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Peter G. Mika, James A. Moore, and John D. Mandzak

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N and K fertilization affect ponderosa pine mortality

Corresponding author:

Peter G. Mika
Department of Forest Resources
University of Idaho
Moscow, Idaho 83843
USA

Telephone: +1-208-885-7205
Fax: +1-208-885-6226
E-mail: fcoop@idui1.csrv.uidaho.edu

Beetle-caused mortality in ponderosa pine: induced by nitrogen fertilization but prevented by potassium amendment

Peter G. Mika[1], James A. Moore[1], and John D. Mandzak[2]

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Dendroctonus ponderosae, mountain pine beetle, *Pinus ponderosa*

Abstract

In 1987 six fertilizer trials were established in ponderosa pine stands in western Montana, USA to test if K amendments to N fertilizers could ameliorate increases in tree mortality associated with N fertilization. Treatments were no fertilizer, 225 kg ha^{-1} of N, or 225 kg ha^{-1} of both N and K. Foliage samples were collected and analyzed for nutrients one year following treatment and tree heights and diameters were measured at the time of and four years after treatment.

Analysis of covariance results showed that fertilization with N alone produced a negative net volume response, but plots receiving both N and K responded positively, producing a highly significant K effect. Treatment differences resulted from heavy tree mortality caused by mountain pine beetle occurring on N treated plots, but not on N+K treated plots. Regression of net volume response on foliar nutrient levels indicated that negative response (beetle mortality) occurred in stands having high initial foliar N concentrations and low K:N ratios. When fertilized with N+K, these stands showed similar net response as all other stands. Fertilization with N alone appears to have made these stands more susceptible to bark beetle mortality, but addition of K to the fertilizer mix

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[1] Dept. of Forest Resources, University of Idaho, Moscow, Idaho 83843, USA

[2] Champion Timberlands, Milltown, Montana 59851, USA

prevents this increase in mortality and allows the stands to respond positively to N additions.

Introduction

In 1980 a group of forestry organizations formed the Intermountain Forest Tree Nutrition Cooperative (IFTNC) to study forest tree nutrition in the intermountain region of the Pacific Northwest, USA. Early IFTNC results from studies of Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco) had shown that nitrogen (N) levels were generally inadequate throughout the region (Mika and Moore 1991) and that positive gross volume response occurred when N fertilizer was applied (Moore *et al.* 1991). However, trees on some sites showed no increased growth 6 years after N fertilization and higher N application rates did not consistently produce higher response. Average mortality rates also appeared to increase with N fertilization (Mika *et al.* 1992); wind and snow breakage and root rot mortality were higher on N treated plots in certain areas.

Analysis of tree nutrient status indicated that tree potassium (K) status was associated with growth response to N fertilization (Mika and Moore 1991). For sites where pretreatment foliar K levels were low, response to N fertilization was reduced and higher rates of N fertilization produced less response. Tree mortality appeared to be increased by N fertilization on such sites, particularly where N rates were high. Across all sites, declines in net growth following N fertilization were associated with decreases in foliar K levels.

Based on these results we concluded that a number of sites in the region lacked sufficient K to allow the maximum expression of tree growth, a condition normally masked by lack of sufficient N. This also led to the hypothesis that, when fertilizing with N, addition of K could prevent some of the negative N fertilizer effects we encountered. To test this, the IFTNC subsequently established a series of 6 N and K fertilizer trials in ponderosa pine (*Pinus ponderosa* Dougl.) in northwestern Montana. In this paper we present evidence that K amendments to N fertilizers prevented mortality associated with N treated plots, thereby increasing net volume response to fertilization.

Materials and Methods

In 1987 the IFTNC established 6 fertilizer trials in northwest Montana, a mountainous region shaped by continental and alpine glaciation. Major formations rise to elevations of 3000 meters and support extensive forests. Precambrian Belt Series metasediments, mostly quartzite and argillite, dominate the surface geology of the region, although alluvial deposits from stream or glacial action are found in most valleys. The region has an inland climate influenced by moist air from the north Pacific Ocean, producing mild, cloudy weather for much of the year. Precipitation, generally snow, falls mostly from November to June while summers are droughty (Pfister *et al.* 1977).

The fertilizer trials, termed installations, were located in second-growth, even-aged, managed ponderosa pine stands; stand age ranged from 33 to 98 years. Stands were either previously thinned or naturally well-spaced; stand basal area ranged from 19 to 33 m^2 ha^{-1}. The stands are dominated by ponderosa pine, but other species contributing substantial basal area include Douglas-fir and western larch (*Larix occidentalis* Nutt.). Two installations were located on valley fill soils--ancient tertiary mixes of clay and rock. Another pair of installations were situated on colluvial material dominated by Belt Series metasediments.

The final pair were located on alluvial deposits resulting from Pleistocene lake beds.

An installation consists of 6 rectangular plots 0.04 ha in size, each containing at least ten ponderosa pine sample trees. Plots were selected to minimize among-plot variation in terrain, vegetation composition, tree stocking, and tree size; within each installation, plots were blocked into 2 groups of 3 plots based on similarity. Three fertilizer treatments--a control, 225 kg N ha^{-1}, and 225 kg N + 225 kg K ha^{-1} --were randomly assigned to the plots within each block. Nitrogen, as urea, and K, as murate of potash (KCl), were applied in the late fall, utilizing hand-held spreaders. To minimize edge effects, a treated buffer strip surrounds all fertilized plots.

All live plot trees were tagged and measured for heights and diameters at the time of treatment and remeasured 4 years after treatment. Any incidence of damage or mortality was noted. Tree volumes were calculated using regional species-specific volume equations (Wykoff *et al.* 1982). Basal areas and total volumes were summed over all trees to obtain plot totals.

One year after treatment, dormant season foliage samples were obtained from two dominant or co-dominant ponderosa pine trees on each plot (12 per installation, 72 total). Current season foliage was collected from the third whorl from the top of each tree by climbing. Foliage was processed and analyzed for content of N, P, K, Ca, Mg, Mn, Zn, Fe, B, and Cu using procedures described by Mika and Moore (1991).

Fertilizer effects on total plot tree growth were estimated using a randomized block analysis of covariance model. The particular model fit was (after Federer, 1955):

$$Y_{ijk} = \mu + I_i + B_{j(i)} + F_k + \beta X_{ijk} + e_{ijk} \tag{1}$$

where Y_{ijk} is the 4-year growth for the plot (ie. the k^{th} fertilizer treatment of the j^{th} block within the i^{th} installation), μ is the overall mean effect, I_i is a random effect due to the i^{th} installation, $B_{j(i)}$ is a random effect due to the j^{th} block within the i^{th} installation, F_k is the effect due to the k^{th} fertilizer treatment, X_{ijk} is the basal area per ha at the start of the experiment for the plot, β is the coefficient for the regression of growth on initial basal area, and e_{ijk} is a random error effect.

The regression coefficient obtained by fitting Equation (1) was used to adjust plot growth rates for within-installation differences in initial basal area per ha. Growth response to fertilization was then calculated by subtracting adjusted growth on control plots from similar growth on fertilized plots. These adjusted fertilizer response rates were used in subsequent analysis. Standard regression techniques were employed to examine relationships between fertilizer response and foliar nutrient levels. Parameter estimates and adjusted means were obtained using a general linear models procedure (SAS Institute Inc., 1985).

Results

Analysis of gross growth (accretion) data for the 4 years following treatment (Table 1) shows that fertilization has a significant effect ($p=0.0115$) on tree volume growth. Estimates of gross volume growth for the various fertilizer treatment have been adjusted to a common initial basal area of 27 m^2 ha^{-1} using Equation (1). The table also includes estimates of differences between treatments and significance levels for tests that those differences are zero. The difference between N fertilized and control plots shows the growth response to N fertilization, while the difference between the N only and N+K treatments represents the effect of K additions.

As expected, N fertilized trees grew significantly more ($p=0.0001$) on the average than unfertilized trees: growth increased by 4.8 m^3 ha^{-1}, an 11.6 % increase over control plot growth rates. Plots treated with N+K grew even more (7.56 m^3 ha^{-1}), but the increase over the N alone treatment (2.76 m^3 ha^{-1}) was not significant ($p=0.2542$).

Similar results for net volume growth are shown in Table 2. Overall variation in growth is larger; the total sum of squares shows a 28 % increase over that for gross growth. The pattern of response is much different: N alone treatments show a negative, non-significant response of -2.58 m^3 ha^{-1} (-6.3 % of the control net growth rate) while N+K plots show a large, marginally-significant response ($p=0.1234$) of 7.87 m^3 ha^{-1}. In this case the K amendment resulted in a large, highly-significant ($p=0.0505$), additional response of 10.45 m^3 ha^{-1}.

This large K effect can be better understood by looking at the cumulative frequency distribution of net volume response presented in Figure 1. The horizontal axis shows values of 4 year net volume response (difference between treated and control plots) while the vertical axis shows the proportion of stands responding at a particular value or less. While all stands showed positive growth response when fertilized with N+K, half of the installations showed negative response to N alone. These negative responders are installations where mortality was higher on the N-treated plots than on the controls. As seen in Figure 2, nearly all mortality was caused by mountain pine beetle (*Dendroctonus ponderosae* Hopkins). While mortality was fairly high on N plots, no bark beetle mortality occurred when N and K were both applied, despite the close proximity of all the plots.

Trees on those plots only treated with N are apparently more susceptible to bark beetle attack.

Regression of adjusted net volume response obtained from equation (1) on control plot foliar nutrient status revealed that response was related to both foliar N concentration and K:N ratios, but differed for the fertilizer treatments. The relationship of response to foliar nutrient level for the two treatments is depicted in Figure 3: the solid line represents the least-squares fit for plots treated with N only, while the dotted line shows the regression for N+K treated plots.

For foliar N concentration, the model shown in Figure 3a was highly significant ($p=0.038$) and accounted for 63 % of the variation in net volume response. The slope of the relationship differed significantly between the two fertilizer treatment ($p=0.0305$). For plots treated only with N, net volume response declined as N concentration of the control plots increased. Large volume losses occurred on sites where N levels were already high. However, when treated with N+K, such sites responded to the same extent as all other sites; the slope of the relationship for N+K treatments is not significantly different from 0 ($p=0.4607$).

The model for foliar K:N ratio shown in Figure 3b was also significant ($p=0.0681$) and accounted for 57 % of the variation in net volume response. Again, slopes differed for the two treatments ($p=0.0549$). Net volume response increased as the K:N ratio of the control plots increased when only N was applied. Large volume losses were confined to those installation where control plots had low K:N ratios. When K was also applied, volume loss did not occur on those sites. Again the slope of the relationship for N+K treated plots was not significantly different than 0 (p=0.5239).

Discussion

We have found evidence that, on some sites in northwest Montana, addition of N through fertilization can lead to increased ponderosa pine mortality from mountain pine beetle. An induced K deficiency is implicated, as addition of K prevented such mortality. Trees on these sites had foliage with fairly high concentrations of N and low ratios of K to N; addition of more N to these sites could easily produce conditions of nutrient imbalance within the trees. While we do not know the exact mechanism by which lack of K produces trees more susceptible to mountain pine beetle attack, combining the existing knowledge about tree resistance to bark beetles with information on the role of K in tree nutrition can give us some good clues.

Unlike most insects that feed on plants, bark beetles need to kill their host in order to successfully reproduce. They are assisted by their mutualistic relationship with microbial phytopathogens. The tree, when attacked, must combat both the insect and its fungal allies; it attempts to do this by isolating the insect and its fungal symbionts within a lesion of dead cells. This process, known as a secondary, or hypersensitive, response to bark beetle attack, is known to occur in all conifers. The process involves a series of activities: local autolysis of parenchyma cells, traumatic resin duct formation, and secondary resin production. The end result is phloem tissue unsuitable for either insect or fungus development (Raffa and Berryman 1982a).

Differences in tree resistance to bark beetle attack result from varying ability to produce secondary resins. Resin production in resistant trees is more rapid and has higher concentrations of monoterpenes (Wright *et al.* 1979, Raffa and Berryman 1982a) and other acetone-soluble compounds (Raffa and Berryman 1983), and increased proportions of more toxic/repellant monoterpenes like limonene and myrcene (Raffa and Berryman 1982b). The secondary response of lodgepole pine (*Pinus contorta* Dougl.) to mountain pine beetle attack is a rapid, localized, generalized reaction, involving an increased abundance of all monoterpenes produced by on-site synthesis and/or transport from adjacent tissue.

Tree vigor is known to influence bark beetle resistance, with trees under various types of stress (disease, crowding, artificial stress) showing increased susceptibility to bark beetle attack. It is thought that stress alters the pattern of tree enzyme activation/synthesis in response to attack (Raffa and Berryman 1982b). The response reaction is energy demanding, switching acetyl-coenzyme A from the Krebs cycle to the mevalonic acid pathway; each molecule of monoterpene produced costs 90 ATP molecules. Amounts of sugars and starches in the inner bark are positively correlated with resin monoterpene concentration, showing the importance of carbohydrate reserves for successful resistance (Wright *et al* 1979).

Potassium functions in a plant include control of water relations through stomatal control and regulation of turgor, energy relations including phosphorylation and photoreduction, starch synthesis, and translocation of carbohydrates, enzyme activation, and nitrogen assimilation and protein synthesis (Mengel and Kirkby 1980, Marschner 1986). Given such a broad role in plant functioning, the likelihood of K impact on plant health is high; in fact, the importance of proper levels of K for plant resistance to insects and disease is well documented. Huber and Arny (1985), in their review of K interactions with disease, state that the role of K as a mobile regulator of enzyme activity involve it in most cellular functions influencing disease severity. Accumulation of inhibitory compounds around infection sites is dependent on the level of K; high K levels promote rapid wound healing and accumulation of fungitoxic compounds around wounds while, at low K levels, compounds with fungicidal properties are rapidly broken down.

Given the important roles of K in the formation and transport of carbohydrates and in enzyme activation, it is easy to see that K deficiency could reduce a tree's ability to produce secondary resins. The next step in our research will be to attempt to show that N and N+K fertilizer treatments do affect this hypersensitive reaction in ponderosa pine. To establish this, we will look at bole chemistry and secondary resin production on these installations. Additional trials will also be established in which bark beetles will be brought to the plots by using attractants; beetle population parameters will be measured to determine if tree resistance varies among treatments.

The nutrient budget of sites and a tree's internal nutrient balance may be altered in ways other than by direct nutrient amendments. Forest practices may remove or redistribute substantial amounts of biomass and, with that, significant amounts of nutrients. Atmospheric depositions may differentially increase or decrease nutrient availability. Events producing the kinds of imbalances observed in this study are likely to have similar consequences for tree health.

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Table 1. Analysis of covariance results for 4-year gross total volume growth ($m^3\ ha^{-1}$).

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Value	Significance Level
Corrected Total	35	7711.0			
Model	14	7049.9	503.6	16.00	0.0001
Installation	5	5394.2	1078.8	34.27	0.0001
Block (Installation)	6	434.3	72.4	2.30	0.0730
Initial Basal Area	1	870.9	870.9	27.66	0.0001
Treatment	2	350.6	175.3	5.57	0.0115
Error	21	661.1	31.5		

Treatment	Volume Growth	Treatment Effect $m^3\ ha^{-1}$	Treatment Effect % of Control	Significance Level
Control	41.49			
225 kg N	46.29	4.80	11.6	0.0001
225 kg N + 225 kg K	49.05	7.56	18.2	0.0001
K Effect		2.76		0.2542

Table 2. Analysis of covariance results for 4-year net total volume growth (m^3 ha^{-1}).

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Value	Significance Level
Corrected Total	35	9868.1			
Model	14	6840.2	488.6	3.39	0.0058
Installation	5	4146.0	829.2	5.75	0.0017
Block (Installation)	6	1748.7	291.4	2.02	0.1079
Initial Basal Area	1	257.3	257.3	1.78	0.1959
Treatment	2	688.3	344.1	2.39	0.1164
Error	21	3027.9	144.2		

Treatment	Volume Growth	Treatment Effect m^3 ha^{-1}	Treatment Effect % of Control	Significance Level
Control	40.92			
225 kg N	38.34	-2.58	-6.3	0.6149
225 kg N + 225 kg K	48.79	7.87	19.2	0.1234
K Effect		10.45		0.0505

Figures

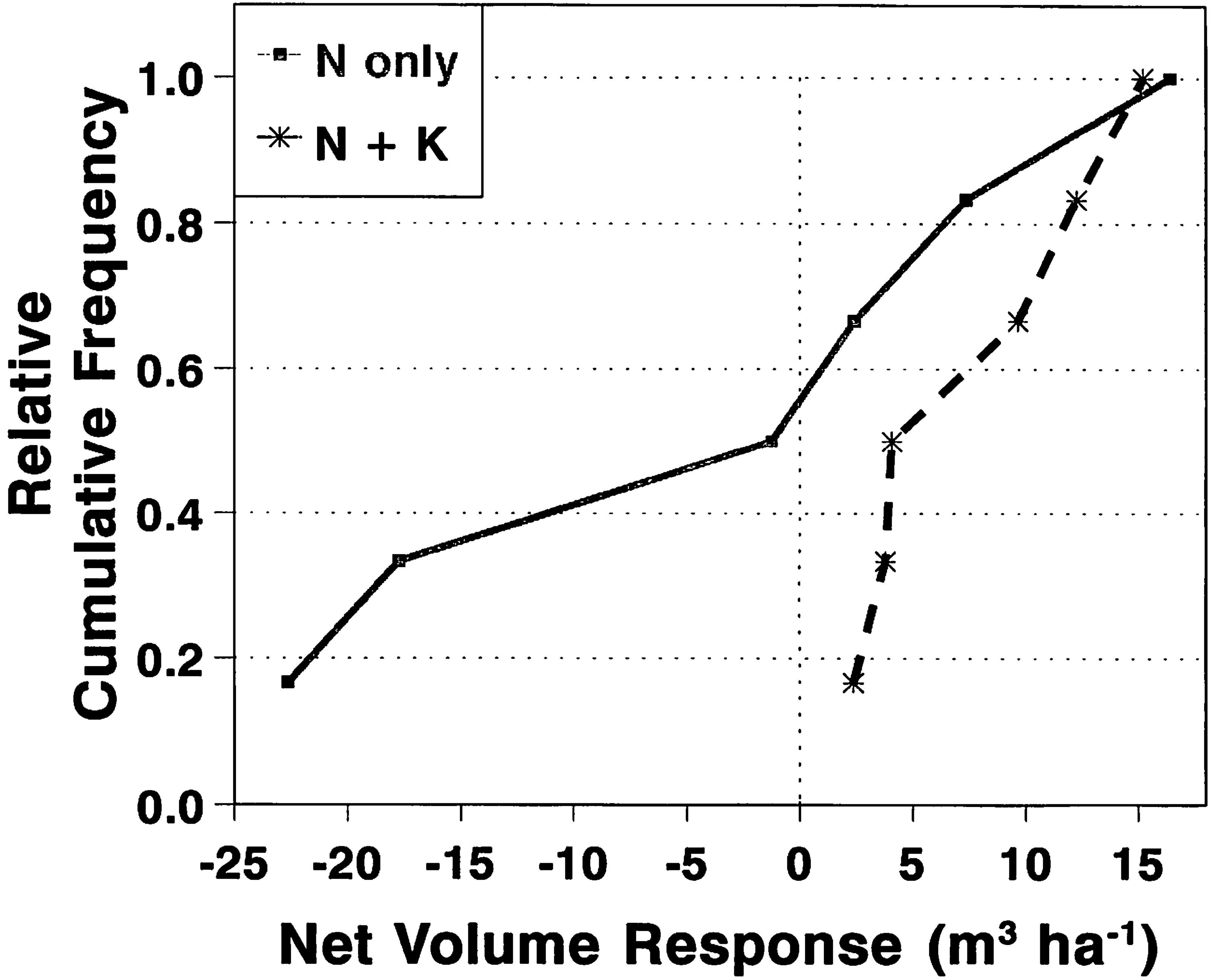
Figure 1. The cumulative frequency distribution for net volume response to N or N+K fertilization. The horizontal axis shows values of response obtained while the vertical axis indicates the proportion of all stands responding at that rate or less. The solid gray line shows the results for N fertilization while the dotted black lines shows N+K fertilization results.

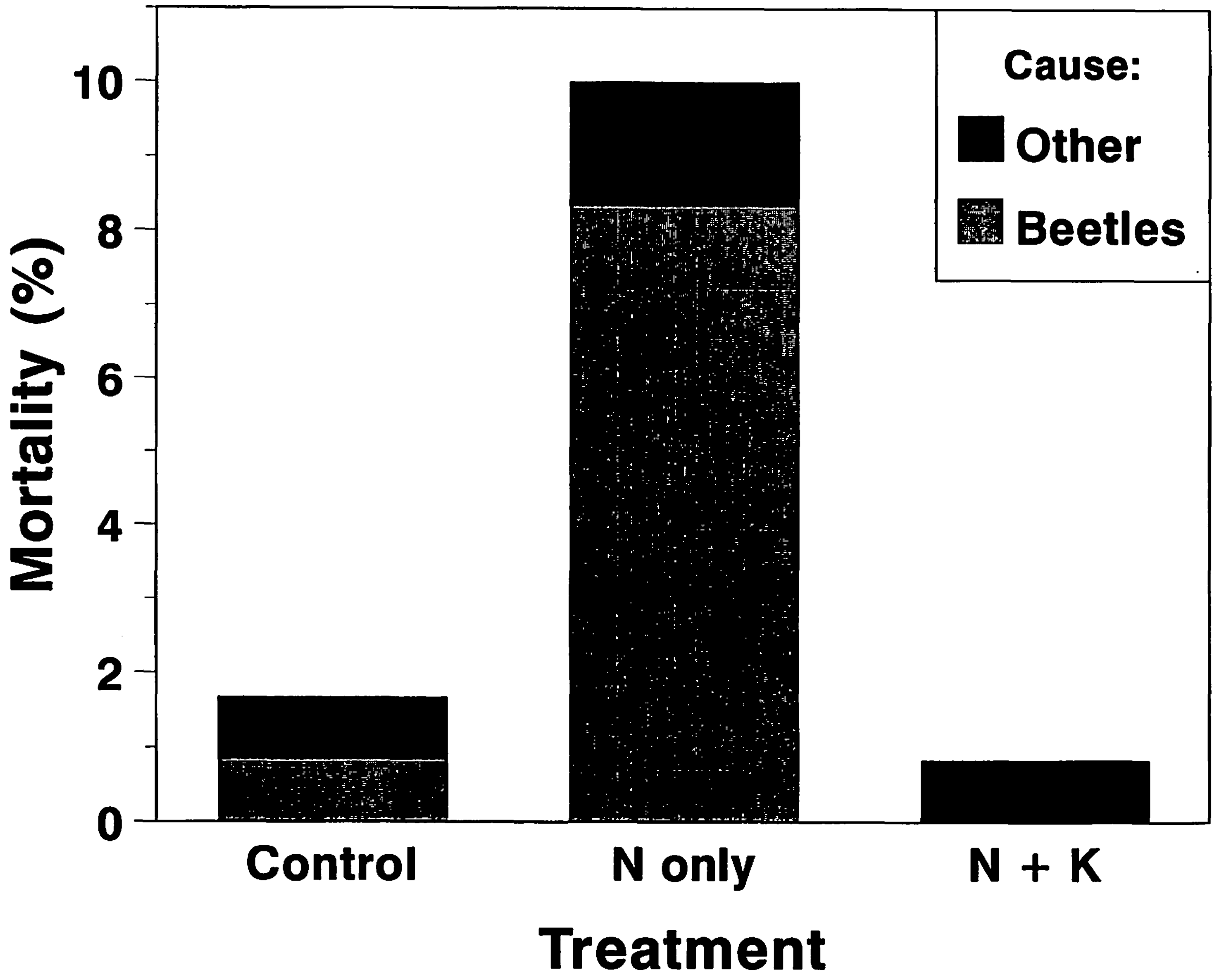
Figure 2. Percentage of trees dying in 4 years by fertilizer treatment and cause of mortality.

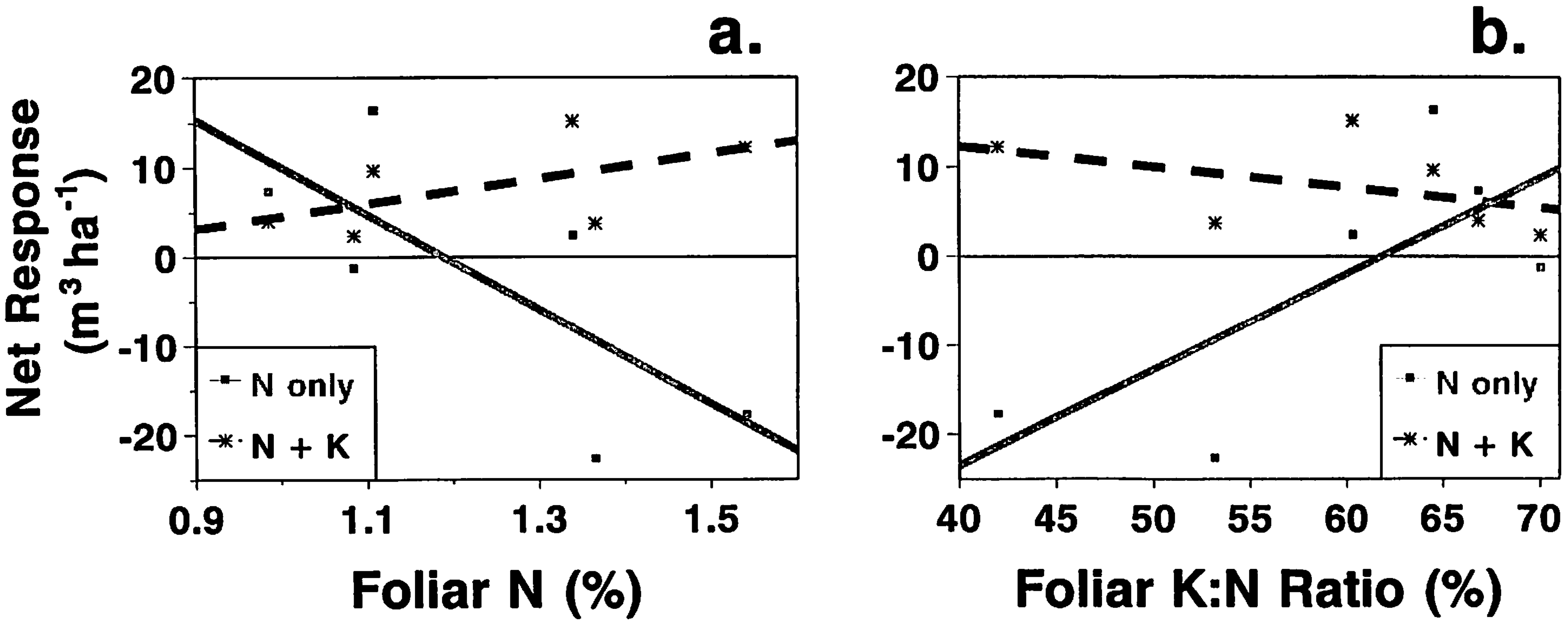
Figure 3. The relationship between foliar nutrient concentration on the control plots and net volume response to fertilizer treatment. The solid gray line shows the regression line while the gray squares indicate the actual data points for N fertilized plots. Similar results for N+K plots are shown by the dotted black line and black asterisks.

a. The relationship for foliar N concentration.

b. The relationship for foliar K:N ratio.


N only
N + K
Relative Cumulative Frequency
1.0
0.8
0.6
0.4
0.2
0.0
-25
-20
-15
-10
-5
0
5
10
15
Net Volume Response (m^3 ha^{-1})


Mortality (%)
0
2
4
6
8
10
Cause:
Other
Beetles
Control
N only
N + K
Treatment


a.
b.
Net Response
(m^3 ha^{-1})
20
10
0
-10
-20
0.9
1.1
1.3
1.5
Foliar N (%)
N only
N + K
40
45
50
55
60
65
70
Foliar K:N Ratio (%)