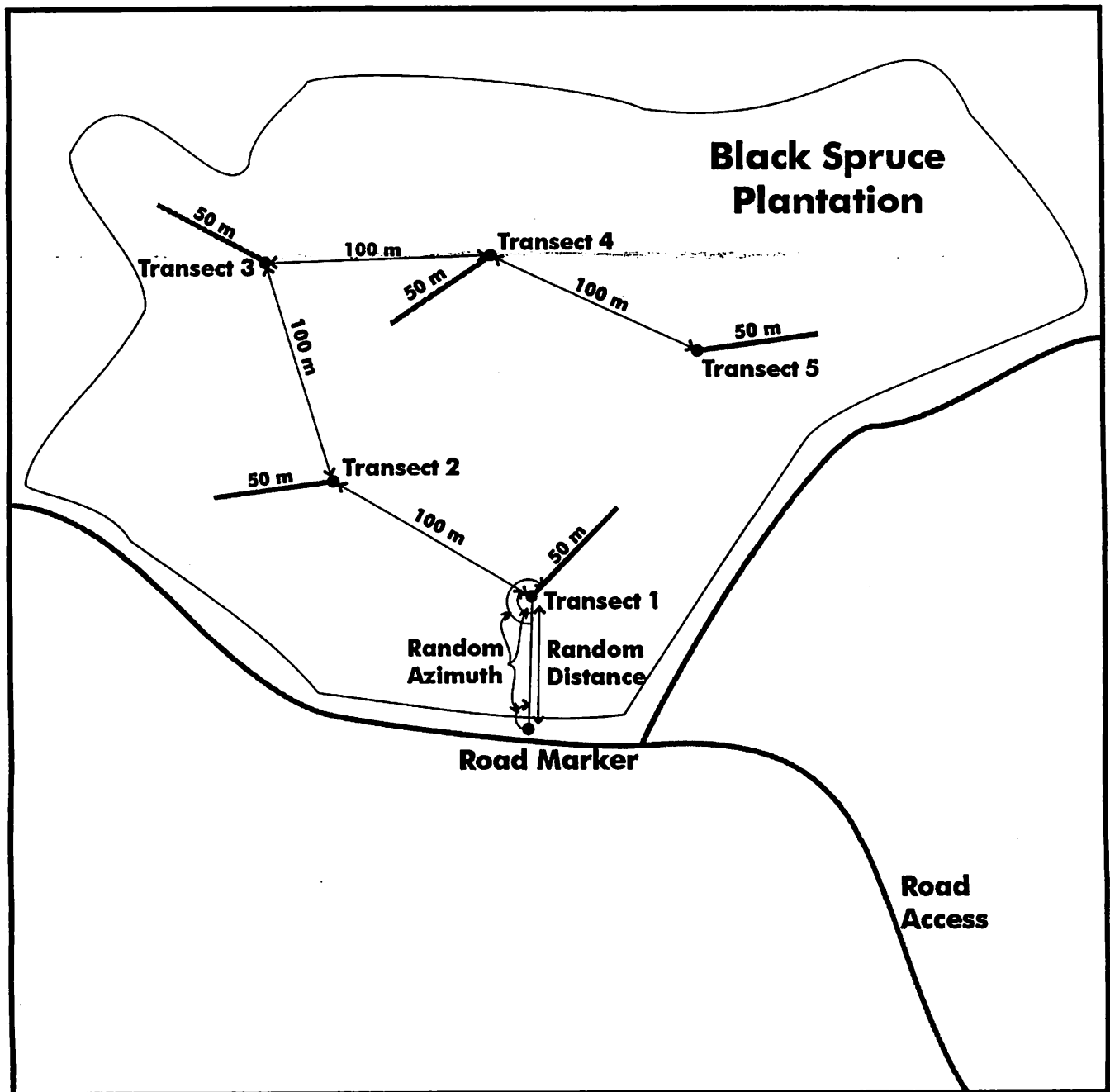


Figure 3. Example of the methodology used to sample the plantations for Armillaria root rot.

Table 1. Variable parameters evaluated for the development of the non linear regression model.

Dependent Variable	Independent Variables	
<i>Armillaria</i> Infection Level	D1, D2, D3, D4	Dummy Variables for FEC Treatment Unit D1-TU B, D2-TU C, D3-TU D, D4-TU E
	Moisture Regime	ordinal scale (-1, 0, 1, 2, 3, 4)
	D9	Dummy Variable for Stock Type 1 - Bareroot, 0 - Paperpot
	Sand, Clay	Percent Sand and Clay in the C-horizon
	Competition Index	Average for each plantation
	Herbs	Average percent ground cover of herbs per plantation
	MdSand, MdClay	Median value from the 5 transects of percent sand and clay in the A-horizon.
	Soil Nutrient Levels	Median values from the 5 transects for Nitrogen, Phosphorus, Potassium, Calcium, Magnesium, Iron, Copper, Manganese, Zinc, Aluminum and Sodium, pH as Hydrogen ion concentration, and Cation Exchange Capacity
	Stumps	Total Number of Stumps Total Basal Area of Stumps Total Number of Infected Stumps Total Basal Area of Infected Stumps

Table 2. Nonlinear regression model expressing *Armillaria* infection level as a function of tree age.

Variable	Regression Equation	MSE	R ²
<i>Armillaria</i> Infection Level	$Arm = 100 * (1 - e^{(-0.00585 * age)})^{0.700077}$	51.30	0.7777

Table 3. Nonlinear regression model expressing the adjusted *Armillaria* infection level as a function of the environmental variables and coefficient estimates, standard errors and 95 percent confidence limits.

Variable	Regression Equation	MSE	R ²		
Model with Phosphorus					
Adjusted <i>Armillaria</i> infection level	Adjarm= $\frac{e^{(\alpha)}}{1 - e^{(\alpha)}}$ where, alpha=(b ₀ +b ₁ *(D1)+b ₂ *(D3)+b ₃ *(D9)+b ₄ *(Clay)+b ₅ *(Total BA of Stumps)+b ₆ *(MdP))	0.0026	0.9402		
Coefficient	Estimate	Units	Asymptotic Std. Error	Asymptotic 95percent Confidence Limits	
				Lower	Upper
b ₀ (Constant)	-1.9703519		0.2562504	-2.4916938	-1.4490100
b ₁ (D1 (TUB))	-0.4719250	1- TU B 0 - all others	0.1810115	-0.8401933	-0.1036567
b ₂ (D3 (TUD))	-0.2023940	1- TU D 0 - all others	0.1487390	-0.5050038	0.1002158
b ₃ (D9 (Stock Type))	0.4191204	1 - bareroot 0 - paperpot	0.1214188	0.1720937	0.6661471
b ₄ (Clay)	-1.720660	percent	0.6536149	-3.0618468	-0.4022851
b ₅ (Total Basal Area of Stumps)	0.1451244	m ² /ha	0.0630260	0.0168978	0.2733510
b ₆ (Phosphorus Level)	0.0306317	ppm	0.0179864	-0.0059617	0.0672252
Model without Phosphorus					
Adjusted <i>Armillaria</i> infection level	Adjarm= $\frac{e^{(\alpha)}}{1-e^{(\alpha)}}$ where, alpha=(-1.69-0.50*(D1)-0.26*(D3)+0.39*(D9)-1.68*(Clay)+0.11*(Total BA of Stumps))			0.0027	0.9353

Anova Table for Model with Phosphorus

Source	DF	Sum of Squares	Mean Square	Prob>F
Regression	7	1.3512767329	0.1930381899	0.0001
Residual	33	0.0859409352	0.0026042708	
Total	40	1.4372082645		

Anova Table for model without Phosphorus

Source	Df	Sum of Squares	Mean Square	Prob>F
Regression	6	1.3441888989	0.2240314832	0.0001
Residual	34	0.0930193656	0.0027358637	
Total	40	1.4372082645		

Table 4. Mean percentage of *Armillaria* infected black spruce trees within FEC Treatment Unit B,C,D,E and F (includes infected healthy, symptomatic, and dead trees).

FEC Treatment Unit	Mean	Standard Deviation	Low	High
B	7.24a ¹	5.23	1.86	13.36
C	15.52a	5.38	5.62	21.72
D	11.64a	8.84	0.84	21.73
E	13.14a	7.72	4.45	24.38
F	16.93a	8.11	6.11	31.65

¹ Means followed by the same letter are not significantly different at the $\alpha < 0.05$ percent level (Student-Newman-Keul test).

Table 5. Mean percentage of cumulative black spruce tree mortality caused by *Armillaria* for FEC Treatment Units B,C,D,E and F.

FEC Treatment Unit	Mean	Standard Deviation	Low	High
B	2.28a ¹	2.13	0.00	6.00
C	3.27ab	1.80	2.00	5.60
D	2.97ab	1.82	0.61	5.59
E	4.37ab	1.94	2.40	8.00
F	5.70b	2.37	2.60	9.98

1 Means followed by the same letter are not significantly different at the $\alpha < 0.05$ percent level (Student-Newman-Keul test).

Table 6. Mean percentage of symptomatic black spruce trees infected by *Armillaria* within FEC Treatment Units B,C,D,E and F.

FEC Treatment Unit	Mean	Standard Deviation	Low	High
B	0.66a ¹	0.74	0.00	2.00
C	0.88a	0.63	0.00	1.60
D	0.63a	0.67	0.20	2.20
E	0.83a	0.32	0.40	1.41
F	0.48a	0.43	0.00	1.20

¹ Means followed by the same letter are not significantly different at the $\alpha=0.05$ percent level (Student-Newman-Keul test).

Table 7. Mean percentage of aspen traplogs infected with *Armillaria* within FEC Treatment Units B,C,D,E and F.

FEC Treatment Unit	Mean	Standard Deviation	Low	High
B	73.72ab ¹	15.74	44	96
C	76.90a	10.82	56	92
D	76.65ab	17.08	40	92
E	49.46b	20.43	20	76
F	61.34ab	29.35	16	96

¹ Means followed by the same letter are not significantly different at the $\alpha=0.05$ percent level (Student-Newman-Keul test).

Table 8. Summary of the numbers, species composition, total basal area and *Armillaria* infected basal area of residual stumps within FEC Treatment Units B,C,D,E and F.

FEC Treatment Unit		Conifer			Hardwood			Total ¹		
		Number (#/ha)	Total Basal Area (m ² /ha)	Infected Basal Area (m ² /ha)	Number (#/ha)	Total Basal Area (m ² /ha)	Infected Basal Area (m ² /ha)	Number (#/ha)	Total Basal Area (m ² /ha)	Infected Basal Area (m ² /ha)
B	Mean	108.89b ²	5.70b	4.82b	191.11b	14.05b	10.79a	318.89a	21.06a	16.20a
	(std)	(103.13)	(6.38)	(6.48)	(141.12)	(11.50)	(9.88)	(174.46)	(13.19)	(12.50)
C	Mean	186.25b	9.21b	7.06b	156.25ab	11.56ab	10.37a	396.25a	24.95a	20.39a
	(std)	(180.98)	(9.34)	(7.18)	(144.02)	(10.64)	(9.60)	(199.28)	(12.54)	(9.81)
D	Mean	316.25ab	21.00a	18.94a	78.75ab	5.26ab	5.08a	442.50a	29.34a	26.34a
	(std)	(168.53)	(10.16)	(9.67)	(48.24)	(2.58)	(2.47)	(184.84)	(11.54)	(11.38)
E	Mean	435.71a	23.67a	19.34a	60.00ab	4.96ab	4.45a	502.86a	28.94a	23.88a
	(std)	(220.14)	(4.47)	(6.50)	(47.26)	(3.40)	(3.28)	(268.00)	(6.19)	(6.88)
F	Mean	416.25a	19.71a	15.70a	48.75a	4.18a	3.84a	467.50a	23.94a	19.54a
	(std)	(217.78)	(8.83)	(8.50)	(64.46)	(7.64)	(7.56)	(194.50)	(7.81)	(9.14)

¹ Totals also include those stumps for which conifer or hardwood could not be determined.

² Means (within columns) followed by the same letter are not significantly different at the $\alpha < 0.05$ percent level (Student -Newman-Keul test).

Table 9. Summary of the data on the occurrence of *Armillaria* infections in healthy (H) and symptomatic (S) black spruce trees within FEC Treatment Units B,C,D,E and F.

FEC TU	Health	Infected with <i>Armillaria</i>	Age (yrs)	Ht (m)	Diameter @ 10 cm (cm)	Relative Shoot Growth	Colour Code
B	H	-	10.00	1.62	3.00	124.35	0.135
B	H	+	10.00	1.43	2.58	107.32	0.125
B	S	-	10.00	1.39	2.49	66.13	0.727
B	S	+	10.00	1.46	2.68	63.42	1.117
C	H	-	9.88	1.70	3.10	113.25	0.018
C	H	+	9.88	1.99	3.45	110.54	0.073
C	S	-	9.88	1.13	1.87	58.64	0.425
C	S	+	9.88	1.32	2.74	62.25	1.000
D	H	-	8.38	1.34	2.59	135.03	0.014
D	H	+	8.38	1.54	3.15	134.41	0.000
D	S	-	8.38	1.42	2.73	70.56	0.333
D	S	+	8.38	1.34	2.55	89.72	0.554
E	H	-	9.43	1.66	3.01	112.39	0.000
E	H	+	9.43	2.07	3.70	118.74	0.000
E	S	-	9.43	1.51	2.55	59.01	0.375
E	S	+	9.43	1.66	2.97	60.92	0.958
F	H	-	9.50	1.64	2.79	119.45	0.014
F	H	+	9.50	1.66	2.91	111.33	0.000
F	S	-	9.50	1.41	2.45	67.66	0.238
F	S	+	9.50	1.46	2.73	68.55	0.821

Colour codes: 0 - healthy; 1 - slightly chlorotic; 2 - very chlorotic