Spatial variation in forest growth after disturbances in a northern hardwood ecosystem and its relationship with underlying environmental factors

by

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Executive summary: Disturbances can change the structure and function of forest stands. How forests respond to disturbance depends on species differences and spatially varying environmental factors. In this study, I analyzed the spatial variation in the growth of two forest stands in Hubbard Brook Experimental Forest. A calcium addition was introduced to one forest stand, and a clear-cut disturbance was introduced to the other. There are hundreds of permanent plots in each forest stand.

Basal area of each species in each plot was used as an indicator of forest growth. To analyze the relationship between forest growth and environmental factors, geographic variables (elevation, slope, aspect, distance to stream) and soil chemistry variables (carbon concentration, nitrogen concentration) were considered potentially influential in this study.

A forest stand level analysis was first conducted to measure the overall forest change during the time of interest. The calcium addition disturbance was not found to have changed the forest growth trend. The clear-cut disturbance decreased the basal area, followed by recovery at a nearly constant rate over the following 25 years. A stand level species-specific analysis revealed that there were large interspecific differences in basal area, and in basal area change. The interspecific differences in physiological properties influenced recovery.

To focus on the influence of environmental factors, I removed the interspecific differences by using a "Forest Change Index" (FCI) to indicate the forest growth condition. The FCI is calculated by summing up the standardized basal area increment of all species in a plot. The FCI measures the combined effect of richness, abundance, and mean individual tree growth. Comparing the inter-plot differences in FCI before and after disturbance, I found that spatial variation patterns to be highly persistent through time, both for calcium addition and clearcutting. After the clear-cut, the spatial variation pattern in forest growth was changed during the first two decades following disturbance, but subsequently reemerged. This result suggests that spatial reorganization with disturbance was temporary.

A regression analysis on the environmental variables shows that geographic variables control the spatial variation in forest growth. Soil carbon concentration was only significant in the clear-cut stand, while nitrogen concentration was not influential in either stand. Furthermore, a generalized joint attribute model (GJAM) analysis showed species differences in response to environmental variables, which explains the persistence in spatial variation.

The persistent spatial pattern likely resulted from nearly constant restrictions on resources. Although species composition and growth was altered by disturbance in the short term, these responses caused a convergence over time. Further research will be needed to test this hypothesis and analyze the mechanism behind the persistent spatial variation in forest growth.

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Keywords: northern hardwood ecosystem; spatial variation in forest growth; environmental factors

1. Introduction

Understanding how ecosystems respond to disturbance has long been an important research topic in ecosystem science. Disturbances affect the structure and function of ecosystems. Disturbances to the forests result from chemical factors, physical factors such as wind (Rich et al. 2010), and biological factors such as pathogens (Needham et al. 2016). Methods for studying disturbance include remote sensing (Rich et al. 2010) and field sampling (Feng et al. 2014). Studies agree that disturbance can influence the spatial structure and function of forest stands (Feng et al. 2014, Rich et al. 2010, Sapkota, Tigabu, and Oden 2009).

In this study, I analyzed the spatial variation in the growth of two experimental forest stands in Hubbard Brook long term ecological research site. Hundreds of permanent plots provide valuable information on spatial variation in forest growth, and its relationship with terrain and soil chemistry variables. Human-caused disturbances in these forest stands provide insights on forest responses. Specifically, I address two questions:

1) Is the spatial variation “pattern” of forest growth changed by disturbances?
2) Which environmental variables (hydrology, landscape, soil) are related to spatial variation in forest growth?

2. Methods

2.1 Site description

Hubbard Brook Experimental Forest (43º56’N, 71º45’W) is a bowl-shaped drainage basin at the top of Mount Kineo in the White Mountain National Forest of New Hampshire. Various studies have been conducted in different watersheds (naturally and experimentally determined) in this hardwood-conifer ecosystem since 1963 (Northeastern Forest Experiment Station 1986).

A calcium addition experiment was conducted in Watershed 1 (W1), an 11.8 ha watershed located at the northeast corner of Hubbard Brook Experimental Forest. On October 1999, 1.2 metric tons Ca/ha were added to the whole watershed (presumably evenly) in the form of wollastonite ($CaSiO_3$) pellets by helicopter (Driscoll 2000).

A whole-tree harvest experiment was conducted in Watershed 5 (W5), a 22.5 ha watershed to the west of W1, from the autumn of 1983 to the summer of 1984 (Siccama and Denny 2000). According to historical records, the forest consisted of trees that had established after an earlier cut between 1909 and 1917 (Bormann and Likens 2012).

2.2 Data description

2.2.1 Vegetation data

The vegetation inventory data were recorded on 25 m by 25 m plots. Included in the dataset are species and dbh of surveyed trees. There are 200 permanent plots in W1, and 360 permanent plots in W5.

In W1, vegetation data were collected first in 1996, before calcium addition, and then after calcium addition in 2001, 2006 and 2011. In the surveyed years, total inventories were conducted on trees >= 10cm dbh in selected plots, while trees >=2 to <=10cm dbh were only sampled in certain areas in those plots (Battles 2015a, b, Driscoll 2015a, b). In W5, vegetation data were collected before harvest on 1982, and after harvest on 1990, 1994, 1999, 2004 and 2009. In 1982, a total inventory was conducted on trees >= 10cm dbh, while trees >=2 to <=10cm dbh were only sampled in 42 of the 360 plots (Battles 2015c). In subsequent years, trees >= 1.5cm dbh were sampled in certain areas of the selected plots (Battles 2015d, e, f, Battles 2016a, b).

To compare forest growth, basal areas (BA) were calculated for trees > 2cm dbh.

2.2.2 Soil chemistry data

To analyze the relationship between soil chemistry properties and forest growth, I analyzed data on percent carbon (%C) and nitrogen (%N) in soil samples in each plot. In W1, %C and %N data were collected before calcium addition in 1996 and 1998, and after disturbance in 2000, 2002, 2006 and 2010 (Johnson 2016). In each surveyed year, the number of surveyed plots and the locations of soil pits in those plots were selected at random (between 58 to 101 plots per surveyed year, one pit in each surveyed plot).

In W5, %C and %N data were collected before harvest in 1983, and after harvest in 1986, 1991 and 1998, using the quantitative soil pit method (Hamburg 2016). In all surveyed years, the surveyed pits were located at the same 60 plots, distributed evenly in W5. For analysis on the relationship between environmental variables and forest growth, the soil chemistry data were matched with the closest year having vegetation data.

2.2.3 Geospatial data

Elevation, slope, aspect and distance to stream were used in this analysis to indicate the terrain related properties of plots. These geospatial data were generated with ArcGIS (ESRI 2015), based on the 10m DEM and GIS shapefiles for hydrology and watershed boundary, as well as the plot maps of W1 and W5 (Campbell 2016a, b, c). For W1, elevation, slope and aspect were obtained from a 10m DEM. Distance to stream was obtained as the Euclidean distance to the nearest stream. For W5, due to the unavailability of coordinate information of plots, only elevation data were used.

2.3 Watershed wide analysis

2.3.1 Forest growth

Total basal area and mean total basal area were calculated to indicate the general forest growth condition in W1 and W5 during the time of interest, as well as forest change after disturbances.

Total basal area of each plot was calculated as

$$TBA_{i,j} = \sum_{k} BA_{i,j,k}$$

where $TBA_{i,j}$ is the total basal area of plot i in year j, and $BA_{i,j,k}$ is the basal area of species k in plot i in year j.

Mean basal area of all plots in each surveyed year was calculated as

$$Mean(TBA)_j = \sum_{i} TBA_{i,j}/I_j$$

where $Mean(TBA)_j$ is the mean total basal area in year j, and I_j is the number of plots surveyed in year j.

2.3.2 Interspecific difference in forest growth

To compare the post-disturbance growth conditions of different tree species, the average basal area of observed species was calculated as

$$Mean(BA)_{j,k} = \sum_{i} BA_{i,j,k}/O_{j,k}$$

where $Mean(BA)_{j,k}$ is the average basal area of species k in year j, $O_{j,k}$ is the number of plots that have observations of species k in year j.

2.4 Plot unit analysis

2.4.1 Inter-plot variation in forest growth

To compare the forest growth across plots, the basal area differences of the same species between successive years were calculated. In this study, plots within the same watershed are nearly even-aged, and are assumed to be exposed to similar degrees of external (experimental and natural) disturbances during the time of interest. Therefore, the spatial variation in the forest growth is attributed either to the plot-related environmental variables or to species differences.

Survival and growth rates differ by species. To average across species, I calculated basal area increments, and then standardized by minimum and maximum values for each species (Jain, Nandakumar, and Ross 2005). This method will transform the original data to a range of [0,1], where the maximum basal area difference for a species is transformed to 1, and the minimum difference is 0. The summed values are my “Forest Change Index” for each plot,

$$Dif(BA)_{i,j+1,k} = BA_{i,j+1,k} - BA_{i,j,k}$$

where $Dif(BA)_{i,j+1,k}$ is the difference between the basal area of species k in plot i in year j+1 and that of the same species in the same plot in the previous surveyed year,

$$StdDif(BA)_{i,j+1,k} = \frac{Dif(BA)_{i,j+1,k} - \min_{l \in P_{j+1,k}} Dif(BA)_{l,j+1,k}}{\max_{l \in P_{j+1,k}} Dif(BA)_{l,j+1,k} - \min_{l \in P_{j+1,k}} Dif(BA)_{l,j+1,k}}$$

where $P_{j+1,k}$ is the set of plots that have observations of species k in either year j or year j+1, $StdDif(BA)_{i,j+1,k}$ is the standardized basal area difference of species k in plot i between year j and year j+1.

$$FCI_{i,j+1} = \sum_{k} StdDif(BA)_{i,j+1,k}$$

where $FCI_{i,j+1}$ is the forest change index of plot i between year j and the next surveyed year, j+1.

Plots showing higher FCIs are considered to have higher forest growth, in a sense of higher richness, higher abundance or higher average basal area increment. The logic in this algorithm is that during the same time period, assuming other species to be the same, the plot where a species has the highest BA increment shows higher growth than other plots where the same species has lower BA increment; the plot where two species have the highest basal area increment shows higher growth than the plot where only one species has the highest basal area increment; the plot where two species have the second highest BA increment may have grown more than the plot where one species has the highest BA increment; the plots where a certain species was not present are not included in the comparison with other plots having the same species, due to the lack of information.

2.4.2 Environmental variables related to the forest growth

To analyze the correlation between environmental variables and the spatial differences in forest growth, I first conducted a linear regression of FCI. For W1, both soil chemistry variables, geospatial variables, and year (as a factor to indicate the random disturbances including climate) were used as predictors. For W5, only soil chemistry variables, elevation and year were used as predictors. An ANOVA (analysis on variance) on each linear regression was used to determine if environmental variables were related to FCI.

To analyze relationships with environmental variables, I used generalized joint attribute model (GJAM). The advantage of GJAM over other species distribution models is that it combines information of all species in a synthetic prediction with full uncertainty (Clark et al. 2016). For W1, both soil chemistry variables and geospatial variables were used in the model as predictors. GJAM analysis was not conducted for W5, due to the limited data.

3. Results

3.1 Overall forest change over years

In both W1 and W5, the total basal area of each plot in surveyed years are nearly normally distributed, with only a few outliers in certain years (Figure 1). Large inter-plot basal area differences exist in all years, but the variances differ.

In W1, mean basal area of all plots increased from 1996 to 2011, but without significant change after disturbance. In W5, the mean basal area of all species in all plots declined significantly after clear-cut disturbance in 1983 to 1984, and increased after disturbance from 1990 to 2009.

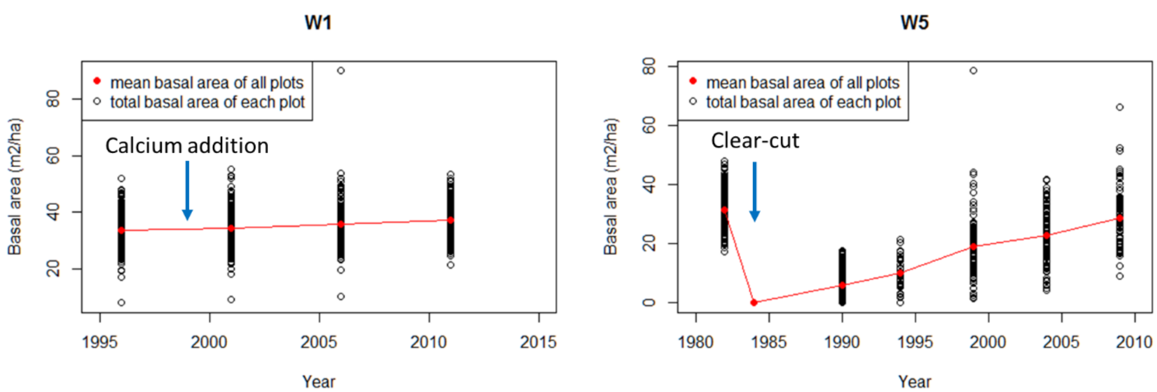

Figure 1. Total basal area of each plot, and the mean basal area of all plots in each surveyed year in W1 and W5

There were large interspecific differences in mean basal area in both W1 and W5 (Figure 2). Especially in W5, some species decline with the clear-cut and recovered afterwards (e.g. *Acer saccharum*). Some increased following this disturbance, but may have been outcompeted by other species (e.g. *Prunus pensylvanica*). Some species disappeared after the harvest. Richness of species in W5 decreased after harvest, but has been recovering since.

In W1, richness of species is nearly constant. The basal area of most species increased steadily.

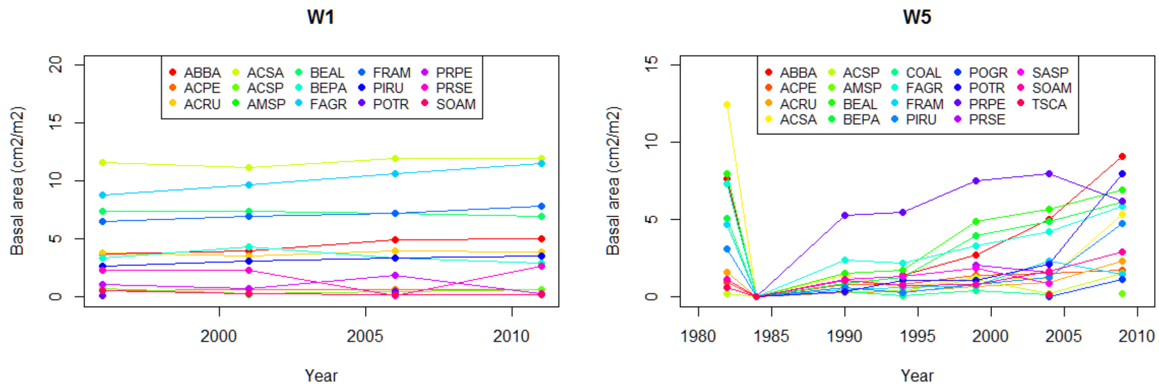

Figure 2. Mean basal area of each species in each surveyed year in W1 and W5

Based on this part of analysis, I analyzed separately pre-disturbance and post-disturbance data for W5 considering the discontinuity in the basal area data. The pre-disturbance and post-disturbance W1 data were analyzed together. Also, it proves the necessity of isolating the species factor in the plot-unit analysis, considering their distinct basal area value and varying response to disturbances.

3.2 Inter-plot forest change comparison

The FCI (min-max standardized basal area increment, summed over species) shows the spatial variation in forest growth. Plots with higher FCI values (higher forest growth) were dyed in warmer (redder) colors, and plots with lower FCI values (lower forest growth) were dyed in colder (bluer) colors.

In addition, to check the spatial variation in forest growth during a longer period, the basal area data of the initial surveyed years in W1 and W5 were processed as basal area difference data to generate pseudo FCIs, which indicate the forest growth since the previous clear-cut in this area (at around 1910).

In W1, the constancy in spatial variation “pattern” is supported by the similar color patterns in maps of forest growth in different periods (Fig. 3). Plots that have shown higher forest growth since around 1910 keeps growing faster in later periods. The constancy is not disrupted by the calcium addition disturbance.

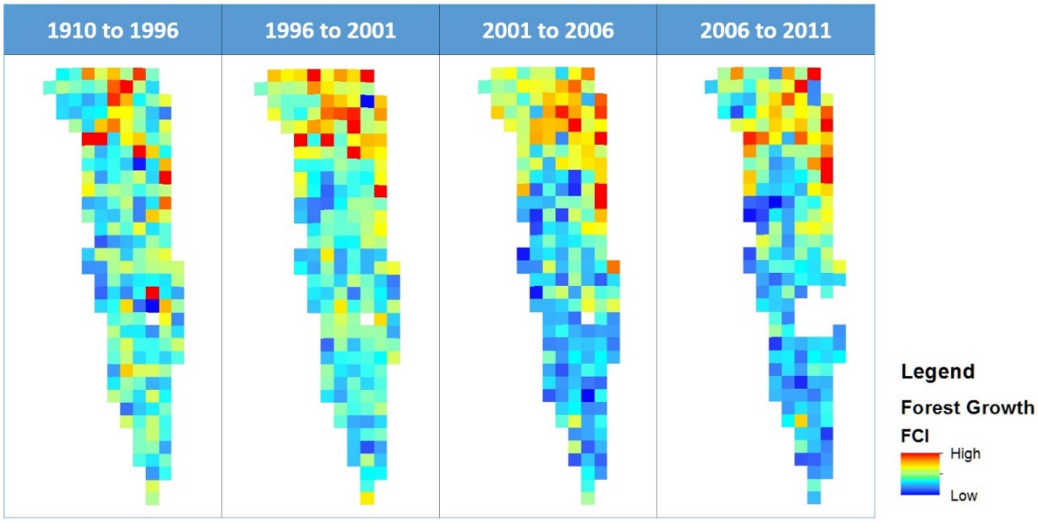

Figure 3. Plot maps of the spatial variation in forest growth over time in W1, indicated by FCI

In W5, however, the lack of data caused the maps to miss a lot of details (Fig. 4), and added to the difficulty in comparing the color patterns in different maps. But still, there seems to be a growing trend for the plots that have shown higher forest growth between two clear-cuts (from 1910 to 1982) to stick out in later periods. Few similarities in color patterns between the 1910 to 1982 map and the 1990 to 2004 maps were observed, but the color pattern in the 2004 to 2009 map became identifiably similar to that in the 1910 to 1982 map. A possible explanation is that the clear-cut disturbance is powerful enough to disrupt the constancy in spatial variation in the first few decades, but the original spatial variation "pattern" gradually recovered with the recovery of the forest stand.

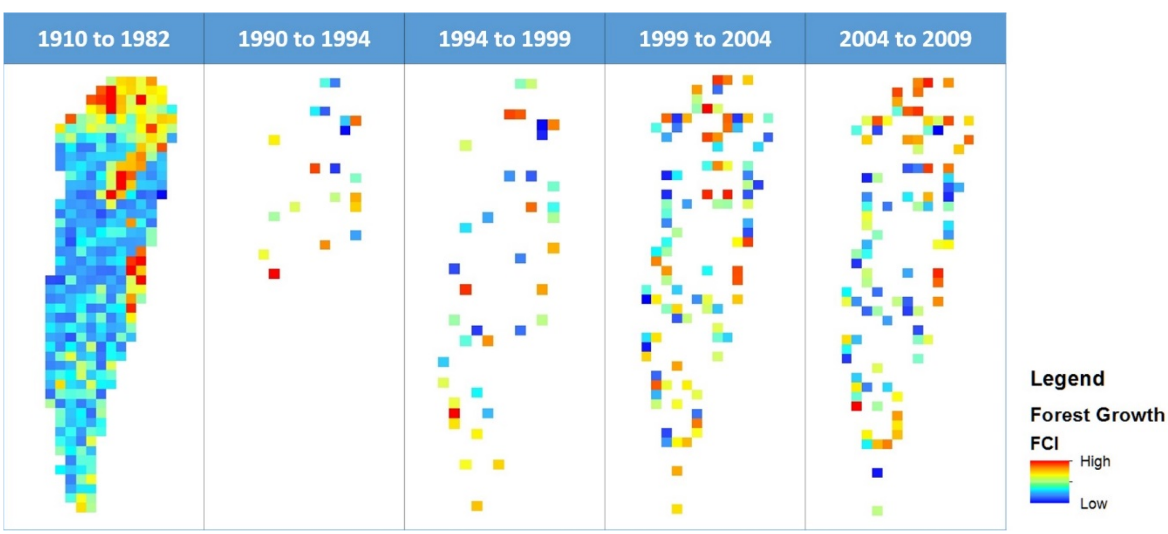

Figure 4. Plot maps of the spatial variation in forest growth over time in W5, indicated by FCI

3.3 Correlation between environmental factors and forest change

Linear regression models were built to analyze which environmental variables are significantly related to the spatial variation in forest growth, and how much of the variation can be accounted for by these variables combined.

For W1 data (Table 1), all geographical variables show significant influences on FCI ($P < 0.05$), among which elevation and distance to stream seem to be the most influential. Soil chemistry variables are not significantly related to FCI ($P > 0.05$).

For W5, soil carbon concentration (%C) is more influential than other variables. Elevation is also significantly related to FCI ($P < 0.05$), while soil nitrogen concentration (%N) is barely significant ($P < 0.1$). The increased correlation between soil carbon and forest growth may result from the higher decomposed below-ground biomass (remnants of the clear cut) in plots that were previously more prosperous.

The high degree of freedom (F value) and low P value of the year factor in both models indicate that the random external disturbances (e.g. precipitation, snow storm occurrence) are significantly influential on the spatial variation in forest growth.

Table 1. ANOVA on the environmental variables and the forest change index in W1 and W5

	W1			W5		
Formula	FCI ~ Elevation + Distance to stream + Easterness + Northerness + Slope + %C + %N + factor(Year)			FCI ~ Elevation + %C + %N + factor(Year)		
	d.f.	**F value**	**P value**	**d.f.**	**F value**	**P value**
Elevation	1	199.92	0	1	5.31	0.024
Distance to stream	1	26.89	0			
Easterness	1	4.66	0.031			
Northerness	1	7.14	0.008			
Slope	1	5.77	0.017			
%C	1	0.56	0.456	1	22.81	0
%N	1	0.8	0.372	1	2.96	0.089
factor(Year)	3	188.95	0	4	47.37	0
Residuals	459			82		
	$R^2 = 0.639$			$R^2 = 0.729$		

The coefficients calculated by the linear models are not listed, to avoid an oversimplified conclusion that a certain variable can positively or negatively influence the forest growth. To understand the effect of each environmental variable, it will be necessary to look at each species separately. Therefore, a generalized joint attributes model (GJAM) was built using environmental variables as predictors and basal area data of each species as responses.

The GJAM analysis shows that different species respond differently to all variables. Some species have negative coefficients with distance to stream while the other species have positive coefficients. This means some species show higher basal area with decreasing distance to streams, while some species have a deceased basal area when getting closer to streams, which may be resulted from the physiological differences. Also, species respond differently to other environmental variables such as slope and aspect.

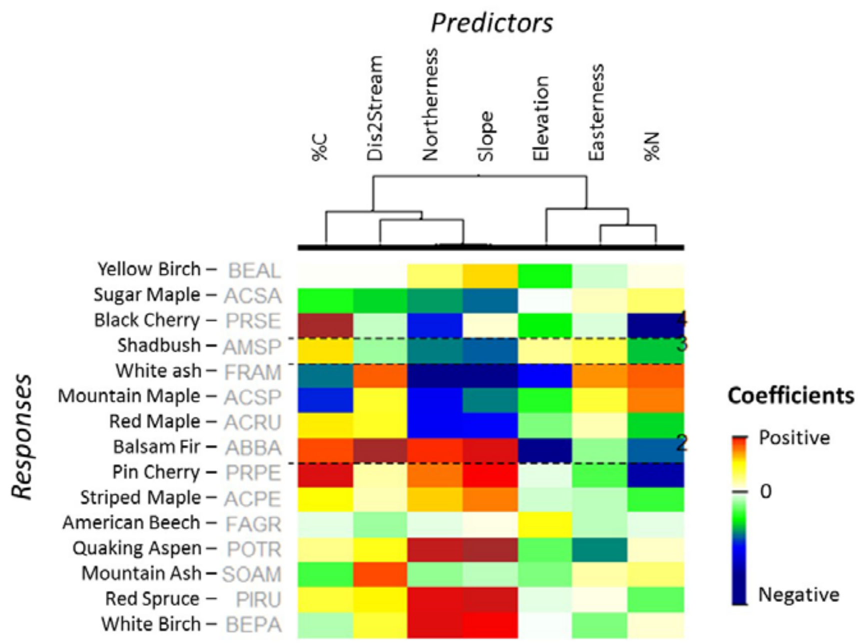

Figure 5. GJAM outputted coefficients between environmental factors and basal areas of different species in W1

Overall, this part of analysis indicates that the nearly constant resource differences determined by environmental factors in each plot may be the main cause of the spatial variation in forest growth. The combination of resources (i.e. light, water, nutrients) varies in different plots, due to the variation in environmental factors. Consequently, the species composition varies to make the best use of the resources, considering different species prefer different environmental factors. When the forest stands reach a steady state of growth (which is when the stands recovered from disturbances in this study), the species composition has become efficient enough to nearly maximize the resource use. Thereafter, species richness and abundance in each plot can still vary, but will keep in accordance with the resource restrictions.

4. Conclusions

Through the analysis on forest growth and its spatial variation before and after disturbances, the first research question is answered. After a calcium addition, the spatial variation in the forest growth was not significantly influenced. The plots with higher forest growth in the past kept on supporting higher forest growth afterwards. When a clear-cut occur, the spatial variation in forest growth can be temporarily changed, indicating a high magnitude disturbance can disrupt the constancy in the spatial variation. But the original spatial variation pattern in forest growth tend to recur with the recovery of the forest. Generally, the prosperous plots are more likely to prosper, regardless of the disturbances.

The second research question on the relationship between forest growth and the environmental variables is partly answered. The geographic variables are significantly related to the spatial variation in forest growth, while soil carbon is only significantly influential in the W5 model. Soil nitrogen is barely influential.

In addition, different species show varying responses to different variables. Therefore, it is hard to determine if any variable has a positive or negative effect on the forest growth. Rather, the nearly constant resource differences determined by environmental factors in each plot may be the cause of the inter-plot variation in forest growth.

Doubts with the conclusions may exist because 1) the algorithm used in the inter-plot comparison (the reasonability of FCI) is not statistically tested; 2) the lack of data in the analysis on W5 plots may decrease the credibility of the conclusions. Further research with large, complete datasets will be needed to fully understand how the post-disturbance spatial variation in forest growth is formed, and to explain why the spatial variation pattern is highly persistent.

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