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Local Ecology Research Papers

Analysis of colonization, growth and mortality within a 30 year maple-basswood forest restoration study in the St. Olaf Natural Lands

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Changes in tree composition and growth in a 30 year old maple-basswood forest restoration

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Abstract

There have been few long term studies of the effectiveness of forest restoration methods. A study of maple-basswood forest restoration on two adjacent formerly agricultural fields within the range of the former Big Woods in southeastern Minnesota, USA began in 1990. Trees planted in 1990 were measured every 2-4 years for 30 years. In 2020, *Fraxinus americana* (white ash) was the most common tree, followed by *Juglans nigra* (black walnut) and *Quercus macrocarpa* (bur oak). Of original trees, *Quercus rubra* (red oak) was tallest on average (17.415m), followed by *F. americana* (13.933m), then *Tilia americana* (basswood) (13.607m). Total mortality of original trees since 1990 was 44.09%, averaging 1.92% of original trees dying yearly. Colonizing trees have been measured since 2013. Colonizers nearly equaled the number of original trees which had died since 1990, increasing species diversity. Since 2013, there have been increasing differences in colonizing tree species, mortality rates and tree size. Total annual average mortality has increased in the prevailing 7 years from 1.74% in 1990-2013 to 2.52% in 2013-2020. Since 2013, the prevalence of *Acer saccharum* (sugar maple), *Ulmus americana* (American elm) and *T. americana* has increased. 42.6% of *U. americana* and 40% of *A. saccharum* colonizers, both shade tolerant, emerged in the last three years, making them the most prolific colonizers as the forest matures. These changes, as the canopy closes and shade intolerant tree mortality increases, suggest the restoration is at a turning point, about to move beyond an early successional forest to a young mature forest.

Introduction

The goal of a restoration effort is to create an ecosystem that is self-sustaining and can survive with very little human influence, which is typically best accomplished by understanding the environmental factors of the site. There has been more research and discussion surrounding the goals of habitat restoration efforts than on the overall results or their effectiveness. In order for a restoration to be successful, it must be self-sufficient with very little outside input while under novel pressures and disturbances, from global warming to invasive species (Hobbs and Cramer 2008). Following this idea, a restoration was planted in the St. Olaf College Natural Lands in southeastern Minnesota, USA in 1990. In order to facilitate more rapid colonization and succession, all the desired species of a maple-basswood forest were planted simultaneously (Shea and Helgeson 2018). This paper will examine how the forest has changed since 2013 when colonizing trees were first measured.

As a forest matures, the composition of trees shift away from the initial colonizing species towards later stages of successional trees. In maple-basswood forests, less shade tolerant trees, such as *Quercus macrocarpa* (bur oak), *Quercus rubra* (red oak) and *Juglans nigra* (black walnut) are replaced over time with more shade tolerant trees, first by *Fraxinus americana* (white ash), then soon followed by *Acer saccharum* (sugar maple), *Tilia americana* (basswood), and *Ulmus americana* (American elm) (Smith 2008, Bray 1956). This occurs because maple-basswood forests follow gap-phase replacement strategies once the canopy closes, wherein the shade tolerant saplings and seedlings outcompete the shade intolerant competitors

(Bray 1956). Based on observations in 2013, a previous study of the restoration by Shea and Helgeson (2018) determined the canopy was beginning to close. 2013 was also the first year colonizing trees were measured in the restoration. Trees which had colonized the transects had either spread from surrounding older enclaves of forest nearby or from reproduction and replacement taking place within the restoration (Hewitt et al. 2019).

Additionally, mortality is another good indicator of changing forest composition. As a forest matures and the canopy closes, the mortality rates of older trees change to reflect the dwindling availability of sunlight. Studies have found that oak in particular is choked out in maturing forests and lags behind more shade tolerant trees (Craig et al. 2014). Therefore, as the forest matures, the more shade intolerant species will increase in their annual average mortality compared to species which are more shade tolerant. On the other hand, late successional species (which are generally shade tolerant) will have high mortality rates as saplings before the canopy is established, leveling off when the canopy closes (Lorimer et al. 2001).

The aim of this study was to examine the changes in composition, mortality and tree measurements over a 7 year period between 2013 and 2020 in a thirty year old restoration.

Methods

The restoration was planted in 1990 in two formerly agricultural fields (Section 1 and Section 2) within the St. Olaf College Natural Lands in Northfield, Minnesota, USA (44°27'36" N, 93°11'25" W). Diameter at the base and height of these original trees were measured every two to four years in a series of 0.1 ha (14x75m) transects across the two fields. Once tree seedlings were tall enough (1.37m), their diameters were measured at breast height instead (DBH). Beginning in 2013, trees ($\geq$ 2.5 cm DBH) which had not been originally planted but had colonized the restoration area were measured as well. In 2017 and 2020, new colonizing trees were measured and added when they met this criteria.

When examining mortality, original trees which had been identified as something other than what they had originally been listed as were included in the original species that they were misidentified as. The formula used to calculate average annual mortality for original trees was as follows (Lorimer et al. 2001):

$$M = 1 - [(N_t/N_0)^{1/t}]$$

Shannon and Simpson's diversity indices were used to calculate diversity in Field 1 and Field 2 and across the whole restoration in 1990, 2013, and 2020. 2013 and 2020 included colonizing trees in their diversity indices. Pairwise t tests were used to calculate significance of changes in diversity.

Results

Mortality

Since 2013, there have been increases in the mortality rates of original-planting shade intolerant species. By examining the average mortality rates over the previous 7 years and comparing it to the thirty year average, we saw this shift in mortality patterns. *J. nigra*, a well established tree in the restoration, had an increase in its average annual mortality of 1.61% over the last 7 years in comparison to the overall thirty year average (Table 1). *Q. macrocarpa* in particular had large amounts of mortality since 2013. Its average annual mortality rate increased 2% from its thirty year average. *Acer rubrum* (red maple) had the highest increase in mortality rate when examining the change since 2013, increasing by 2.70%. All three of these species are intolerant of shade, and were also planted originally in the restoration in large numbers. Other species with fewer original trees that increased their average mortality in comparison to the thirty year average include *Ostrya virginiana* (ironwood), *Prunus serotina* (black cherry) and *Prunus americana* (wild plum). *P. serotina* and *P. americana* are intolerant of shade, while *O. virginiana* is extremely tolerant of shade.

Since 2013, the average annual mortality rate of several other originally planted species has decreased. *Q. rubra* fell slightly from a 30 year average of 1.43 % to a 1.05 % 7 year average (Table 1). *A. saccharum*, *F. americana* , and *Quercus alba* (white oak) all decreased even more so in their average annual percent mortality in the last seven years. In the last 7 years, no *T. americana* have died or went missing, giving it a 0 overall annual mortality rate since 2013. All of these species were planted in large numbers in the restoration. *F. americana* is somewhat shade tolerant, while *A. saccharum* and *T. americana* are both shade tolerant (Smith 2008).

Diameter and Height

Since 2013, in original trees, both *A. saccharum* and *J. nigra* have surpassed *Q. macrocarpa* in average height. Canopy cover across the restoration increased from 2015 to 2020, from 90.60% to 96.425%. Canopy cover increased most in Section 2 of the restoration. Amongst original trees, *Q. rubra* (25.196 ± 1.629cm), *T. americana* (18.225 ± 1.963cm), and *Q. alba* (15.621 ± 0.488cm) are the trees with the largest average DBH in 2020 (Figure 1). *Q. rubra* had the tallest average height, 17.415 ± 0.277m, *F. americana* had the second tallest,13.933 ± 0.219m, and *T. americana* had the third tallest height, 13.607 ± 0.781m.

Over time, *Q. rubra*, *Q. alba*, and *F. americana* were the first to accelerate their growth above other trees, distinctly grouping them ahead of the other common trees in the restoration (Figure 2). *Q. macrocarpa* has steadily fallen to the shortest average height of the common trees in the restoration, as *A. saccharum* and *J. nigra* surpass it.

Diversity, Composition and Colonization

In both 2013 and 2020, *F. americana* was the most prolific colonizing species. In 2013, 34.60% of all colonizing trees were white ash (Table 2). The second most frequent colonizing species in 2013 was *Acer negundo* (boxelder), 15.20%. The third most common colonizers in 2013 were *Q. rubra*, 9.00%. The composition of colonizers has changed since 2013. Since 2013, there have been increasing numbers of *U. americana* and *A. saccharum* colonizing the transects. *U. americana* replaced *Q. rubra* as the third most common colonizing species in 2020. Different species of elm were differentiated for the first time in 2020, prior to which they had been labeled as *U. americana*. Furthermore, *Carya cordiformis* (bitternut hickory) and *Juglans cinerea* (butternut) were identified for the first time in 2020, although *C. cordiformis* had previously been misidentified as other species of tree in 2013 and 2017.

Diversity across both Sections 1 and 2 increased from the original planting to 2013 and increased further from 2013 to 2020 (Table 3). The Simpson's diversity of the restoration for 2013 ($t_\infty = 2.431$, $p < 0.05$) and 2020 ($t_\infty = 2.990$, $p < 0.05$) were both significantly different from 1990's diversity, according to pairwise t tests. However, the diversities of the restoration in 2013 and 2020 were not significantly different from one another. The diversity of colonizing species was significantly greater from 2013-2020 than in 1990-2013 ($t_\infty = 2.216$, $p < 0.05$). Both periods of colonization were more diverse than the original planting in 1990.

Discussion

Colonizers and Composition

For analyzing colonizers, all new trees recorded in 2013 were taken to represent all colonizers over a 23 year period, since 1990. New trees found in 2017 and 2020 were combined to represent the colonizing trees since 2013, over a 7 year gap. Colonizing trees in transect 17 were measured for the first time in 2020. This may explain the proliferation of *Populus tremuloides* (quaking aspen) as a common colonizer in the last seven years. Since transect 17 contained new trees which had grown in the last thirty years, many colonizers in 2020 could have been measured in 2013. This could have inflated numbers of trees like *P. tremuloides*, of which most of its colonizing individuals found in 2020 were solely in transect 17.

F. americana was by far the most prolific colonizer of the transects, and makes up a majority of the trees within the restoration. Studies have found that air bound dispersal colonizing species tend to be the most prolific colonizers, which could explain why white ash and American elm have had so many new trees emerging in the restoration (Gardescu and Marks 2004). Some of these seeds were likely blown in from reservoir populations surrounding the restoration (Hewitt et al. 2019). However, the huge numbers of *F. americana* colonizers show that the population of white ash within the restoration is likely self-sufficient and reproducing. *F. americana* and other fast colonizing plants tend to be found in greater numbers in new fields, as compared to old growth forests (Singleton et al. 2001).

The high numbers of new *P. americana* are likely due to the already established population replacing itself, as plum is not a long lived tree and quickly begins fruiting (Smith 2008). Other trees, such as basswood and aspen, use sucker strategy to spread themselves, which could explain why they increased in colonization as their colonizers and original trees became established and were then able to reproduce in this method (Gardescu and Marks 2004).

Overall, the differences in colonizing species between 2013 and 2020 are important as trees less tolerant of shade have decreased their share of the colonizing trees. This is likely due to the closing canopy, as canopy cover was observed to have increased between 2015 and 2020 across both sections of the restoration. The average canopy coverage across the restoration increased from 90.60% in 2015 to 96.425% in 2020. The differences in colonizing species has furthermore been reflected in the changes of the overall forest composition as more shade tolerant trees have become increasingly prevalent in the restoration. Furthermore, novel colonizing species that were not originally planted, such as *C. cordiformis* and *U. americana* have contributed to the increasing biodiversity within the transect. These trees in particular are a part of the historical composition of remnant Big Woods ecosystems, which makes their appearance within the restoration significant (Daubenmire 1936).

Mortality and Tree Growth

The average annual mortality rates since 2013 of *A. rubra* and *J. nigra* are higher than their average annual mortality rates between 1990 and 2020. This shows both these species are dying off in higher numbers in the last 7 years than in the years prior (Table 1). Typically, it is the smallest trees of these species that have been disappearing or dying. Their growth had been stunted, and they remained below 1.5 m in height for over two decades, before finally being shaded out by the growing height of the rest of the canopy. This is why even though they have been dying at increasing rates, their original trees' average DBH has increased since 2013. Since the smaller trees are dying off, this increases the averaging weight of the larger trees that survived, resulting in their overall species greatly increasing in diameter over the last three years. Both *A. rubra* and *J. nigra* had some of the highest increases in their mortality rate over the last 7 years of any of the well established original trees. Neither of these trees are shade tolerant (Smith 2008).

Original *Q. macrocarpa*'s 7 year average annual mortality rate is much higher than its 30 year average, by 2% (Table 1). This is reflected by how its height and DBH have barely changed since 2013 as well. Overall, this species of tree appears to be at the beginning of a steep decline, as it is rapidly falling behind other species, such as *J. nigra*, *F. americana*, and *Q. alba* in height, to name the other most common species in the transects. During field measurements, we rarely observed a bur oak that looked healthy, and the data shows they have stalled in growth and increased in their mortality in comparison to other species (Table 1). Bur oak is extremely intolerant of shade and is slow growing, which has resulted in the more shade tolerant trees outcompeting it as it falls below the canopy line (Smith 2008). This is likely why their mortality has increased in recent years as the rest of the canopy closes around them and they fall behind other trees (Craig et al. 2014). Historically, on forest-prairie edges, fire was the main system to prevent shade tolerant species colonization, however, since this disturbance no longer occurs in the restoration, it is beginning to attain the composition of a more mature maple-basswood forest (Grimm 1984). This is supported by Figure 2, as *Q. macrocarpa* has now become the shortest common tree in the restoration on average. This leads to it being frequently shaded out by the other trees that are now outpacing it in terms of height.

Finally, the reason many shade tolerant species, such as *A. saccharum*, had high mortality rates to begin with is because they are late successional gap-phase replacement trees. Studies have found that trees which follow this reproductive strategy of being late successional gap-phase replacement trees, outlined in Bray (1956), tend to have high mortality rates early on.

Until the forest is established as mature, the saplings of these seeds have high mortality rates, before leveling off and dominating the overall colonizer composition (Lorimer et al. 2001). This again supports the idea that the decrease in the average annual mortality rates in the last 7 years for *A. saccharum* and *T. americana* coincide with increasing canopy coverage across the restoration.

Despite its decreasing mortality, *A. saccharum* is still smaller on average in DBH and height than less shade tolerant species in the restoration, such as *F. americana*, *Q. alba* and *Q. rubra* (Figure 1). Although, since these less tolerant trees are now established in the canopy, they create the shade necessary for *A. saccharum*, *U. americana* and *T. americana* to outcompete any new seedlings from other species in gap-phase replacement (Bray 1956). We see that the three tallest trees have long been the tallest trees on average in the restoration (Figure 2). Only now, in the last seven years, are shade tolerant trees, such as *A. saccharum* beginning to grow taller than less tolerant trees like *Q. macrocarpa*. With the establishment of the canopy, we will likely see a similar growth spurt in *A. saccharum* in the coming years as was seen in the current tallest trees 15-20 years ago. It is likely that *A. saccharum* will begin to catch up in size to the other trees in the restoration, now that *F. americana* and *Q. alba* have provided the perfect environment for *A. saccherum* to emerge into the canopy.

Conclusions and Looking Ahead

Overall, throughout the restoration, since 2013, we have seen a trend of more shade tolerant species decreasing in mortality, increasing in diameter and increasing in colonizers. Amongst these species which are becoming more established in the restoration are principally *F. americana*, *A. saccharum*, and *U. americana*. *F. americana* mainly occurs in Minnesota forest canopies in mid to late successional states, often behaving as a climax species (Smith 2008). As the forest is maturing, especially in the last seven years, the canopy is closing and the less shade tolerant species, such as *Q. macrocarpa*, *J. nigra* and *A. rubra* are being slowly pushed out. Light tends to be the limiting factor of a species' overall success in a forest as it matures (Craig et al. 2014). Our results confirm this is likely the case for trees in both Fields 1 and 2 as the forest composition shifts to be more tolerant of shade.

One worry moving forward is the impact of emerald ash borer on the composition of the forest. *F. americana* being the most common species of tree is problematic, as studies have found emerald ash borer to decimate ash populations on its first introduction to a region (Engelken et al. 2020). Currently EAB has infested Farmington and Faribault, Minnesota (Minnesota Department of Agriculture 2021). This places EAB under 15 miles away from the restoration. This is especially problematic as shade tolerant species are reliant on the large amount of canopy shade provided by mostly *F. americana*. If 36% of the forest disappeared, it is unlikely that the other canopy species, such as basswood, white oak, red oak, and black walnut would be able to compensate for the loss in shade to facilitate shade tolerant species' growth and colonization (Singleton et al. 2001). Climate change is another factor which is concerning in regards to the success of the restoration (Hobbs and Cramer 2008). This may affect seedling growth patterns and may already reflect the prevalence of *F. americana* colonization in the restoration. It will likely alter growth and colonization patterns, and could drastically alter the canopy environment in years to come.

However, despite these risks, the forest composition is increasingly shifting towards a more shade tolerant, more mature forest, meeting part of the restorations' goals. Several species within the transects appear to be able to sustain and even increase their populations through colonization and low mortality rates: *F. americana*, *T. americana* and *A. saccherum* (Table 1, Table 2). Since 2013, several novel species have emerged, such as *C. cordiformis* and *U. americana* (Table 2). These trees historically made up maple-basswood forests and are now colonizing the restoration in large numbers (Daubenmire 1936). Overall, with the increasing frequency of *A. saccherum*, *T. americana*, *U. americana* and *C. cordiformis* colonizers, the future forest composition will likely represent a present day Big Woods forest ecosystem. Since 2013, the forest has become more diverse and the shade intolerant species which were part of the dominant make-up of 2013's observations, such as *Q. macrocarpa* and *A. negundo* are dying off. We predict these trends will continue as the forest begins to mature into a successful, self-sufficient restoration, meeting the original goals of the project and helping to preserve the maple-basswood forests of southern Minnesota.

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Tables and Figures

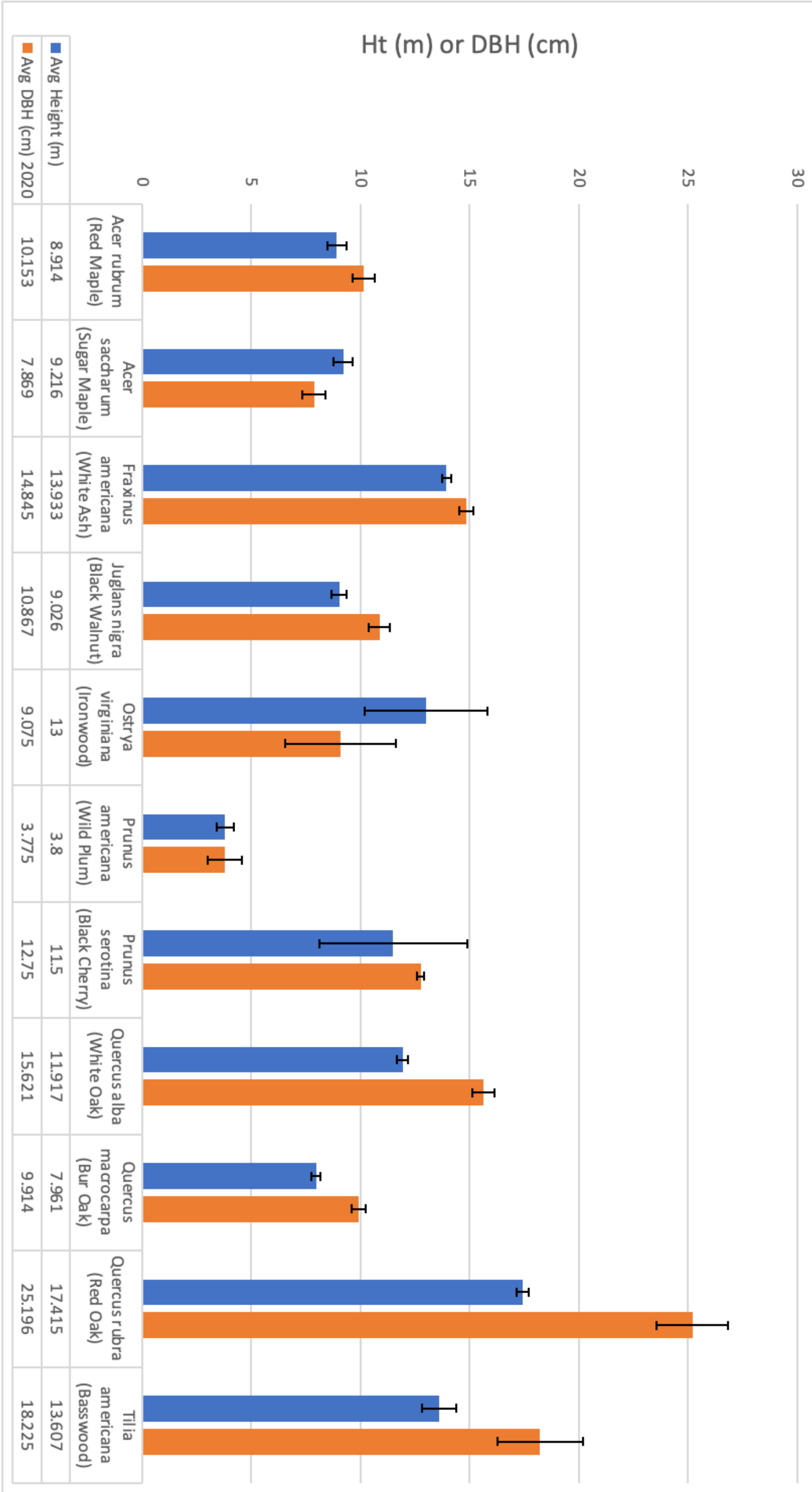
Ht (m) or DBH (cm)
0
5
10
15
20
25
30
Acer rubrum (Red Maple)
Acer saccharum (Sugar Maple)
Fraxinus americana (White Ash)
Juglans nigra (Black Walnut)
Ostrya virginiana (Ironwood)
Prunus americana (Wild Plum)
Prunus serotina (Black Cherry)
Quercus alba (White Oak)
Quercus macrocarpa (Bur Oak)
Quercus rubra (Red Oak)
Tilia americana (Basswood)
Avg Height (m) 8.914 9.216 13.933 9.026 13 3.8 11.5 11.917 7.961 17.415 13.607
Avg DBH (cm) 2020 10.153 7.869 14.845 10.867 9.075 3.775 12.75 15.621 9.914 25.196 18.225

Figure 1. Average height and DBH of original trees within the restoration in 2020. Red oak had the tallest average height, followed by white ash, then basswood. Red oak also had the greatest DBH, followed by basswood, then white oak.

Table 1. Mortality rates of original trees. The mortality percent is the percentage of the original trees which have died off by 2020. The annual mortality is a calculation of the average percent of the original tree population that dies each year. *A. saccharum*, *F. americana*, *Q. alba*, and *T. americana* all decreased in annual mortality percent since 2013. *A. rubrum*, *J. nigra*, *O. virginiana*, and *Q. macrocarpa* all increased in annual mortality since 2013.

species	Number of OR trees in 2020	1990-2020 Mortality %	Annual Mortality 1990-2020 (%)	Annual Mortality 1990-2013 (%)	Annual Mortality 2013-2020 (%)
Acer rubrum (red maple)	63	38.89	1.63	0.79	4.33
Acer saccharum (sugar maple)	58	58.28	2.87	3.41	1.09
Fraxinus americana (white ash)	297	29.44	1.16	1.43	0.27
Juglans nigra (black walnut)	194	52.30	2.44	1.94	4.05
Ostrya virginiana (ironwood)	2	80.00	5.22	1.42	16.72
Prunus americana (wild plum)	2	95.00	9.50	5.46	21.61
Prunus serotina (black cherry)	2	33.33	1.34	0.00	5.63
Quercus alba (white oak)	107	48.04	2.16	2.54	0.91
Quercus macrocarpa (bur oak)	125	47.81	2.14	1.53	4.14
Quercus rubra (red oak)	13	35.00	1.43	1.54	1.05
Tilia americana (basswood)	14	17.65	0.65	0.84	0.00
Total	**880**	**44.09**	**1.92**	**1.74**	**2.52**

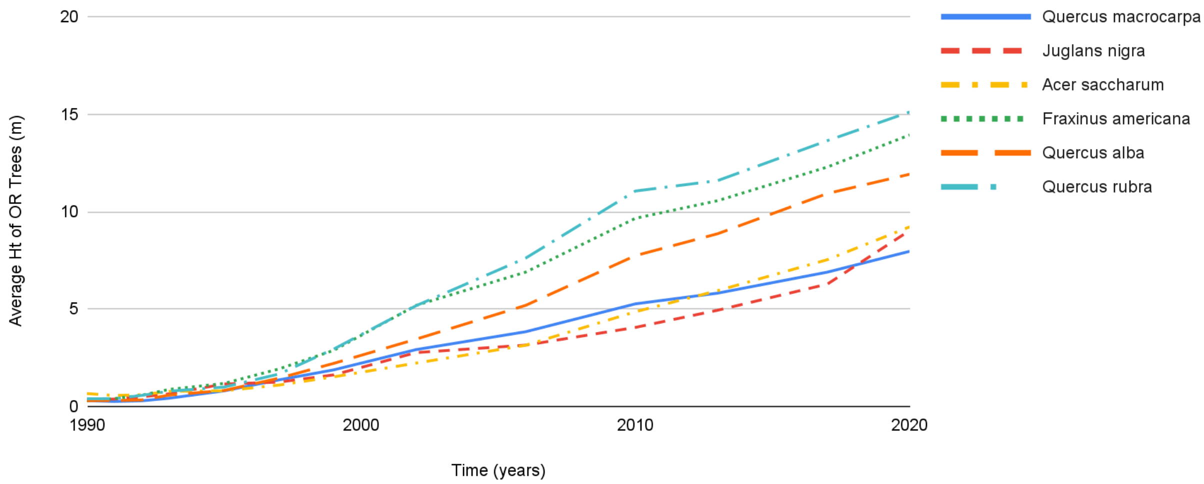

Figure 2. Linear average heights of the most common original trees over the last thirty years. Eight years into the restoration, *Q. alba* and *Q. rubra* began to grow taller on average than other original trees. *F. americana* began to do the same in 2006. They became the top three tallest trees on average in the restoration and have been since. *J. nigra* and *A. saccharum* recently surpassed *Q. macrocarpa* in average height since 2013.

Table 2. Colonizers between 1990-2013 and 2013-2020. *A. saccharum*, *C. cordiformis*, *J. nigra*, *U. americana*, and *T. americana* all increased their percentage of the colonizing species in the last six years of colonization. *F. americana*, *A. negundo*, and all oak species decreased their percentage of colonizing species over the same time period.

Species	**# of Colonizers 1990-2013**	**# of Colonizers 2013-20**	**% of Colonizers 1990-2013**	**% of Colonizers 2013-20**
Acer negundo (boxelder)	76	26	15.20	7.43
A. rubrum (red maple)	2	2	0.40	0.57
A. saccharum (sugar maple)	9	17	1.80	4.86
Carya cordiformis (bitternut hickory)	8	10	1.60	2.86
F. americana (white ash)	173	94	34.60	26.86
Gleditsia triacanthos (honeylocust)	4	0	0.80	0.00
Juglans cinerea (butternut)	0	1	0.00	0.29
J. nigra (black walnut)	10	19	2.00	5.43
O. virginiana (ironwood)	15	8	3.00	2.29
Populus tremuloides (aspen)	18	31	3.60	8.86
P. americana (wild plum)	34	54	6.80	15.43
P. serotina (black cherry)	15	12	3.00	3.43
Q. alba (white oak)	17	2	3.40	0.57
Q. macrocarpa (bur oak)	10	0	2.00	0.00
Q. rubra (red oak)	45	5	9.00	1.43
T. americana (basswood)	26	26	5.20	7.43
Ulmus americana (American elm)	36	40	7.20	11.43
Ulmus rubra (slippery elm)	2	2	0.40	0.57
Ulmus thomasii (rock elm)	0	1	0.00	0.29
Total # of Trees	**500**	**350**	**100.00**	**100.00**

Table 3. Diversity comparisons from 1990 to 2020. The diversity of the restoration increased from 1990 to 2013, and again increased slightly from 2013 to 2020. Values from the year 1990 only include original plants. 2013 and 2020 values include colonizing trees. Statistical comparisons (a 2-sample t test) were conducted on Simpson's diversity for species compositions in 1990, 2013 and 2020. Pairwise comparisons indicated the diversity differed significantly from 1990's population in 2013 ($t\infty = 2.431$, $p < 0.05$) and 2020 ($t_\infty = 2.990$, $p < 0.05$). Simpson diversity between 2013 and 2020 were not significantly different ($t_\infty = 0.598$, $p < 0.05$).

Year	**Species Diversity Index**	**Field 1**	**Field 2**	**Entire Restoration**
1990	Shannon ('H)	0.82	0.69	**0.84**
	Simpson (Ds)	0.81	0.75	**0.82**
2013	Shannon ('H)	0.96	0.83	**0.95**
	Simpson (Ds)	0.86	0.77	**0.84**
2020	Shannon ('H)	1.04	0.84	**0.99**
	Simpson (Ds)	0.89	0.76	**0.84**