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Effects of climate change across seasons on litterfall mass and chemistry in a northern hardwood forest

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Thesis

**EFFECTS OF CLIMATE CHANGE ACROSS
SEASONS ON LITTERFALL MASS AND CHEMISTRY
IN A NORTHERN HARDWOOD FOREST**

by

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ABSTRACT

Northern hardwood forests are expected to experience an increase in mean annual air temperatures, and a decrease in winter snowpack and greater frequency of soil freeze/thaw cycles (FTCs) by the end of the century. As a result of these anticipated changes, northern hardwood forests in the northeastern U.S. will also have warmer soil temperatures in the growing season and colder soils in winter. Prior studies show that warmer soils in the growing season increase net primary productivity (NPP) and C storage as a result of increased soil net N mineralization, while increases in soil freezing in winter reduces plant uptake of N and C as a result of root damage. However, the combined effects of warmer soils in the growing season and increased soil freeze/thaw cycles in winter on tree litter mass and chemistry are unknown. We report here results from the Climate Change Across Seasons Experiment (CCASE) at Hubbard Brook Experimental Forest in New Hampshire, USA to characterize the response of leaf litter mass and chemistry to growing season warming combined with soil freeze–thaw cycles in winter. Across the years 2014-2017, litterfall mass and chemistry (%C, %N, C:N) were not significantly affected by changes in soil temperature; however, there was a trend of higher total litterfall mass and litter N mass from plots where soils were warmed in the growing season, but this increase disappeared with the addition of FTCs in winter. These results indicate that while rates of NPP and the total mass of N could be increased with

rising soil temperatures over the next century in northern hardwood forests, the combination of warmer soils in the growing season and colder soils in winter may ultimately have little to no impact on litter mass or chemistry. We conclude that considering the combined effects of climate changes in the growing season and in winter is vital for the accurate determination of the response of litterfall mass and chemistry in northern hardwood forests.

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Introduction

Mean annual air temperatures in the northeastern U.S. are expected to be 2.9 to 5.3 degrees C greater than the 1970-1999 mean by the year 2100 and heat waves are expected to occur with increased frequency (Hayhoe et al 2007). The depth and duration of winter snowpack is also expected to decrease (Reinmann et al 2019), which will cause soil freeze/thaw cycles in winter to increase in frequency (Campbell et al. 2010). Some models project a 49%-95% decrease in overall forest area undergoing winter snowpack in the northeastern United States by the year 2099 (Reinmann et al. 2019). As a result of these anticipated changes, northern hardwood forests in the northeastern U.S. will likely experience warmer soil temperatures in the growing season and colder soils in winter over the next century.

As temperatures continue to change over the next century, ecosystem processes, including primary productivity and nutrient cycling may be impacted. Warmer air and soil temperatures have been shown to increase rates of gross photosynthesis, net primary productivity (NPP), and above and belowground C storage (Lu et al. 2013). A soil warming experiment in a mixed temperate forest at Harvard Forest demonstrated that warmer soils result in greater tree growth and net primary productivity, which was attributed to warming induced increases in N availability (Melillo et al. 2011). Greater soil N availability with warmer soil temperatures has been attributed to increased rates of net nitrogen mineralization (Melillo et al. 2011; Harrison et al., *in press*, Biogeochemistry), a process carried out by soil microbes that breaks down soil organic matter to produce inorganic forms of nitrogen plants can take up. An increase in net N

mineralization, and subsequent increase in soil N availability could increase plant N uptake, and N content in leaf litter (Bai et al. 2013; Lu et al. 2013). As a result of the increase in tree growth and NPP under warmer soils, the size of plant C pools (Lu et al. 2013). While these results indicate warming air temperatures could potentially increase the capacity of northern hardwood forests as C sinks, if temperatures increase too far, increases in NPP could reach a cap for two reasons. While an initial warming of soils increases N available to trees, and thus results in increased NPP (Melillo et al. 2011), continued warming of soils could lead northern hardwood trees to become limited by other nutrients such as phosphorus (Gonzales and Yanai 2019). Trees and microbes could also be subject to heat stress if temperatures are increased beyond their range of tolerance, which could offset the benefits of increased rates of N mineralization for NPP at lower temperatures (Teskey et al. 2015).

In addition to warmer temperatures increasing NPP and soil nutrient cycling during the growing season, they also impact winter processes, namely snowpack and soil freezing. Winter snowpack provides an insulating effect on forest soils, and aids in regulating the severity and frequency of soil frost (Hardy et al. 2001). Past studies have indicated that reduced winter snowpack and increased depth and duration of soil freezing can result in a significant reduction in aboveground woody biomass and carbon stored in wood of maple trees (Reinmann et al. 2019). An increase in soil freeze/thaw cycles caused by a smaller snowpack in winter may also reduce C uptake by trees during the growing season as a result of damage to tree roots (Campbell et al. 2014; Sanders-DeMott et al. 2018). Damage to roots by soil freezing results in reduced ability of trees to

uptake nitrogen and other nutrients in the following growing season (Campbell et al. 2014; Comerford et al. 2013; Sanders-DeMott et al. 2018). Increased soil freezing also changes soil microbial communities and leads to decreased rates of N mineralization, which may contribute to the decreased rates of N uptake by trees (Sorenson et al. 2019). The negative impacts of a reduced snowpack and increased soil freezing in winter could therefore offset any potential benefit of warmer soil temperatures in the growing season on root health, nutrient uptake, rates of tree growth, and NPP of northern hardwood forests. It is possible that these changes in forest function could also result in changes in litterfall chemistry.

Litterfall chemistry plays an important role in the regulation of nutrient cycling in northern hardwood forests, and the combined effects of climate change across seasons could affect litterfall %C, %N, and C:N ratios, impacting rates of nutrient recycling and biogeochemical cycling of these elements in northern hardwood forest ecosystems. Nitrogen is considered the most limiting nutrient for plants in northern forests (Schlesinger and Bernhardt 2013). During the growing season trees take up and assimilate nutrients like nitrogen into their biomass. In Autumn each year, both C and N can be retranslocated before foliage falls from trees as litterfall. As the leaves fall from the trees to the forest floor and begin to decompose, the C and N that was used in the creation of the leaf matter is returned to the soil where microbes can once again break down organic material to inorganic forms of nitrogen and other elements that trees take up (Likens 2013). The total mass of litterfall that falls from deciduous trees in Autumn is often used as a metric for rates of aboveground NPP, since the mass of leaves produced is

positively related to total rates of tree growth and aboveground C sequestration (Clark et al. 2001). While northern forests are currently considered to be net C sinks, the combined effects of climate change across seasons could alter their capacity for C storage if changes in soil temperature affect their rates of growth (Pan et al. 2011). Further, the combined effects of climate change across seasons could affect litterfall %C, %N, and C:N ratios, affecting rates of nutrient recycling and biogeochemical cycling of these elements in these forest ecosystems.

To our knowledge, no study has evaluated effects of climate change on total mass of litter or litterfall chemistry in northern hardwood forests. Understanding the combined impacts of a warmer growing season, reduced winter snowpack, and increased soil freeze thaw cycles in winter on litterfall mass and chemistry, will help us to predict how rates of forest growth, C storage, and nutrient cycling in northern hardwood forests may change in the future. We hypothesize that trees that experience warmer soils in the growing season have a higher amount of total litterfall mass and higher concentrations of carbon (C) and nitrogen (N) in litterfall compared to forests with ambient conditions, and that soil freeze/thaw cycles in winter offset growing season warming-induced increases in total litterfall mass and C and N in litterfall. Since warming has been shown to increase rates of N uptake (Lu et al. 2013; Melillo et al. 2011) and soil freeze/thaw cycles have been shown to have the opposite effect (Campbell et al. 2014; Sanders-DeMott et al. 2018), we also expected that the ratio of C:N in litterfall would be reduced when trees experience growing season soil warming, but come back to baseline C:N ratios when they

also experience a small winter snowpack and greater frequency of soil freeze/thaw cycles in winter.

Methods

Study Site

Our research was conducted at the Hubbard Brook Experimental Forest (HBEF), a United States National Science Foundation Long-Term Ecological Research (NSF LTER) site, in New Hampshire, USA (43°56'N, 71°45'W). HBEF is principally populated by northern hardwood trees; however, higher elevations and steeper slopes have coniferous tree species. Soils at HBEF are primarily Typic Haplorthods, a base-poor spodosol formed in glaciofluvial sand and gravel, and depth to bedrock is approximately 14m deep (Winter et al. 2008). The climate is cool, humid and continental with an average annual rainfall of 1400 mm falling evenly all year round. Soil frost occurs about two out of every three years, with a mean annual max depth of 6cm (Campbell et al. 2010), and winter air temperatures average -4.7°C (Bailey et al. 2003; years 1969-2000). While HBEF has gone undisturbed since 1920, the conifer-hardwood forest was logged for 30 years.

Climate Change Across Seasons Experiment (CCASE)

During the summer of 2012 at HBEF, we established CCASE (Templer et al. 2017) to explore the impacts of a 5 °C temperature increase during the snow free season (Hayhoe et al. 2007) and the rise of soil freeze/thaw cycle frequency in winter (Campbell

et al. 2010) anticipated in this area over the next century. Red Maple is the dominant species in our experimental plots, which makes up $63 \pm 7\%$ basal area with an understory comprised of mainly American beech (*Fagus grandifolia*) saplings (Templer et al. 2017).

We established six plots (each 11 X 13.5 m²) that are all centered on a minimum of three mature red maple trees, a typical canopy tree in northern hardwood forests. Other tree species present in our plots include sugar maple (*Acer saccharum*), yellow birch (*Betula Alleghenies*), big tooth aspen (*Populus grandidentata*), white ash (*Fraxinus Americana*), and red oak (*Quercus rubra*) trees. In an attempt to standardize the plots, all six plots were intentionally situated to have comparable tree species composition and aboveground biomass. Notably, across the six plots in 2012, litterfall mass of red maple trees was not significantly different across the six plots (prior to the start of the experiment; $p = 0.54$).

Ongoing snow manipulation and soil temperature treatments began in December of 2013. There are two plots where soils are warmed to 5 °C above ambient (“warmed”) between spring snowmelt (early April) and the first snowfall in November or December (hereafter referred to as the growing season); two plots with the same warming treatment in addition to soil freeze/thaw cycles induced in winter (“warmed + FTC”); and two plots with ambient soil temperature (“reference”). The *warmed* and *warmed + FTC* plots combined make up the four “treatment” plots and are fitted with heating cables that were buried in parallel lines, 20 cm apart, and 10 cm deep by hand using a flat shovel in 2012. While no warming cables were installed in *Reference* plots, the soils were likewise cut to mimic cable installation disturbance.

In the *warmed + FTC* treatment plots, the first snow of winter is lightly packed down to preserve albedo and reduce disturbance to the forest floor with succeeding shoveling. We induce soil freezing by removing snow via shoveling within 24 hours of snowfall events in winter. Soil freezing is operationally defined as soil temperatures less than $-0.5\text{ }^{\circ}\text{C}$. The heating cables are switched on to warm soils to $1\text{ }^{\circ}\text{C}$ to induce a 72-hour thaw, after soils are frozen for 72-hours. One soil FTC is created by the whole process of frozen soils for 72 hours and thawing soils for 72-hours total. We attained four FTCs in the winters of both 2013/2014 and 2014/2015, two in 2015/2016, one in 2016/2017 and two in 2017/2018.

Litterfall collections and chemistry

Between the years of 2014-2017, we placed four baskets in each plot in early September to collect litterfall throughout Autumn ($n = 24$ baskets total). Each basket is lined with a fiberglass mesh door screening (mesh size $1/16''$) to avoid loss of litter from baskets and has a top interior area of 55 cm by 42 cm for a total collection surface per plot of 0.924 m^2 . All litter is removed biweekly throughout Autumn, typically for about 8-10 weeks. Litterfall is brought back to the laboratory and dried in an oven at 55 degrees Celsius for a minimum of 48 hours and sorted by tree species and plot each fall. Sorted litter is weighed to determine mass by tree species and ground using a Wiley Mill or liquid N with a mortar and pestle and weighed into tin capsules on a microbalance prior to CN analysis. We analyzed all litter samples on a C and N autoanalyzer at Boston University.

Statistical Analyses

Statistical analyses were completed using R statistical software (version 3.6.1; R Core Team, 2019). All error is reported as standard error (SE) of the mean for total litterfall mass, %C, %N and C:N across the three treatment types (*reference*, *warmed*, *warmed + FTC*) for 2014-2017. In all statistical analyses, treatment was designated as a fixed effect and plot was the random effect to account for the repeated sampling over time.

We used linear mixed effects models to examine potential treatment effects on total litterfall mass, mass of C, mass of N, %C, %N, and C:N values in specific years between 2014-2017. All linear mixed effects models were implemented using the package “nlme” in R (Pinheiro et al. 2012). Plot was designated as the random effect for these tests, with total litterfall mass, mass of C, mass of N, %C, %N, and C:N as the fixed effects respectively. Tukey's HSD tests were used for all pairwise comparisons among treatments. We were unable to have more than two *reference*, two *warmed*, and two *warmed + FTC* plots, as a result of the cost and infrastructure necessary to implement the experimental treatments.

Results

Growing Season and Winter Environmental Variables

Soil temperatures in *warmed* plots were higher than *reference* plots by 5.1 ± 0.05 °C and 5.0 ± 0.05 °C, for *warmed* and *warmed + FTC*, respectively (Harrison et al. 2020). The depth of snow and minimum winter soil temperatures were both lower, while

soil frost depths and number of soil FTCs were greater in the *warmed* + *FTC* plots compared to the *reference* plots (Harrison et al. 2020).

Litterfall Mass

While not statistically significant, we found a trend whereby there was greater litterfall mass in the *warmed* compared to the *reference* plots, but this difference disappeared with the addition of soil freeze/thaw cycles in winter (Figure 1). While we observed a trend for greater total mass of N (g N m^{-2}) in litterfall in the *warmed* plots compared to the *reference* plots, these differences were not significantly different. Similarly, there was no difference in total mass of C (g C m^{-2}) across treatments (Figure 2).

Litterfall Chemistry

We found no statistically significant differences in %C, %N or C:N ratio between *reference*, *warmed* only, and *warmed* + *freeze thaw* cycle plots across 2014-2017 (Figures 3-9). However, we found statistically significant differences in %C, %N, and C:N between the three treatments within individual years for some tree species (Figures 3-9). For example, litterfall %C for red maple in the year 2016 was significantly higher in *warmed* + *freeze thaw* cycle plots than in *reference* plots (Figure 3). For yellow birch, litterfall %C was significantly higher in *warmed* + *freeze thaw* cycle plots than in *warmed* only plots in 2014 (Figure 6). Also, for yellow birch, litterfall %N was significantly higher in *warmed* only plots than in *reference* or *warmed* + *freeze thaw*

cycle plots in 2017 (Figure 6). In 2017 litterfall C:N was significantly lower in *warmed* plots than in *reference* or *warmed + freeze thaw* cycle plots for yellow birch (Figure 6). In 2016 for big tooth aspen, *warmed + freeze thaw* cycle plots had significantly more litterfall %N than *reference* plots (Figure 7). In 2014 for big tooth aspen, *warmed* only plots had significantly lower litterfall C:N than *warmed + freeze thaw* cycle plots, while in 2016 *warmed + freeze thaw* cycle plots had significantly lower litterfall C:N than *reference* plots (Figure 7). In 2017 for white ash, litterfall %C in 2017 was significantly higher in *reference* plots than *warmed* only, and *warmed + freeze thaw* cycle plots (Figure 9).

Discussion

Despite the lack of significant differences, the observed trend for greater litterfall and litter N mass in the *warmed* plots compared to the *reference* plots indicates that rates of NPP and the total mass of N could be increased with rising soil temperatures over the next century in northern hardwood forests. The fact that a smaller snowpack and greater frequency of soil freeze/thaw cycles in winter completely offset these warming-induced gains suggests that over the next century we are unlikely to see large shifts in rates of NPP and inputs of N to the forest floor in northern hardwood forests during Autumn senescence in these forests. These results are important because they show that past studies that only focus on projected increases in temperatures, that do not take into account the shrinking winter snowpack and greater incidence of soil freeze/thaw cycles, are likely to overestimate warming induced increases in nutrient cycling and C

sequestration. While litterfall mass may not have been significantly different, *warmed* plots could still have increased NPP, and litterfall may not capture the full story.

Belowground productivity and growth of roots were not measured in this study, and we could be missing a portion of the increase in NPP by only measuring changes in aboveground growth.

The lack of effect of changing soil temperatures on C concentrations in litter may have resulted from a simultaneous increase in both C uptake (plant growth) and C loss (plant respiration) both being stimulated by the warmer soils in the growing season and canceling each other out, for a net result of no change in the *warmed* plots from the *reference* plots (Lu et al. 2013). The C concentrations in litter from *warmed + freeze thaw* cycle plots also did not differ significantly from *reference* plots, which could be explained by an inability of trees to fully utilize the increase in N availability during the warmer growing season as a result of damage done to the roots during the increased freeze/thaw cycles in the winter season (Sanders-DeMott et al. 2018). If root damage prevented trees in the *warmed + freeze thaw* cycle plots from utilizing an increase in N that was made available by warmer growing season soils, then there would be no subsequent increase in NPP and aboveground C storage, and thus C content of litter.

The lack of effects of warmer soils and increased freeze/thaw cycles on N content in litter could be a result of changes in net nitrification and tree root uptake of N. Prior studies at Hubbard Brook have shown that disturbances like soil freezing, which lowers the ability for trees to take up N (Campbell et al. 2014; Sanders-DeMott et al. 2018), result in higher nitrification rates as the ammonium released through

decomposition builds up in the soil, and increased nitrate leaching from soils occurs as a result (Houlton et al. 2003). While warmer soils may have increased rates of net nitrogen mineralization (Harrison et al., *in press* Biogeochemistry) and NPP in the forests at CCASE, increased soil FTCs damaged roots to the point that they did not take up significantly more N in the *warmed + freeze thaw* than *reference* plots, and the excess N that may have been in the soil as a result of warming in the growing season, may have leached out or been converted to nitrate (Sanders-DeMott et al. 2018). Therefore, the lack of significant difference in litterfall N concentration and N mass among the treatments may reflect the lack of difference in N uptake among the plots. The damage from freeze/thaw cycles to tree roots, which in turn may limit how much N trees can take up, may have also limited the amount of C the plant could take up and assimilate despite warmer growing season soil temperatures resulting in no significant change in C concentration between *reference* plots and *warmed + freeze thaw* cycle plots.

While not statistically significant, we observed lower C:N ratios of litter in *warmed* compared to *reference* plots, which may indicate that soil warming makes leaf litter more labile, which allows litter to be more easily decomposed by soil microbes. The *warmed + FTC* plots did not differ significantly from *reference* plots for litter C:N, which again may be attributed to damage to tree roots from soil freeze/thaw cycles which in turn hampered the C and N uptake ability of trees so that they could not utilize any increase in N that may have been present in the growing season due to warmer soils. If repeated damage to tree roots from consecutive winters of being subjected to increased freeze/thaw cycles, results in a continuous decrease in root function each year, including

root uptake of N, then nitrate leaching could eventually occur at a high enough rate that C:N values actually increase in the *warmed + freeze thaw* cycle plots.

Conclusions

A continued increase in air temperatures (Hayhoe et al 2007) and the increased frequency of winter soil freeze/thaw events (Campbell et al 2010) are expected to occur over the next century in New England, which is likely to impact NPP of northern hardwood forests. Our results demonstrate that the combined effects of climate change across the growing and winter seasons may result in no net change in litterfall mass or chemistry in northern hardwood forests. While past studies have shown warmer growing seasons result in increased NPP and aboveground carbon storage as a result of increased N availability, our results indicate that a reduction in winter snowpack and increase in soil freeze/thaw cycles cancels out any increase in NPP gained during a warmer growing season. These results indicate that over the next century we are unlikely to see large shifts in forest productivity and inputs of C and N to the forest floor during Autumn senescence in northern hardwood forests.

Due to the cost of setting up our plots, we were limited in plot number, plot size, and number of trees in each plot. Future studies could attempt to warm soils and induce freeze/thaw cycles at a larger scale to see if plot area or tree number impacts the results. While we did not find any effects of tree species on litterfall mass or chemistry, future studies could include additional tree species that are found in northern hardwood forests, to determine if species not included in this study may respond differently to the

treatments. We also only measured changes in aboveground NPP, so future studies could consider whether warmer soils and increased freeze/thaw cycles result in changes to belowground biomass. This study included four years of data, as the plots are subjected to warmer soils and increased freeze/thaw cycles for a longer period, we can assess whether there are any cumulative effects that become apparent in the long-term.

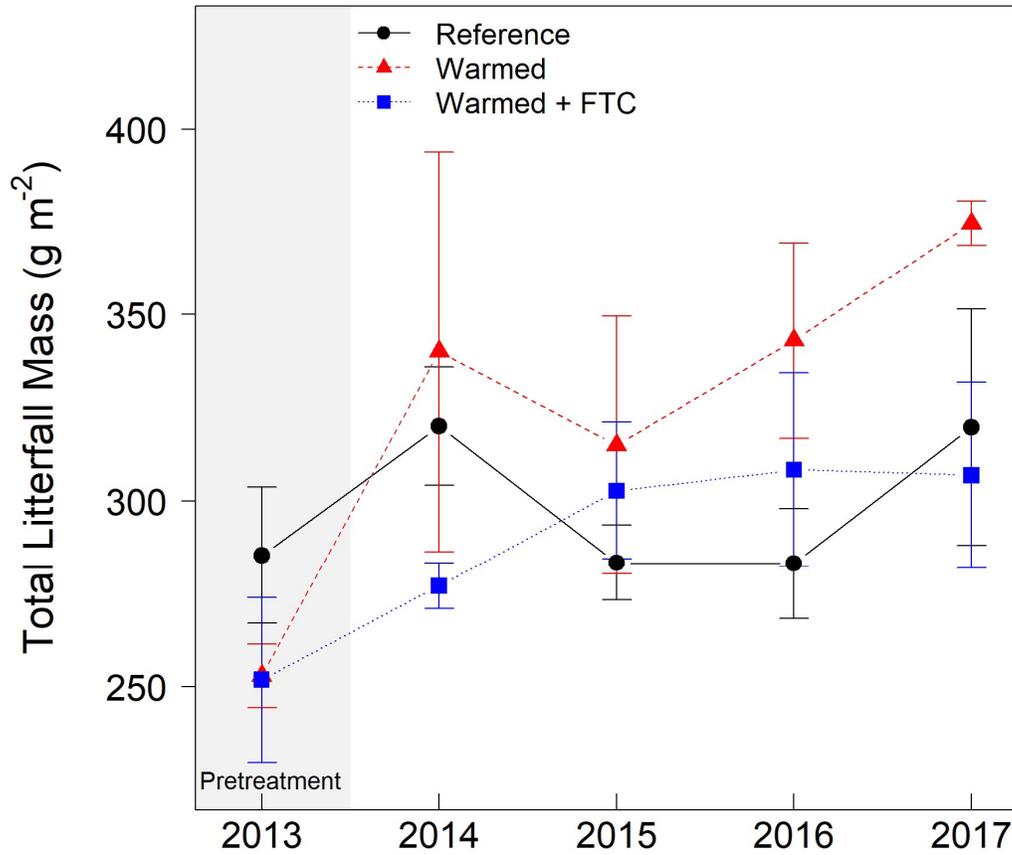


Figure 1. Total litterfall mass (g m^{-2}) across all tree species measured from litterfall collected in CCASE plots between 2013 and 2017. Values are means with standard error. Gray shaded region indicates period of time before we initiated experimental treatments (treatments began in December 2013).

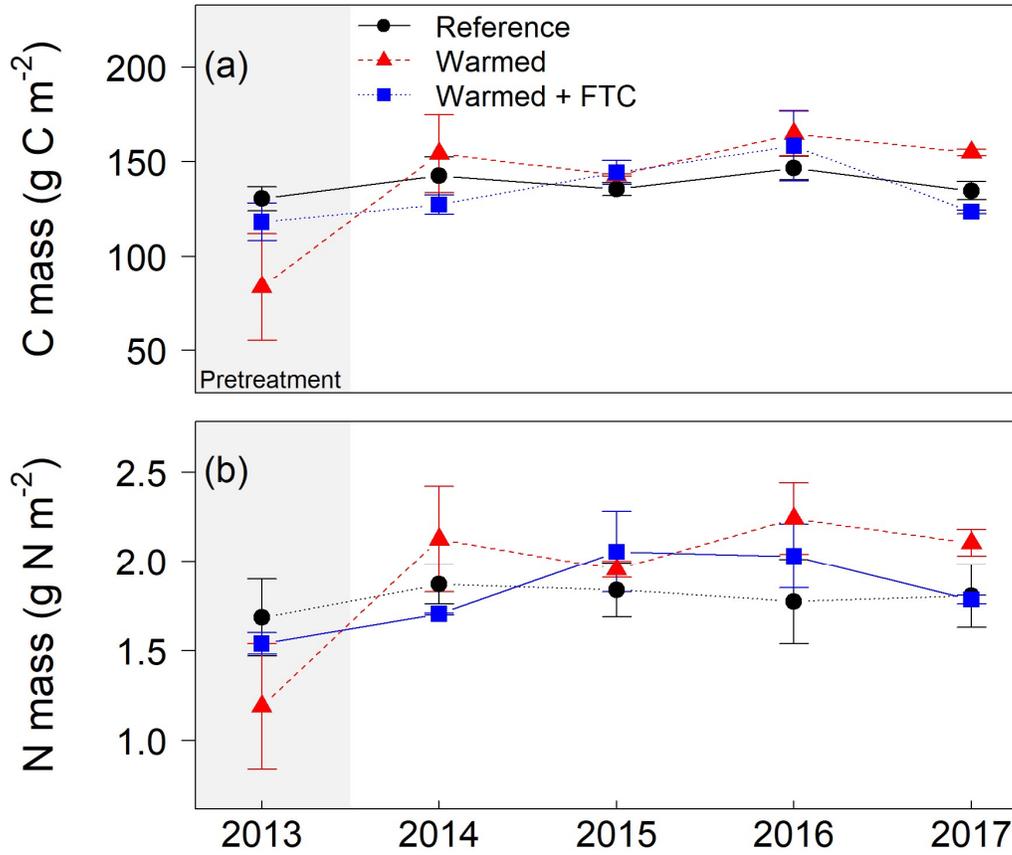


Figure 2. Total mass of N (g N m⁻²) and mass of C (g C m⁻²) across all tree species measured from litterfall collected in CCASE plots between 2013 and 2017. Values are means with standard error. Gray shaded region indicates period of time before we initiated experimental treatments (treatments began in December 2013).

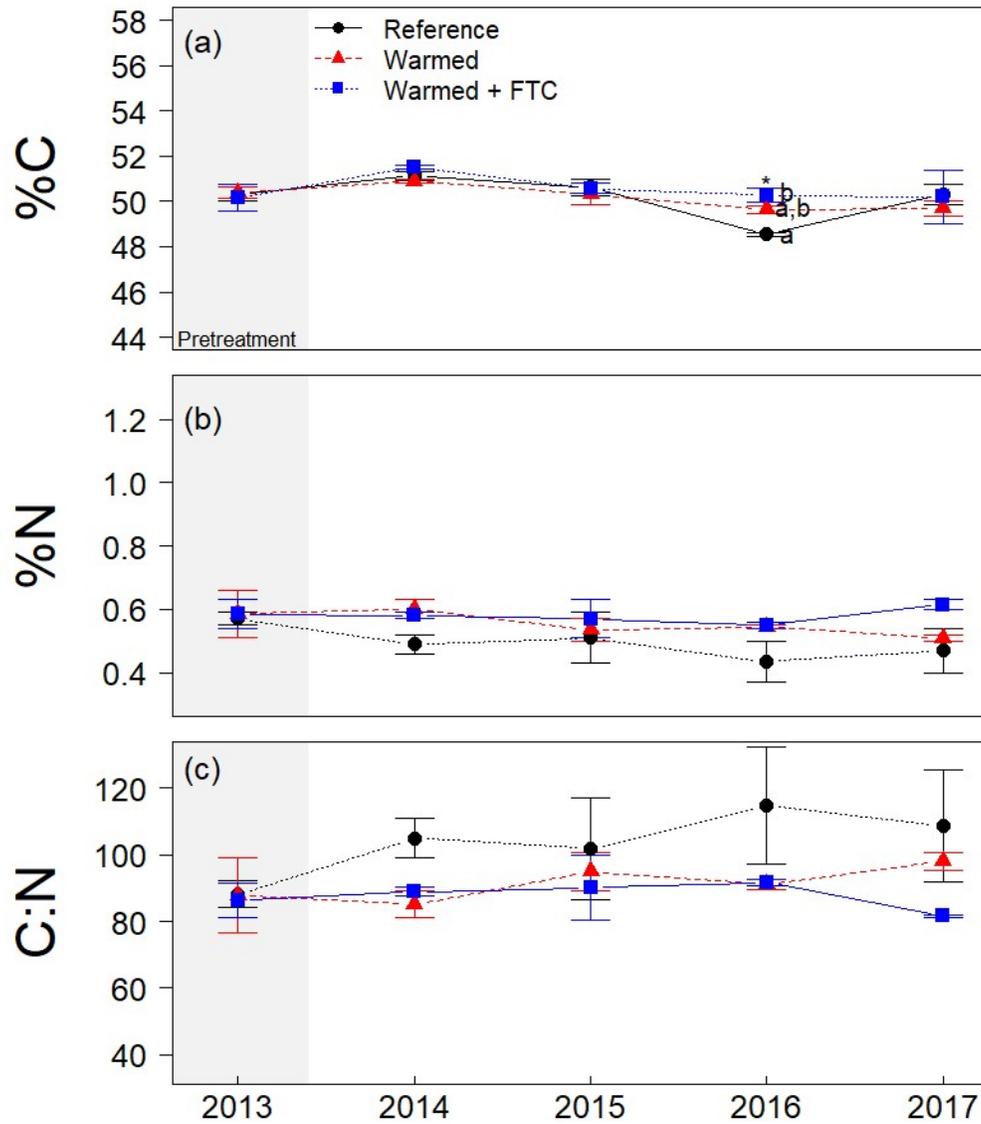


Figure 3. Red maple %C, %N and C:N measured from litterfall collected in CCASE plots between 2013 and 2017. Values are means with standard error. Gray shaded region indicates period of time before we initiated experimental treatments (treatments began in December 2013).

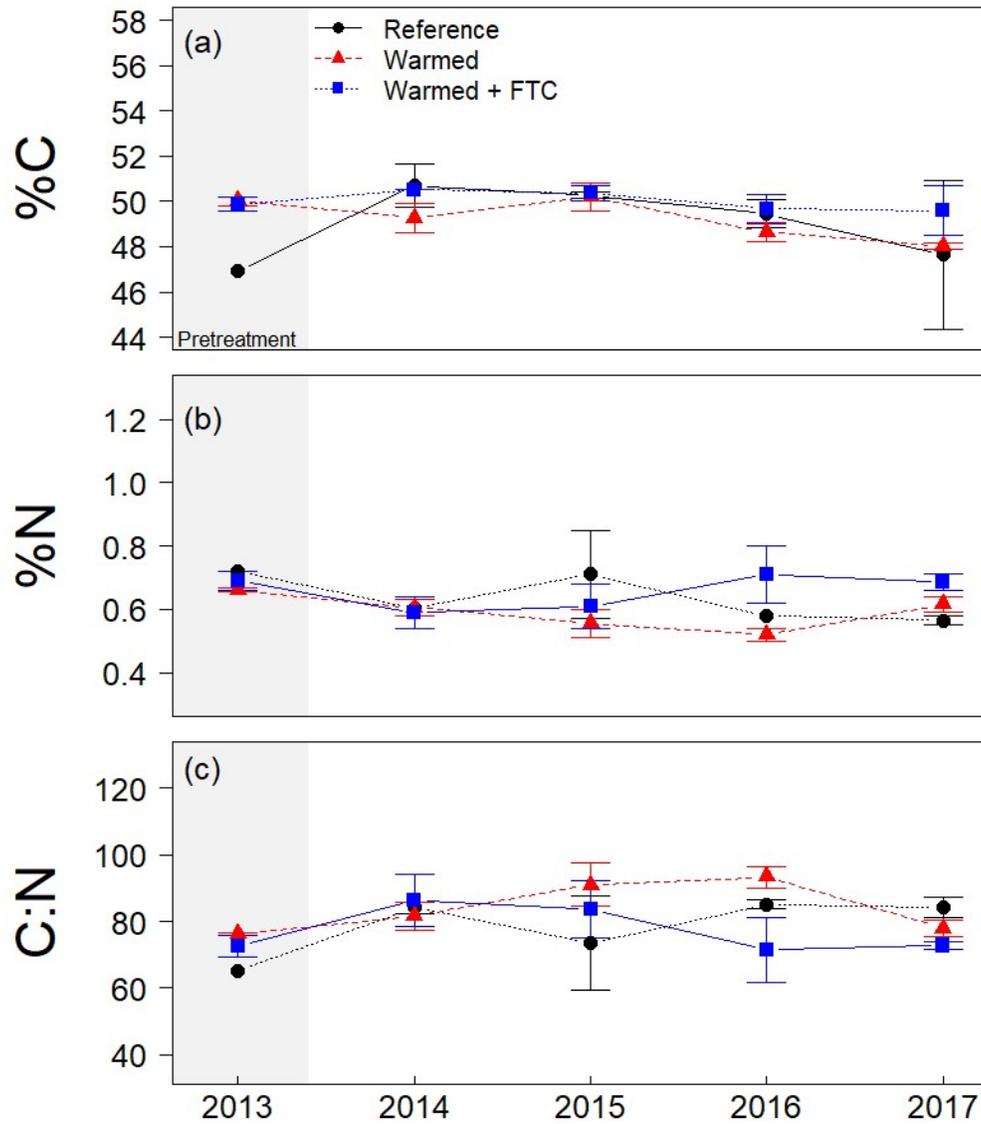


Figure 4. Sugar maple %C, %N and C:N measured from litterfall collected in CCASE plots between 2013 and 2017. Values are means with standard error. Gray shaded region indicates period of time before we initiated experimental treatments (treatments began in December 2013).

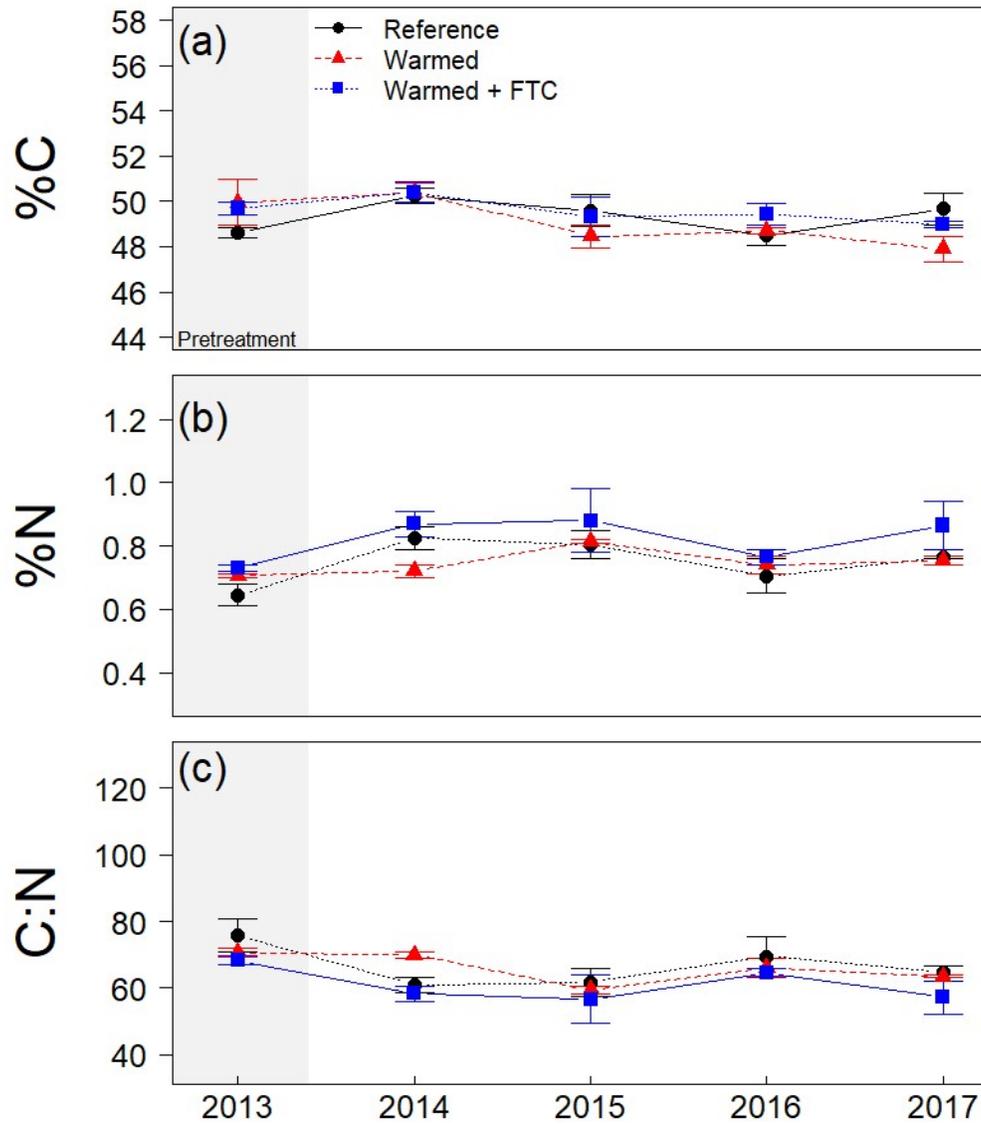


Figure 5. American beech %C, %N and C:N measured from litterfall collected in CCASE plots between 2013 and 2017. Values are means with standard error. Gray shaded region indicates period of time before we initiated experimental treatments.

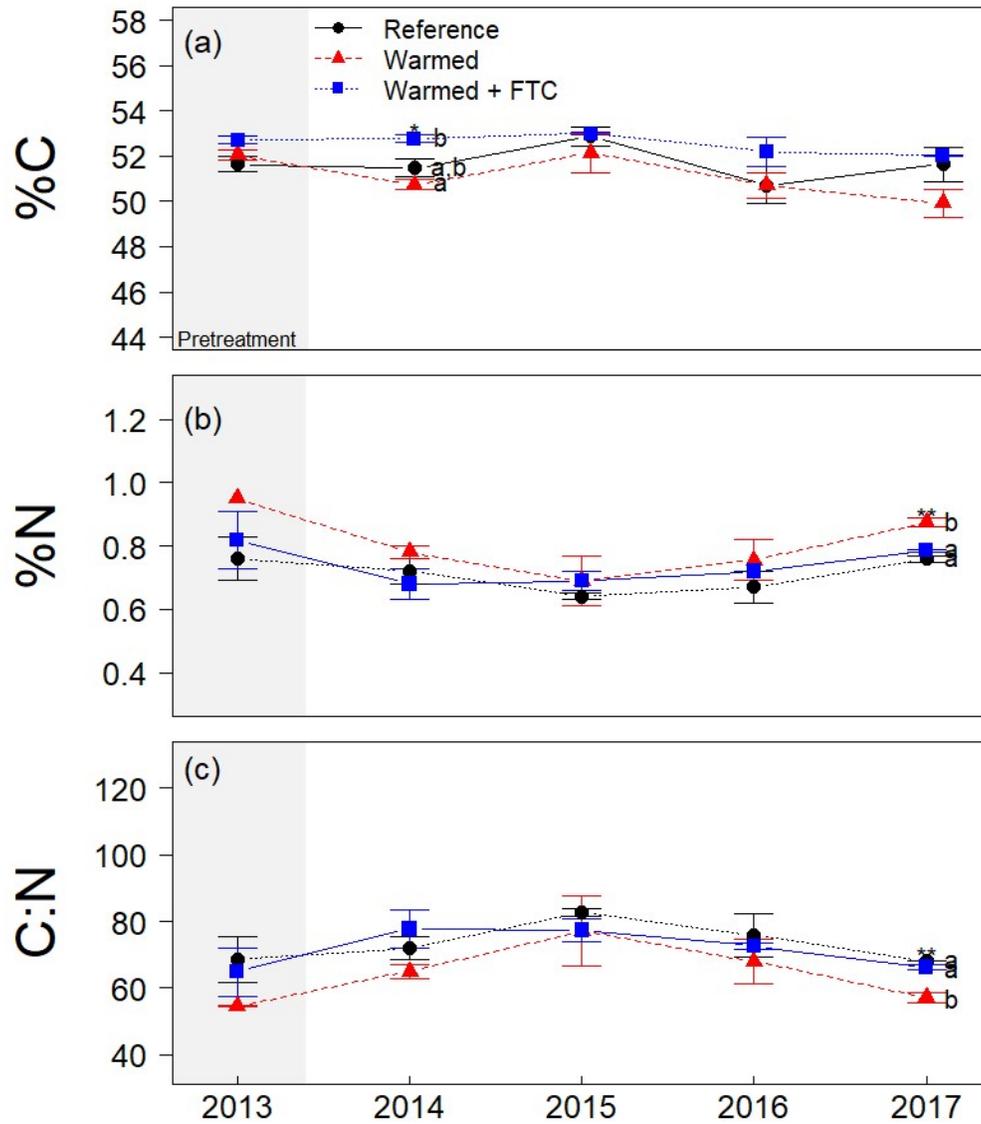


Figure 6. Yellow birch %C, %N and C:N measured from litterfall collected in CCASE plots between 2013 and 2017. Values are means with standard error. Gray shaded region indicates period of time before we initiated experimental treatments.

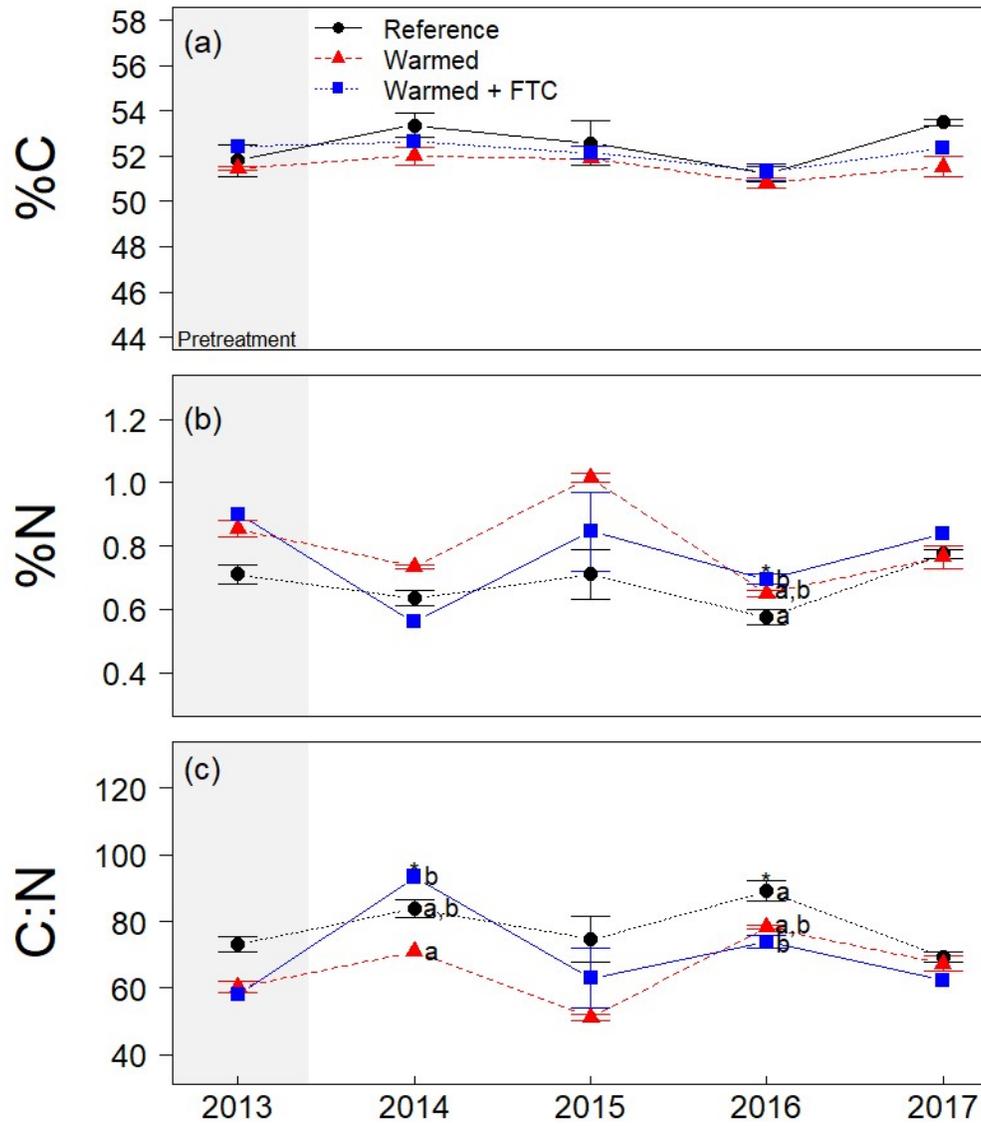


Figure 7. Big tooth aspen %C, %N and C:N measured from litterfall collected in CCASE plots between 2013 and 2017. Values are means with standard error. Gray shaded region indicates period of time before we initiated experimental treatments.

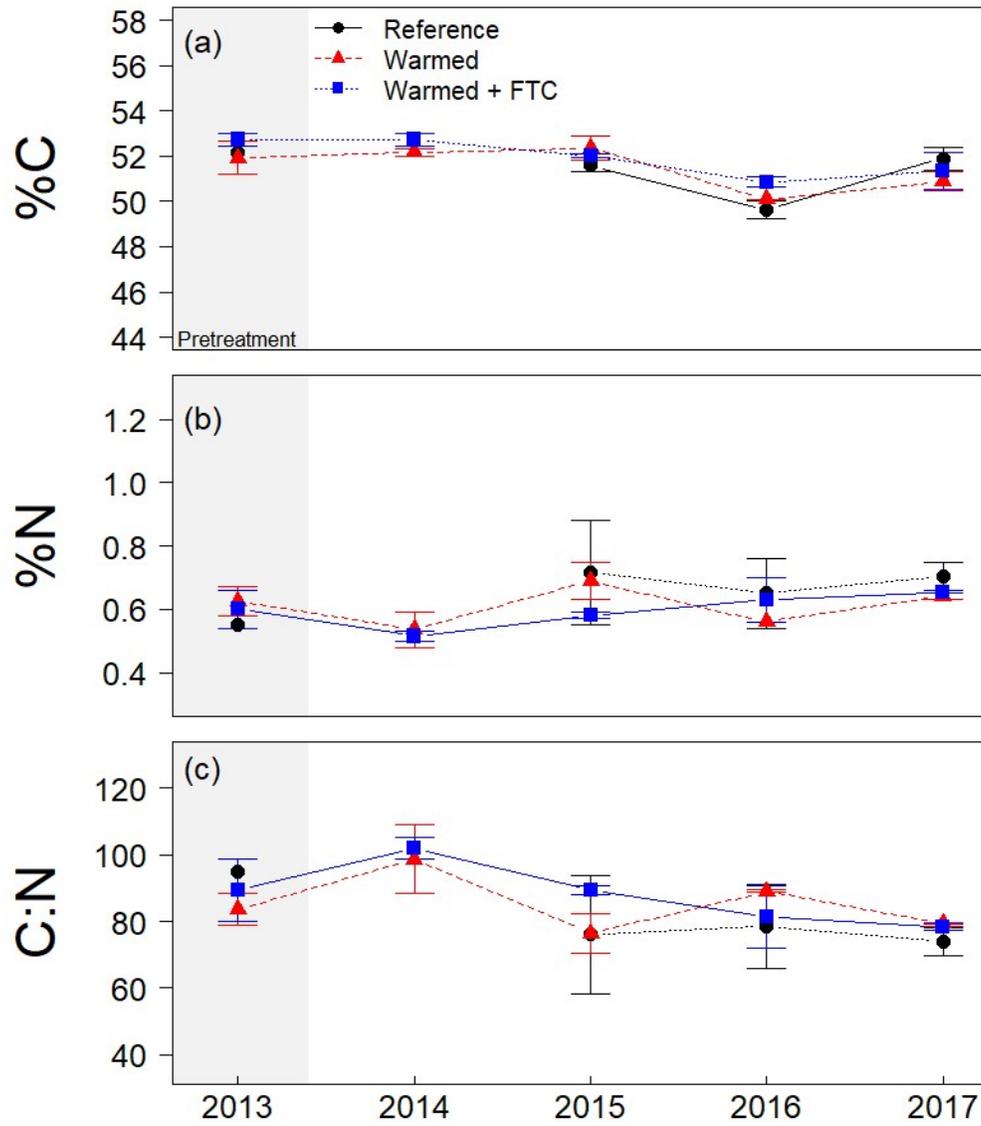


Figure 8. Oak %C, %N and C:N measured from litterfall collected in CCASE plots between 2013 and 2017. Values are means with standard error. Gray shaded region indicates period of time before we initiated experimental treatments.

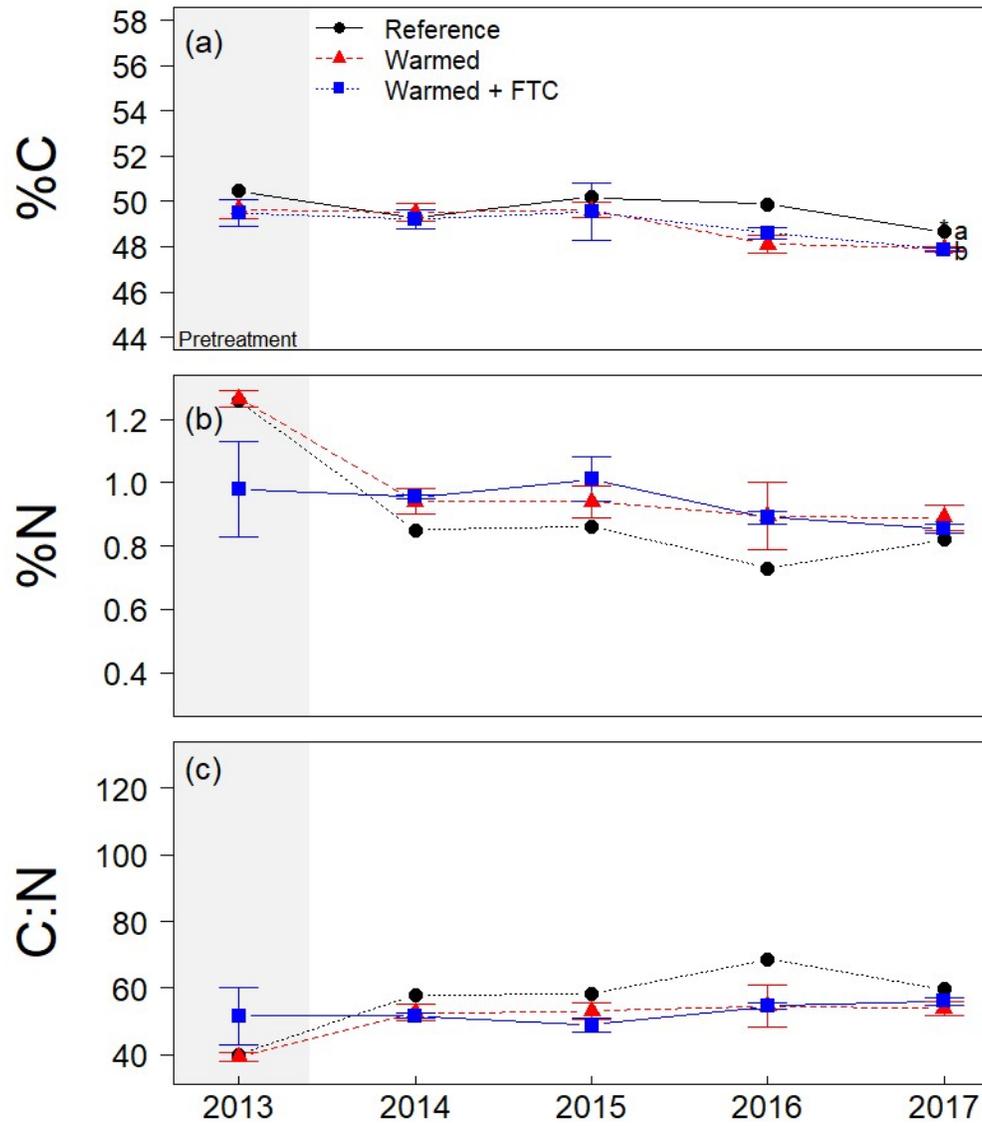


Figure 9. White ash %C, %N and C:N measured from litterfall collected in CCASE plots between 2013 and 2017. Values are means with standard error. Gray shaded region indicates period of time before we initiated experimental treatments.

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