Secondary Succession and its Effects on Soil Nutrients and Fungal Communities

Amanda Cayo

Abstract

Fungi serve many purposes in ecosystems—from fixing nitrogen for plants to decomposing detritus. Their positive effects on forest ecosystems are well documented, but how fungal communities are affected by disturbances and change during succession is less well understood. We studied fungal communities and levels of nitrogen and carbon in the soil of forests in different stages of secondary succession following a burn chronosequence. In our study we surveyed seven species of fungi common in Northern Michigan in three burn plots at the University of Michigan Biological Station in Pellston, Michigan. We surveyed each plot three times. We also took soil samples from each plot to assess their nitrogen and carbon levels. We found no significant difference in the diversity of fungal species between plots, levels of soil nitrogen and carbon, or the carbon to nitrogen ratio between plots. However, the proportions of mycorrhizal and decomposing fungi were significantly different between plots. These data are useful for determining how fungal communities differ in different successional stages, which has not been extensively studied. Fungal community composition has a large impact on carbon and nitrogen cycling, as well as the rate of decomposition in forest ecosystems. This affects the plant communities that can thrive in these environments.

Introduction

Fungi are important organisms in many forest ecosystems—they aide in decomposition, nitrogen fixation, and nutrient cycling. Fungi are a food source for animals and can also be disease causing agents in many plants and animals (Ostry, Anderson, and O'Brien 2011). Many

fungi form symbiotic relationships with plants and live in their roots. The two major fungi functional groups are decomposers, which break down detritus, and mycorrhizal fungi, which fix nitrogen, although some fungi are both decomposers and mycorrhizal.

Fungi play a vital role in forest ecosystems as decomposers. They break down detritus, such as leaf litter and dead organisms, and allow their nutrients to be recycled and returned to the soil (Ostry, Anderson, and O'Brien 2011). While bacteria break down the sugars and amino acids in leaf litter, most of the litter is composed of cellulose, which is easily broken down by fungi. The priming effect of fungi (use of atmospheric carbon as an energy source) allows them to break down this cellulose and return its nutrients into the soil (Fontaine et al. 2011). This is vital for the growth of new plants and organisms in a forest ecosystem.

Decomposing fungi also have a large effect on nitrogen and carbon cycling in ecosystems. A study by Frey, Six, and Elliott (2003) tested this by labeling wheat straw with C^{13} and allowing it to decompose on the surface of N^{15} labeled soil. They found that carbon and nitrogen were exchanged back and forth between plants and nearby fungi. They also found that inhibiting these fungi reduced the movement of carbon and nitrogen in this system by 50%, meaning that fungi are essential for moving soil nitrogen and carbon from plant litter though ecosystems (Frey, Six, Elliott 2003).

Decomposing and mycorrhizal fungi both contribute to nutrient cycling in forest ecosystems; however their roles are distinct. Each type of fungi uses a different type of litter (mycorrhizal use the deeper layers while decomposers use the surface layers) which leads researchers to believe that they have separate roles in carbon and nitrogen cycling, although their exact roles are still unknown (Hobbie and Horton 2007).

While fungi have a great effect on the nitrogen available in soil, nitrogen availability also has a large effect on fungi. Arbuscular mycorrhizal fungi abundance and its importance in the local mycorrhizal community increases with soil nitrogen availability (Nave et al. 2013). Nitrogen availability affects the types of fungi that can live in a particular area, which in turn affects the plant and animal communities that can thrive there. This is particularly important in forests undergoing succession after a disturbance because fungal bodies are generally located underground and are rarely destroyed during disturbances such as fire. These fungi will eventually help shape the plant and animal communities of the new forests.

Successional forests go through many stages of plant growth before reaching a stable community. Fungal communities also change in different stages of succession. These communities change over time, as competition among plants and predation change the organisms present in the forest. This affects nitrogen and phosphorus levels in the soil, with older successional forests having a higher ratio of nitrogen to phosphorus in the living leaves of plants (Huang, Zhou, and Liu 2012). When leaves fall and become litter, these levels will in turn affect the fungal species present below the soil surface. Forests in higher successional stages have higher fungi species richness as well as a higher fungal biomass (King 2010).

For our study we investigated the effect of succession on nitrogen levels in the soil and how the age of the forest, as well as nitrogen levels in the soil, affect the fungal species and functional groups (mycorrhizal vs. decomposers) present. We studied fungi in three plots that had been burned at different times (1936, 1954, and 1998) and were in different stages of succession.

We hypothesized that the older plots will have more decomposing fungi because they have more leaf litter available. Also older plots will have higher soil nitrogen levels because of the greater rate of decomposition of plant litter. We predicted that there will be a significant difference in fungal functional groups and abundance between successional forests of different ages. The soil from the older plots will have less nitrogen and carbon than the newer plots and therefore the older plots will have more decomposing fungi and the newer plots will have more mycorrhizal fungi. We expect there to be the greatest fungal species diversity in the older plots because there has been the most time for colonization to occur.

Methods

We surveyed three burn plots (1936, 1954, and 1998) located at the University of Michigan Biological Station in Pellston, Michigan on three separate occasions (7/23/14, 7/26/14, and 7/30/14) (figure 7). These forest plots were each clear-cut, burned, and then left undisturbed. We surveyed the 1936, 1954, and 1998 burns three times each.

To measure fungal species and functional group diversity we focused on seven species of fungi common in northern Michigan. We surveyed four species of mycorrhizal fungi: golden chanterelles, aspen bolete, birch bolete, king bolete, and a category for "other." We also surveyed three species of decomposer fungi: oyster mushrooms, artist's conk, smokey polyphore, and a category for "other."

For each survey we used five transects for the 1936 and 1954 plots and four transects for the smaller 1998 plot. Each transect ran the length of the plot (100 m for the 1936 and 1954 plots and 50 m for the 1998 plot) and was four meters wide and 20 meters apart. Edge effects were eliminated by moving inward 10m from the border of each plot.

To see how much nitrogen was present in the soil of each plot, we took a soil sample on each transect in a diagonal manner across the entire plot (five samples total for 1936 and 1954 plots and four samples total for the 1998 plot). After each survey and soil collection we sifted, dried, and ground the soil from each transect at each plot. We then tested the soil samples for levels of nitrogen and carbon.

We calculated the Shannon diversity index of each plot on each day. To compare these data between plots we ran an ANOVA. We also used the average carbon and nitrogen levels found in the soil of each plot to calculate their carbon: nitrogen. We then used an ANOVA to compare the nitrogen levels, carbon levels, and the carbon:nitrogen between plots. We used a chi square test to determine if there was a significant difference between proportions of mycorrhizal and decomposer fungi between plots.

Results

The 1936 and 1954 plots have a higher species evenness that the 1998 plot (figures 1, 2, and 3). The dominant species in the 1936 and 1954 plots were golden chanterelles and "other" mycorrhizal fungi (figures 1 and 2), while the dominant species in the 1998 plot was by far "other" mycorrhizal fungi (figure 3). Golden chanterelles constituted only 1% of the fungi population found in the 1998 plot (figure 3).

There was no statistically significant difference in the Shannon index values between plots ($F=3.967$, $df=8$, $p=0.08$) (table 1). However the ratio of mycorrhizal to decomposer fungi differed between plots. The 1936 and 1954 burns have a similar mycorrhizal to decomposer fungi ratio, while that of the 1998 burn is much higher (figure 4). There is a statistically

significant difference in the proportions of mycorrhizal and decomposing fungi between plots (X^2=101.522, df=1, p>0.01).

There was no statistically significant difference in the percentage of soil nitrogen (F= 0.948, df=38, p=0.397), percentage of soil carbon (F=0.839, df=38, p=0.441), or the carbon:nitrogen ratios (F=0.772, df=38, p=0.47) between plots (figures 5 and 6).

Discussion

Overall, fungal community composition and soil nutrient levels were similar between plots and did not support our hypotheses. This could be because most fungal biomass is located underground as hyphae growing in plant roots or in the soil, making them difficult to locate (Ostry, Anderson, and O'Brien 2011). Macrofungi are fungi that produce fruiting bodies or mushrooms that contain spores. It is difficult to find these fungi because their fruiting body production is heavily dependent on temperature and precipitation and varies greatly over time (Ostry, Anderson, and O'Brien 2011). We likely did not include many species of fungi that had not yet produced fruiting bodies or are located entirely underground in our study, which may have skewed our results. Also, several species of fungi are nitrogen-fixing as well as being decomposers, so we may have oversimplified our categories for data collection.

The comparison between Shannon indexes for the plots does not support our hypothesis that the 1936 would have a greater fungal diversity than the younger plots. Our average values for Shannon indexes were slightly higher for the 1936 and 1954 plots than the 1998 plot. Previous research has shown that after a disturbance there is a higher arbuscular mycorrhizal fungal diversity in plots that are "medium aged" as opposed to those that were disturbed within the last 20 years (Hart et al. 2014). There is also a decrease in mycorrhizal fungal diversity

during the final stages of succession when a forest has reached its climax community (Suzuki 2002).

The proportions of mycorrhizal and decomposing fungi were significantly different between plots, confirming our hypothesis that the 1998 plot had a larger proportion of mycorrhizal fungi while the 1936 plot had a larger proportion of decomposer fungi. In general, older trees tend to have more mycorrhizal fungi living in close proximity than younger trees, which could explain this observation (Hart et al. 2014). However, because a disturbance, such as a fire, does not destroy every species present in a forest, especially those who live partially below ground, the composition of fungal communities can be largely dependent on the fungal and tree species present before the disturbance (Suzuki 2002). Most fungal communities are greatly influenced by the species of trees present, which could also be a factor in fungal diversity during succession (Weand et al.). Because of this, the communities in the 1998 plot may never resemble those in the 1936 over time unless their original fungal communities were similar.

Because the soil carbon and nitrogen percentages did not differ significantly between plots our hypothesis was not supported. This is contrary to what we would expect because previous research by Hobbie and Horton (2007) has shown that mycorrhizal and decomposer fungi has different roles in and impacts on soil nutrient cycling. Therefore we would expect that forests with significantly different proportions of mycorrhizal and decomposing fungi would have significant differences in nutrient cycling and the carbon and nitrogen content of their soils. It has also been shown that large proportions of mycorrhizal fungi contribute to soil carbon losses, which would cause plots like the 1936 and 1954 plots to have less soil carbon than the 1998 plot (Cheng 2012). Our results could indicate that the forests do not differ in age substantially enough to experience a difference in soil nutrients.

These observations can be useful in determining the successional stages of other forests. The changes in fungal community composition are unique to several successional stages and can prove useful in other surveys in successional forests (McMullan-Fisher and Keane 2002). Fungi are key components of nutrient cycling in these ecosystems so their community composition is important for determining the nutrients present in the soil that are available for plant use and growth. They are also essential for litter decomposition, which can affect the resources available to plants and animals in the forest.

These fungal communities could also be greatly affected by higher levels of CO_2, as CO_2 enhancement of arbuscular mycorrhizal fungi has been found to reduce levels of soil carbon significantly (Cheng 2012). Therefore forests with higher proportions of mycorrhizal fungi are at risk of having low nutrient soil as atmospheric CO_2 levels increase. This means reduced plant growth and diversity, as well as potentially low animal species diversity because of reduction in plant food resources and physical habitat.

In conclusion, the age of a forest does not affect the levels of nitrogen and carbon present in the soil or the level of fungal species diversity. However, forests in intermediate successional stages have higher proportions of mycorrhizal fungi compared to decomposer fungi, which can have a large effect on the tree communities present, as well as the nutrient content of the soil as levels of atmospheric CO_2 rise. However, fungal community composition after a fire disturbance is determined by several factors and exact community composition is unpredictable. Nonetheless, this is an area that requires more research because fungi are and will continue to be an essential part of forest ecosystems.

References

Cheng, L., F. L. Booker, C. Tu, K. O. Burkey, L. Zhou, H. D. Shew, T. W. Rufty, and S. Hu. 2012. Arbuscular Mycorrhizal Fungi Increase Organic Carbon Decomposition Under Elevated CO2.

Fontaine, S., C. Henault, A. Aamor, N. Bdioui, J. M. G. Bloor, V. Maire, B. Mary, S. Revaillot, and P. A. Maron. 2011. Fungi mediate long term sequestration of carbon and nitrogen in soil through their priming effect. Soil Biology and Biochemistry 43:86–96.

Frey, S. D., J. Six, and E. T. Elliott. 2003. Reciprocal transfer of carbon and nitrogen by decomposer fungi at the soil-litter interface. Soil Biology and Biochemistry 35:1001–1004.

Hart, M. M., M. Gorzelak, D. Ragone, and S. J. Murch. 2014. Arbuscular mycorrhizal fungal succession in a long-lived perennial 1. Botany 92:313–320.

Hobbie, E. A., and T. R. Horton. 2007. Evidence that saprotrophic fungi mobilise carbon and mycorrhizal fungi mobilise nitrogen during litter decomposition.

Huang, W. J., G. Y. Zhou, and J. X. Liu. 2012. Nitrogen and phosphorus status and their influence on aboveground production under increasing nitrogen deposition in three successional forests. Acta Oecologica 44:20–27.

King, K. 2010. Abundance and Diversity of Mushrooms in Differently-Aged Forests of Northern Michigan.

McMullan-Fisher T. W.; Keane, P. J., S. J. M. . M. 2002. The macrofungal community and fire in a Mountain Ash forest in southern Australia. Fungal Diversity 10:57–76.

Nave, L. E., K. J. Nadelhoffer, J. M. Le Moine, L. T. A. van Diepen, J. K. Cooch, and N. J. Van Dyke. 2013. Nitrogen Uptake by Trees and Mycorrhizal Fungi in a Successional Northern Temperate Forest: Insights from Multiple Isotopic Methods. Ecosystems 16:590–603.

Ostry, M. E., N. A. Anderson, and J. G. O'Brien. 2011. Field Guide to Common Macrofungi in Eastern Forests and Their Ecosystem Functions.

Suzuki, A. 2002. Fungal succession at different scales. Fungal Diversity 10:11–20.

Weand, M. P., M. a Arthur, G. M. Lovett, R. L. McCulley, and K. C. Weathers. 2010. Effects of tree species and N additions on forest floor microbial communities and extracellular enzyme activities. Soil Biology & Biochemistry 42:2161–2173.

Figures

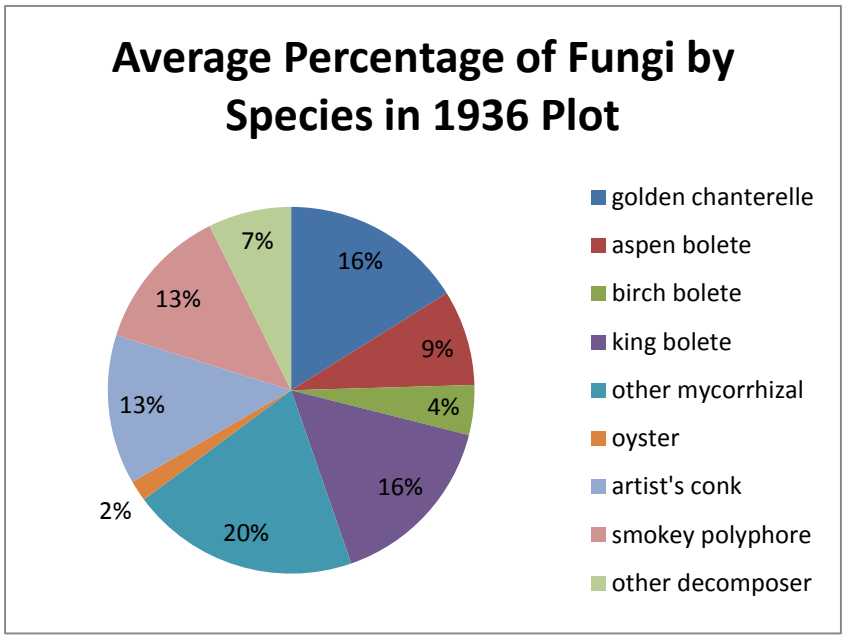

Figure 1—The percentage of each fungi present in the 1936 burn plot by species calculated using the average number of each species counted over three days.

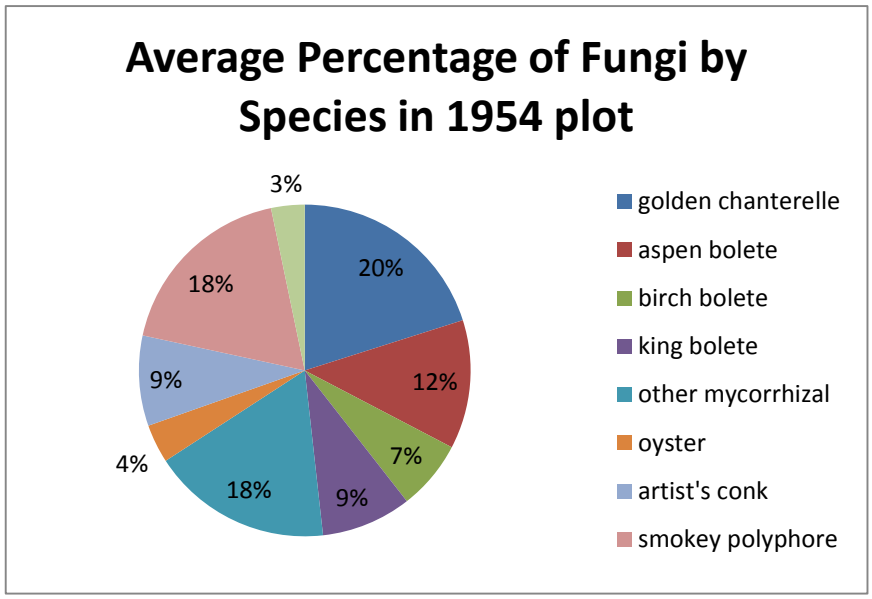

Figure 2—The percentage of each fungi present in the 1954 burn plot by species calculated using the average number of each species counted over three days.

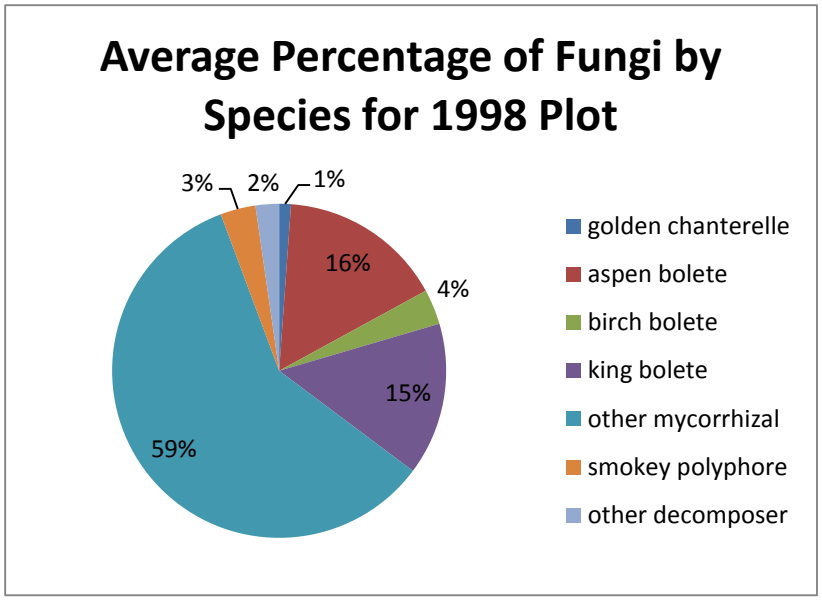

Figure 3—The percentage of each fungi present in the 1998 burn plot by species calculated using the average number of each species counted over three days.

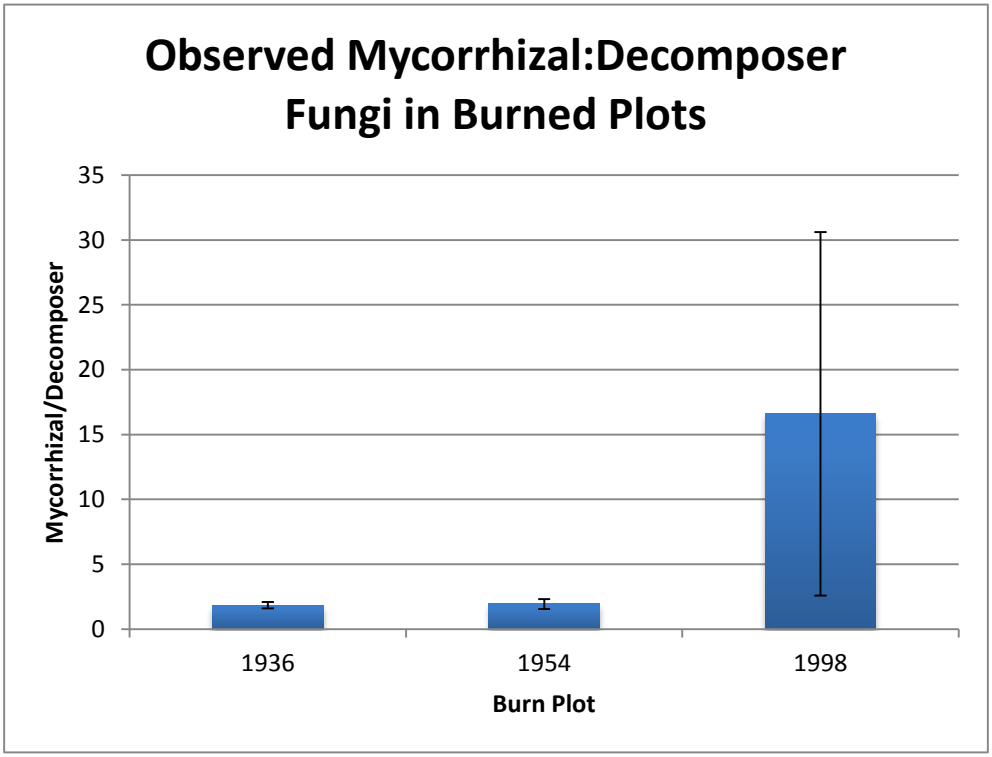

Figure 4—The average ratio of mycorrhizal to decomposer fungi in the burn plots.

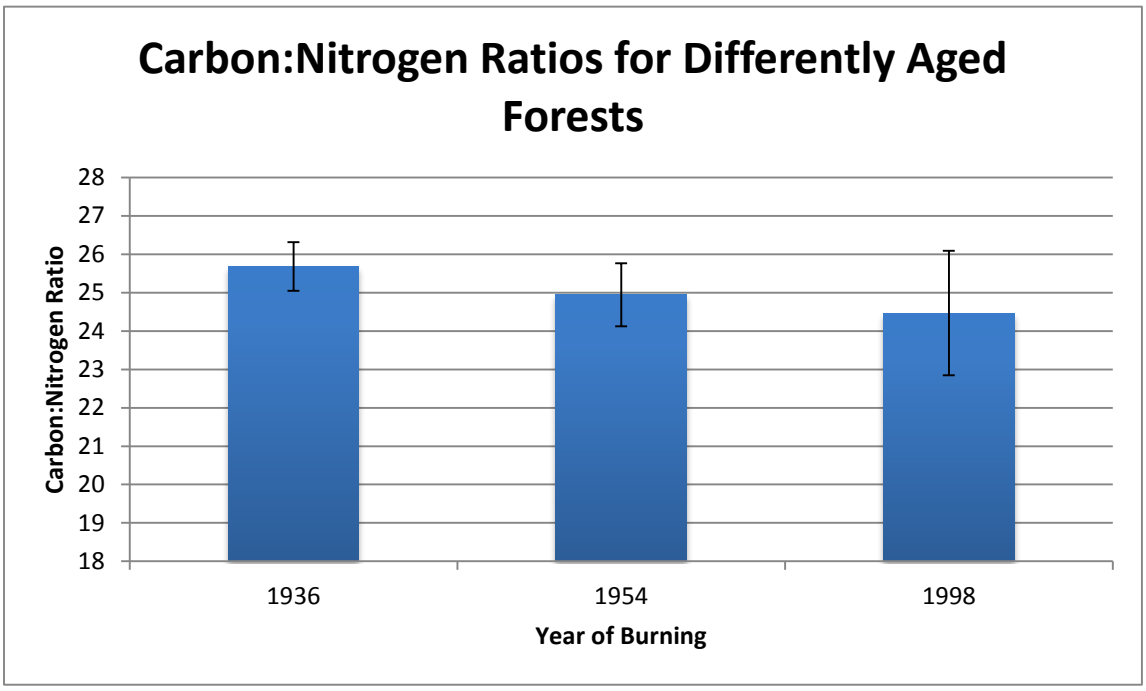

Figure 5—The average carbon:nitrogen ratios for each plot.

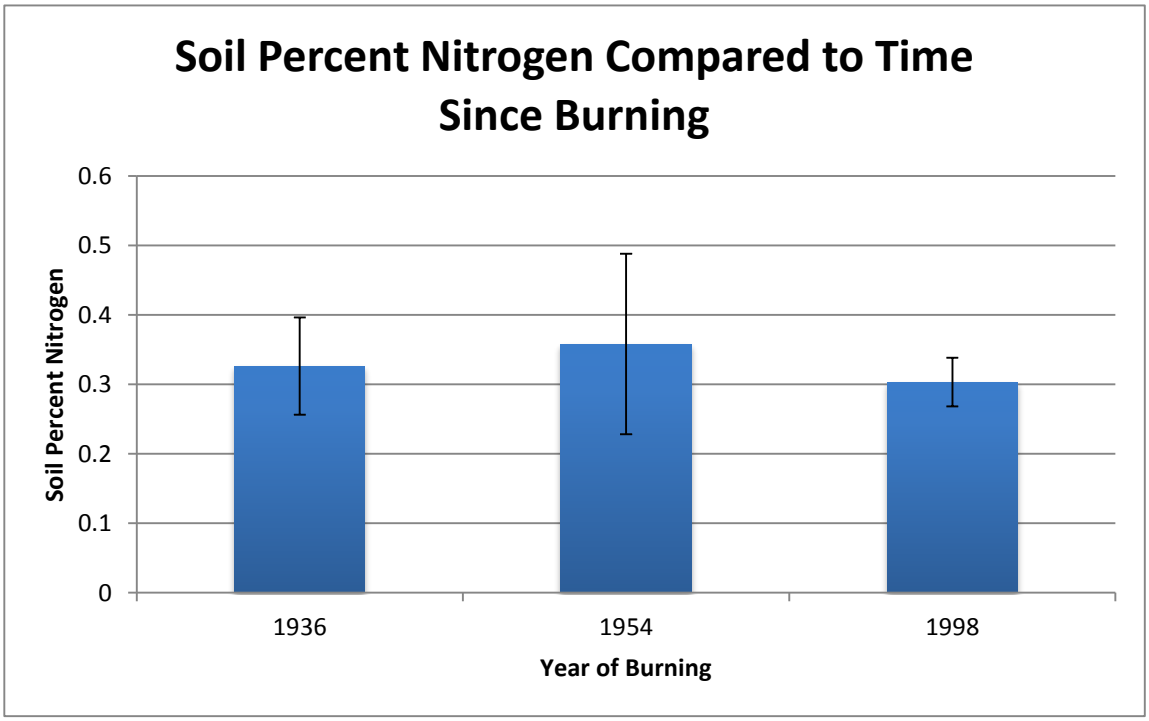

Figure 6—The average soil nitrogen percentages for each plot.

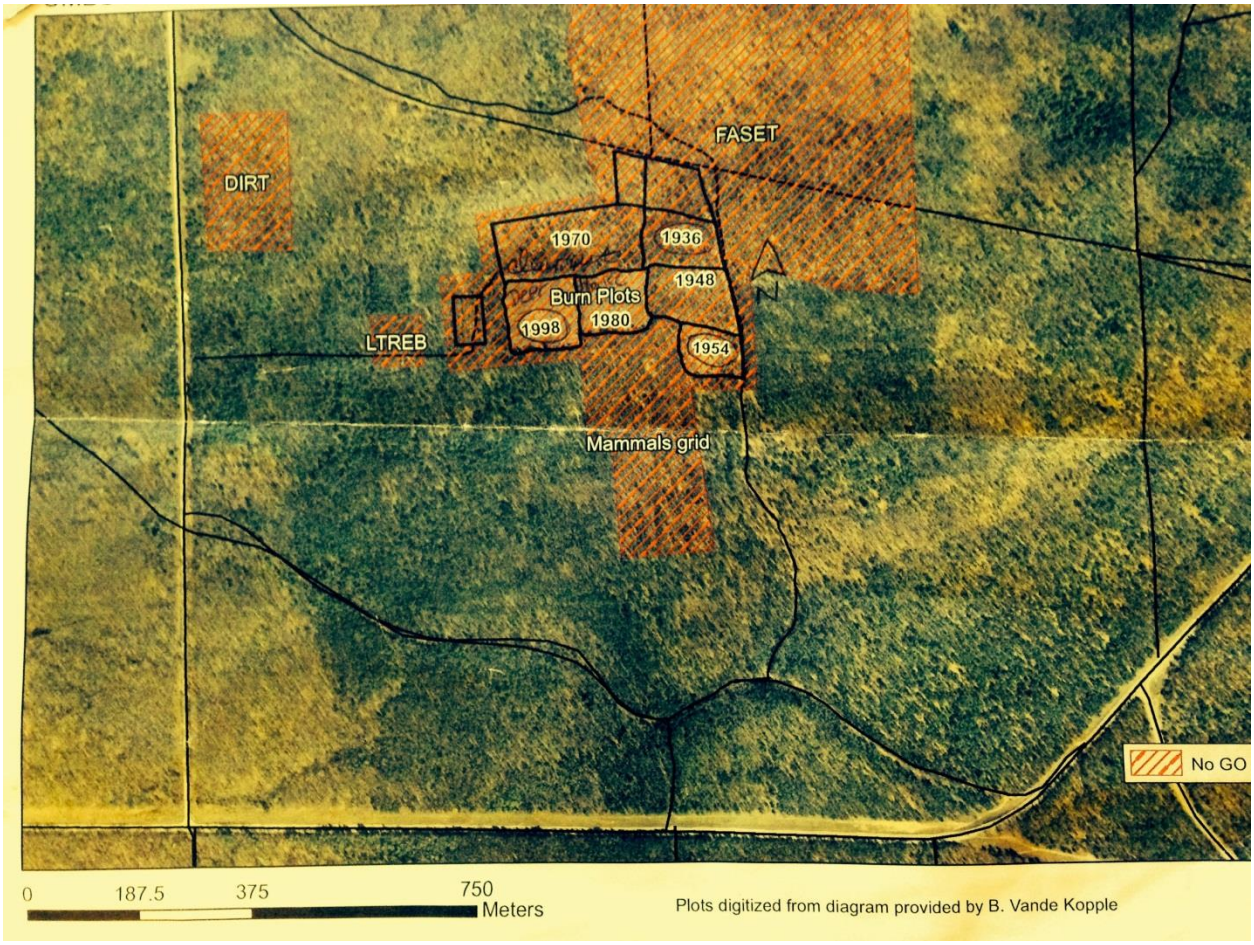

Figure 7—Burn plot layout at the University of Michigan Biological Station in Pellston, Michigan.

Tables

Shannon Index Value for Average Number of Each Species By Plot

	trial 1	trial 2	trial 3	average
1936	1.859	2.034	1.942	1.945
1954	1.81	2.017	2.025	1.951
1998	0.551	1.715	1.424	1.23

Table 1—The Shannon index value calculated for each trial then averaged for each plot.