

Tree Species Effects on Soils: Implications for Global Change

Edited by

Dan Binkley and Oleg Menyailo

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IV. Earth and Environmental Sciences – Vol. 55

Tree Species Effects on Soils: Implications for Global Change

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Series IV: Earth and Environmental Sciences – Vol. 55

Tree Species Effects on Soils: Implications for Global Change

edited by

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Chapter 1

GAINING INSIGHTS ON THE EFFECTS OF TREE SPECIES ON SOILS

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INTRODUCTION

The interactions of trees and soils have fascinated scientists, farmers, and foresters for centuries. The success of trees depends strongly on the properties of the soils beneath them, as recognized by A.A. Nartov in the 17th Century (cited in Remezov and Pogrebnyak 1969):

“The properties of spruce and pine are such that 100 years are required for pine on dry soil, and for spruce on humid soil... However, pine growing on humid soil will hardly reach a height of 6 feet in this span of time... spruce cannot succeed on hard and dry hillocks or similar locations unless its roots, which spread far underground, will reach the moisture they require.”

By the early 20th Century the influence of trees on soil development was well recognized. G.F. Morozov noted (cited in Remezov and Pogrebnyak 1969):

“The idea that forest is an agency of soil formation was never really alien to forestry; the idea became more and more definite in the course of its development...foresters began using such expressions as “beech soil,” “oak soil,” etc., not merely in the sense of a soil suitable for the given species, but with emphasis on the idea that the soils are actually being influenced by the tree stand.”

By the late 20th Century, interests in the effects of tree species on soils had broadened to include ideas of sustainability of long-term soil fertility, responses to air pollution, and influences on understory vegetation diversity. Concerns about concentrations of trace gases that absorb infrared radiation and warm the atmosphere intensified interest in forest biogeochemistry, and the differences in trace gas fluxes from forests dominated by different species. The effects of changing climate on forest biogeochemistry may be moderated directly by the effects on species composition of forests (and the differences in biogeochemistry among species) rather than by the simple effect of temperature or moisture. For example, the rate of nitrous oxide production and methane consumption differed by 3-fold under the influence of different species in the Siberian afforestation experiment (Oleg and Hungate, this volume).

This volume presents a summary of ideas, data, and perspectives from a NATO Advanced Research Workshop held in Krasnoyarsk, Siberia (August 26-29, 2004) on the effects of tree species on soils, including implications for global changes. The chapters cover a broad range of projects; some deal with landscape-scale patterns across forested landscapes, and others deal with species planted in common garden settings. The experimental designs are equally diverse, with some scientists confident that the effect of species is far stronger than any pre-existing differences among soils in their plots. Other scientists used replicated designs that did not require this assumption. Our introductory chapter provides a context to help readers evaluate the strength of evidence in later chapters, and also highlights some of the key findings from our workshop.

UNRAVELING THE EFFECTS OF TREE SPECIES FROM OTHER SOIL-FORMING FACTORS

The scientific investigation of soils blossomed in the late 19th Century, with the leadership of Vasily V. Dokuchaev in Russia and Eugene W. Hilgard in the United States (Jenny 1961a). These scientists began to see soils as something more than geology or chemistry, emphasizing interactions among climate, geology, and biology:

“The still young discipline of these relations is of an exceptional inspiring scientific interest and meaning. Each year it makes greater and greater strides and conquests; gains daily more and more of active and energetic followers, eager to devote themselves to its study with the passionate love and enthusiasm of adepts.” (Dokuchaev 1898, quoted by Jenny 1961a)

At the end of the 19th Century, Dokuchaev (1951) summarized his view of soil formation in an equation:

$$S = f(\text{cl}, \text{o}, \text{p})t^{\circ}$$

where S = soil, cl = climate, o = organisms, p = geologic substrate, and t° is a measure of relative age (this version of the equation was related by Jenny 1961b). A similar equation was proposed by an American ecologist, Charles Shaw (1930), who was unaware of Dokuchaev's work:

$$S = M(C+V)^T+D$$

where S = soil, M = parent material, C = climate, V = vegetation, T= time and D = deposition or erosion. The most familiar form of a soil-forming equation is probably Hans Jenny's (1941):

$$S = f(\text{cl}, \text{o}, \text{r}, \text{p}, \text{t}, \dots)$$

where S = soil, cl = climate, o = organisms, r = topography, p = parent material, t = time, and "... " is a place holder for other factors that might later be determined to be important. All of these expressions provide a key variable for the effect of biological factors such as tree species.

Recognition of the potential effect of vegetation on soils was an important step, but a century of forest soil investigations leaves a great deal to be investigated in the next century. Earl Stone's (1975) classic summary of the state of knowledge on tree species effects on soils concluded that many beliefs were no better than myth; aside from the N-fixing species, he thought the evidence supporting generalizations was too weak to support confident interpretations. A body of evidence has accumulated since Stone's review to document that species dramatically affect soils (see reviews by Binkley 1995, Binkley and Giardina 1998, Augusto *et al.* 2002). The mythological themes remain strong; Sverdrup *et al.* (2002) claimed that the idea that tree species differ in their effects on mineral weathering is only myth, yet their rationale included no empirical evidence to support or refute their own claims. We remain far from our goal of a generalizable understanding about the magnitude of species effects, and how consistent these effects might be across soils types and along environmental gradients. We hope this volume is a notable step in spurring progress on these themes.

DESIGN OF STUDIES

The chapter by Zechmeister-Boltenstern and coauthors (this volume) examined rates of turnover of microbial N and C, as well as gas flux rates, in twelve types of natural forests. These forests span the range of forest types in Central Europe, and the differences among these forests relate to both the dominant tree species, and the environmental conditions at each site. These

confounding differences among sites were avoided in one study reported in the chapter by Cortina and Maestre (this volume), where the survival of *Pistacia* shrubs was mapped at a single site. However, the apparent within-site uniformity of the slope was disproven by the spatial pattern of shrub mortality; clusters of high mortality indicated that the slope was very non-uniform. The Siberian afforestation experiment described in several chapters tried to overcome within-site variations in soil properties by removing the 0-20 cm mineral soil, mixing it, and redistributing the soil across the site. Unfortunately, the yield of a wheat crop planted on the site revealed that within-site variation was still sizable (Shugalei, this volume). These limitations can be addressed by experimental designs that include replication of treatment; however, even designs with replicate plots may not meet the definition of experimental replication. Common-garden experiments that test only monoculture effects may not extrapolate well to diverse forests; Roy et al. (this volume) use a creative approach of examining soil influences of species near the boundaries of monoculture plots, relating soil features to the chemistry of litter inputs rather than simply to species names.

DEFINING REPLICATION

We may believe many things about the effects of trees on soils. For example, we might believe that decomposition of deciduous hardwood litter is more rapid than that of conifers. Beliefs may be true, but they need to be tested with challenging experiments before strong confidence is warranted. The decomposition belief could be tested in a beech forest using litterbags filled with beech and spruce litter. If the beech litter decomposed more quickly than the spruce litter, the confidence warranted in the belief would be increased – but not by very much because of a long list of unexamined assumptions. Would the same results have developed if the bags were placed on a spruce soil rather than a beech soil? Did the results depend on the chosen mesh size for the litterbags? Not all spruce needles are alike; would the use of leaves from another site (with higher nutrient supply) have shown different results? Beech and spruce may not be representative of the full range of hardwood and conifer species, so the pattern in this experiment provides no degrees of freedom for a statistical inference about the classes of species. And in any case, could a difference in decomposition rates of fresh litter really tell us very much about the longer-term differences in soils that would develop as humified material accumulated?

Classical experimental design in a chemistry laboratory would test ideas about chemical reactions by holding all variables constant (including temperature, air pressure, volume, and procedures) except for the variables involved in the hypothesis test. The experiment may involve testing 4 concentrations of a chemical, and the scientist might do 4 replications of each to be sure the observed results are consistent and repeatable. This general

design has been adopted in many forestry studies (and strongly advocated, e.g. Mead *et al.*, 1990), often without realization of the weakness that comes from holding all other variables constant. In many cases, we need answers that apply across diverse sites, and testing the effects of treatments in a replicated study within a single site cannot provide these answers.

Confidence in ideas about the effects of species needs to be developed from a clear context that defines the population of interest (in a statistical sense), and experimental designs that draw representatively from the population. In the case of decomposition of hardwood and conifer litters, the populations of all hardwood species and all conifer species could not be represented by only beech and spruce, and the population of soil and forest types could not be represented by a single beech forest.

The definition of “replication” needs to be considered carefully in designing an experiment, and in the interpretation of results. Statistical analyses rely on carefully designed replication to account for the influence of factors (such as prior differences in soils) other than the factor of interest (such as tree species effects).

We illustrate some of these key points with a case study that contrasted the N content of soils under *Eucalyptus saligna* and N-fixing *Falcataria moluccana* (Garcia-Montiel and Binkley 1998). A comparison of two adjacent plots indicated that the N-fixer increased soil N by $36 \text{ g m}^{-2} \text{ yr}^{-1}$ over a 12-year period (Figure 1). However, the random assignment of species to each of these plots could have placed the N-fixing species in a plot that already had higher soil N initially, so any prior difference would confound the estimate of N accretion. These plots were relatively small ($30 \times 30 \text{ m}$), and perhaps larger plots would reduce the likelihood of the species overlying prior differences in the soil. Alternatively, the soils could have been removed, mixed, and reapplied to the landscape as in the Siberian afforestation experiment.

To account for the possible prior variation in initial soil conditions, or in the influence of initial conditions on N fixation and accretion, this study in Hawaii was replicated in 4 blocks. With 4 replicate plots of each species, it would be unlikely that all 4 replicates of one species would fall on higher N soils than the 4 replicates of the other species. Across all 4 replicates, the average rate of N accretion was $18 \text{ g m}^{-2} \text{ yr}^{-1}$, just half of the rate indicated by the single pair of plots.

Even this replicated design has limitations for making inferences about N accretion under *Falcataria*; no amount of replication (or prior soil mixing to increase uniformity) within a single site can provide degrees of freedom for testing a hypothesis about a population of sites. Even with high confidence in the species effects at this site, we don't know if the species effect would be consistent on similar soils at other sites. Fortunately this experiment was replicated at a total of 3 sites (with 4 replicate blocks at each site), and across all these plots the average rate of N accretion was just $12 \text{ g m}^{-2} \text{ yr}^{-1}$. The strength of this experimental design is rare in studies that have examined the

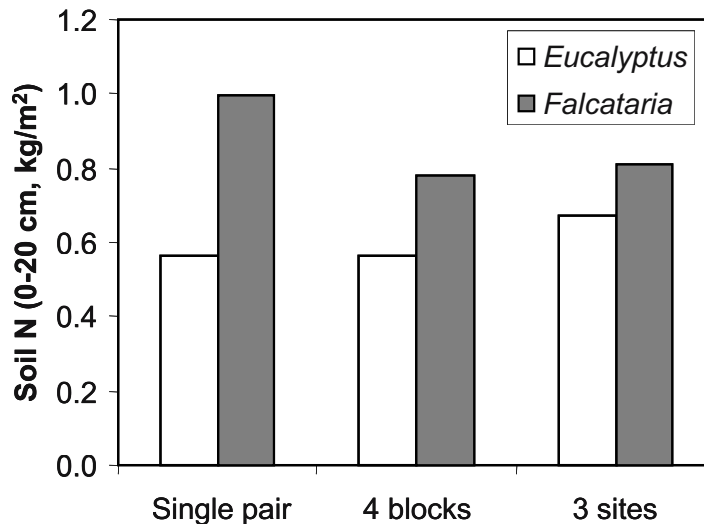


Figure 1. The difference in soil N beneath *Eucalyptus saligna* and *Falcataria moluccana* indicated an annual rate of N accretion (over 12 years) of $36 \text{ g N ha}^{-1} \text{ yr}^{-1}$ when comparing a single pair of plots; $18 \text{ g N ha}^{-1} \text{ yr}^{-1}$ based on 4 blocks (with a pair of plots in each block) within one site; and $12 \text{ g N ha}^{-1} \text{ yr}^{-1}$ across 3 sites (with 4 blocks/site; from data of Garcia-Montiel and Binkley 1998).

effects of tree species on soils, but even this design was limited by the fact that the three replicate sites were all on the same soil series; we have no statistical basis for inferring the likely effect of *Falcataria* on any other type of soil (Figure 2).

The bottom line is that replication in statistics is based on the definition of the population of interest, and what comprises a representative sample of that population. If the population in the N-fixation study were defined as “these two plots,” then the first estimate of N accretion would be valid, because the entire population was assessed. If the population were defined as a 10-ha landscape, then the single pair of samples would represent a single sample, with no degrees of freedom to assess the variability across the 10 ha that would be unrelated to N fixation. The 4 replicate blocks provide degrees of freedom relative to the population of 10 ha, but nesting all 4 replicates within this single location gives no estimate of the variation that would be encountered on similar soils at other sites. Repeating the study on 3 sites provides an estimate of the variation among sites across the 10,000 ha of this Kaiwika soil series, but if the population of interest included other types of soils, even this design would be insufficient. If this study could afford a total of 12 pairs of plots (as it had 4 blocks at 3 sites), the most powerful design would have involved placing single pairs of plots (one *Eucalyptus*, one *Falcataria*) at 12 separate locations across the entire population of interest (see Stape *et al.* 2004 for a fertilization trial using this approach).

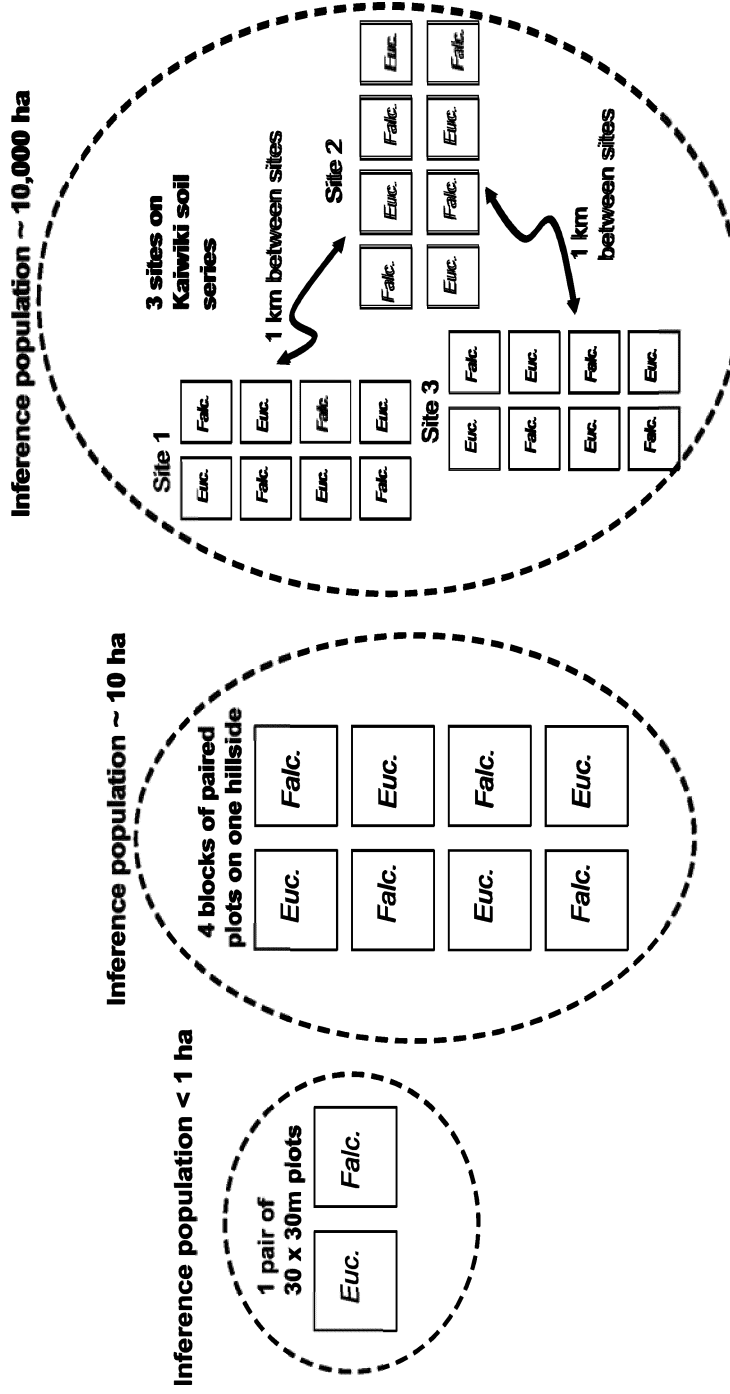


Figure 2. Diagram of experimental design for study in Figure 1, examining effects of *Eucalyptus* and N-fixing *Falcataria* on soils. A stronger design would have spread the 12 pairs of plots across a random set of locations on this single soil type (or even across soil types), giving a population of inference of 100 km² or more

Many forestry experiments use a classic replicated, randomized (sometimes blocked) design, with 3 or 4 replicates plots for each treatment (e.g., Mead *et al.* 1990). This design is powerful if the replicates (or blocks) are spread throughout the population of interest, but if they are clustered at a single location (and the population not even defined!), then any inference to the population is limited to non-statistical sorts. Non-statistical inferences may still be drawn, based on professional judgment about whether interactions across sites will be zero, linear, or non-linear, but these inferences are typically too weak to support important decisions.

In some cases, a broad question about the effects of a tree species can be examined by a “meta-analysis” that considers the consistency of effects across many studies. If all studies with N-fixing trees show strong increases in soil N, then we have high confidence that this effect is a general one that is not limited to a particular type of site. We may have enough case studies of N fixing species for this sort of analysis (see chapter in this volume), but meta-analyses have not yet been developed for other species. For example, Binkley and Giardina (1998) noted that 5 common-garden experiments found that Norway spruce acidified soils more strongly than other species, and that larch seemed to reduce soil acidity. Larch also significantly reduced soil acidity compared to most other coniferous and deciduous species at the Siberian afforestation experiment (Menyailo *et al.*, 2002). The need for further meta-analysis of common garden experiments is evident, especially if factors could be identified that accounted for some of the variation in results among studies. For more insight on limitations of designs commonly used in forest research, see Bennett and Adams (2004).

DETERMINING THE EFFECT OF TIME

We also note that the points raised above on spatial variation and replication also apply to testing hypotheses about changes over time. An experiment might compare the effects of beech and spruce on soil invertebrates, and how these effects change over a 20 year period. If sampling were limited only to the beginning and the end of the 20 year period, one could test whether the two periods differed, but 0 degrees of freedom for the effect of time would preclude a statistical inference about the effects of time. If the initial sampling occurred when the O horizon was moist, and the second sampling (20 years later) happened during a dry period, then the significant difference between samplings could result from moisture rather than time. If the sampling in time had been repeated at years 0, 5, 10, 15, and 20, then one could explicitly test for the effect of time, expecting that any variation in moisture content would represent “noise” (unexplained variance) that would not mask a strong effect of time.

In some cases, an evaluation of change over decades might focus on a soil property that shows very little variation among seasons or soil moisture

conditions. An evaluation of changes in the C content of a soil horizon over a 20 year period may be unreplicated in time, but scientists (and readers) may still be confident that the significant difference between the time periods was a result of the passage of time (and all the processes that happened over that period).

Statistical inferences provide us with “blind” evaluations of the probability that an observation may have happened at random; we are free to use other criteria (such as our confidence that soil C contents do not vary substantially within seasons) to gauge the confidence warranted in experimental results, as long as we are very clear about when we are using “blind” statistics, and when we are using other information to make an inference. We also note that the issues raised above apply to other factors in the development of forests and soils. For example, the use of a single genotype (or provenance) to represent a species provides no statistical basis for inferring the effects of other genotypes (or provenances) of the same species. We may be willing to infer that a single genotype is representative of the population of genotypes of the same species, but this inference is based on judgment rather than statistics.

EXPERIMENTAL LIMITATIONS

A dozen studies around the world have examined the effects of tree species on soils by planting species in common gardens. This is an elegant design that removes a broad range of factors that could confound the test of species’ effects. However, common garden designs typically include several important limitations. Many of them have been established on former agricultural soils, so the apparent effect of tree species develops from a very unnatural starting point. Former agricultural soils would typically have a legacy of prior fertilization, a dearth of seeds of typical understory species, and the absence of an O horizon. The species included in some common gardens may be unlikely to be found on the same soil type across forested landscapes, so the impacts on an unusual soil may not represent broad-scale impacts of each species.

The changes that develop over the time span of most individual research projects may not represent important, long-term changes in soils. We have too little information on the effects of tree species to chart the time course over which soils change. For example, soils may change more rapidly under white pine than under Norway spruce, but the “endpoint” conditions could be the same after enough time had passed.

We might also want to infer the mechanism behind the effects that tree species exert on soils, but even well-designed common garden experiments cannot test alternative ideas. For example, Son and Gower (1991) examined the effects of 5 tree species on annual net N mineralization in Wisconsin, USA. The species differed by more than 2.5 fold in N mineralization, and

76% of the variation in net N mineralization was explained by the ratio of lignin:N in aboveground litterfall (Figure 3). The evidence failed to refute the idea that lignin:N influences N supply, but it could not prove lignin:N was the driver. Indeed, the differences among species in N mineralization related even better with the total fungal biomass, with 89% of the variance accounted for (Scott 1998). The fungal biomass may or may not have been the key to the variation among species in N mineralization; the total biomass of bacteria showed a strong negative trend with fungal biomass (Figure 3), highlighting the risk of assigning special importance to any individual covariate. Indeed, the direct drivers of change beneath the tree species might be the soil community of microbes and animals; we know that soil animal communities differ strongly under the influence of tree species (see Bezkorovaynaya this volume, Elmer et al. 2004), but we know almost nothing about the implications of these changes for rates of biogeochemical cycling.

Some features of soils can be very dynamic, complicating any questions about the effect of tree species. In the Wisconsin common garden, which species showed the greatest N mineralization? The answer to this question depended on the time period of incubation; the ranking of species shifted dramatically across time periods (Table 1).

Issues of scale are also important in tree and soil studies. Long bridges span wide rivers, but lengthening bridges does not widen rivers. In soils, higher pH and base saturation may be associated across landscapes with greater growth rates of trees, but increasing pH and base saturation within a single site may not increase growth. Forest productivity increases across Scandinavia with increasing soil pH and base saturation and pH (Dahl *et al.* 1967, Lahti and Vaisanen 1987), but dozens of liming experiments have shown that raising pH within a single site does not increase growth in this region (Nihlgård and Popovic 1984, Popovic and Andersson 1984, Derome *et al.* 1986, Andrason 1988, Derome and Pätälä 1989). This apparent contradiction between within-site and across-landscape perspectives may relate to a positive correlation across landscapes in soil N supply and soil pH (Giesler *et al.* 1998), and changing pH within sites may or may not increase the supply of growth-limiting nitrogen.

ADVANCES IN METHODOLOGY, AND SURPRISES

Over the past 20 years, our ability to delve into soil processes has expanded dramatically. In the past, experiments on the influence of tree species were often limited to characterizations of one or more soil horizons, or in some cases to a nutrient budget of a whole stand (Bergkvist and Folkesson 1995). A lack of overall mass balance typically limited the confidence warranted by any particular component of these budgets. The Krasnoyarsk Workshop (and this book) highlighted several promising approaches for new investigations, as well as surprises. Dr. Phil Ineson presented information on

the stable isotopes of carbon in vegetation and worms in microcosms; the rapid appearance of the labeled C indicated that the worms must be feeding in part on plant roots and not just on plant detritus (which remained unlabelled in this short-term experiment). Santruckova (this volume) and Mukhortova (this volume) demonstrated the insights that could be developed by analyzing the kinetics of reaction rates in the laboratory and the field. Butterbach-Bahl and Kiese (this volume) demonstrated that variation in time may be as important as variation in space; the annual total flux of trace N gases depended on short-lived “spikes” in gas efflux. Intermittent sampling that missed these rare spikes would underestimate the efflux in a plot by several-fold, and catching these spikes would be fundamental to determining the influence of different species. Dr. Cindy Prescott discussed ideas about differences among species in preference for forms of nitrogen; the ericaceous shrub salal (*Gaultheria shallon*) was expected to prefer organic forms of N, but its utilization of ammonium and nitrate rivaled that of other species. In fact, molecular techniques demonstrated that salal shrubs formed mycorrhizal associations not only with ericoid mycorrhizae, but also with arbuscular and ectomycorrhizae.

THE CASE FOR EVIDENCE-BASED FOREST SCIENCE

As scientists, we benefit from a legacy of decades and centuries of development of science in dozens of fields, and this includes valuable approaches to conducting science. We suggest that forest science should embrace standards of evidence established for other scientific fields, and consider explicitly the level of confidence warranted in our ideas. One example of this approach is “evidence-based medicine,” which developed as a means for health practitioners to evaluate the confidence warranted in the value of medical treatments. Cochrane (1972) launched the idea that randomized controlled experiments are vital for assessing the effectiveness of medical treatments. Prior to this initiative, the efficacy of treatments was often judged with anecdotal evidence, or evidence from trials with poorly

Table 1. The ranking of species in relation to cumulative net N mineralization depended strongly on the time period of comparison (from Son and Gower 1991, Scott 1996).

Time period	Species ranking
Annual, in situ incubations	Norway spruce < red pine = red oak < white pine < European larch
0-20 days laboratory	Norway spruce < red oak < red pine < white pine < European larch
0-60 days laboratory	White pine < red pine < red oak < Norway spruce < European larch
0-387 days laboratory	White pine = red pine < European larch < Norway spruce < red oak

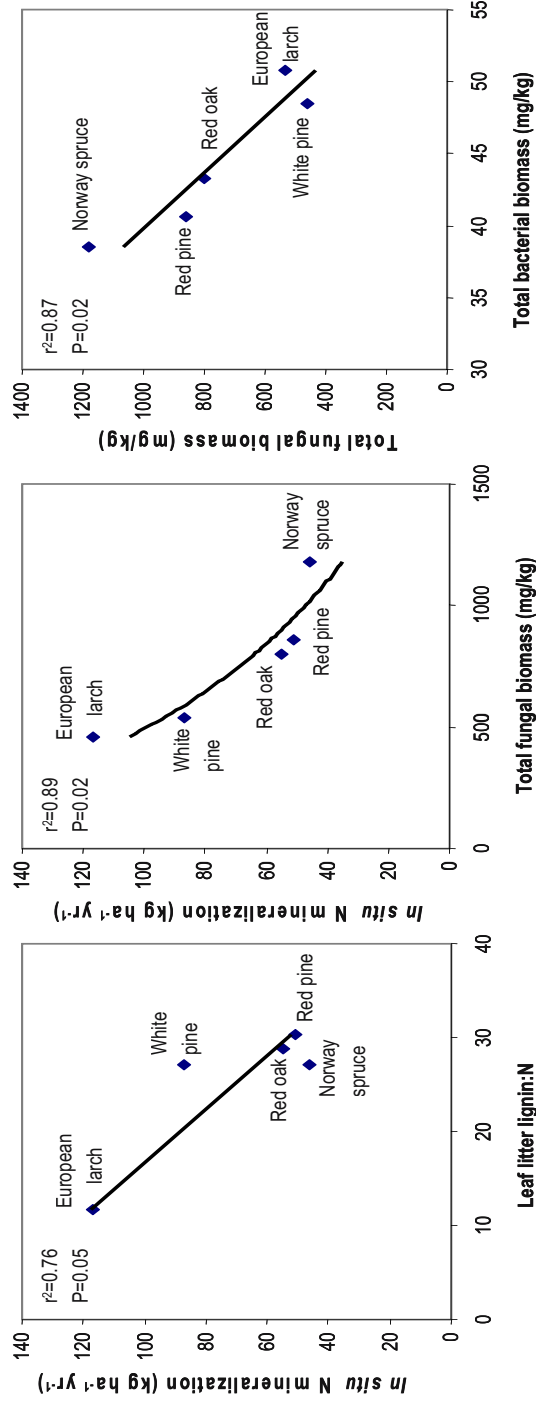


Figure 3. Annual net N mineralization in the field related well to the lignin:N of aboveground litterfall in a common garden experiment (left; Son and Gower 1991), but lignin:N may not have a causal effect on net N mineralization as evidenced by other patterns among these stands. Net N mineralization correlated strongly with fungal biomass (middle), and fungal biomass related well with bacterial biomass (Scott 1998). Simple correlations cannot be relied upon to test mechanistic hypotheses.

Table 2. A preliminary scheme for rating the confidence warranted in forestry experiments. Many forest studies (including those of species effects on soils) are type 3 or 4; few study designs support Level-1 or Level-2 confidence in applying results to forest landscapes.

Level	Type of evidence
1	Meta-analysis of several similar experiments, showing consistent effects
2a	Replicated experiment at several sites, with explicit extrapolation to the population of interest
2b	Replicated experiment at several sites, but no formal <i>a priori</i> plan for extrapolating to the population
3a	Experiment at a single site with replication of treatments
3b	Case studies across environmental gradients with potentially confounding spatial factors
4	Case studies, no replication of treatments within a single site
5	Expert opinion or inferences from expected first principles

controlled factors. Fletcher and Sackett (1979) took the next step and developed “levels of evidence” to rate the value of medical treatments. Formal rating systems are now standardized in medicine. (See: Oxford Centre for Evidence-Based Medicine <http://www.cebm.net/index.asp>, The Cochrane Collaboration and Library <http://www.cochrane.org/docs/descrip.htm>, and the University of Toronto’s Centre for Evidence-Based Medicine, <http://www.cebm.utoronto.ca/>). Professional medical societies have developed similar schemes to evaluate the strength of evidence, and the power of this approach is so persuasive that over 100 grading scales are used among medical journals to gauge the confidence warranted in experiments and recommendations for patient care (Ebell *et al.* 2004).

We should endeavor to be as straightforward and effective in relating science and practice in forestry, and provide explicit statements about the power of our experimental evidence. This power goes beyond the simple P value from a statistical test to include critical details about the design of individual experiments, and groups of experiments. We offer a preliminary example of this approach in Table 2, and readers can refer to this table when evaluating confidence warranted by the experimental designs in this volume and in other publications.

LOOKING TO THE FUTURE

Our workshop identified major advances in our understanding of the effects of species on soils, and how these might shape the responses of forests to changing climate. The advances in methodology and the surprises that came from recent studies, combine to illustrate the potential for future gains in knowledge. We would highlight several key areas for development.

1. Future research projects should define the populations of interest, and design experiments to address these populations. If the population of interest happens to be beech and Norway spruce forests on limestone soils in Bavaria, then experimental plots need to be established to provide a fair, representative sampling of this population.
2. The effects of tree species should be examined by testing challenging hypotheses that go beyond simple descriptions of the magnitudes of effects. For example, if a species happens to increase the supply of N in soils, does this increase lead to an increase in growth? Only an experimental manipulation of N supply could test this hypothesis. Hypothesis testing will be especially important for determining the mechanisms that underlie observed effects of species.
3. Few forests are dominated by single tree species, yet almost all of our information on the effects of tree species on soils comes from monoculture experiments. Are the effects linear functions of the proportion of species, or do interactions reduce or enhance these effects? We may gain preliminary insights on the effects of species in mixtures by examining the borders between monoculture plots, but explicitly designed experiments will be needed to test many important hypotheses.
4. The effects of tree species on soils may be moderated (or enhanced) by the influence of overstory trees on understory vegetation. We have seen many cases where understory vegetation differs dramatically beneath the influence of overstory species, but no studies have manipulated understory vegetation to isolate this effect. Similarly, tree species have major influences on soil biota, and experiments must address these biotic differences that may determine the overall effect of tree species.
5. We recommend that studies on tree-species effects take advantage of the constraints offered by mass balance in nutrient cycling studies. Confidence in experimental results will be high if the various pools of nutrients among treatments add up to the same total contents for the entire tree+soil system. Substantial deviations from mass balance would indicate caution is needed in interpreting the findings (Fisher and Binkley 2000). A classic estimate of fine root production in a forest was so high that canopy photosynthesis could not provide enough C to grow the roots (as pointed out by Ryan 1991). Another study reported greater rates of fine root growth on a poor site than on a fertile site, but calculations of the N requirement for both stands (J. Aber, personal communication) indicated the poor site would have to have a greater supply of N than the fertile site (which seems unlikely). An unreplicated comparison of burned and unburned spruce forests claimed that burning increased soil calcium (Ca) by 5000 kg/ha, yet the total Ca content of the trees was just 1000 kg/ha; the 4000 kg/ha gap in the budget suggests that little confidence is warranted in this estimate of fire impact. Multiple lines of evidence can provide insights about the “reasonableness” of production and nutrient budgets.

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Chapter 2

EFFECTS OF BRITISH COLUMBIA TREE SPECIES ON FOREST FLOOR CHEMISTRY

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INTRODUCTION

Although the question of tree species effects on soils has been of scientific interest for decades, two big questions remain largely unanswered. First, are there consistent effects of tree species on soil and forest floor properties? And second, how large are species effects compared with influences of other site factors? Here we address these questions by reviewing studies of the effects of tree species native to British Columbia, Canada, on forest floor chemistry, to determine if there are consistent patterns. Then we examine studies that provide some indication of the relative influences of tree species and other site factors, to assess the importance of species effects.

The province of British Columbia (BC), by virtue of its size and variety of climatic zones, has a large number of tree species, which also occur in neighboring provinces and U.S. states. In addition to comprising the natural and planted forests of BC, several of these species have been introduced into reforestation and afforestation projects in many European countries. The effects of BC tree species on forest floor properties have been investigated in several studies in North America and in Europe. In this paper we review what is known about the forest floors created by tree species native to British Columbia, particularly with respect to nutrient concentrations, rates of nitrogen mineralization, proportions of ammonium and nitrate, and microbial communities. Given the substantial influence of foliar litter on nutrient cycling in the forest floor (Prescott, 2002), we also discuss nutrient concentrations and rates of decay of foliar litter of BC tree species. Much of this information is drawn from common garden experiments both in BC