Name: Andrew M. Pierson

Title: Primary succession on the basin of a catastrophically drained lake in the boreal forest

Running Title: Primary succession in the boreal forest

Abstract

This study examined primary succession on the basin of a catastrophically drained lake in northern Minnesota. The site, Bass Lake, suffered this drainage as a result of logging operations in 1925, which reduced the total area of the lake from approximately 2 km^2 (494 ac.) to its present day size of 1.05 km^2 (260 ac.). I hypothesized that succession occurring on this newly exposed area would follow the relay floristics model of Clements. Specifically, I expected a change from shade-intolerant trees, such as *Betula papyrifera* (paper birch), to shade-tolerant trees, such as *Abies balsamea* (balsam fir). To test this hypothesis, I used data collected using the Point-Centered Quarter Method for trees found below the old shoreline between the years of 1978 and 2010. The results indicated that there was a transition from paper birch to balsam fir on the north side of the lake. However, paper birch remained as the most significant tree on the south side of the lake throughout the study's duration with no such transition. As a result, it appears that the north side of Bass Lake follows the relay floristics, but this hypothesis must be rejected for the south side. Factors such as soil texture, water availability, canopy openings, and growing season may have caused this difference.

Keywords: Bass Lake, northern Minnesota, point-centered quarter method, relay floristics, shade tolerance

Introduction

Ecological succession in terrestrial habitats is the gradual process by which ecosystems change in species composition and/or structure over a period of time (Walker et al. 2010). Succession can be divided into two different categories: primary succession and secondary succession. Of these two, secondary succession is more commonly found and involves changes in a previously established ecosystem after a disturbance (Bergeron et al. 2014). A disturbance, in relation to secondary succession, can be an event ranging from a windstorm, a fire, or pathogenic and insect outbreaks. These disturbances can be widespread throughout the forest or only affect a small portion of it leading to a gap forming in the tree canopy. Regardless of the severity of the disturbance, succession afterwards is aided by factors such as soil and seed sources, which existed in the forest community prior to the disturbance. In contrast to secondary succession, primary succession is ecosystem development on barren surfaces with no prior vegetation history (Walker and Del Moral 2003). Soil is often not initially present with this succession and must develop over time. Examples of primary succession occur along the newly exposed shorelines of receded rivers (Hollingsworth et al. 2010), on the basins of drained lakes (Nielsen and Moyle 1941), on lava domes (Elias and Dias 2004), and on the glacial moraines in the wake of glacial retreat (Fastie 1995).

Many factors that drive or affect succession have already been identified. For instance, facilitation, the idea that the interactions of one plant species positively benefiting the invasion and growth of later successional species, is regarded as being critically important when it comes to primary succession; Nitrogen-fixing symbionts are often the drivers behind successional change because of their facilitative actions (Walker et al. 2003). The individual characteristics of various tree species, such as shade-tolerance and longevity, are all important factors in the growth and development of the boreal forest following a fire disturbance (Bergeron et al. 2014). Shade tolerance seems to be the key characteristic in determining the age of a forest community. In the boreal forest, the successional pathway after a catastrophic fire moves from shade-intolerant species of trees, such as *Betula papyrifera* (paper birch) and *Populus tremuloides* (quaking aspen), to a more shade-tolerant species of trees, such as *Thuja occidentalis* (white cedar) and *Abies balsamea* (balsam fir) (Frelich and Reich 1995; Bergeron and Dubue 1988). However, while shade-tolerance determines the pattern of succession, other factors also play a role in succession. For example, changes in competitive balance provide the mechanism for changes in species dominance (Chapin et al. 1994). Meanwhile, initial site conditions, which along with facilitation affect the rate of change and final community composition and productivity.

The search for a model of plant succession has a long history behind it. Frederic E. Clements (1936) first proposed a model of succession called the *relay floristics model*, which he developed from his observations of the prairie vegetation of Nebraska and the forest communities of the western United States (Fig. 1). Under Clements' theory, the plant community continuously developed until it reached a final climax stage. At this climax stage, the vegetation present in the area is best suited for the environment. This development towards the climax happens in stages in which species arrive and depart in batches with the earlier species preparing the way for later species. Succession was predictable and deterministic. In contrast to relay floristics, Frank Egler (1954) proposed a hypothesis called the *initial floristic composition* from his studies concerning old-field (abandoned farmland) succession. Under this hypothesis, succession did not proceed with orderly states as proposed by Clements, but rather succession is dependent on which species occupied the site first. The species that are present all develop simultaneous until some species drop out of succession because of their limited longevity. Trees, with the longest lifespan, dominate in the final equilibrium stage. These initial ideas were further refined by Connell and Slatyer (1977) who proposed three models of succession: *facilitation*, *tolerance* and *inhibition*. Under the facilitation model, early successional species arrive to a location because they have "colonization" traits such as fast growth, good dispersal abilities, and able to propagate to large numbers and then these species modify the environment to be more suitable to later successional species to grow and develop. The facilitation model was attributed by Connell and Slatyer to the relay floristics model of Clements and stated that this model was associated with primary succession which often have extreme environmental conditions that make invasion difficult. In the tolerance model, later successional species can invade a site independently and establish themselves independently of the pioneer species that preceded them because they can tolerate a lower level of resources compared to the earlier colonizing species. Eventually, this tolerance of conditions allows later successional species to become dominant over the earlier species, which require more resources. In the inhibition model, the first species invades and holds the site against all other invaders and they maintain this position until an event occurs that causes them to become damaged or die off allowing other species to move in. Both the tolerance and inhabitation models are related to Egler's hypothesis. While current evidence suggests that relay floristics is the model applicable to primary succession, this assumption has not been fully tested.

In this study, I used a long-term data set (30 yr) to examine succession on the catastrophically drained basin of a lake in the boreal forest region of northern Minnesota. The goal of this study was to determine how succession occurred in this area. I hypothesized that succession in this area would occur in a pattern similar to the relay-floristics model as put forth by Clements and that I would find a transition from shade-intolerant trees (paper birch) to shade-tolerant trees (balsam fir).

Methods

The study area, Bass Lake, is located 9.7 km (6 mi.) north of the city of Ely, St. Louis County, Minnesota (Fig. 2). As noted by Nielsen and Moyle (1941), Bass Lake suffered a severe drainage on May 15, 1925, when the ridge of glacial gravel that acted as a dam between Bass Lake and Low Lake gave way. The cause of the ridge's breakdown was a sluiceway built by loggers to move logs from Bass Lake to Low Lake. The drainage took ten hours to complete and caused the lake to be lowered by 15.9 m (52 ft.) and its area reduced from approximately 2 km^2 (494 ac.) to its present day size of 1.05 km^2 (260 ac.). The area that was opened up by the drainage had no prior exposure to plant invasion, which makes succession on this surface primary succession. Neither side of the lake has been disturbed since 1925.

Field data was collected between 1978 and 2010 by groups of Wilderness Field Station students using the Point-Centered Quarter Method at locations on the north side and south side of the lake. Under this method, the different groups established four transect lines with two above the old shoreline and two below. At regular intervals along the transect line, a point was established. At these points, imaginary perpendicular lines created four quarters of an infinitely large circle. Within each of the quarters, the tree closest to the center was identified and measurements were made of the distance to the tree from the center point and the diameter of the tree at 1.4 m (4.5 ft.) height. This process was done on both the north and south side of Bass Lake.

These data was analyzed to create four metrics: Relative Density, Relative Frequency, Relative Dominance, and Importance Value. Relative density reports a comparison of the numbers of trees of one species against all of the trees of all of the species sampled. Relative frequency reports information about the dispersion of a species in the forest relative to all of the species sampled. Relative dominance reports the relative age of a particular set of trees in comparison to other trees. Importance value is the sum of the relative density, relative frequency, and relative dominance; it indicates the relative importance of the particular tree species in the forest. Occasionally, more than one area was sampled for north shore and/or the south shore during a specific year. In these instances, data from the multiple sites was averaged. Some species of trees were then removed from the analysis because they appeared too infrequently in the data (in only 1 or two years) or their population was significantly small (relative density <0.5 across multiple years).

Results

South side of Bass Lake

The major tree species that had a significant impact in the forest of this area were *Abies balsamea* (balsam fir), *Betula papyrifera* (paper birch), *Populus tremuloides* (quaking aspen), and *P. grandidentata* (large tooth aspen). Several other species were noted to appear in the data for this section including *Picea glauca* (white spruce), *P. mariana* (black spruce), *Thuja occidentalis* (white cedar), *Pinus resinosa* (red pine), and *P. strobus* (white pine). However, these species did not exert a similar amount of influence on this section of the forest compared to the other four. There was a steady decline in coverage by the large tooth aspen between 1978 and 2004 (Fig. 3A). A similar decline is noted in Figure 4A for relative density and Figure 5A for relative dominance which created a trend for large tooth aspen as seen in Figure 6A. Quaking aspen, on the other hand, initially suffered a decline between 1985 and 1995 for relative frequency (Fig. 3A), density (Fig. 4A), and dominance (Fig. 5A) before increasing between 2004 and 2012. Finally, paper birch and balsam fir proved to be rather mirror opposites of each other. At the start in 1978, paper birch was the most dominant in terms of density and frequency while balsam fir was relatively unimportant. Then, balsam fir steadily increased in density and frequency, while paper birch steadily declined until 2004. After 2004, paper birch increased in density and frequency, while balsam fir stopped increasing and then declined. Relative dominance for balsam fir followed the same pattern as its frequency and density. Paper birch's relative dominance consistently declined.

North side of Bass Lake

An apparent difference between the south side and north side can be found in the number of tree species that were significant at the north side compared to the south side. The actual species present at both the north and south sides are essentially the same (Table 1 and Table 2). However, more species were significant at the north side than at the south side. *Populus balsamifera* (balsam poplar), red pine, white pine, and *Pinus banksiana* (jack pine) all exerted some influence on succession for this side of the lake compared to the south side of the lake, where these species were infrequently found. Furthermore, large tooth aspen, which was found to be significant at the south side, was not significant at the north side. Paper birch, similar to the south side data, starts out as the most dominant in all categories of relative frequency (Fig. 3B), relative density (Fig. 4B), and relative dominance (Fig. 5B). However, it undergoes a steady decline in all three of these values between 1978 and 2008 with one minor exception with relative dominance between 2004 and 2008, which increased slightly. Balsam fir increased steadily in all categories with a rather large jump between 2004 and 2008 at which time it became the most dominant species. Quaking aspen decreased in terms of frequency and density overall, but its relative dominance increased slightly in the later part of the study. Out of the four remaining trees (balsam poplar, red pine, white pine, and jack pine), only white pine increased consistently with respect to density and frequency while the others were either consistently declined (balsam poplar) or inconsistently increased and then decreased (red pine and jack pine).

Discussion

My hypothesis is that the primary succession that would be found to occur at Bass Lake below the old shoreline would take on a pattern that resembled the relay floristics model (Fig. 1). Under relay floristics, I expect a change from shade-intolerant trees to shade-tolerant trees. In other boreal forest communities, the final tree community is dominated by either balsam fir, white cedar, black or white spruce (Bergeron et al. 2014). Neither black spruce, white spruce, or white cedar has a major presence at Bass Lake, but balsam fir does. So if my hypothesis is correct, the dominant tree in below the old shoreline should be balsam fir. There appears to be a transition from paper birch to balsam fir on the north side of Bass Lake, which confirms my hypothesis. Furthermore, two other species provide evidence of this transition. Quaking aspen, another shade-intolerant tree, performed poorly over time on the north side while white pine, a moderately shade-tolerant tree, increased in significance (Dovciak et al. 2005; Kneeshaw et al. 2006). Because these shade-tolerant trees are becoming increasing important over shade-intolerant, I believe that relay floristics can be regarded as the applicable model to the north side of Bass Lake.

However, no transition from paper birch to balsam fir was seen at the south side of Bass Lake. Quite the opposite, the density and frequency of paper birch is rising in the later years at this area of the lake. More importantly, the dominance of the paper birch appears to be dropping at the south side, which indicates that the average age of the paper birch trees present there is getting younger. Younger trees indicate that paper birch will continue with its current trend and remain as the most important species on the south side of Bass Lake in the years to come (barring disturbance). For the south side of Bass Lake, I reject my hypothesis that the relay floristics model is applicable to the south side of Bass Lake.

There are several possible explanations for the differences between the north and south side that have been noted. The most likely explanation could be the effect of soil texture on invading tree species. According to the early work of Nielsen and Moyle (1941) with Bass Lake, well-drained areas of coarse gravel were invaded by paper birch to the exclusion of almost all other species.

Furthermore, it was also noted by Nielsen and Moyle (1953) that the paper birch stand on the north side of the lake was considerably less dense compared to the south side. The reason why this is important is because edaphic conditions are very different on these two sides of the lake; the south side of Bass Lake was considerably rockier and thinner soil when compared to the north side (Fig. 7). Amount of available water was also considered to be a possible factor. Water availability being a factor is also supported by post-fire observations in which stands converge to white cedar and black spruce on xeric sites and balsam fir and white cedar on more mesic sites (Bergeron and Dubuc 1988). The areas I studied are likely to be xeric sites because they are drained, but black spruce and white cedar were not major factors for either the north or south side of the lake below the old shoreline and will most likely not be for some time. Canopy openings are another possible explanation for the maintained appearance of paper birch on the south side. Under conditions of only 25% full sunlight, paper birch can outgrow more shade-tolerant trees such as black spruce and white cedar (Frelich and Reich 1995). Thus, as long as the south side's tree canopy does not become too dense, paper birch would have enough light to thrive. A final factor to consider is the length of the growing season. Snow on the south side of the lake remains longer than it does on the north side of the lake, thus shorting the growing season on the south side. A shorter growing season could possibly benefit paper birch at the expense of balsam fir. However, what effect a shorter growing season ultimately has at Bass Lake is currently unknown.

There are several limitations/difficulties within the context of this study. The entire analysis of succession at Bass Lake was based on pre-existing data from 1978 to 2010. Some of these data were unusable because they lacked sufficient metadata. There was also the possibility that calculation of the point-centered values could have been more indicative of the succession occurring in the local area that was sampled rather than the forest as a whole. An example of this issue can be found by looking at the importance value of quaking aspen in 1985 for the north side of the lake (Fig. 6B) in addition to the relative frequency (Fig. 3B), relative density (Fig. 4B), and relative dominance (Fig. 5B). In 1985, quaking aspen is significantly greater than when it was measured in 1979 or 1986. The sampling in 1985 was most likely restricted to a singular area on the north side and this discrepancy was the result. However, sampling area was most likely not a significant issue. Another issue that came up was that the point-centered quarter method also lacked the means of performing statistical analysis such as confidence intervals and the data had to be interpreted qualitatively. Despite the lack of statistical analysis, general vegetation trends over time were successfully discovered. Future directions based on this study should consider methods to identify the impact of water availability and canopy openings in the studied areas of Bass Lake. Additionally, the timeframe of sampling should be increased for both sides of the lake. With the north side, we should see whether other later successional species come into play or whether balsam fir continues to dominate this area. With the south side, we should see whether the importance of paper birch continues in this section or whether something happens that disrupts its significance.

Conclusions

The relay floristics model can only be partly applied to the primary succession that is occurring at Bass Lake and only at the north side. More research has to be done at the south side of Bass Lake find an applicable model to the succession to this area. Factors such as soil texture, water availability, canopy openings, and growing season should be considered in future studies.

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Table 1. Tree species present at the north side of Bass Lake between 1978-2010.

Scientific name	**Common name**
Abies balsamea	Balsam fir
Acer rubrum	Red maple
Alnus incana	Speckled alder
Betula papyrifera	Paper birch
Fraxinus nigra	Black ash
Picea glauca	White spruce
Picea mariana	Black spruce
Pinus banksiana	Jack pine
Pinus resinosa	Red pine
Pinus strobus	White pine
Populus balsamifera	Balsam poplar
Populus grandidentata	Large tooth aspen
Populus tremuloides	Quaking aspen
Thuja occidentalis	White cedar

Table 2. Tree species present at the south side of Bass Lake between 1978-2010.

Scientific name	**Common name**
Abies balsamea	Balsam fir
Acer rubrum	Red maple
Acer spicatum	Mountain maple
Alnus incana	Speckled alder
Alnus viridis	Green alder
Betula papyrifera	Paper birch
Picea glauca	White spruce
Picea mariana	Black spruce
Pinus resinosa	Red pine
Pinus strobus	White pine
Populus balsamifera	Balsam poplar
Populus grandidentata	Large tooth aspen
Populus tremuloides	Quaking aspen
Thuja occidentalis	White cedar

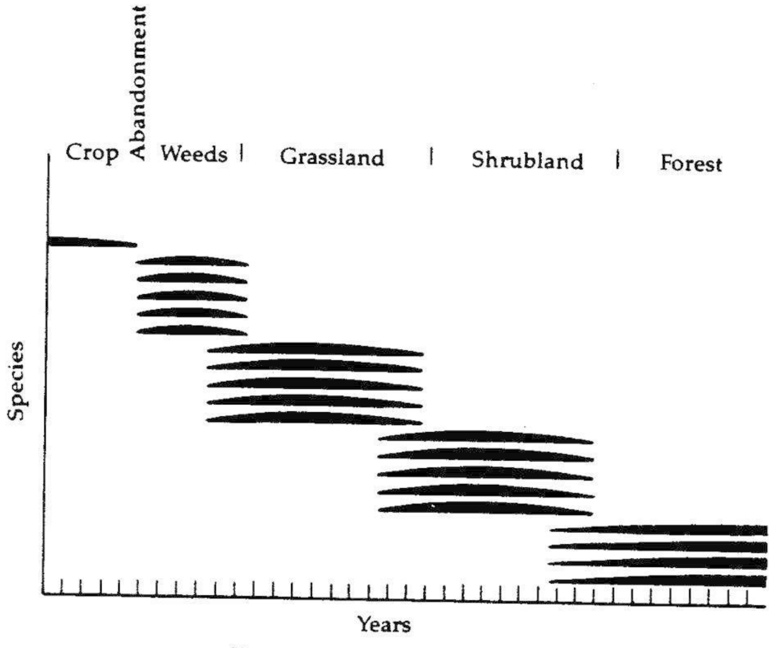

Figure 1. The relay floristics model for an old field succession in an abandoned agricultural land in North America. After abandonment, Pioneer species, such as weeds, enter a farmland and modify it for a later successional species. The final community is composed of shade-tolerant trees. Adapted from Egler (1954).

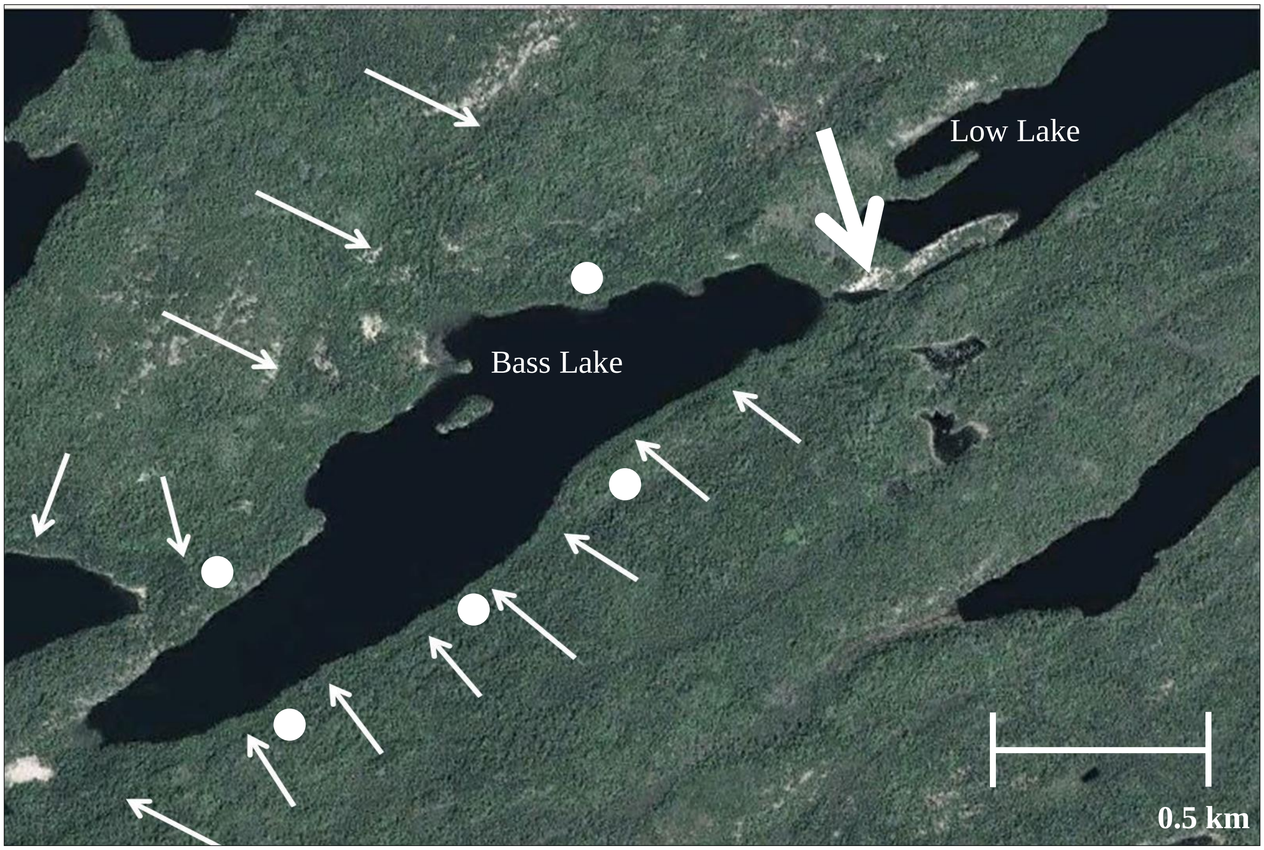

Figure 2. Overhead view of Bass Lake. The white arrows around Bass Lake indicate the location of the shoreline in 1925. The larger white arrow indicates the location of the former glacial gravel ridge the separated Bass Lake and Low Lake. The white dots indicate the approximate locations of sampling areas.

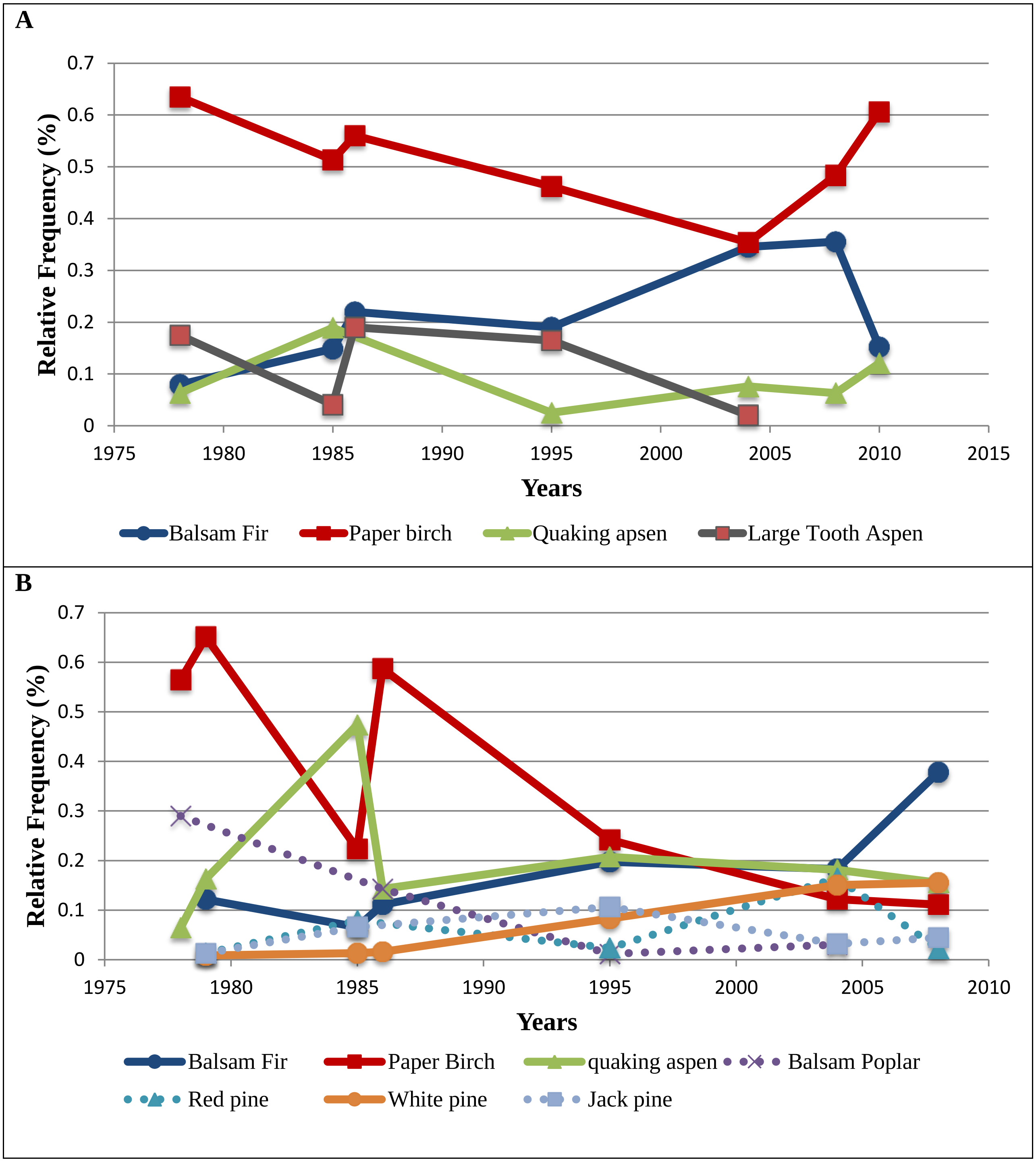

Figure 3. Relative frequency values of tree species below the old shoreline of Bass Lake. A: Covers the area below the old shoreline at the south side of the lake. B: Covers the area below the old shoreline at the north side of the lake.

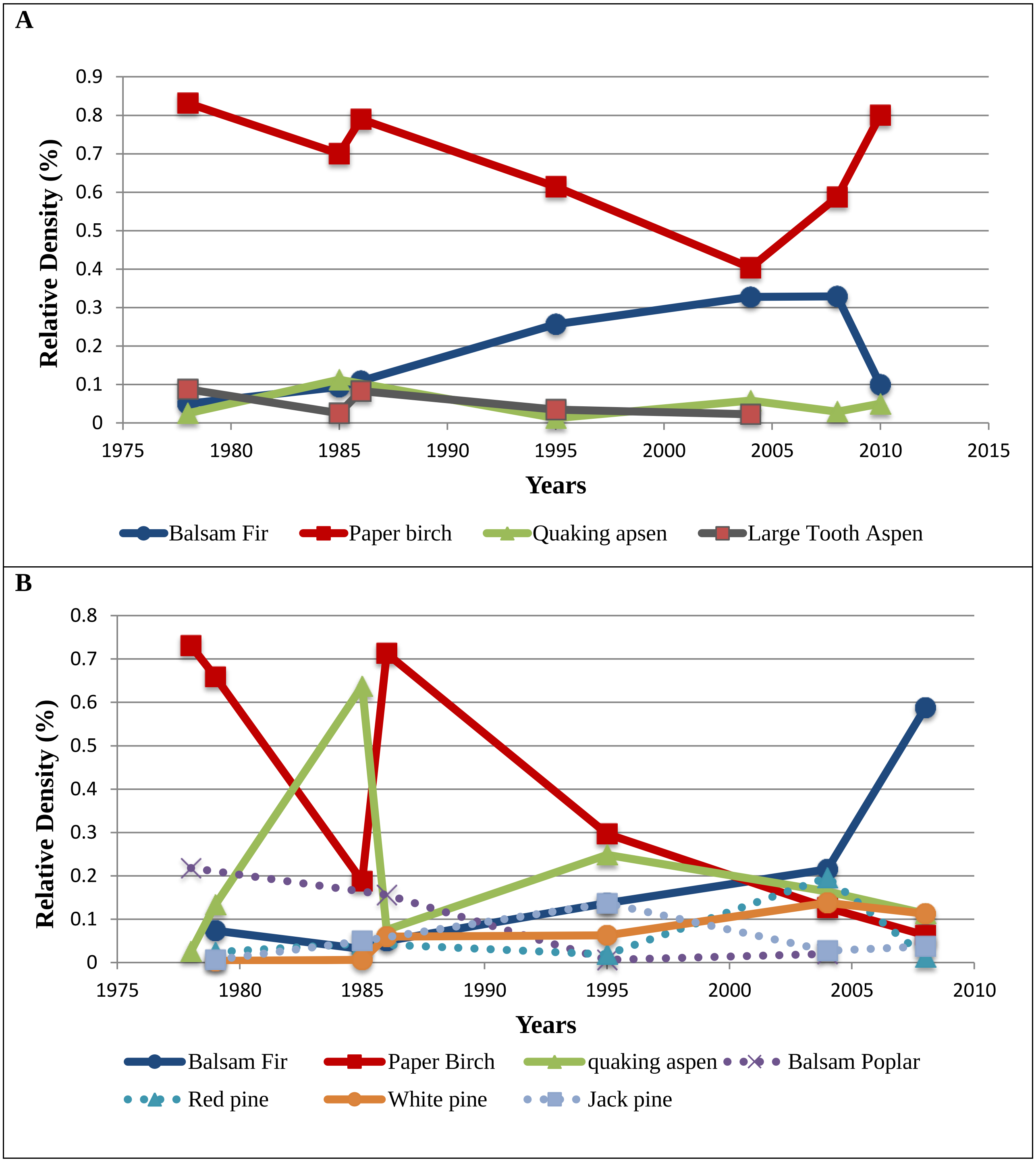

Figure 4. Relative density values of tree species below the old shoreline of Bass Lake. A: Covers the area below the old shoreline at the south side of the lake. B: Covers the area below the old shoreline at the north side of the lake.

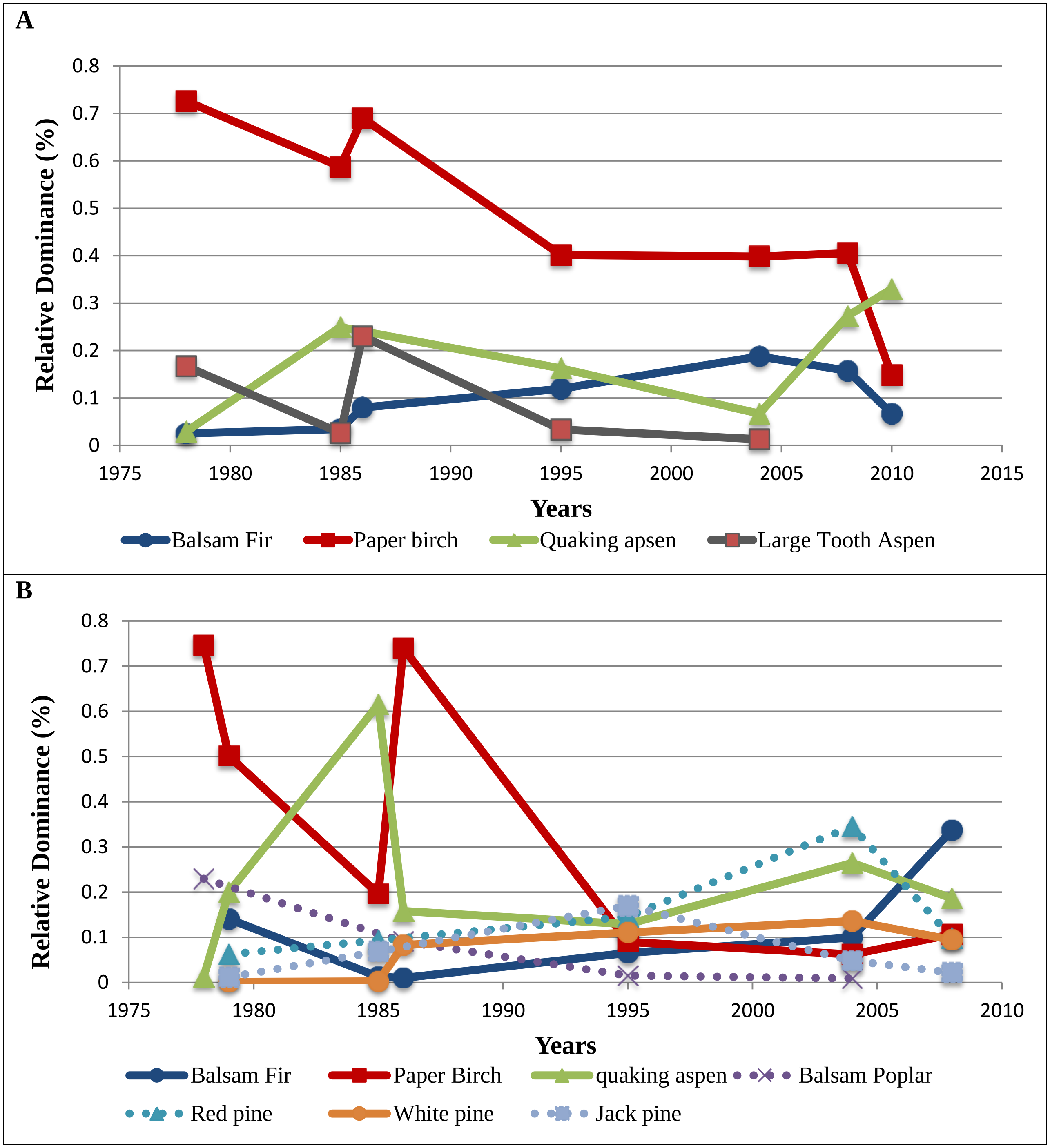

Figure 5. Relative dominance values of tree species below the old shoreline of Bass Lake. A: Covers the area below the old shoreline at the south side of the lake. B: Covers the area below the old shoreline at the north side of the lake.

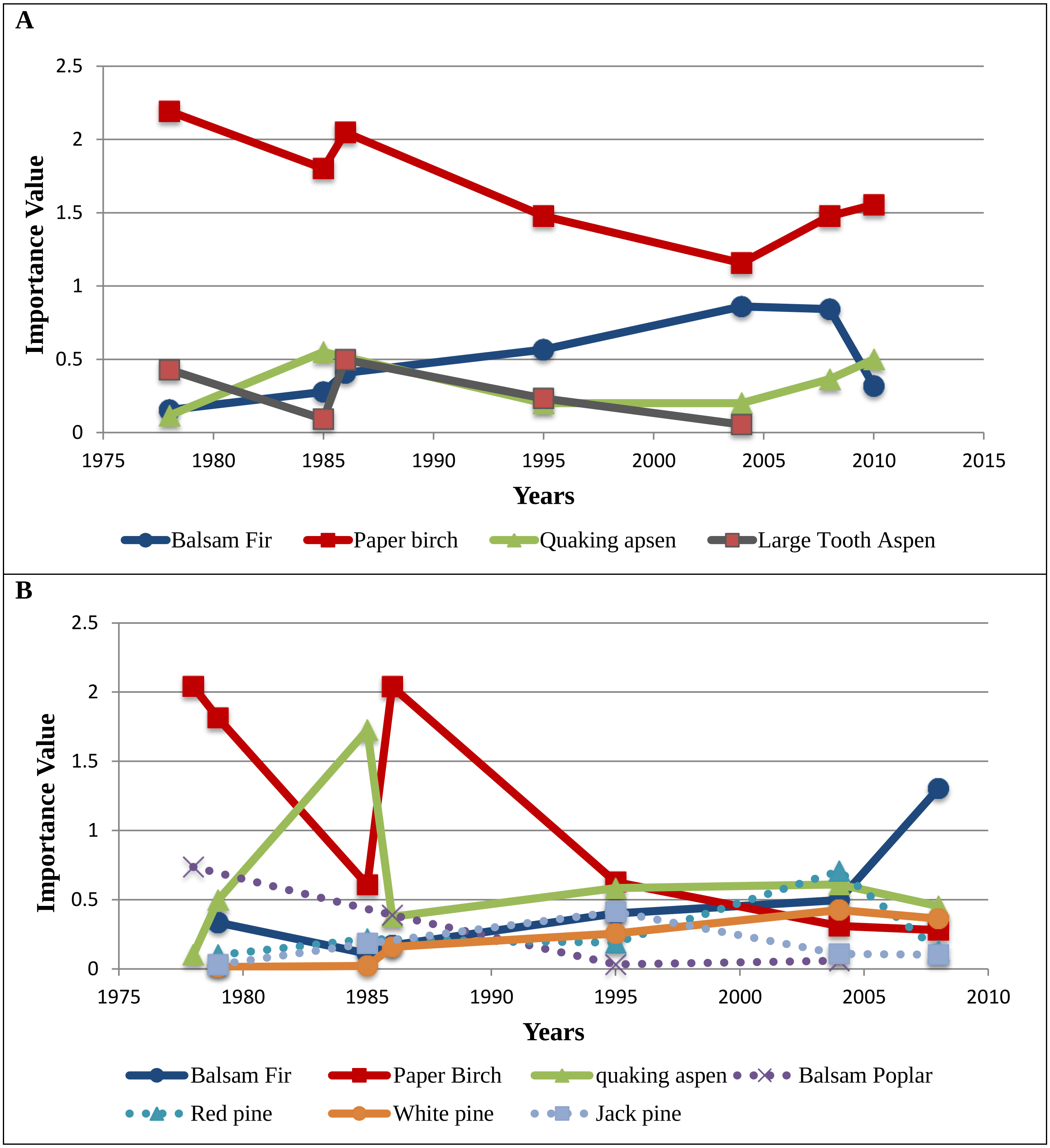

Figure 6. Importance values of tree species below the old shoreline of Bass Lake. A: Covers the area below the old shoreline at the south side of the lake. B: Covers the area below the old shoreline at the north side of the lake.


A


B

Figure 7. A comparison of the soil texture below the old shoreline for the north (A) and south sides (B) of Bass Lake. The south side of Bass Lake is significantly rockier than the north side and is dominated by paper birch trees growing in the spaces between the rocks.