ABSTRACT

The Janzen-Connell hypothesis proposes that tropical tree diversity is maintained through distance and density-dependent mortality of tree seedlings and saplings due to host-specific seed, seedling, and sapling predation. Numerous studies with varied results have been conducted to see if the Janzen-Connell hypothesis can be applied to temperate climates. However, no study has ever been done to see if there is a relationship between shade-tolerance in temperate trees and observed patterns consistent with those predicted by the Janzen-Connell hypothesis. Because shade-tolerant trees tend to remain saplings for a longer period of time than shade-intolerant trees, they should be vulnerable to host-specific predation for a longer period of time than shade-intolerant trees. It was therefore hypothesized that an increasing degree of shade-tolerance would be accompanied by a stronger trend towards the pattern of regular distribution predicted by the Janzen-Connell hypothesis. Three tree species— *Betula papyrifera* (white birch), *Betula alleghaniensis* (yellow birch), and *Picea glauca* (white spruce)—respectively increasing in their degree of shade tolerance, were studied and their sapling height, density, and distance from the lone maternal tree were measured. Observed patterns of white birch sapling distributions were furthest from those predicted by the Janzen-Connell hypothesis and were closer to aggregated distribution patterns. Observed patterns of yellow birch sapling distributions were significantly closer than white birch sapling distributions to those predicted by the Janzen-Connell hypothesis, but were somewhat different to what was expected in the initial hypothesis. White spruce showed a distribution closest to the regular distribution predicted by the Janzen-Connell hypothesis, and all slopes were in accordance with the slopes that were to be expected if the Janzen-Connell hypothesis was in effect. However, most likely due to the small sample pool of white spruce saplings, there was a lack of significant results with the white

spruce. Nevertheless, a possible trend was observed that could suggest that shade-tolerance in temperate tree species on the UNDERC property can account for the degree of sapling distribution that is consistent with the predictions of the Janzen-Connell hypothesis.

INTRODUCTION

Background of the Janzen-Connell Hypothesis:

The Janzen-Connell hypothesis (Janzen 1970, Connell 1971) proposes that tropical tree diversity is maintained through distance and density-dependent mortality of conspecific seedlings and saplings due to host-specific seed, seedling, and sapling predation (Crawley 1997, Hyatt et al. 2003, Peters 2003). Janzen (1970) used the terms “seed/seedling predator” and “seed/seedling parasite” to indicate whether the organism’s feeding on the juvenile plant was enough to kill it or not, respectively; terms such as “herbivore,” “frugivore,” and “gramnivore” were regarded as insufficient because they did not tell the fate of the seed, seedling, or sapling. Janzen (1970) used the concepts of density-dependent and distance-dependent seed, seedling, and sapling predation to explain the observations that many tree species appeared to be more regularly distributed than would be expected if the probability of a new adult tree appearing was only proportional to the amount of seeds that arrive at that point (Janzen 1970). In general, more seeds tend to land closest to the maternal tree and seed density decreases as distance from the maternal tree increases (Janzen 1970). Without host-specific seed/seedling predators, Janzen (1970) argued that more conspecifics would grow to a mature juvenile stage closer to the maternal tree, and thus a more aggregated distribution would result. The Janzen-Connell hypothesis predicts that due to both distance-dependent and density-dependent predators, a pattern of repelled recruitment in which seedling survival increases with distance from the maternal tree will result (Janzen 1970, Crawley 1983). These host-specific “predators” could include rodents (Manson and Styles 1998, Janzen 1970), deer (Janzen 1970), insects (Janson 1970), even fungi (Janzen 1970) and pathogens (Packer and Clay 2000).

Density-dependent seed/seedling predators feed where food is most abundant until there is no longer enough food for it to be energetically efficient to forage in that spot (Janzen 1970). Distance-dependent seed/seedling predators that are classified by Janzen (1970) as parasites to the maternal tree can often be predators to the seedlings or saplings (Janzen 1970). This is because saplings can't withstand loss of leaves and shoot tips to the degree that adult trees can (Janzen 1970).

Out of the five general predictions of the Janzen-Connell hypothesis, this study focuses on the first and the fourth prediction. The first of these predictions was that survival of a seed to a well developed sapling stage should increase with distance from the maternal tree (Janzen 1970). The fourth of these predictions was that the survival of a juvenile should be an inverse function of the density of conspecific juveniles (Janzen 1970).

Janzen-Connell Hypothesis and Temperate Climates:

Although the Janzen-Connell hypothesis was originally applied to trees in the tropics, recent studies have attempted to apply this hypothesis to temperate forests. A meta-analysis on the Janzen-Connell hypothesis compiled studies published in ten major journals that involved the Janzen-Connell hypothesis in both tropical and temperate climates (Hyatt et al. 2003). It suggested that in temperate climates only, distance from maternal plant could possibly reduce seed/seedling survival (Hyatt et al. 2003). The concept of host-specificity was one explanation as to why this regular distribution of species and also a greater diversity of tree species are more prevalent in the tropics than in temperate climates (Hyatt et al. 2003). Tropical climates have more host-specific plant predators and parasites while many plant predators and parasites in temperate climates are generalists (Harper 1977, Howe and Westley 1988, Hyatt et al. 2003). Janzen (1970) states that although the probability of a sapling reaching maturation should increase with distance, it will never equal one due to factors outside host-specific predation such as competition or predation by generalists. As the degree of generalist predation increases, it can be inferred therefore that the host-specific effects will be less easily seen, because the impact of the generalists will be much greater.

However, recent studies have found that the Janzen-Connell hypothesis can apply to some trees in temperate climates. A study by Myster and McCarthy (1989) showed that herbivore predation on seeds and seedlings was the number one factor in affecting seedling dispersal patterns. It had a much greater effect than competition did, and in many cases the herbivores were host-specific (Myster and McCarthy 1989). A study by Caccia and Ballare (1998) applied the Janzen-Connell hypothesis to the regeneration of Douglas-fir (*Pseudotsuga menziesii*). In order for a tree to show significant effects of repelled recruitment in an environment where host-specific seedling/sapling predators are rare, it would most likely have to remain vulnerable to predation for a longer period of time. A trade-off exists in shade-tolerant trees in which seedlings and saplings can survive in the shade of the forest understory but as a result grow slowly (Barnes and Wagner 1981, Molles 2003). Because Connell (1971) noted that the effect of distance-dependent predation on juveniles declined with plant height, it can be predicted that juveniles of the faster growing shade-intolerant trees will be more likely to escape predation and therefore can grow closer to the maternal tree than the slower growing, shade tolerant trees. Thus, because they grow slower, shade-tolerant trees should show a stronger trend towards the regular distribution predicted by the Janzen-Connell hypothesis than shade-intolerant species of temperate trees. Although the meta-analysis suggested a slight trend in temperate plants towards a reduced survival as distance from the maternal plant increased, 50% of the plants were shrubs and herbs, and the trees considered were of varying degrees of shade-tolerance (Hyatt et al. 2003). No studies have focused on the concept of shade tolerance in relation to the Janzen-Connell hypothesis. Shade-tolerant temperate trees may be the exception to the pattern seen in the meta-analysis and will instead show distribution patterns similar to those predicted by the Janzen-Connell hypothesis.

Hypothesis and Predictions:

Three temperate tree species— *Betula papyrifera* (white birch), *Betula alleghaniensis* (yellow birch), and *Picea glauca* (white spruce)—that were shade-intolerant, moderately shade-tolerant, and shade-tolerant, respectively were used in this study. I hypothesized that patterns of conspecific seedling and sapling dispersal around a maternal tree would be consistent with predictions 1 and 4 of the Janzen-Connell hypothesis, and that these patterns would be most strongly seen in the shade-tolerant white spruce, while the shade-intolerant white birch would show a trend more consistent with aggregated distribution, and yellow birch distribution patterns would be somewhere in between the other two trees. Height was considered an indicator of sapling age or the degree of parasitism or predation on saplings. Both younger saplings that have not yet had time to feel the effects of host-specific predation and smaller saplings whose growth has been slowed due to a struggle to survive parasitism or predation were predicted to be found in areas closest to the maternal tree or with the greatest conspecific sapling density. Because according to the Janzen-Connell hypothesis seedlings/saplings have a lesser chance of survival closest to the maternal tree and closest to conspecific seedlings/saplings, I predicted that seedling/sapling height would increase with distance from the maternal tree, and that height would decrease with conspecific seedling/sapling density. This pattern was supposed to be greatest for white spruce and decrease with decreasing shade tolerance. I also looked at the effect of distance on conspecific seedling/sapling density to see if out of the three tree species, white spruce had a juvenile distribution closest to a regular distribution, and if white birch had an aggregated distribution. Yellow birch was expected to have a distribution somewhere in between that of white spruce and that of white birch.

MATERIALS AND METHODS

Study site:

The University of Notre Dame Environmental Research Center (UNDERC) is located in a northern hardwood forest that spans part of the Upper Peninsula of Michigan as well as a portion of Vilas County, Wisconsin. Since it was heavily logged in the years between 1880 and 1910, the forest is largely second-growth (Stearns 1950).

Data collection:

Six to eight plots were selected for each of the three species–*Betula papyrifera* (white birch), *Betula alleghaniensis* (yellow birch), and *Picea glauca* (white spruce)—that were shade-intolerant, moderately shade-tolerant, and shade-tolerant, respectively. Lone adults were considered to be adult trees that were over 50m away from any conspecific adult tree. They were selected to prevent the interaction of seedlings with other conspecific adults, and each plot consisted of one of these lone adults. From the base of the adult tree, belt transects were set up running in the four cardinal directions. The width of the belt transects were 2m around trees with a very large abundance of surrounding conspecific seedlings and saplings, 3m around trees with an intermediate abundance, and 4m around trees with a very low abundance of conspecific saplings. Transect lengths tended to be 20m except for a few trees where saplings were especially sparse and so the transect lengths were extended to 25m. Within each transect, the number of seedlings and saplings that were greater than 5cm tall were counted and their height and distance from the maternal tree were measured in centimeters.

Data Analysis:

A stepwise multiple regression analysis was used to determine for each of the three tree species the relationships between sapling height and the distance of the sapling from the maternal tree, and if the slope of the white birch was significantly different from that of the yellow birch and the white spruce. A stepwise multiple regression was also used to determine the relationships between seedling/sapling height and conspecific seedling/sapling density for each of the three tree species, and if these slopes differed significantly among any of the three species. Because the Janzen-Connell hypothesis predicts that as distance from the maternal tree increases the probability that the seedling/sapling will survive increases as well, seedling/sapling density should remain somewhat constant or increase as distance increases. It can therefore be inferred that the probability of finding a tree every .1 square meter should also remain constant or increase as distance increases. A multiple logistic regression analysis was run to determine for the three tree species the relationship between distance and the probability of finding a conspecific seedling/sapling. Post hoc analyses were used to determine which trees had slopes that were significantly different from what would be expected of a regular distribution.

RESULTS

Height vs. distance:

Stepwise multiple regression analysis indicated that the slope coefficient of seedling/sapling height vs. distance for yellow birch was negative but not significantly different than a slope of zero (B= -0.002, SE=0.005, p=0.676) (R-squared=0.032, Fig. 1a). White birch was shown to have a negative slope coefficient that was significantly different than that of yellow birch (B=-

0.018, SE=0.007, p=0.007) (R-squared=0.032,Fig. 1b). The positive slope of seedling/sapling height vs. distance for white spruce was not shown to be significantly different than that of white birch (B=0.023, SE=0.020, p=0.244) (R-squared=0.032). When yellow birch was removed and just white birch and white spruce were compared, white birch was shown to have a negative slope that was significantly different than a slope of zero (R-squared=0.035, B=-0.02, SE=0.005, p<0.001), and the coefficient for the slope of white spruce was almost significantly more positive than that of white birch (R-squared=0.035, B=0.041, SE= 0.021, p=0.056, Fig. 1c).

Height vs. density

Stepwise multiple regression analysis showed that the positive coefficient for the slope of height vs. density for yellow birch was not significantly different than a slope of zero (B=0.188, SE=0.114, p=0.1) (R-squared=0.147, Fig. 2a), and that the slope coefficient for white birch was significantly more positive than that of yellow birch (B=0.380, SE= 0.516, p=0.033) (R-squared=0.147, Fig. 2b). The negative slope coefficient of height vs. density for white spruce was not significantly different than that of white birch (B=-0.838, SE=0.904, p=0.355) (R-squared=0.147). When yellow birch was once again removed from the regression analysis, the positive slope coefficient for white birch (x=0.085) was significantly different than a slope of zero (R-squared=0.179, B=0.568, SE=0.150, p<0.001). White spruce showed a negative slope coefficient (Fig. 2c) that was not significantly different from that of white birch (R-squared=0.179, B=-1.218, SE=1.002, p=0.228).

Distance vs. density:

Multiple logistic regression indicated that the slope coefficient of distance vs. probability of finding a yellow birch sapling was positive and was significantly greater than a slope of zero (B=0.037, SE= 0.011, p=0.001). The slope coefficient of distance vs. the probability of finding a conspecific seedling/sapling for white birch was negative and was significantly less than that of yellow birch (B=-0.086, SE=0.016, p<0.001). White spruce showed a slightly negative slope that was not significantly different than that of white birch (B=-0.003, SE=0.038, p=0.930). Post-hoc analyses revealed that white birch had a negative slope coefficient that was significantly less than a slope of zero (B=-0.049, SE=0.012, p<0.001, Fig. 3b). Although white spruce was shown to have a slightly positive slope coefficient, it was not significantly different from a slope of zero (B=0.033, SE=0.036, p=0.356, Fig. 3c). Yellow birch was shown to have a positive slope that was significantly greater than a slope of zero (B=0.037, SE=0.011, p=0.001, Fig. 3a).

DISCUSSION

White birch:

The slopes of white birch were all statistically significant and all were contrary to what was predicted to have been observed if the Janzen-Connell hypothesis affected white-birch distribution. A negative slope coefficient that was significantly less than both that of yellow birch and that of a zero slope for the distance vs. height stepwise multiple regression (Fig. 1b) indicated that as distance increased, sapling height decreased. Because as far as this study is concerned, a decreased sapling height can be seen as suggestive of a lesser chance of sapling survival, these results are contrary to those predicted by the Janzen-Connell hypothesis. A slightly positive slope coefficient for the density vs. height stepwise multiple regression analysis (Fig. 2b) indicates that sapling density does not have the inverse effect on sapling survival that is consistent with prediction four of the Janzen-Connell hypothesis (Janzen 1970). A slope that was significantly less than zero for the distance vs. density analysis indicated that as the distance from the maternal tree increased, the probability of finding a white birch sapling, and therefore most likely the density of white birch saplings, decreased (Fig. 3b). This is contrary to the Janzen-Connell hypothesis which is supposed to account for a trend close to regular distribution (Crawley 1983, Hyatt et al., Janzen 1970). The observed distribution of white birch saplings suggests that, in accordance with the trend in temperate trees suggested in the results of the meta-analysis (Hyatt et al. 2003), distance from the maternal tree reduces survival for this particular species of temperate tree. The results of the three regression analyses for white birch indicate that white birch, a shade intolerant tree species, has an aggregated distribution which would be expected if seeds had an equal chance of survival and patterns of sapling distribution represented the initial pattern of seed dispersal (Janzen 1970). This is in accordance with the hypothesis that because white birch is so fast growing, it will spend the least amount of time out of all three species in the vulnerable stage and therefore will be less susceptible to the effects of host-specific predation that is less common than generalist predation in temperate climates (Harper 1977; Howe and Westley 1988; Hyatt 2003).

Yellow birch:

Yellow birch showed a trend consistent with the first prediction of the Janzen-Connell hypothesis which states that chances of seed/seedling/sapling survival should increase with distance from maternal tree (Janzen 1970). The positive slope that yellow birch had for the distance vs. density multiple logistic analysis (Fig. 3a) indicated an extreme case of repelled recruitment because more saplings were found far from the maternal tree than were found close to it. Consistent with the results in a study by Houle (1998), the results of this study could suggest that yellow birch is density independent and therefore observed patterns were not in accordance with the fourth prediction of the Janzen-Connell hypothesis. This can be seen in the zero slope generated by the stepwise multiple regression analysis of density vs. height (Fig. 2a).

Because one of the predictions of the Janzen-Connell hypothesis is that conspecific saplings closer to one another will have a lesser chance of survival than those more spaced out (Janzen 1970), and a small sapling indicated a young sapling or a sapling that was weakened by some sort of parasitism, saplings should have been larger in less dense areas. However, this is not necessarily contrary to the predictions of the Janzen-Connell hypothesis due to the sapling distribution patterns that are consistent with an extreme case of repelled recruitment. No pattern in height was seen in relation to distance either. Because density was greater with increasing distance from the maternal tree, host-specific density-dependent predators could have been affecting sapling growth far from the maternal tree, but it may not have been noticeable due to the distance-dependent host-specific predators that could have been limiting sapling growth closest to the tree. These two factors taken together could cause a constant sapling height. Either way, as seen through the extreme pattern of repelled recruitment suggested in Figure 3a, patterns of yellow birch sapling distribution appear to be more dependent on distance than density.

White spruce:

Although none of the results of white spruce showed that the slopes were significantly different than those of white birch, all of the slopes suggested a trend that was consistent with both predictions of the Janzen-Connell hypothesis. The lack of significance in the results could have been due to the small sample pool of white spruce. Unlike the birch saplings which tended to be numerous at many of the birch sites, there were only a few white spruce saplings at each white spruce site. The strongest results for white spruce were in the stepwise multiple regression analyses with distance and height. With a p-value of 0.056, the positive slope for white spruce (Fig. 1c) was almost significantly different than the negative one for white birch (Fig 1b). Because saplings tended to be larger further from the maternal tree, these results suggest that, consistent with the first prediction of the Janzen-Connell hypothesis, white spruce sapling survival increases with distance from the maternal tree. Although it was not significantly different than the positive slope of white birch, the negative slope resulting from the density vs. height stepwise multiple regression for white spruce (Fig. 2c) suggested a pattern in accordance with prediction four of the Janzen-Connell hypothesis that conspecific sapling density is inversely related to sapling survival (Janzen 1970). Multiple logistic regression and post-hoc analyses for density vs. distance suggested that a pattern of regular distribution might exist among white spruce saplings. Although multiple logistic regression revealed a slightly negative slope for white spruce, post-hoc analysis revealed a slightly positive slope that was not significantly different than zero (Fig. 3c), indicating a pattern of regular distribution. The Janzen-Connell hypothesis was formed in order to account for such observed patterns of regular distribution (Crawley 1983, Hyatt et al. 2003, Janzen 1970). Although results were not significantly different than white birch in most of the analyses, the trend in the slopes suggested that out of the three tree species studied, white spruce was most consistent with the expected patterns suggested by the predictions of the Janzen-Connell hypothesis.

Although not all of the results were significant, they suggest that a trend exists among shade-intolerant, intermediately shade-tolerant, and shade-tolerant species of temperate trees found on the UNDERC property. Results suggest that an increase in shade-tolerance could cause an increase in the tendency to show patterns of distributions consistent with those predicted by the Janzen-Connell hypothesis. Even if the results of the white spruce were discarded due to the small sample size and lack of statistical significance, there is a definite difference between the slopes of yellow birch and white birch for all three tests. The patterns observed in the moderate shade-tolerant yellow birch sapling distributions and heights were much more consistent than the shade-intolerant white birch sapling patterns with the patterns predicted by predictions 1 and 4 of the Janzen-Connell hypothesis.

Future studies:

Problems with identification of birch saplings were an issue in the field and could have affected results. Therefore, this experiment should be repeated using species other than birch to prevent confusion between the saplings of both species, and also to see if the same trend towards the patterns predicted by the Janzen-Connell hypothesis can be seen in relation to shade tolerance for most of the temperate tree species found on the UNDERC property. Because the sample pool was so small for white spruce, this study should be repeated using more adult white spruce. However, most of the UNDERC property was searched for lone adult white spruce and all the ones found were used in this study, so extending the range outside of UNDERC may be necessary in order to obtain more lone adult white spruce.

This study just looked at patterns of sapling distribution and compared them to those expected if the predictions of the Janzen-Connell hypothesis were effective on that particular tree species, but it could not prove that host-specific predators were causing the observed patterns. Further studies should be done to determine if the distribution patterns observed in yellow birch and white spruce were actually due to the Janzen-Connell hypothesis. Studies should be done to determine the host-specific predator. A study by Packer and Clay (2000) showed that pathogens were host-specific to black cherry and were affecting sapling distribution consistent with the predictions of the Janzen-Connell hypothesis. It was conducted by growing black cherry (*Prunus serotina*) seedlings in soils taken from near the maternal tree, from far away from the maternal tree, and in both soils after they were sterilized. A similar experiment should be conducted for white spruce and yellow birch to see if a host-specific pathogen is the cause of the observed sapling distribution patterns. If pathogens are not the cause, insect and animal host-specific predators should be considered.

Because it has been shown that the white-footed mouse (*Peromyscus leucopus*) does not show a regular pattern in seed predation in terms of distance-dependence or density-dependence but instead a pattern based off of the type of protection from predators available in the understory which is independent of any of the study trees (Manson and Stiles 1998), it can be ruled out as the cause of the observed patterns consistent with the predictions of the Janzen-Connell hypothesis. Because deer can be considered facultatively host-specific predators (Janzen 1970) and deer are very abundant in temperate climates, especially where hunting is not permitted (Horsely 2003), the effects of deer browsing should be studied for each of the three tree species. Deer should be kept out of the experimental plots using fences. Plots with 20m radii with the study tree in the center should be used and the same data that was collected for this study—height, density, and distance from maternal tree—should be collected after the saplings have been permitted to grow without the threat of deer predation for a few years and compared to control plots where deer were permitted to browse. If a specific insect is thought to be a host-specific predator on any of the tree species, experimental plots could involve regularly spraying the plot with some form of pesticide for a few years to ensure that these insects do not affect sapling distribution in those plots and the same data that was collected for this study should be collected again and compared to the control plots where the insect has not been kept away.

ACKNOWLEDGMENTS

I would like to thank my advisor, Dr. Walt Carson for his help in designing this project and providing sources for the basic information required to begin this study. I would especially like to thank my TA, Luke DeGroote, for the immense aide he provided in everything including proposal editing, tree identifications, sapling measurements, and statistics. Other thanks to the members of the UNDERC class of 2007—Katherine Davila Olmo, Meghan Mohrman, Charlie Vogelheim, Jessica Lee, Nick Ward, and Dano Heatwole—each of whom accompanied me once in the field to keep me company or record measurements.

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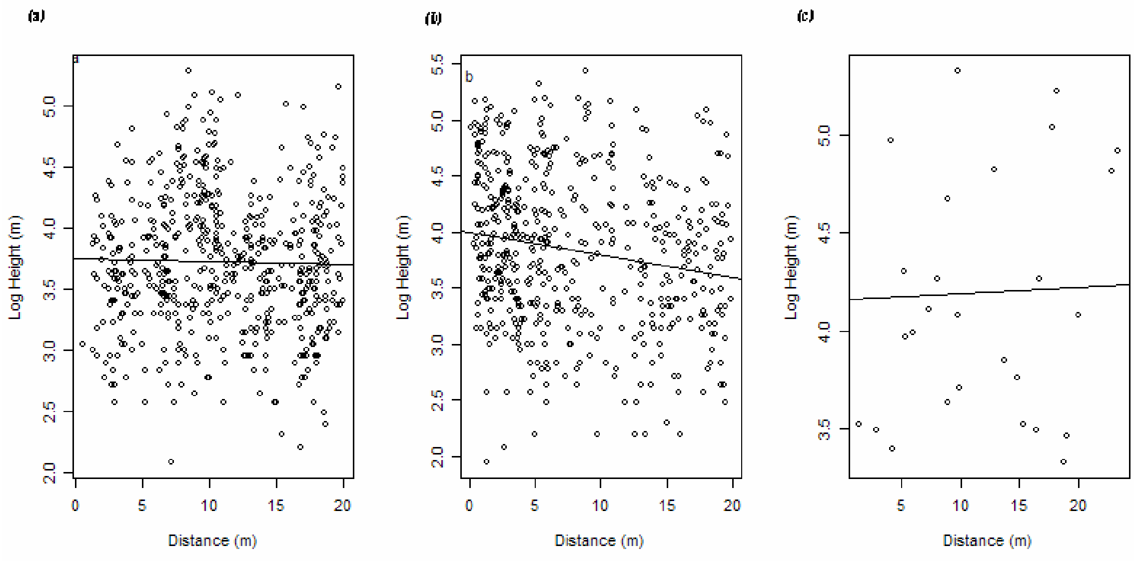

Figure 1: Height vs. distance for the three tree species. (a)Yellow birch: a slope similar to zero suggests that distance has no effect on sapling height. (b) White birch: a negative slope indicates that height and distance are inversely related. (c)White spruce: a slightly positive slope suggests that seedling maturation might be improved as distance form the maternal tree increases. However, most likely due to the small sample size of white spruce, the white spruce slope is not significantly different than the slope of white birch.

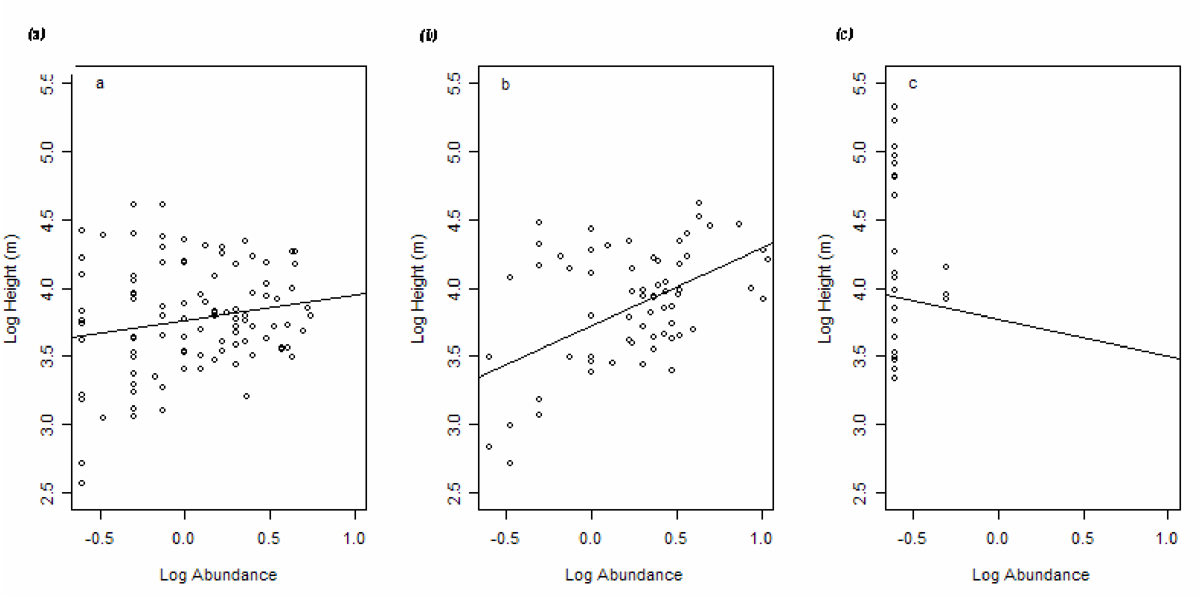

Figure 2: Height vs. density for all three species of temperate trees studied. (a)Yellow birch: the slightly positive slope is actually not significantly different than zero, therefore suggesting that density has no effect on sapling height. (b)White birch: the positive slope suggests that, contrary to prediction four of the Janzen-Connell hypothesis, density and height are positively related. (c)White spruce appears to have a negative slope that would be in accordance with the expected patterns consistent with prediction four of the Janzen-Connell hypothesis. However, most likely due to the small white spruce sapling sample size, there was not a great variation in density and the white spruce slope is not statistically significantly different than the slope of the white birch.

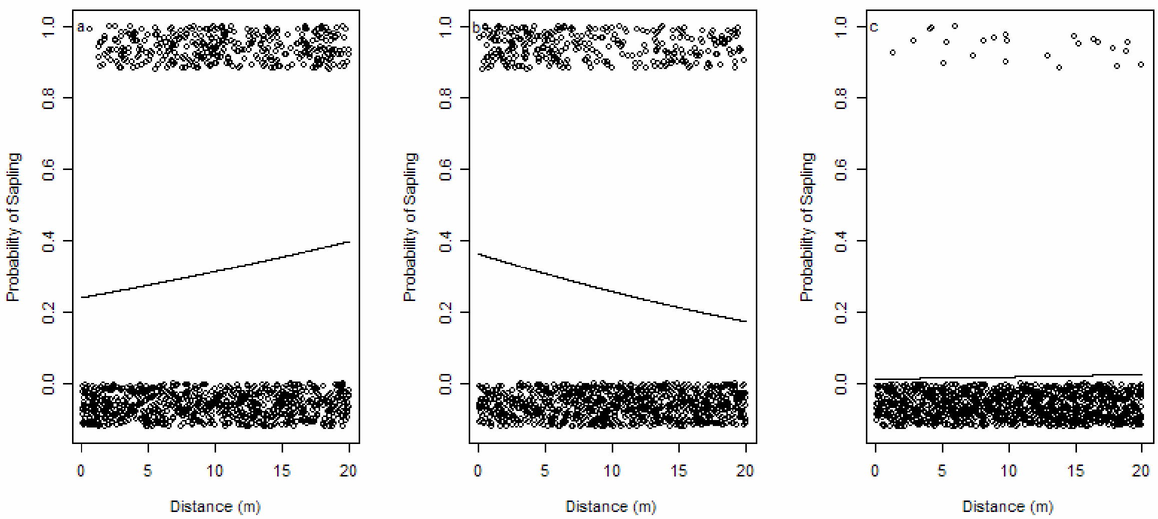

Figure 3: Distance vs. density for each of the three species of tree studied. The probability of a sapling being found was considered an indication of the sapling density at that specific area. Post-hoc analyses were run for each species of tree to see if any trees displayed patterns consistent with the pattern of regular distribution predicted by the Janzen-Connell hypothesis. (a) Yellow birch: a positive slope implied that sapling density increased with distance from the maternal tree indicating an extreme case of repelled recruitment (b)White birch: a negative slope indicated an aggregated distribution instead of what was predicted by the Janzen-Connell hypothesis. (c) White spruce: a slope that is similar to zero indicated a distribution very similar to the pattern of regular distribution predicted by the Janzen-Connell hypothesis.