Greenfall Dynamics Across Maple, Birch, and Aspen Stands of an Eastern Deciduous Forest in
Relation to Wind Disturbance
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## **Abstract**

Greenfall, or live leaf matter that prematurely falls to the forest floor, is an important and often overlooked component of forest systems. Although it accounts for less than five percent of foliar production, live leaf material on the forest floor is much more nutrient rich than senesced leaves. Factors such as insect herbivory and hurricane-strength winds that influence greenfall have been studied in the past. However, correlations between lower wind speeds and greenfall have not been studied. The major objectives of this study were to determine if the greenfall masses of aspen, birch, and maple forests in the University of Notre Dame Envrionmental Resarch Center correlate with wind speed, and whether the greenfall masses of the three species differ from each other. A secondary objective was to observe whether maple greenfall differed across habitat and how maple leaf rolling insects correlated with maple greenfall mass. My results reveal that greenfall mass differed between maple sites and aspen and birch sites, with birch and aspen sites exhibiting no difference. Only maple species greenfall mass exhibited a positive correlation with windspeed, while birch species exhibited a negative correlation. Maple leaf rollers correlated with decreased maple greenfall mass, while maple sites differed from aspen and birch sites in roller percentages. Future studies sampling wider areas of forest may be needed to determine whether similar correlations exist within larger forest systems.

## **Introduction**

Deciduous forests are dynamic communities, with nutrients constantly cycling from the soil of the forest floor, up into growing trees, and back to the floor again through litterfall. Numerous factors contribute to the cycling process and alter the overall vegetation structure of

the forest. Some examples of such factors include mammalian herbivory, abiotic disturbance, and insect herbivory in the canopy layer (Hunter and Forkner 1999). An often overlooked component of this system is greenfall, live leaves that prematurely abscise from their tree resulting in green leaf litter on the forest floor. Greenfall, while only accounting for less than five percent of foliar production is nonetheless an important aspect of forest communities(Risley and Crossley 1988). Although it is only a small part of the leaf litter, greenfall can contain as much as two times the amount of nitrogen and phosphorus as senesced leaves and as a result provides higher quality resources to the forest floor for potential consumers (Grace 1986). In addition, greenfall is important to forest systems because it occurs during the growing period, providing a nutrient input to the forest floor during a period of time when there is no input from senesced leaves (Meehan *et al.* 2010).

Leaf abscission, the process by which trees shed their leaves, is one factor that contributes to greenfall. The shedding is controlled by an abscission zone located at the base of the leaf, comprised of cells smaller than the surrounding leaf cells. These cells undergo a biochemical process where they break down along the point of detachment before the leaf falls off the tree (Sexton and Roberts 1982). Abscission occurs when the leaf undergoes damage, triggering the biochemical process leading to the leaf falling off (Bowling and Vaughn 2011). Trees affected by disturbances such as heavy storms can lose live leaves that they would have retained under ideal conditions. This live leaf loss could be a response of the tree to damage caused by the disturbance. If a leaf is damaged by a disturbance it may not be efficient for the tree to allocate resources to it anymore. This may cause the tree to resorb the leaf's nutrients in a process similar to when leaves undergo senescence (Lu *et al.* 2010). This may lead to the leaf being shed so nutrients can be translocated to healthier leaves capable of effective

photosynthesis. However, if a leaf is abscised from a tree before its nutrients can be resorbed any translocation of nutrients from the leaf will be prevented. This in turn may result in green leaves on the forest floor that are rich in nutrients (Risley and Crossley 1992).

Another set of factors that contribute to greenfall is activity by herbivorous insects and their predators in the forest canopy. Predator-prey interaction between birds and caterpillars frequently influence greenfall and which live leaves fall to the ground. Birds such as the black-capped chickadee use morphological clues such as rolled leaves and leaf discoloration to search for caterpillars (Heinrich and Collins 1983). As a possible response some palatable caterpillar larvae, in an effort to mask feeding activity from predators, chew live leaves off of their stem after feeding on them and cause them to fall to the forest floor (Heinrich 1979).

Wind speed is another common factor that may contribute to greenfall. Prior studies have examined large-scale disturbances such as hurricanes and their influence on greenfall, forest structure, and tree response (Lodge *et al.* 1991). Boucher *et al.* (1990) have reported that there are differences in responses to wind disturbance between tree species. Moreover, Cooper-Ellis *et al.* (1999) found wind different wind disturbance related mortality and damage among trees of differing size. In addition, there is evidence showing that hurricane damage results in pulses of nutrient availability from greenfall on the forest floor (Hunter and Forkner 1999). However, while several studies have investigated the effects of hurricane strength winds on greenfall there is little information about the effects of more moderate wind speeds on greenfall.

My first aim in this study was to determine whether there is any relationship between typical variations in wind speed and the amount of greenfall of three types of trees, maple, birch, and aspen, over the course of the summer. I also attempted to determine if these three tree types

exhibited any difference in the amount of greenfall in comparison to each other. Furthermore, since maple species are present in birch and aspen stands I tried to determine whether there is any variance in maple greenfall between the three forest types. Lastly, I looked at herbivory in maple species by studying the percentage of leaf rolling insects in maple greenfall across the three forest types and the relationship between maple leaf roller percentage and greenfall mass. I hypothesized that greenfall mass would be positively correlated with wind speed among all all tree types, and that all tree types would exhibit different greenfall masses in comparison to each other. I also expected maple greenfall mass to show no difference across all three forest types, with the reasoning that there should not be physiological differences between maple trees across the study property. Lastly, I expected the percentage of leaf rolling insects in maple leaves to exhibit no difference across the forest types, and that higher percentages of leaf rolling insects would correlate with an increase in greenfall mass.

## **Materials and Methods**

*Study Site*

This study was conducted during the months of June and July, 2012, at the University of Notre Dame Environmental Research Center (UNDERC), a 7500 acre property situated along the border of the Upper Peninsula of Michigan and northern Wisconsin. The property is surrounded by the Ottawa National forest and houses a variety of early succession trees such as birch and aspen, as well as late succession trees such as maple.

*Plot Selection*

Using a vegetation map of UNDERC property three study areas were selected, one where maple trees were dominant, one where birch trees were abundant and one where aspen trees were

abundant (Figure 1). Within each of the study areas I arbitrarily selected plots that were relatively clear of dense understory growth with at least one adult specimen. The selection process consisted of finding a maple, birch, or aspen tree within its respective study area with a diameter at breast height (DBH) greater than or equal to five centimeters and centering a fifty square meter plot around it. Plot coordinates were marked using a handheld global positioning system device and labeled with a flag at each corner. Within each plot the DBH and species was recorded for all maple, aspen, and birch with a DBH above or equal to five centimeters. This selection process continued until eight plots were established within each forest type for a total of 24 plots.

*Plot Sampling*

Each plot was visited weekly and all maple, birch, and aspen greenfall within the plot was collected and placed in a labeled bag. Once all plots had been collected the leaves from each bag were sorted and counted by species, with the percentage of maple leaves affected by leave rolling organisms also recorded for each plot. The bags were then placed in a drying oven set to sixty degrees Celsius for three days, after which the biomass for each species within each plot was recorded. Basal area of each tree within each plot was calculated and the number of leaves per species, as well as the leaf mass per species, was divided by the total basal area of trees of that species to quantify how many leaves and how much greenfall mass occurred per square meter of basal area for each species. This data was further divided by the amount of days between each collection to obtain a per day value for leaf count and mass. A weather station on property was utilized to obtain daily wind speed data and the maximum hourly wind speed during each given collection interval was recorded.

*Analysis*

All statistical analyses were run using the SYSTAT program. The only normally distributed variable was the maple leaf roller percents for each forest type ( Shapiro-Wilk P-Values = 0.418, 0.755, and 0.302 for maple, aspen, and birch, respectively). The remaining non-normally distributed variables collected were transformed by taking the natural logarithm of recorded values in order to normalize them. Data normalized in this matter include the maple forest maple greenfall mass, aspen forest aspen greenfall mass, aspen forest maple greenfall mass, birch forest birch greenfall mass, and birch forest maple greenfall mass, all of which originally had Shapiro-Wilk P-Values less than 0.05 but upon transformation had values of 0.170, 0.145, 0.171, 0.579, and 0.898, respectively. To test for a correlation between maximum wind speed and greenfall mass I performed linear regressions with greenfall of each forest type's main species as the dependant variable and maximum wind speed during each collection interval as the independent variable. I performed a one-way ANOVA to test for the differences between greenfall mass across forest types, as well as differences in maple leaf roller percents and maple greenfall mass across forest types. To test for a correlation between maple greenfall mass and leaf roller percentage I performed a linear regression with the maple greenfall mass in all forest types as the dependant variable and leaf roller percentage across all forest types as the independent variable.

## Results

The linear regression analyses indicated a significant positive correlation between maximum wind speed and maple greenfall mass in the maple forest type (Figure 2, P=0.0000059, $R^2$=0.50, SE=0.54, df=1,30), a significant negative correlation between maximum

wind speed and birch greenfall mass in the birch forest type (Figure 3, P=0.023, $R^2$=0.16, SE=0.70, df=1,30), and no significant correlation between maximum wind speed and aspen greenfall mass in the aspen forest type (Figure 4, P=0.95, $R^2$=0.00015, SE=0.796, df=1,30). There was a significant difference between the greenfall mass of the aspen, maple, and birch trees within their respective sites (Figure 5, P=0.00000000002, SE=0.58, $F_{2,93}$). A post-hoc analysis revealed that of the forest types, maple and birch (P=0.00001) and maple and aspen (P=0.00001) were significantly different while birch and aspen forest types did not significantly differ (P=0.344). There was significant difference in maple greenfall mass across all three forest types (Figure 6, P=0.0015, SE=0.67, $F_{2,93}$). However, a post-hoc analysis indicated that the only significant difference was between maple and birch sites (P=0.00096), with no significant difference between aspen and birch sites (P=0.127) or aspen and maple sites (P=0.185). There was significant difference in the maple leaf roller percentage across all three sites (Figure 7, P=0.00000000002, SE=14, $F_{2,93}$), with a post-hoc analysis indicating significant difference between aspen and maple (P=0.00001) as well and between birch and maple (P=0.00001), but there was no significant difference between birch and aspen sites (P=0.067). Lastly, there was a significant negative correlation between maple greenfall mass and leaf roller percentage (Figure 8, P=0.013, $R^2$=0.06, SE=0.85, df=1,94).

**Discussion**

Contrary to my expectations, birch greenfall showed a negative correlation with wind speed and aspen greenfall showed no correlation with wind speed. However, as I expected, maple greenfall showed a positive correlation with wind speed. Secondly, I only found partial evidence in support of my hypothesis that all three tree types would differ from each other in greenfall mass. Specifically, only maple differed from birch asnd aspen, with aspen and birch

exhibited no significant difference in greenfall mass. There was significant difference in maple greenfall between maple and birch sites, discounting my expectation that maple greenfall would not significantly differ between all three sites. In addition, contrary to my expectation that leaf roller percentages would not difer with forest type, I found evidence of significant differences in maple leaf roller percentages between maple and birch as well as maple and aspenm forests. Lastly, maple greenfall mass exhibited a significant negative correlation with an increase in maple leaf roller percentage, which is the opposite of what I hypothesized.

One reason why not all species exhibited a significant positive correlation between greenfall mass and wind speed may be because low level wind speed is not the most important factor influencing greenfall. Rather, barring large wind events such as hurricanes and tornadoes, prior studies have indicated that insect herbivory may be the most important factor affecting greenfall. In a deciduous forest in the southern Appalachians where greenfall was studied in thirty-six sites there were only six sites that had more greenfall mass attributed to causes other than herbivory (Risley and Crossley 1988). Impact of herbivores could also be a reason why aspen and birch exhibit different greenfall masses than maple but not from each other. If there are insects that preferentially feed on one tree type over another the amount of greenfall for each tree type could be different. It is possible, however, that high wind in combination with heavy precipitation could significantly impact greenfall. In the same study the only cases where non-herbivory related greenfall was significantly greater than herbivore caused greenfall were due to thunderstorms. Future studies into greenfall could attempt to quantify the relative importance of wind-induced greenfall related to herbivore-induced greenfall. Such a study could also attempt to find a threshold speed where wind replaces herbivory as the dominant greenfall cause.

The negative correlation between greenfall mass and windspeed for birch could also be attributed to insect herbivory choices. Caterpillars are very selective in choosing which leaves they consume (Schultz 1983). Their selectivity is due to their preference for plant parts with high nitrogen, so greenfall inducing insects may preferentially select young leaves that are rich in nitrogen (Mattson 1980). As a result they may selectively feed on smaller, younger birch leaves that are richer in nitrogen than surrounding leaves and cause them to fall. In effect, the decreasing birch greenfall mass with increasing wind speed could be unrelated to wind speed and instead be due to herbivorous insects clipping small birch leaves from trees. In the future it could be interesting to examine the prevalence of herbivory in birch forests to determine whether preference for younger, smaller leaves produces a correlation between wind speed and greenfall mass. It would also be interesting to examine if herbivory has an effect on maple trees within birch forests, and whether that can explain any of the difference that exists between maple growing in birch sites and maple growing in aspen or maple sites.

Maple leaf roller results may also be explained by herbivorous insect activity. In general young leaves on trees are preferred by insects because they contain more nitrogen and moisture and less harmful substances than mature leaves (Rhoades and Cates 1976). Insects feeding on maple leaves and utilizing them to roll up for shelter could seek out younger, smaller maple leaves. Caterpillars rolling leaves for shelter have been known to create their shelter then clip the leaf to allow it to fall to the forest floor (Risley and Crossley 1988). If the leaves that contained rollers in the aspen and birch sites were young and wind related greenfall was not significant, then the maple roller activity could have accounted for the correlation between increased leaf roller percent and decreased greenfall mass. In the future a more in-depth study of leaf rolling insects could indicate how much greenfall mass relates to leaf roller activity.

Greenfall is a very important and often overlooked component of forest system dynamics. While only contributing to less than five percent of leaf litter, its input is more nutrient rich in comparison to senesced leaves that fall to the ground. The higher nutrient content of greenfall and the fact that greenfall occurs during the growing season makes it a valuable input to herbivores and decomposers on the forest floor. In the future more in-depth studies into greenfall may be useful in assessing its importance and underlying causes. Examining widespread forest areas and other tree species, as well as insect herbivory, will add to the understanding of greenfall processes. Furthermore, lab experiments could indicate more about underlying physical processes behind non-herbivore induced greenfall, such as testing what wind speeds will cause different tree species to lose green leaf material. Studying wind effects in the lab will help indicate how much greenfall is due to herbivores and how much is a result of abiotic processes. Considering its unique place in forest systems, further studies into greenfall and its significance could prove to be very useful.

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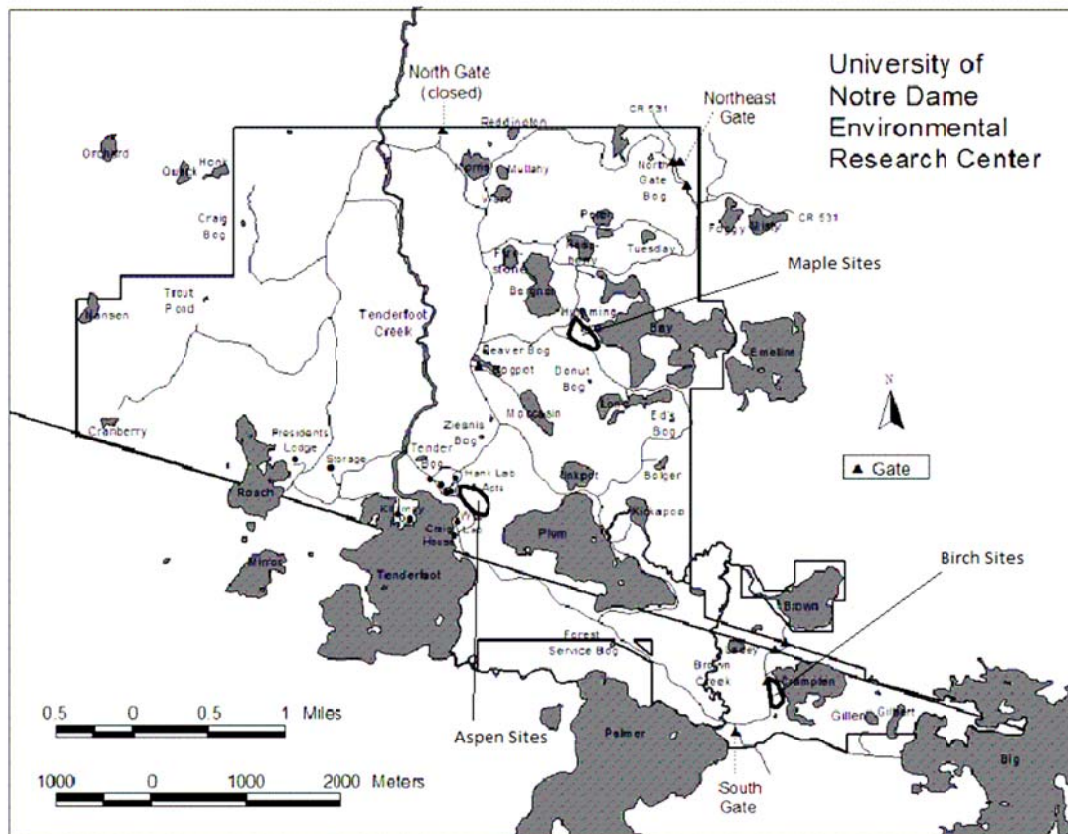   for plant anti-herbivore responses to defoliation. *Oecologia* 61:208-210.

**Figures**



**Figure 1**     Location of Aspen, Maple, and Birch forest sites used for study

## Maple Mass Vs Max Wind



**Figure 2**     Relation between the natural logarithm of maple greenfall mass in maple sites and the maximum wind speed recorded during each collection interval. $P<0.05$, $R^2=0.50$, SE=0.54, df=1,30.
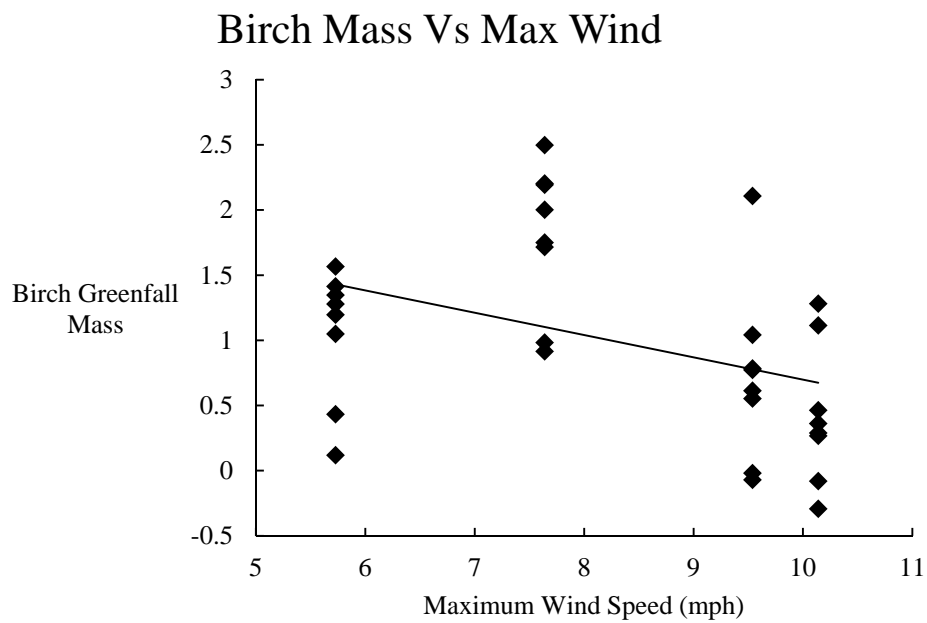
## Birch Mass Vs Max Wind



**Figure 3**     Relation between the natural logarithm of birch greenfall mass in birch sites and the maximum wind speed recorded during each collection interval. $P=0.023$, $R^2=0.16$, SE=0.70, df=1,30.
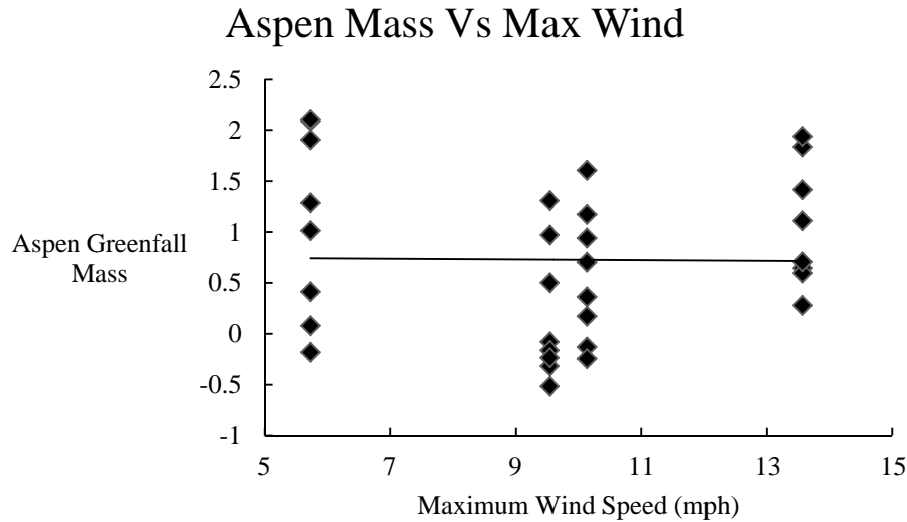
## Aspen Mass Vs Max Wind



**Figure 4**    Relation between the natural logarithm of aspen greenfall mass in aspen sites and the maximum wind speed recorded during each collection interval. $P>0.05$, $R^2=0.00015$, SE=0.796, df=1,30.
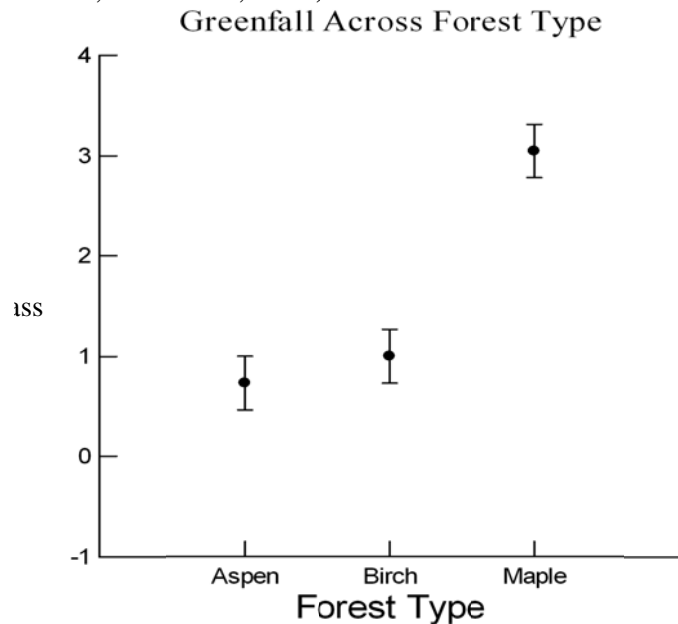


**Figure 5**    Least squares means of the logarithm of aspen, birch, and maple greenfall mass in respective forest types. ANOVA indicated sites differed significantly ($P<0.05$, SE=0.58, $F_{2,93}$), with a Tukey test indicating no significant difference between birch and aspen ($P=0.344$) and significant difference between maple and birch ($P<0.05$) and maple and aspen ($P<0.05$).
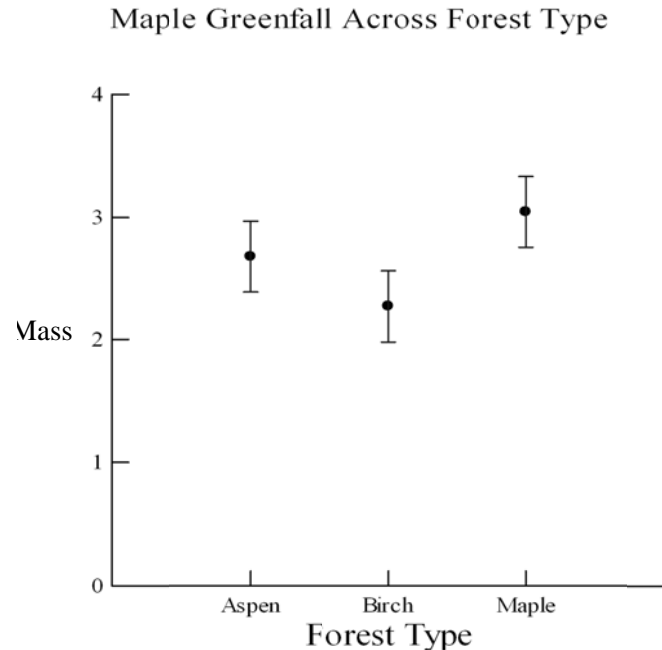
Maple Greenfall Across Forest Type



**Figure 6**   Least squares means of the logarithm of maple greenfall mass across forest
types. ANOVA indicated sites differed significantly (P=0.0015, SE=0.67,
$F_{2,93}$), with a Tukey test indicating significant difference between maple
and birch (P=0.00096), and no significant difference between aspen and birch
(P=0.127) or aspen and maple (P=0.185).
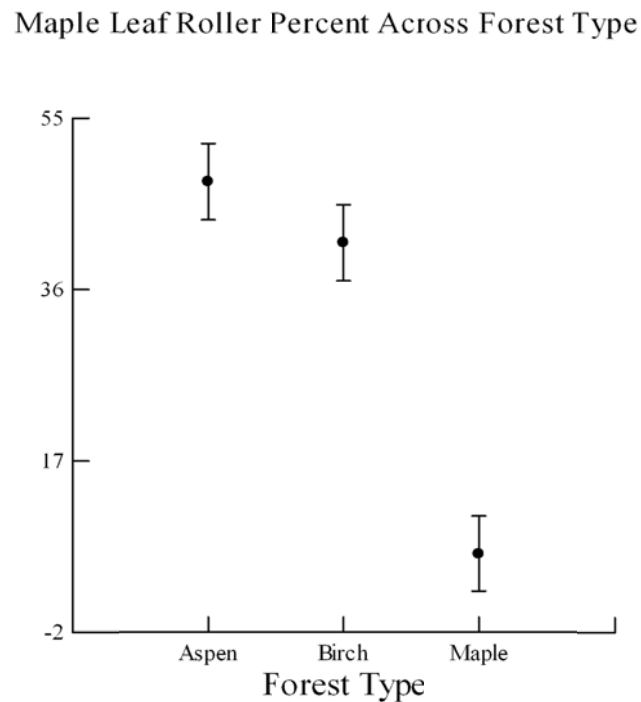
Maple Leaf Roller Percent Across Forest Type



**Figure 7**   Least squares means of maple leaf roller percent across forest types. ANOVA
Indicated significant difference between sites (P<0.05, SE=14, $F_{2,93}$), with a
Tukey test indicating significant difference between aspen and maple sites

(P<0.05) as well as birch and maple sites (P<0.05), but no significant difference
Between birch and aspen sites (P=0.067).
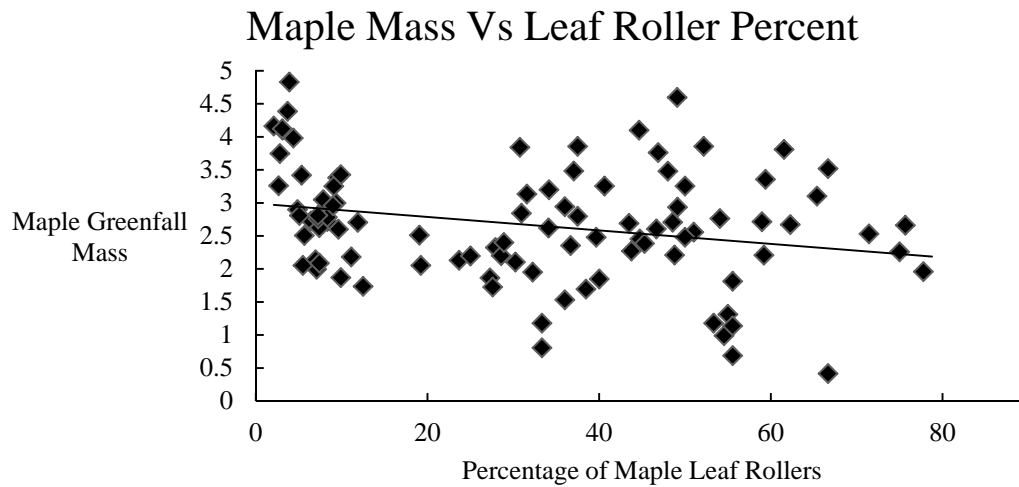
## Maple Mass Vs Leaf Roller Percent



**Figure 8**    Relation between the natural logarithm of maple greenfall mass across all sites
and maple leaf roller percentage across all sites. (P=0.013, $R^2$=0.06, SE=0.85,
df=1,94).