Ash and Non-Ash Nitrogen and Moisture Levels in Whitaker's Forest Canopy Gaps

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Abstract Creation of canopy gaps is an innovative forest management technique that provides space and light for new growth while maintaining the ecology and biodiversity of the forest. A current study on the canopy gap regeneration of giant sequoia (*Sequoiadendron giganteum*) in Whitaker's Forest (southern Sierra Nevada Mountains, California) shows a marked difference in the size and vigor of seedlings growing in ash beds, which resulted from burning logging debris, compared with those growing in bare mineral soil. To investigate this difference, I collected soil and foliar samples, as well as soil moisture measurements, from both ash and non-ash areas of four 1-acre gaps. The soil and foliage samples were analyzed using extractable nitrate and ammonium tests. Soil sample nitrogen levels range from 0.1 ppm to 64.5 ppm, foliage samples range from 5 ppm to 650 ppm, and soil moisture readings range from –0.044% to 0.36%; none of the three shows statistically significant difference between ash and non-ash. Levels of soil nitrogen don't appear to be related to those of foliar nitrogen, and nitrogen levels do not appear to be related to soil moisture. Neither ash nor non-ash areas in large gaps show the expected high moisture levels near gap center. This pilot study outlines the high variability in nitrogen and moisture levels in the system, and also illuminates the spatial scale at which the variability occurs. Future work can use these baselines to continue the examination of potential influences of ash on conifer regeneration.

Introduction

If current even-aged forest management is to be converted into more ecologically beneficial uneven-aged management, we must thoroughly understand the factors influencing seedling growth within canopy gaps (Gagnon et al. 2004). Seedlings within gaps can grow in ash beds and bare mineral soil. To quantify the differences in growing conditions provided by these two substrates, I measured their soil nitrogen and moisture content. I also measured the foliar nitrogen content of seedlings grown in ash and soil. The influence of ash on regeneration in gaps is an important consideration because it has the potential to enable increased growth, yet further study is necessary to determine whether this occurs.

Regeneration of the giant sequoia (*Sequoiadendron giganteum*) within canopy gaps is currently being studied at Whitaker's Forest in the southern Sierra Nevada. Twenty canopy gaps were created in 2003 by small group selection harvests. Differences between gaps and surrounding forest have been shown to persist for a minimum of two years from gap formation (Ritter et al., 2005*a*), so these areas can still be expected to have exhibited gap characteristics when the data for this study was collected in 2005.

Within each canopy gap, logging debris was piled in a north-south strip, called a windrow, and burned. Seedlings and seeds were planted in the resulting ash beds and in the adjacent bare mineral soil. Seedlings planted in ash have exhibited higher growth rates when compared to those in bare mineral soil, but, in the context of York's study, this difference was less powerful than the effect of gap size on growth (R. York 2006, manuscript in progress). However, when considered independently, growth differentials between ash and non-ash hold interesting implications, and I seek to explore these differences in this study.

Seedling growth is regulated by the availability of three basic variables: sunlight, moisture, and nutrients. These three variables are all closely intertwined; for example, rates of soil nutrient cycling are determined by soil temperature and moisture (Prescott 2002) and soil nitrogen levels are determined partially by soil moisture (Kennedy and Pitman 2004). It is impossible to gain a clear understanding of the seedling responses at Whitaker's Forest without examining all of these factors.

Gaps in the forest canopy allow greater amounts of sunlight to reach the ground, which may cause interactions with soil moisture. Despite the increased evaporation implied in gap scenarios, conditions of reduced competition result in higher soil moisture within canopy gaps when compared with surrounding forests of both beech and Douglas-fir. In fact, moisture levels are often at capacity within gaps while being as low as 50% of capacity outside (Gray et al. 2002, Ritter et al. 2005*a*, Ritter et al. 2005*b*). Conditions of high water and high sunlight are beneficial to seedling growth, but the color and texture of an ash substrate may react in a different way from soil, and provide very different growing conditions.

Nutrient availability is the final essential factor in seedling growth, and nitrogen has been found to be the only nutrient that promotes forest growth when administered individually to conifers (Nohrstedt 2001). For centuries, the availability of nutrients such as nitrogen has been thought to be augmented by the introduction of ash to the soil. This can easily be done in managed forests by the on-site burning of logging debris. The comparison of ash and soil is particularly interesting in my study because the windrow technique of debris burning used has been found to have “dramatic and lasting effects on soil development” in the southeastern United States (Johnston and Crossley 2002), yet its effects on regeneration have not been investigated.

There is some disagreement regarding the effects that wood ash has on seedling growth. One study showed that ash did not affect foliar nutrients, growth, or biomass production in a willow plantation (Park et al. 2005). Another study showed an overall increase in biomass after burning in a pine forest but attributed this partially to an increase in light availability (Skre et al. 1998). A third study found that ash results in minor conifer growth stimulation in nitrogen rich sites while it decreases growth in nitrogen poor sites (Nohrstedt 2001). Some canopy gaps, even those as small as 0.1 hectare, have exhibited increased soil nitrogen availability (Prescott 2002), which supports the idea that gaps are excellent places to examine the effects of ash.

It has been shown that a fire event can exert great influence over vegetation patterns, through increased moisture retention by burned conifer forest litter versus unburned litter (Whitney 1979), and through variations in soil nutrients caused by patterns of ash distribution (Rice 1993). Some of the nutrients distributed by ash include extricable phosphorus, potassium, calcium, and magnesium (Park et al. 2005, Whitney 1979). Complex uptake requirements must be met before a plant can use nutrients in the soil, however. A study conducted in a willow plantation showed that ash increased soil nutrients but did not affect foliar nutrients (Park et al., 2005). Measuring nitrogen content in seedling foliage as well as soil will allow levels of nitrogen present in soil to be compared with levels of nitrogen actually incorporated by plants.

The presence of ash in Whitaker's Forest mimics to some degree the natural state of the giant sequoia-mixed conifer forests of the southern Sierras, which were historically maintained by a regular fire regime (Stephenson et al. 1991). Fire has a direct influence on giant sequoias by providing the only conditions under which their seeds can germinate (Stephenson et al. 1991). Fire suppression in the 20th century has led to dramatically decreased sequoia regeneration compared to 19th century sequoia establishment, and these decreased rates are not sufficient to maintain existing sequoia groves (Stephenson 1992). Because sequoias are theoretically adapted to sprouting in ash, it is especially interesting to examine the reasons behind their different growth rates in ash and soil.

Canopy gaps play an important role in the regeneration of all types of forests by providing areas of decreased competition in which young trees can become established. Studies have shown that seedling numbers and root size increase with distance from mature trees in longleaf pine forests (Gagnon et al. 2004). Seedling growth rates were found to be the same or higher in defined beech canopy gaps than in large open areas (Guo and Werger 2004). This suggests that regeneration after harvests could be more efficient using gaps than using more common techniques such as clearcuts.

However, most current forest management regimes do not incorporate gap formation. Some managers attempt to imitate natural disturbances by utilizing harvesting methods that leave behind an evenly-spaced overstory rather than clearcutting (Palik et al. 2003). When a heterogeneous, or "clumped" overstory was created in a longleaf pine harvest, leaving dense areas alternating with canopy gaps, competition was shown to decrease and regeneration improve (Palik et al. 2003). This means that timber production may actually be increased by the presence of gaps. Because gaps also provide extensive benefits to the forest ecosystem, such as by increasing species diversity (Pederson and Howard 2004), it has been indicated that the costs in terms of deciduous forest management are outweighed by the ecological benefits of canopy gaps (Pederson and Howard 2004).

As worldwide deforestation rates increase, it is becoming more and more crucial to understand the ecological processes of forest systems and how they are affected by harvesting methods (Coates and Burton 1997). There is increasing pressure to develop sustainable management plans that will maintain the stability of the forest ecosystem while also fulfilling our natural resource demands (Coates and Burton 1997). Illuminating the differences between ash and soil as potential seedling substrates within canopy gaps may initiate the integration of debris burning and gap formation into management plans, and this would be a decisive move toward the practice of more ecologically conscious forestry.

Methods

Study Site Rob York of the UC Berkeley Forest Ecology Lab under John Battles is conducting a canopy gap regeneration study at Whitaker's Forest in Tulare County, a University of California property which adjoins Kings Canyon National Park in the southern Sierra Nevada Mountains (Fig. 1). Whitaker's Forest contains 320 acres of mixed-conifer and giant sequoia forest, on moderate to steep slopes. As a giant sequoia research site, Whitaker's is ideal: over 200 old growth sequoias (>2.4 m diameter) remain on the site, and the second-growth sequoia stands are considered to be the most advanced in the Sierras (UC Center for Forestry 2006).

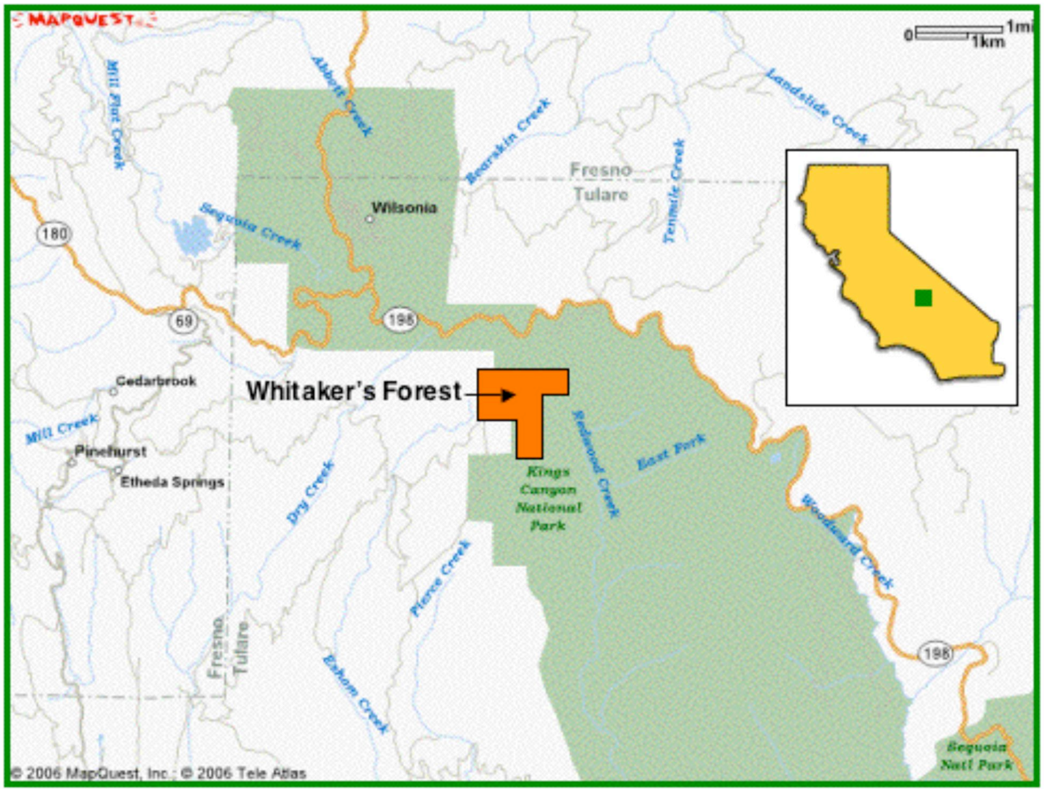

Figure 1. The 320-acre Whitaker's Forest property is located adjacent to Kings Canyon National Park, in Tulare County, California. The inset map locates the detail map within the state.
inset credit: http://agecon.nmsu.edu/mediation/State%20Contacts/California.htm
detail credit: http://www.mapquest.com

To conduct his study, York directed the creation of twenty canopy gaps of various sizes in 2002 by small group selection harvests (Mitchell 2003). After the harvest operation, logging debris was piled in a north-south strip down the middle of each gap and burned, leaving a five-meter-wide ash bed behind. In the spring of 2004, giant sequoia seeds and seedlings were planted at intervals of three meters in north-south rows both in the ash bed and in the nearby bare mineral soil. The two-year-old seedlings had been grown under nursery conditions, had 20-cm root cones, and were planted with the accompanying cone soil. The seed and seedling rows were located three meters apart (Fig. 2).

In the summer of 2005, I collected samples from Whitaker's Forest under agreement with York and the UC Forest Ecology Lab. Due to time and resource limitations, I could not examine all 20 of York's gaps. To ensure that I did not introduce an additional (unreplicated) variable into my study, I only took nitrogen measurements in gaps of a single age category, and I concentrated my moisture sampling there. I chose the largest gap size (approximately one acre) because larger gaps are more efficient to harvest and my results may therefore be more influential in forest management. In order to take measurements that would be most relevant to both seed and seedling growth in this experimental setting, I located my sample sites equidistant from the seed and seedling rows in both the ash bed and the bare mineral soil (Fig. 2).

Temperature and moisture levels in canopy gaps have been found to form systematic north-south gradients in a beech forest (Ritter et al. 2005*a*). In order to detect any such gradient in this case, I took measurements in three distinct positions: the north edge of the gap, the center of the gap, and the south edge of the gap. Location of edge measurement sites were determined by the extent of the ash bed in each gap: the sites were located between the seed and seedling spots that were closest to the edge of the gap while still remaining in the ash bed. Then the seed and seedling pairs directly opposite in the bare mineral soil served as the location for the corresponding soil measurement sites (Fig. 2). In each gap, there were 3 sites per treatment, for a total of 6 sites.

Sampling sites were intitially located equidistant from the seed and seedling rows in order that I might apply my results to both seed and seedling growth, but very few seeds actually germinated, so I was unable to factor seed growth into my analyses.

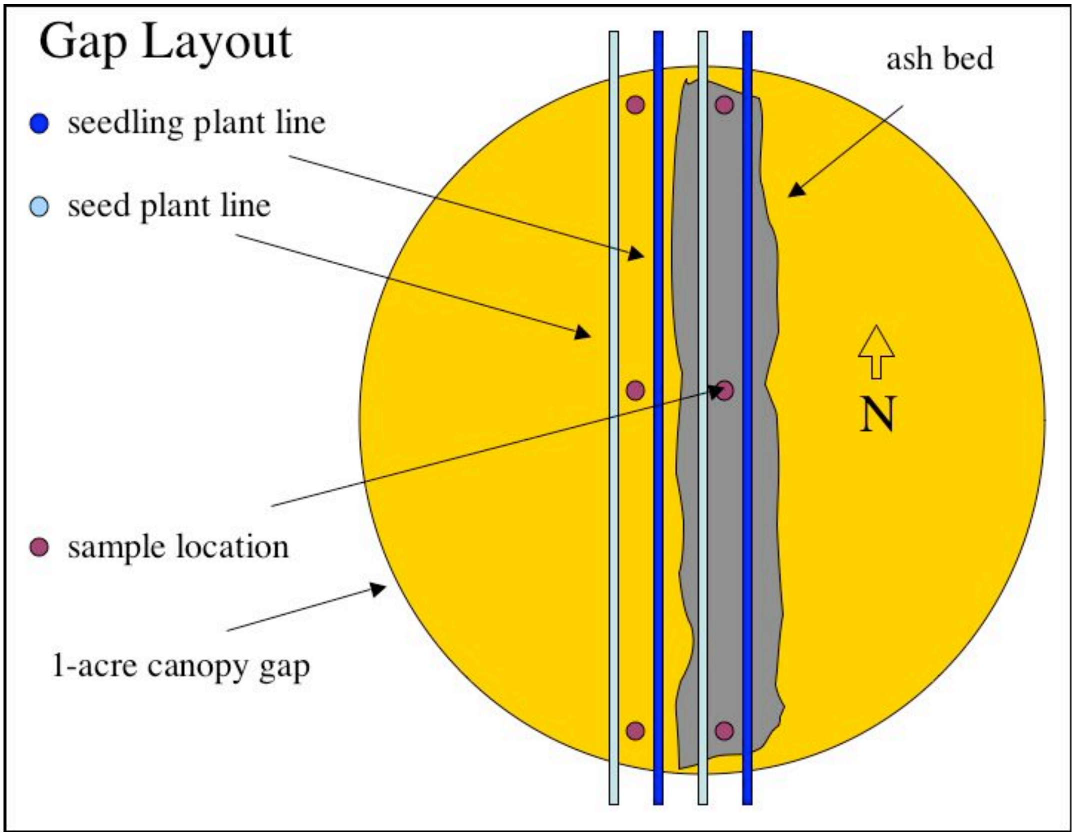

Figure 2. Within each 1-acre gap is a 5-meter-wide ash bed. Within the ash bed are lines of seedlings and seeds (two seedlings and several seeds planted every 3 meters) that are 3 meters apart. Corresponding lines of seeds and seedlings were planted in the bare mineral soil adjacent to the ash bed. All lines extend beyond the gap, into the forest matrix. Sample locations are chosen between corresponding pairs of seeds and seedlings as close as possible to the edges of the gap while maintaining ash presence, and as close as possible the center of the gap.

Soil Nitrogen Measurements At each site, I collected approximately 500 g of soil with a trowel from about 10 cm depth. This is half the length of the seedling root cones, so measurements are relevant to seedling nitrogen utilization. Human contact with the samples was minimized in order to prevent contamination. Samples were collected in plastic bags, but the bags were opened to allow the soil to air dry for a minimum of 24 hours.

I transported the samples to the DANR lab in Davis, where they were analyzed for total nitrogen content. The lab used Protocol 312: Soil Nitrate and Extractable Ammonium - Flow Injection Analyzer Method. This is a type of soil fertility test that uses potassium chloride to perform an equilibrium extraction of nitrate and ammonium (Hofer 2003 and Knepel 2003). The test was chosen because nitrogen is crucial to plant growth and has also been found to be affected by ash deposition (Park et al., 2005).

The lab used Standard Reference NORD, tested as 68 and acceptable +/- 6. Test results are reported as ppm NO_3-N. Duplicate tests of three out of 24 samples allowed me to calculate a root mean square error of 0.0757 percent ppm. When the original measurement and duplicate measurement differed, I use the average of the two in analysis.

Foliar Nitrogen Measurements At each site, I also collected approximately 20 g of foliage from a healthy member of each sample pair of seedlings (all seedlings were double-planted by York). Sample seedlings were chosen based on foliage color and quality, seedling size and morphology, and overall vigor. I used pruners to trim away young to middle-aged foliage. I avoided the older foliage beyond the first two bud scars, because it represents growth during the seedlings' first two years, when they were in the nursery. I also avoiding the newest foliage, because nitrogen can be unusually concentrated there and might bias the samples. Contact with material was again minimized, and samples were air dried for a minimum of 24 hours.

These samples were analyzed by the DANR lab using Protocol 512: Extractable Nitrate and Ammonium in Botanical Materials - Flow Injection Analyzer Method. This test uses 2% acetic acid to perform a total extraction of nitrate and ammonium (Wendt 1999, Switala 1997, Carlson et al. 1990). Extractable nitrate and ammonium tests were used to analyze both the soil and the foliage in order to enable comparison of the levels of nitrogen present in soil and levels taken up by seedlings growing in the soil.

The standard reference used in this case was UCD 157, tested as 1402 and acceptable as 1480 +/- 200. Test results are reported as ppm NO_3-N, but many readings are "<10." In these cases, I use a value of five in analysis. Again, three out of 24 tests were duplicated, and because the only difference was between 10 and <10, the error for this test is not calculable, and so is considered to be zero (J Battles, personal communication).

Soil Moisture Measurements I used a portable soil moisture probe (ThetaProbe type ML2x, Dynamax Delta-T Devices product line, Cambridge, UK) to measure soil moisture in percent water content by volume (accuracy: +/- 1% or +/- 0.01 m^3/m^3). Because soil moisture can vary immensely based on microhabitat differences (R York, personal communication), I took a large number of moisture measurements: I sampled every six meters along the seedling rows in both ash and mineral soil. This placed my sample points at alternating seedling planting spots. At each sample point, I took three readings.

The prongs of the probe penetrate to a depth of about 10 cm, which is half the length of the seedling root cones, so measurements should be relevant to seedling moisture utilization. All moisture measurements were taken during solar noon (between noon and two o'clock pm), when soil is relatively dry and variations due to daily changes in humidity and condensation are minimized (GLOBE 2004). Some measurements were taken in "volts," but duplicate measurements in both "volts" and "soil moisture" were used to generate an equation ($y = 0.5231x - 0.0629$) by which to translate all measurements to "soil moisture" in % water content.

Statistical Analysis I used Microsoft Excel (version 10.1.0 for Macintosh) to organize data, perform simple calculations, create figures, and execute regression analyses. To perform single sample, paired sample, and unpaired t-tests, I used an online Internet calculator by GraphPad Software, found at http://graphpad.com/quickcalcs/ttest2.cfm (accessed Apr 11, 2006).

The extremely fine grain of soil moisture variability allows me to use individual measurements independently, but I am using the averages of the three measurements at each point because they provide a somewhat more normalized view of the moisture regime. Also, I am treating my individual nitrogen measurements as independent, rather than averaging through gaps. This is because nitrogen dynamics such as mineralization have been found to depend on localized site characteristics at the relatively fine scale of two to four meters (Smithwick et al. 2005). All of my sample sites were at least five meters apart, and microsite variability is so high within those distances that independent samples are not considered pseudoreplicated within gaps (J. Battles, personal communication). Because it is quite possible that my samples were taken too far apart to overcome the spatial scale of variability, I have also abandoned my sample pairings in many analyses.

Results

Nitrogen I pooled the ash and non-ash soil nitrogen results and calculated the means and standard errors (Fig. 3). The ash mean is certainly higher than the non-ash mean, but the two do not differ by statistically significant standards when compared using an unpaired t-test (df = 22; P = 0.2666). If the pairing aspect is retained, and paired differences between ash and non-ash are compared to zero with a one-sample t-test, the result is also non-significant (N = 12; P = 0.1533). However, it is interesting to note that in five out of the six pairs that do show obvious variation, the ash nitrogen levels are greater.

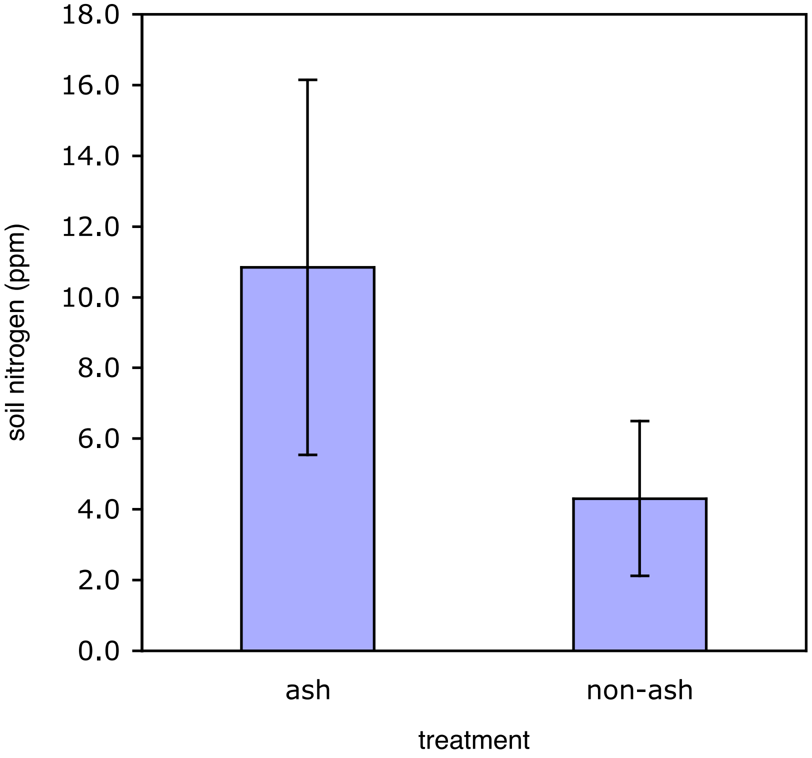

Figure 3. I collected soil samples from ~10 cm depth in both ash and non-ash in four canopy gaps. Samples were analyzed for total nitrogen content (NO_3) in ppm. The results range from 0.1 ppm to 64.5 ppm. There is no statistically significant difference between ash and non-ash soil nitrogen levels (unpaired t-test; df = 22; P = 0.2666).

I performed the same calculations on the foliar nitrogen measurements (Fig. 4). In this case, the non-ash mean is higher, but, again, the two are not statistically significantly different (unpaired t-test; df = 22; P = 0.4641). When the foliage pairing is maintained and the ash/non-ash differences compared to zero with a one-sample t-test, the result is also non-significant (N = 12; P-value = 0.4809).

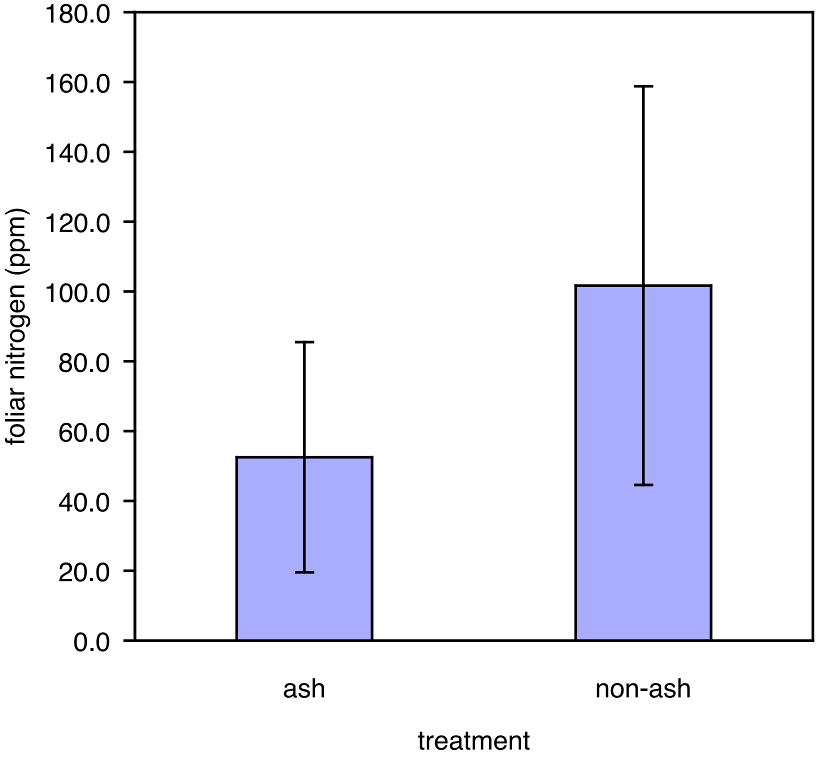

Figure 4. I collected foliage samples from seedlings in both ash and non-ash in four canopy gaps. Samples were analyzed for total nitrogen content (NO_3) in ppm. The results range from 5 ppm to 650 ppm. There is no statistically significant difference between ash and non-ash foliar nitrogen levels (unpaired t-test; df = 22; P = 0.4641).

I plotted soil nitrogen against foliar nitrogen, regardless of ash or non-ash status (Fig. 5). If foliar nitrogen levels were proportionate to levels of nitrogen in the nearby soil, then a strong correlation should be visible. However, correlation analysis results in a non-significant R value of 0.1565. It is interesting to note that there is a cluster of points around zero here, as well as extreme outliers along both axes, yet no points showing high levels of both types of nitrogen. Repeating the regression using only ash pairs and only non-ash pairs yields similar non-significant R values, as well as similar patterns.

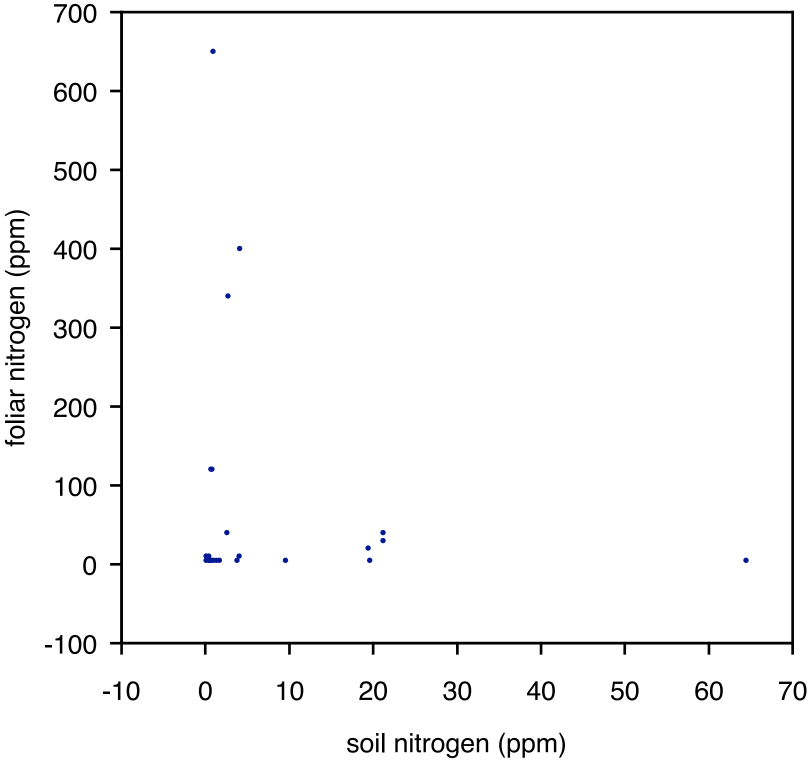

Figure 5. I collected soil samples and foliage samples from nearby seedlings in both ash and non-ash in four canopy gaps. Samples were analyzed for total nitrogen content (NO_3) in ppm. Corresponding soil and foliage measurements are plotted against each other in a correlation analysis which is not statistically significant (N = 24; R = 0.1565).

Moisture I took the means of the ash and non-ash soil moisture data sets, whose points are already means of three, and calculated the standard error (Fig. 6). Non-ash shows a higher mean, but the unpaired t-test yields a very non-significant P value of 0.7182 (df = 280). When I maintain the moisture pairing system and compare corresponding ash and non-ash moisture points in a correlation, the R value is statistically significant (N = 141; R = 0.3081). However, this still means that moisture levels in one treatment only explain about 10% ($R^2 = 0.0949$) of moisture levels in the other treatment. If there were systematic differences in moisture dynamics between ash and non-ash, a stronger correlation should be detected. I also performed a paired-sample t-test on the data, but the resulting P-value was 0.6667 (N = 141); again, not significant. Repeating these analyses using the 849 individual readings (before averaging of the three per point) yields similar results.

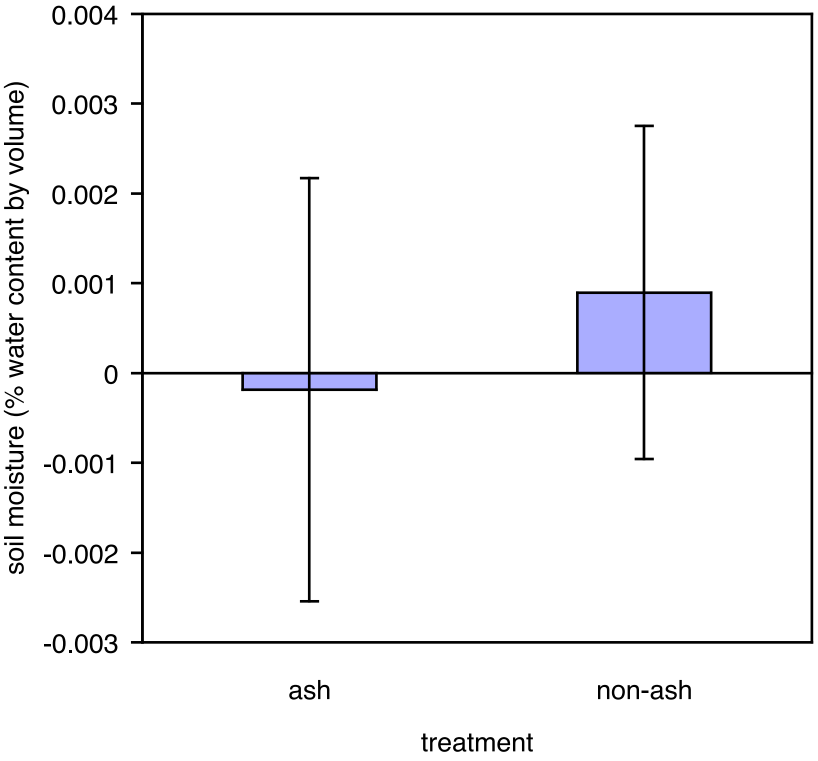

Figure 6. I used a soil moisture probe to take measurements (% water content by volume) in both ash and non-ash in 12 canopy gaps. At each point, I took three readings and then averaged them. Before averaging, the data ranged from –0.044% to 0.36%. After averaging, the range is –0.039% to 0.12%. There is no statistically significant difference between ash and non-ash soil moisture levels (unpaired t-test; df = 280; P = 0.7182).

Interactions Correlation analyses comparing nitrogen (both soil and foliar) and moisture levels, in ash, in non-ash, and in both treatments combined, did not yield significant R values. (In order to form corresponding pairs of moisture measurements, which were taken at every odd-numbered planting spot, and soil/foliage samples, which were occasionally taken at even-numbered planting spots, averaging of several nearest moisture measurements was sometimes necessary.)

North-South gradient No comparison of nitrogen level with position within gap proved significant or indicated a pattern, so I eliminated position as a variable in my nitrogen calculations. This is a viable solution considering that nitrogen dynamics vary at a scale of two to four meters (Smithwick et al. 2005). With the soil moisture, however, I was able to examine a more continuous gradient from north to south, because an averaged group of three soil moisture readings had been taken every six meters in both ash and soil. I concentrated on three of the four largest gaps because gap effects are more obvious in larger gaps.

Moisture measurements had been taken at odd-numbered planting spots from north to south, so I averaged the three measurements across gaps for each planting spot number, then used planting spot as a proxy for distance from north edge and plotted the data for ash and non-ash (Fig. 6). The planted lines from York's study actually extend beyond the gap edges into the forest matrix (Fig. 2), so the moisture gradient incorporates any edge effects. It is interesting to note that this graph does not show the high central gap moisture and low edge/matrix moisture that one would expect based on previous studies (Gray et al. 2002, Ritter et al. 2005*a*, Ritter et al. 2005*b*) and on a simple moisture competition model.

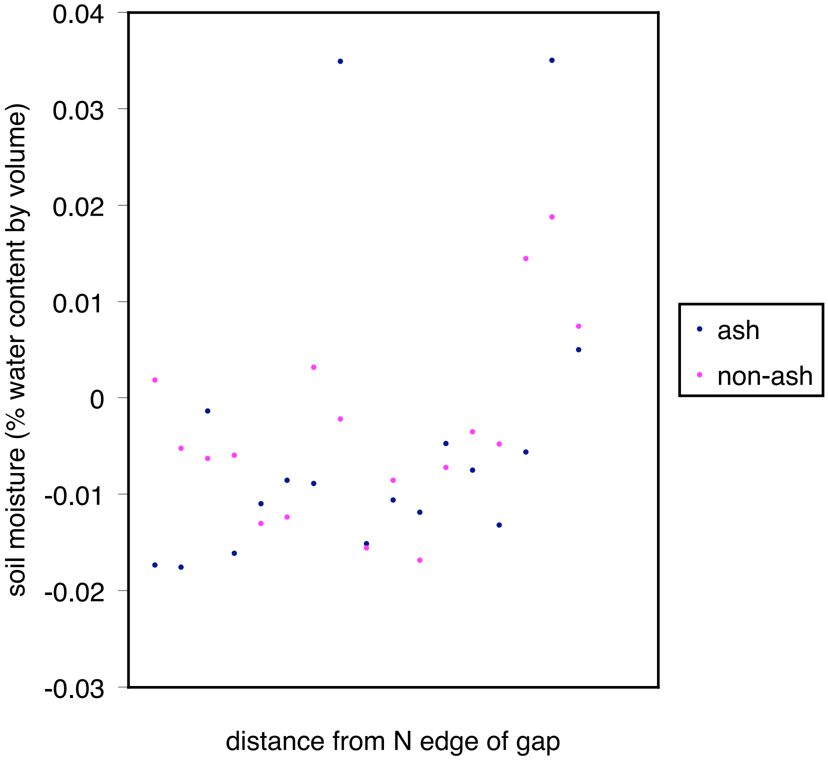

Figure 6. I used a soil moisture probe to take soil moisture readings (% water by volume) about every six meters along the north-south ash gradients in three canopy gaps. At each point, I took three readings and then averaged them. Then, I averaged the three values for each sampling spot. This does not show the high moisture levels expected in the center of large gaps.

Discussion

Nitrogen My nitrogen analyses are handicapped by extremely low power, but they can be used to help estimate expected variability when designing future studies. Microsite spatial variability is obviously very high in this system, in agreement with Smithwick et al.'s 2005 indication of a two to four meter nitrogen dynamics scale. I cannot reject the null hypothesis that nitrogen levels do not differ between ash and non-ash, but this could be due to my large spatial scale of about 40 meters north-south and about eight meters east-west between nitrogen sample points. Sampling on a smaller scale will better justify pairing between ash and non-ash, and differences between the two treatments may well be discovered. I found no indication of proportionate soil and foliage nitrogen levels. With low power, I cannot say definitively that this means seedlings do not or cannot make use of nitrogen present in the local soil, but similar findings have been documented (Park et al. 2005).

Because I do not know how deep any effect of surface ash penetrates the substrate, my soil sampling depth of ~10 cm may have been inappropriate. In future, sets of samples could be taken from various depths and compared. Also, the trowel technique is not very precise; some kind of soil corer would yield more uniform results.

My foliage samples were extremely small, because some of the seedlings I was sampling were very small and weak. Therefore, the lab tests may have been less reliable, and results may have been biased by single unusual sections of foliage in the samples. The poor health of some seedlings may have introduced unknown variables affecting nitrogen sequestration. Future investigators should make an effort to ensure collection of large sample sizes from plants that are all in a similar state of health.

Moisture I was able to take many more soil moisture measurements than nitrogen measurements, but my power to detect differences between ash and non-ash may still be extremely low. This is possible because my moisture measurements were taken six meters apart north-south and about eight meters apart east-west and soil moisture can vary on a scale of single centimeters. In fact, I did notice large variation even among the three samples I took within 10 cm at each sample spot; the largest difference lies between 0.4%, 0.01%, and 0.003% water content. I cannot reject the null hypothesis that soil moisture levels do not vary between ash and non-ash, but, again, this result is applicable only to my sampling scale.

Because soil is consistently very dry, a more sensitive moisture probe could perhaps be used to reveal low-magnitude patterns. Also, future studies could be focused on identifying more factors in the system, such as experimentally determining the effects of color and texture on soil moisture dynamics. Ash and soil color may create different albedos and evaporation rates, and these could be infinitely variable, considering that ash can range in color from white to black. Variations in ash and soil texture could also create varying abilities to absorb, retain, and release moisture.

Interactions My small sample sizes, combined with the fact that there are so many factors that interact along with nitrogen levels and soil moisture made it impossible for me to identify any patterns in nitrogen-moisture relationships, though patterns have been found in the past (Prescott 2002; Kennedy and Pitman 2004). The fact that outliers tend to exist near zero and at both extremes (little nitrogen, high moisture; little moisture, high nitrogen) highlights the variability in types of interactions that can occur, but it also raises the question of why few interactions seem to result in intermediate levels of nitrogen and moisture. In the future, studies could be conducted to address the reason this is occurring. Investigators may also ask the question of whether nitrogen or moisture is the more limiting seedling growth resource in this system, and the answer may explain some of these interactions.

North-South Gradient I rejected the within-gap position variable when dealing with nitrogen, because I had too few samples to adequately cover the two to four meter nitrogen dynamics scale (Smithwick et al. 2005). However, an interesting pattern (or rather, lack of pattern) is indicated by the moisture data when averaged over the gradient in three of the largest gaps. Neither the ash nor the non-ash presents the "high at the center, low at the edges" distribution that would be expected based on a pure tree competition model. Instead, moisture levels are more evenly distributed, with some outliers and a general rising trend toward the south edge.

Increased moisture to the south might be explained by increased shading from that side caused by the angle of the sun in the northern hemisphere, but future investigators could examine moisture gradients in more detail, such as by studying the potential effects of encroaching root competition and the edge effect of moisture drip from surrounding mature trees.

In general, however, very small-scale heterogeneity (<10 cm: the "seedling scale") has been shown to have greater effects on regeneration than does within-gap position (Gray and Spies

1997). So, future gap regeneration studies may benefit from a shift in focus from north-south gradients to other factors, like localized substrate characteristics, nutrient availability, and moisture levels. My study can be used as an initial pilot investigation to encourage future work in examining those factors.

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