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Patterns and controls of aboveground litter inputs to temperate forests

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ABSTRACT

Aboveground litter production is an important biogeochemical pathway in forests whereby carbon and nutrients enter soil detrital pools. However, patterns and controls of aboveground litter production are often based on an understanding of how autumnal, foliar inputs are related to aboveground tree production. Here we use three separate data sources of aboveground litter production in temperate forests to ask how aboveground woody productivity affects foliar litter production in light of other factors, such as the climate sensitivity of litter production and the seasonality of not only foliar but also fine woody debris and reproductive litter inputs. We find that foliar litter production increases with aboveground woody production, and this relationship is modified both by plant functional group and climate. Basal area also provides a crucial control on litter production. Conifer forests produce approximately half as much foliar litter as broadleaf deciduous forests. Litter production is sensitive to both among-site and among-year variation in climate, such that more litter is produced in warmer, wetter locations and years. On average 72% of aboveground litter is foliar material, with the remaining split about evenly between fine woody debris and reproductive material, and although about 88% of broadleaf litter falls during autumn, only about 61% of needles, 37% of fine woody debris and 43% of reproductive material falls during the same period. Together these results illustrate key differences in the controls of litter production in coniferous and deciduous forests, and highlight the importance of often overlooked litter fluxes, including non-autumn and non-foliar litterfall.

Keywords: aboveground litter production, biomass allocation, temperate forest, plant functional type, litter decomposition, terrestrial biogeochemical models

INTRODUCTION

The production and decomposition of litter represents a crucial pathway by which carbon and nutrients enter the soil in forested systems. Much effort has gone into quantifying the controls on litter decomposition (Schimel et al. 1994; Moorhead et al. 1999; Harmon et al. 2009; Bradford et al. 2017). Yet controls on litter production have not received the same level of attention, even though the amount of litter produced is considered to strongly influence belowground food webs (Wu et al. 2021) and carbon and nutrient stocks and turnover (Leff et al. 2012; Xu et al. 2013; Huang and Spohn 2015).

One way of assessing how controls of litter production are currently quantified is to consider how litter is treated in process-based models. In most terrestrial biogeochemical models, carbon is allocated to plant pools such that aboveground litter production is estimated as a fixed proportion of net primary productivity (NPP) (Raich et al. 1991; Rastetter and Shaver 1992; Potter et al. 1993; Fisher et al. 2014; Wieder et al. 2015). Ultimately then, these terrestrial biogeochemical models explicitly make the assumption that factors, such as climate, vegetation type, or soil fertility, influence litter production through control of NPP. These assumptions are consistent with earlier observational work that investigated controls on patterns of litter production rates (Meentemeyer et al. 1982; Vogt et al. 1986; Matthews 1997). Yet at the same time there is awareness that other factors may modify the relationship between tree productivity and allocation to litter, which then generates significant uncertainty in ecosystem C stocks and fluxes (Mitchell et al. 2009; De Kauwe et al. 2014; Negrón-Juárez et al. 2015). Plant growth strategies mediate the relationship between NPP and litterfall rates. This is approximated in many terrestrial biogeochemical models by using different parameter values for allocation of NPP to foliar biomass for broadleaf and coniferous forests (Kattge et al. 2009; Alton 2011). The use of different values is consistent with empirical work showing that plant functional types allocate biomass differently (Duursma and Falster 2016; Jevon and Lang 2022). However, although the use of distinct parameter values for different forest types implies that the relationship between productivity and foliar litter production differs among plant functional types (e.g. broadleaf deciduous vs. evergreen coniferous), the quantitative importance of this assumption for litter input rates in light of other modifying factors seems more uncertain.

Climate, like plant functional type, may be a strong modifier of the relationship between total plant productivity and allocation to litter inputs. Although there is debate over how plants allocate carbon to different tissues (Mccarthy and Enquist 2007), experimental data suggests that allocation patterns are sensitive to temperature, with the fraction of biomass found in leaf tissue increasing with increasing temperature (Poorter et al. 2012). Evidence that these experimental results translate to what is generally observed across climate gradients is much more limited, but there is evidence that in colder climates the proportion of total forest biomass in foliage is smaller for both angiosperm and gymnosperm forests (Reich et al. 2014). These temperature relationships may be more pronounced for gymnosperms (Reich et al. 2014) and allocation to needles is also observed to be less for conifers growing in locations with stronger summer droughts (Delucia et al. 2000). Therefore, in addition to direct climate effects on NPP, climate sensitivity of biomass allocation may at least partially explain why litter production in both coniferous and deciduous forests tends to increase with mean annual temperature and precipitation (Liu et al. 2004). Yet the extent to which these relationships reflect generalizable and distinct patterns for leaf and needle litter production remains uncertain.

Biomass allocation by trees may also be dependent on interannual climate variation (e.g. within site but among year variability), with resultant differences to litter production from year to year. Indeed, there is some observational evidence that interannual variation in litter production is sensitive to climate, particularly in coniferous forests (Berg and Meentemeyer 2001; Lehtonen et al. 2008) and additional evidence from other ecosystems, such as grasslands (Ukkola et al. 2021). Overall, climate-driven changes to how individual plants allocate carbon to leaves, roots and wood may cause variation in litter production over both space and time, and these relationships may differ among forests and plant functional types.

In addition to these unknowns in the controls of foliar litter production, there has been very little work quantifying the other components of aboveground litter. Indeed, aboveground litter is often treated as an undifferentiated pool, with controls that assume all aboveground litter is foliar (Xu et al. 2013; Fisher et al. 2014, 2018; He et al. 2021). However, aboveground litter comprises multiple other tissues including fine woody debris (FWD) and reproductive organs. These different components of aboveground litter can vary dramatically in their timing of input to the forest floor, in their chemistry (Gosz et al. 1972), decomposition rates (Freschet et al. 2013), and ultimately in how they affect soil organic carbon pools and nutrient availability (Crow et al. 2009; Bowden et al. 2014). Thus, variation in the absolute and relative amounts of different litter types, and whether NPP, climate and plant functional type influence production of these litter types similarly to their influence on foliar litter production, is important to understand given their downstream effects on forest biogeochemistry, food webs, and the overall ecosystem carbon and nutrient cycling.

Here we use a combination of datasets from temperate forests to test the sensitivity of aboveground litter production to forest type and climate. Temperate forests represent approximately one quarter of global forested land area, and account for more than a third of the global forest carbon sink (Pan et al. 2011). The striking seasonal leaf phenology in temperate forests makes them an excellent testbed for questions about litter production, timing, and composition. They are also convenient systems to ask questions about plant functional types, as they often contain a diversity of both deciduous broadleaf trees as well as evergreen conifers. We collate various datasets to test alternative hypotheses describing the relationship between aboveground woody growth and litter production (Figure 1). We additionally include basal area, as we expect that both litter production and woody production should increase with greater standing stock in a forest. We use annual aboveground woody growth (or woody ANPP) to act as a proxy of NPP for predicting litter production because it allowed us to evaluate relationships between NPP and litter production at a common, fine spatial grain and hence avoid pitfalls of data aggregation ((Ruel and Ayres 1999; Bradford et al. 2021).

Our first hypothesis was based on the common assumption in terrestrial biogeochemical models that aboveground litter production is a fixed proportion of net primary productivity (NPP) or standing vegetation biomass (Raich et al. 1991; Rastetter and Shaver 1992; Potter et al. 1993; Fisher et al. 2014). We therefore hypothesized that if aboveground litter production is a common proportion of productivity, then it should increase in tandem with aboveground woody productivity (H_1, Figure 1). Conversely, some models assume different parameter estimates for allocation to litter production by broadleaf versus coniferous forests (Kattge et al. 2009; Alton 2011). As such, we hypothesized that relationships between aboveground litter production and aboveground woody production are dependent on plant functional type (H_2, Figure 1). Similarly, given extensive experimental evidence that biomass allocation can be climate sensitive (Poorter et al. 2012), we hypothesized that if experimental findings extrapolate to observed patterns, then allocation to litter production should be greater under warmer and wetter conditions (H_3, Figure 1). Given observations that allocation, especially in coniferous forests, is climate sensitive (Reich et al. 2014), we further hypothesized that litter production by evergreen coniferous trees may be more sensitive to climate variation than for deciduous broadleaf species (H_4, Figure 1). We also test whether statistical models that predict foliar litter production as a function of aboveground woody growth, basal area, and climate can similarly predict the other components of aboveground litter (fine woody debris, and reproductive litter), and quantify the relative timing of each pool throughout the year. Finally, we quantify the amount and proportion of each type of aboveground litter (foliar, fine woody, and reproductive) in temperate forests using three independent data sources with different spatial and temporal extents.

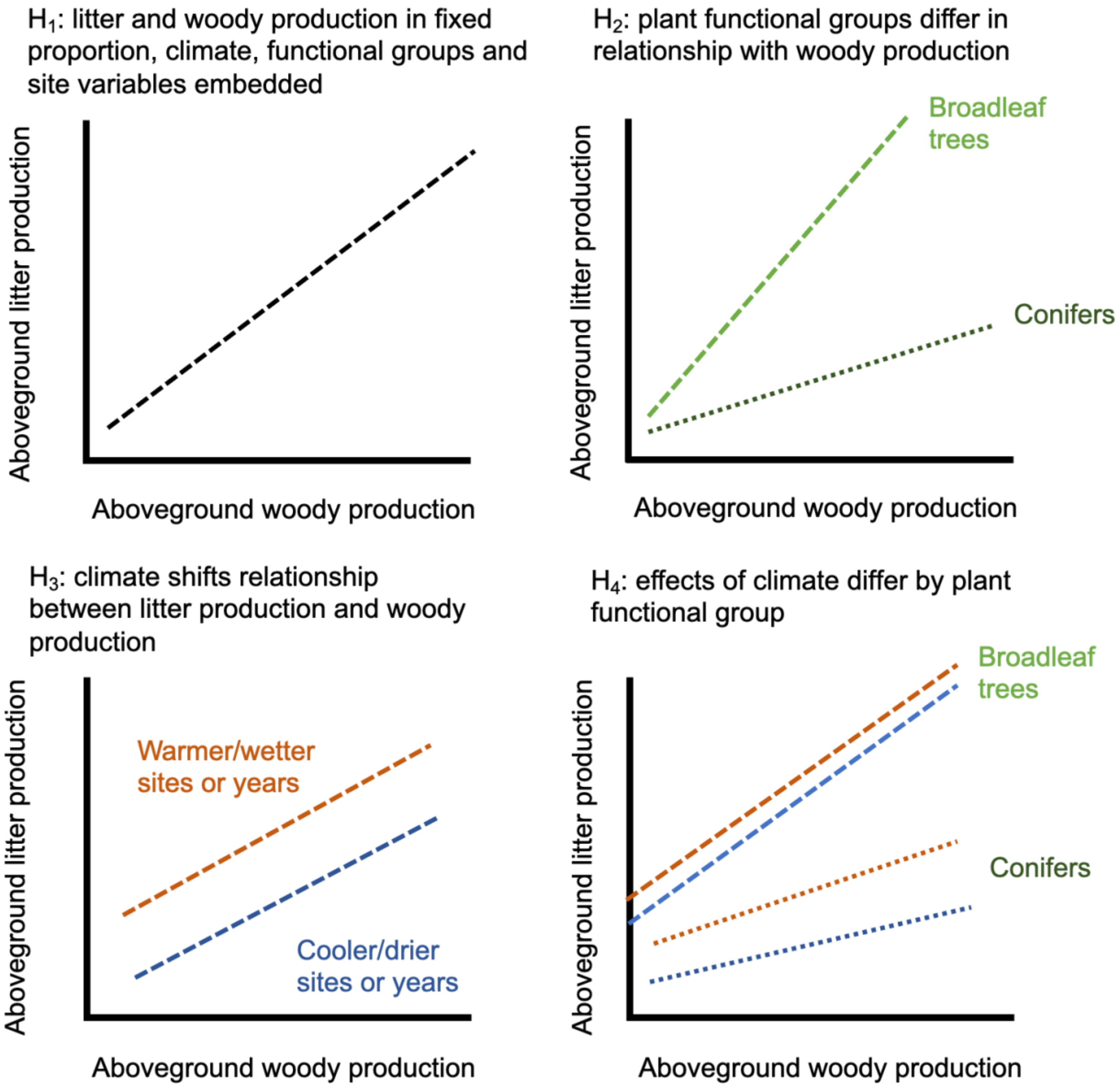

Figure 1. Hypotheses describing alternative relationships between aboveground litter and woody productivity. In many theoretical and empirical models, (H_1) aboveground litter production is conceived as a static fraction of productivity. This approach implicitly accounts for differences in overall productivity among sites or years that could be driven by plant functional group, climate, or other site factors (e.g., soil fertility). Alternatively, (H_2) plant functional types may differ in the fraction of productivity associated with wood *vs*. leaves, due to differences in relative turnover times and allocation. Similarly, (H_3) the effects of climate on carbon allocation among

plant organs may cause a shift in the proportional coupling of aboveground litter production and woody production (e.g. in a warmer year, there may be greater litter production but not greater woody production). Finally, (H_4) plant functional types and climate may interact such that climate could differentially alter the slopes of the relationships in H_1, or climate sensitive biomass allocation could cause a greater shift in the proportional coupling in one functional group but not another.

METHODS

We use three separate data sources with different spatial and temporal extents. First, we use data from 13 eastern US forests that are part of the National Ecological Observatory Network (NEON) to test whether geographic climate patterns and/or forest type (e.g. conifer or deciduous broadleaf) modify the relationship between aboveground productivity and aboveground litter production. We used only 13 of the 60 NEON sites, which collectively capture ecoclimatic variability in the United States, to focus our primary analysis on advancing understanding of controls that operate within a region (i.e. mixed temperate forest). Specifically, our understanding of controls is scale dependent (Levin 1992) and so we opted for a within-biome analysis (temperate forests), instead of an among biome comparison, given our expectation that understanding controls at the region versus broader scales is plausibly most relevant for informing decadal forecasts of ecological change. These 13 sites represent all deciduous and mixed temperate forests in the network, except for three longleaf pine ecosystems with markedly different dynamics given their regular management with active burns. We also use this NEON dataset to quantify the amount and seasonality of aboveground litter fall in each litter type (foliar, woody, and reproductive). Second, to test whether litter production is similarly sensitive to temporal variation in climate, we use a 14-year record of litter production at the Harvard Forest in central Massachusetts. Finally, we compare estimates of aboveground litter production in each litter type to temperate forests in a global database of litter production (Holland, E. A., Post, W. M. et al. 2015). Together, these three datasets capture variation within and among sites (NEON), over time at a single site (Harvard Forest), and globally (Holland).

NEON dataset (1)

To perform a regional analysis of the controls on aboveground litter production, we use 13 temperate forested NEON sites in the eastern US that range in ecological and climatic characteristics (Supplemental Fig. 1). These sites include Bartlett Experimental Forest (BART), Blandy Experimental Farm (BLAN), Dead Lake (DELA), Great Smoky Mountains National Park (GRSM), Harvard Forest (HARV), Lenoir Landing (LENO), Mountain Lake Biological Station (MLBS), Oak Ridge National Laboratory (ORNL), Smithsonian Conservation Biology Institute (SCBI), Smithsonian Environmental Research Center (SERC), Steigerwaldt-Chequamegon (STEI), Treehaven (TREE), and University of Notre Dame Environmental Research Center (UNDE). General sampling designs at these sites are described in (Thorpe et al. 2016) and in-depth at https://www.neonscience.org/.

Litter fall

To estimate aboveground litter production, we used the litter fall record at each site (NEON (National Ecological Observatory Network) 2022a). Within each site, there are approximately 20 40-m x 40-m vegetation monitoring plots made up of four 20-m x 20-m subplots. Within two subplots, litter fall traps are randomly located and collected regularly throughout the year. Data was available for a total of 464 subplots within 236 plots across the 13 sites. The number of subplots per site varied from 13 (BLAN) to 44 (BART), but was generally 40 (DELA, GRSM,

HARV, ORNL, SCBI, SERC, TREE, UNDE). LENO had 21, MLBS had 32 and STEI had 34. Within each subplot, there are two types of litter fall trap: elevated traps, designed to capture all types of aboveground litter (0.5 m^2), and larger, ground traps (1.5 m^2), which are intended to capture woody litter that may not be well captured by the smaller elevated traps. The elevated traps are lined with 1-mm mesh, which captures the majority of aboveground litter mass but may underestimate a few coniferous species with very small needles (e.g some *Larix*, *Tsuga*, *Picea* species- see NEON TOS Protocol and Procedure: Litterfall and Fine Woody Debris for details).

However, not all traps are actively collecting litter for the entire year, as traps are occasionally overturned or damaged, resulting in gaps in the litter fall record. In addition, the interval between collection times differs by site, trap type, and season (with more regular collections occurring in the autumn at deciduous sites). For the elevated traps, which are collected more regularly, we account for gaps in litter fall collection and differences in sampling interval in our annual litter fall estimate by first calculating a daily seasonal litter fall rate by dividing the total litter mass of each class that fell during that season (either autumn or not autumn) by the number of “trapping days”: the number of days that trap was actively collecting litter during that season. We then multiplied this rate by the length of that season, which was independently estimated using phenological observations (see below). Finally we add together the two seasonal totals to get an annual estimate of litter mass.

For the ground traps, which are generally only collected approximately once per year, we also divided the total mass by the number of trapping days then multiplied this by 365 to obtain an annual estimate. We only used the ground trap estimates for the fine woody debris class, as the ground traps are not designed to properly capture other litter classes. After comparing annual estimates of fine woody debris from the elevated and ground traps within the same subplot, we found similar total estimates but weak correlation between estimates within the same plot (Supplemental Figure 3); therefore, when both estimates are available we use the average of the two trap types within each subplot.

Phenology

To estimate the length and timing of autumn at each site, we used the in-depth phenological observation data taken at each NEON site (NEON (National Ecological Observatory Network) 2022b). At each site, at least 10 individual trees from at least three dominant tree species (n= 31 - 100 individuals per site per year) are visually monitored for their phenological stage, including when the individual has falling leaves. Monitoring frequency varies: during seasons when phenophases are rapidly changing it occurs multiple times per week, but monitoring occurs regularly throughout the year. A phenophase is always recorded. Therefore we used the observations of the “falling leaves” phenophase to define autumn at each site as the period of time after July 1 during which 99% of the “falling leaves” observations occur (e.g. autumn begins when 0.5% of these observations have occurred and ends when 99.5% of them have occurred in a given year). We used a site level estimate by taking the mean autumn start and end dates across years for each site to account for some site:year combinations with missing phenology observations. Note that these estimates are taken nearby to, but independently from, the litter collections described above. Thus we could estimate the beginning and end of the autumn season even when litter collections contain gaps.

Vegetation

To estimate productivity in each plot with a litter fall trap, we used the NEON data product DP1.10098.001 reporting the DBH of all stems within the vegetation plots (NEON (National Ecological Observatory Network) RELEASE-2022) We calculated the total basal area within each subplot, as well as the basal area broken down by plant functional group (deciduous broadleaf or conifer). We estimated wood mass for each individual stem (> 1-cm DBH) using generalized allometric equations from (Jenkins et al. 2003). We then calculated aboveground woody growth as the change in estimated wood mass between sampling years across all trees in each subplot. We also assessed how the distribution of plant functional types changes across the climate gradient of the 13 NEON forests (Figure S4).

Climate data

Temperature and precipitation data from 2016-2021 were extracted from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) datasets created by the PRISM Climate Group at Oregon State University (www.prism.oregonstate.edu). We used mean annual temperature and total annual precipitation estimates at the latitude and longitude of each NEON site.

Harvard Forest dataset (2)

The second dataset we used is a long-term record from the Harvard Forest, a mixed deciduous forest in central Massachusetts, USA (Munger and Wofsy 2022). Litter fall at the Harvard Forest was collected from three baskets (0.13 m^2), which were randomly placed in each of 34 plots (10-m radius; 102 baskets total). Each year litter was collected regularly throughout the fall and once the following spring, dried and weighed. Litter collection, along with sorting of litter to species (including reproductive and woody litter) occurred from 2000-2015, except that in 2003-2005 litter was not fully sorted and therefore those years were excluded from this analysis. We do note that the mesh size (2.54 mm spacing) used in these traps may allow for the loss of some of the smaller needles (including some of the smaller *Tsuga canadensis* needles, the dominant conifer at this site) and therefore needle litter production values may be underestimated.

Using the same approach as described above for the NEON dataset, we estimate aboveground woody biomass using the generalized allometric equations from (Jenkins et al. 2003), and the aboveground woody growth as the change in biomass from one year to the next. As trees in these plots are measured several times a year, biomass estimates for individual trees are based on the maximum DBH recorded for the individual tree in a given year. These data are then scaled to the plot level. Climate data from this site is collected at the nearby meteorological station (Boose and Gould 2022).

Statistical analysis for datasets 1 and 2

To test the effect of plant functional group and climate on litter production, we built hierarchical, linear mixed effects models to evaluate controls on annual foliar litter fall that included plant functional group, aboveground woody growth, basal area, annual mean temperature, annual total precipitation, and all two-way interactions with aboveground woody growth. The aboveground woody growth and basal area terms only included trees of the applicable functional group (e.g. for a needle litter observation, the basal area and aboveground woody growth terms were both calculated based on conifers only). As our goal was to test the strength of the relationship between production and litter fall at fine spatial scales, we use aboveground woody growth as a proxy for productivity. However, we also include basal area as we expect, *a priori*, that the standing stock in the forest will be a strong control on both the litter and the woody production. For this reason we also test the interaction between aboveground woody growth and basal area, as well as the collinearity between these two predictors. We used variance inflation factors to test models for multicollinearity, using a VIF > 2 as an indication of when two variables could not be included in the same model: in all models reported in the main text, all VIFs were < 2. Variables were standardized by subtracting the mean and dividing by 2 standard deviations, to allow for direct comparison with the binary variable, plant functional type (Gelman 2008). The standardized coefficients also allow for the direct comparison of the relative effects of variables with very different units (e.g. what is the effect of a change of 1 standard deviation in each variable); however, we also report unstandardized coefficients for each model in the Appendix. We applied this model structure separately to the NEON dataset and the Harvard Forest dataset. For the NEON dataset, we included Year and Plot nested within Site as random effects. For the Harvard Forest dataset, we included Plot as a random effect. Models were run in lme4 (Bates et al. 2015) and visualized using ggeffects (Lüdecke 2018) and sJplot (Lüdecke 2021) in R version 4.0.5.

To test further the effects of climate on litter fall, which we hypothesized would differ between the plant functional types if allocation was differentially influenced by climate, we created separate models for broadleaf litter and needle litter. These models had identical model structures (including random effects) to the first set, but did not include plant functional types. We tested whether the results from our analysis of the NEON dataset were sensitive to the choices we made in terms of scaling the available data to annual estimates, as it is possible that our estimated length of the autumn season could bias our annual estimates of litter production. Therefore we also ran our models using the individual estimates of daily litter fall rate. In these models, we retained the structure of the above models but included “season” (values of either “fall” or “not fall”) as an additional fixed effect, and trap nested within plot and site as the random effects (Table S3).

When assessing the importance of climate in the Harvard Forest dataset, we first identified which season’s climate had the greatest effect on litter production for both broadleaf and needle litter. To do this, we used the mean annual leaf and needle production at the site. We then used the daily temperature and precipitation to identify the window of time during which annual litter production was most highly correlated with climate, using the ‘dendroTools’ package in R (Jevšenak and Levanič 2018). We allowed the window to vary in length from 55 to 90 days, including the previous year’s climate, and tested correlations with annual litter production. Because of the different climate windows identified for the two plant functional types, significant collinearity occurred between the climate variables and the plant functional types in the overall model (VIFs > 2). Therefore, for the Harvard Forest dataset, we report an overall model including plant functional type using mean annual climate variables. For the individual models of each plant functional type we use the mean air temperature and precipitation during the identified windows.

Global dataset (3)

Finally, we used a global database of litter production (Holland, E. A., Post, W. M. et al. 2015) to quantify average litter production in each functional type (foliar, fine woody debris, and reproductive material) over a wider range of temperate forests. The details of the database are described elsewhere (Holland, E. A., Post, W. M. et al. 2015). Briefly, the database includes annual litter fall estimates in grams of dry mass per m^2 per year in various pools, reported as site level means. We included only the “small woody” category for our fine woody debris estimate, as this is mostly consistent with our other data sources. However, not all studies included in the database used the same definition of “small” (ranges from 2-5 mm in diameter, with some studies not reporting the size threshold used). We also selected data only from studies which reported all three categories, and calculated the total aboveground litter fall as the sum of these three pools. Overall this resulted in 59 mean estimates from 22 forests, with some forests contributing multiple observations of different stands (Figure S1).

RESULTS

Overall, foliar litter production generally increased with aboveground woody productivity (Figure 2). However, the strength of the relationship differed by both plant functional type and dataset. In the NEON dataset, coniferous litterfall increased from 162 to 320 g DM m^{-2} yr^{-1} across the observed range of aboveground woody productivity (0 to 2078 g DM m^{-2} yr^{-1}). This corresponds to an 8% increase in litter production as aboveground woody productivity increases from 200 to 400 g DM m^{-2} yr^{-1}. In contrast, there is no significant main effect of aboveground woody growth and broadleaf litterfall in the NEON dataset (Table 1). In the Harvard Forest dataset, broadleaf litter and coniferous litter increased similarly with above ground woody growth, such that an increase in aboveground woody productivity from 200 g m^{-2} yr^{-1} to 400 g m^{-2} yr^{-1} was associated with an 8% and 9% increase in coniferous and broadleaf litter, respectively (Table 2). Thus the effect of aboveground woody productivity on coniferous litter production was similar across the two datasets, while the effect on broadleaf production was only apparent in the HF dataset (Figure 2).

Plant functional type was a strong predictor of foliar litter production in both the NEON and HF datasets. In the NEON dataset, coniferous litter production ranges from being 38-69% lower than broadleaf deciduous litter production, when adjusted for average basal area, aboveground woody growth, and climate (Table 1). In the HF dataset the difference is more consistent: coniferous litter production is typically 47-49% lower than broadleaf deciduous litter production, even when adjusted for basal area, aboveground woody growth, and climate (Table 2). Thus overall, broadleaf litter production tends to be approximately twice that of coniferous litter production at the same basal area, aboveground woody growth, and climate.

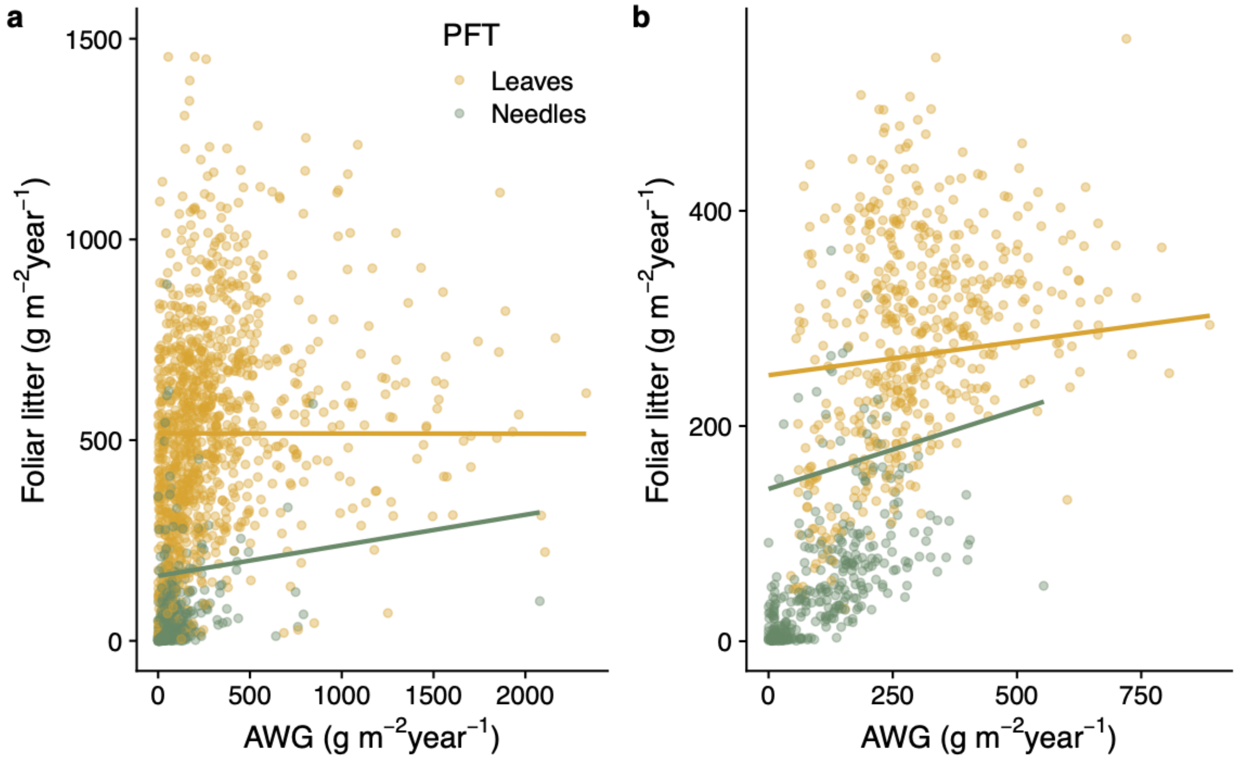

Fig. 2 Plant functional types (PFT) differ in their relationship between foliar litter and aboveground woody production (AWG) across 13 forests from the NEON dataset (a) and 34 plots over 14 years at the Harvard Forest (b). Points represent raw observations, while lines depict the marginal, modeled effects of the interaction between AWG and plant functional group for annual foliar litter production using the unstandardized coefficients from the statistical models (see Table S1 and Table S2 for model coefficients and model fit). Thus the lines represent the isolated effects of PFT and AWG while holding the other variables in the model constant at their mean values, while the points represent the full variability in litter production, which is controlled by multiple factors (including a strong effect of basal area- see Figure 3).

The effect of aboveground woody productivity on litter production was consistently much smaller (e.g. less than half) than the effect of basal area (Table 1, Table 2). There was a positive effect of basal area on foliar litter production for both the broadleaf and conifer litter in both datasets, as well as a negative interaction between the effect of aboveground woody growth and basal area in the overall models. Thus the effects of aboveground woody growth on foliar litter production are contingent on basal area.

Indeed, both litter production and aboveground woody growth increased strongly with basal area (Figure 3). In the NEON dataset, woody production and foliar litter production in broadleaf deciduous forests both increased with basal area, but woody production increased much more strongly. Therefore at low basal area, the production of foliar litter is much greater than aboveground woody growth, while at higher basal area they are approximately equal. Similar patterns emerge in the HF dataset, except that at higher basal area woody production surpasses foliar litter production. In coniferous forests of both datasets, foliar and woody production is similar at low basal area, but woody production increases more rapidly with basal area than foliar production such that there is nearly always more woody production than foliar litter production.

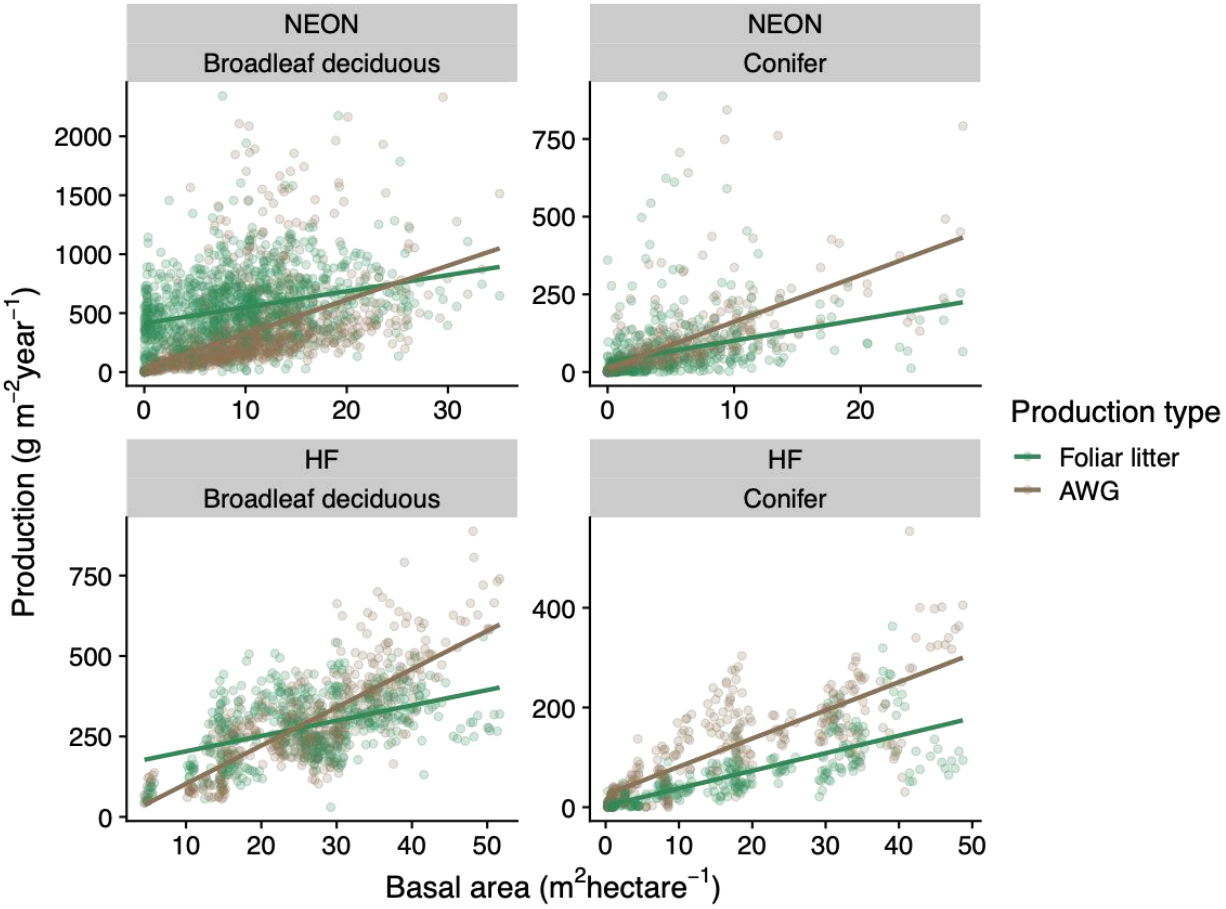

Fig. 3 Relationship between basal area and aboveground woody production relative to aboveground foliar production differs between forest types. Green points and lines represent foliar litter production, brown points and lines represent aboveground woody growth. Lines are univariate linear regressions. A, B: NEON sites, C, D: Harvard interannual data. Note different axis ranges.

Spatial variation in mean annual climate had a strong effect on broadleaf, but not conifer, litter production across the NEON forests (Table 1). Indeed, the effect of temperature and precipitation on broadleaf litter production were similar in magnitude to the effect of basal area (Table 1). We found that broadleaf litter increased with temperature, such that more foliar litter was produced at higher temperatures regardless of other controls, including aboveground woody growth (Figure 4). In effect, a site with a MAT less than 5 °C produced about 28% less litter than a site with MAT greater than 15 °C, after accounting for differences in basal area and aboveground woody growth. Broadleaf litter production also increased with higher precipitation but interacted with aboveground woody growth such that lower precipitation resulted in lower overall litter production and a negative association between aboveground woody growth and foliar production.

Litter production was also sensitive to interannual variation in climate. In the Harvard Forest dataset, broadleaf litter increased with higher spring temperatures (from April 11 to June 18) and increased precipitation from the previous autumn (October 27 - January 6). Conifer litter was most sensitive to the previous year's climate: needle litter production increased with higher preceding autumn temperatures (September 15th - November 18th) and winter precipitation (December 19th - February 10). The effect of temperature on litter production was similar for broadleaf and needle litter, with warmer temperatures during the preceding seasons associated with increased litter production (Table 2, Figure 5). Increased precipitation also drove greater broadleaf and needle litter production: for needle litter production, there was also a positive interaction such that needle litter production was increased relative to aboveground woody growth in years with higher winter precipitation (Figure 5). For broadleaf litter, the effects of temperature and precipitation were greater in magnitude than the effects of aboveground woody growth; for needle litter, the magnitude of the climate effects and aboveground wood growth were similar (Table 2).

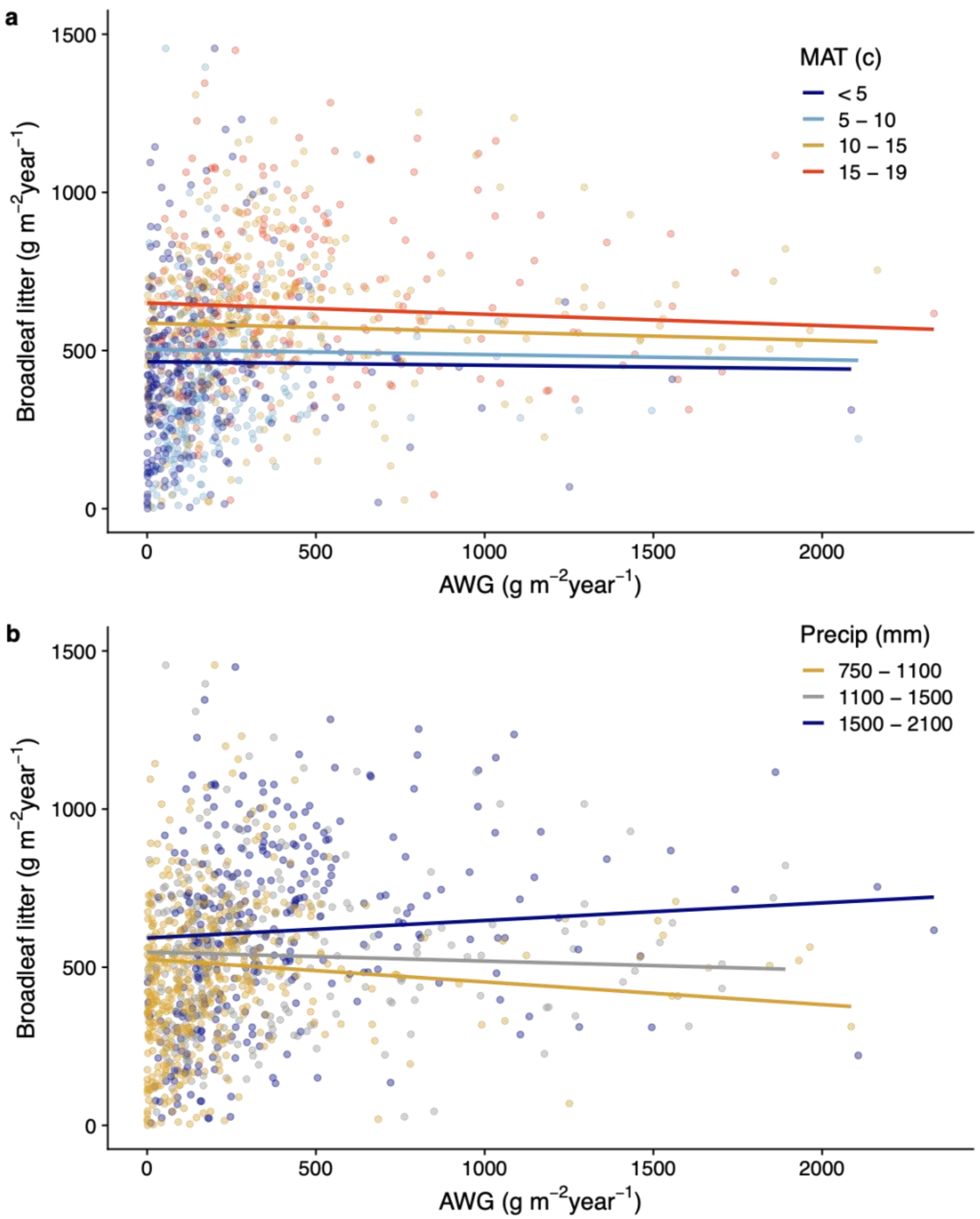

Fig. 4 Mean annual climate modifies the relationship between aboveground woody production (AWG) and foliar production in broadleaf deciduous forests in the NEON dataset. Points represent raw observations, while lines depict the modeled, marginal effects of the interaction between AWG and either annual mean temperature (a) or total annual precipitation (b) for annual foliar litter production using the unstandardized coefficients from the statistical models (see

Table S1 for model coefficients and model fit). The regression line is plotted while holding the other variables in the model constant at their mean values to isolate the effects of AWG and the climate variable, using the unstandardized coefficients from the statistical model in Table S1, while the points represent the full variability in litter production, which is controlled by multiple factors (including a strong effect of basal area- see Figure 3). In each case, the colored lines represent predictions for the set of data that falls within that climate range.

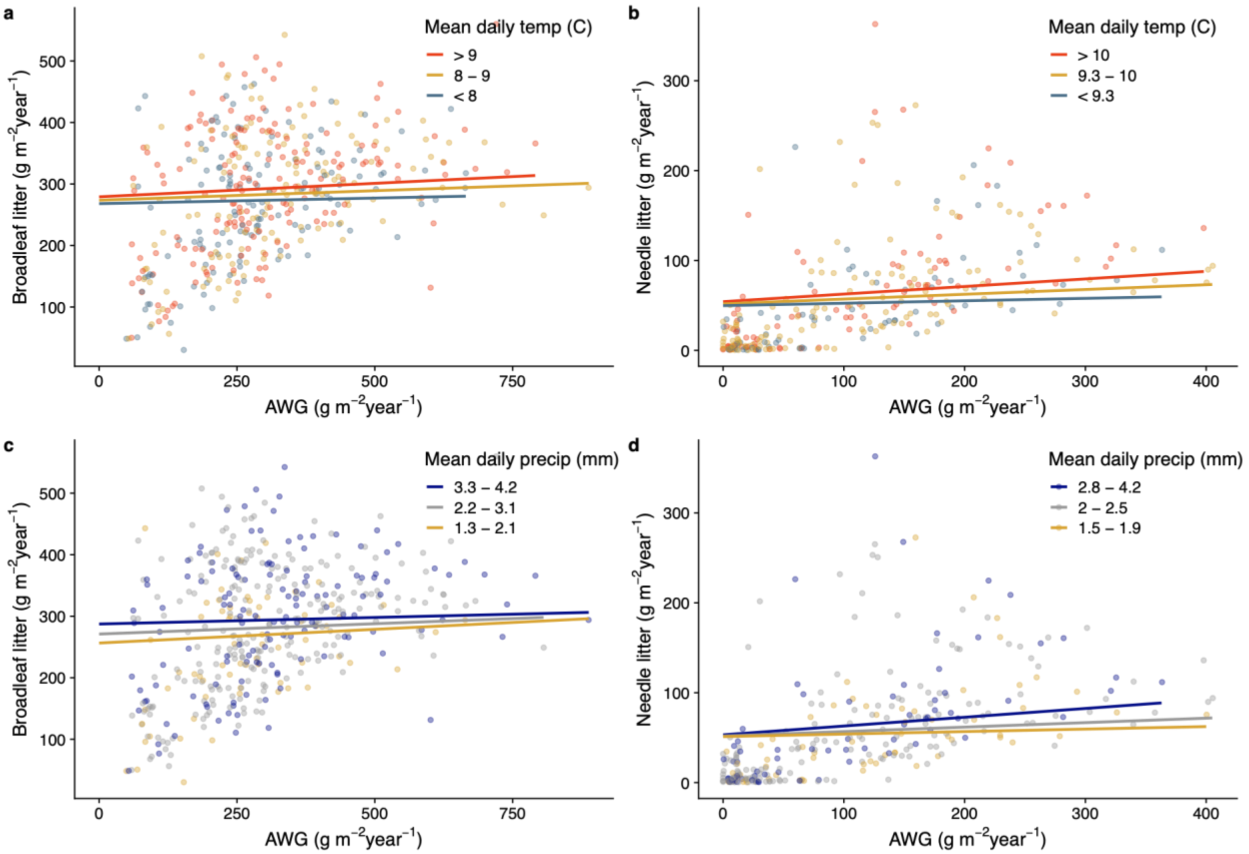

Fig. 5 Interannual variability in climate modifies the relationship between aboveground woody production (AWG) and foliar production in broadleaf deciduous (a, c) and coniferous (b, d) litter at the Harvard Forest. Points represent raw observations, while lines depict the modeled, marginal effects of the interaction between AWG and either mean daily temperature (a, b) or mean daily precipitation (c, d) during the identified climate window (Table S6) for annual foliar litter production using the unstandardized coefficients from the statistical models (see Table S2 for model coefficients and model fit). The regression line is plotted while holding the other variables in the model constant at their mean values to isolate the effects of AWG and the climate, but the points represent the full variability in litter production, which is controlled by multiple factors (including a strong effect of basal area- see Figure 3). In each case, the colored lines represent predictions for the set of data that falls within that climate range.

Aboveground litter production in temperate forests from the global dataset varied from 192 to 1661 g DM m^{-2} yr^{-1}, 62-97% of which was foliar. Temperate forests in the eastern US NEON sites produced 522-1042 g DM m^{-2} $year^{-1}$, of which 70-88% was foliar. Variation within a single forest across years was much smaller than variation among forests: on average, the Harvard Forest produced 420 g DM m^{-2} $year^{-1}$ dry litter, with a range of 355-459. In all three data sets the contribution of FWD and reproductive parts to total litter was only 19-25% (Table 3). Fine woody debris and reproductive tissue litter followed similar patterns as foliar litter with respect to aboveground woody production, basal area and climate; however, they were much less predictable (Table S4, Table S5).

The different types of aboveground litter (leaves, needles, FWD, and reproductive material) also exhibited different seasonal patterns of production. The length of autumn, based on phenological observations at each of the NEON sites, ranged from 65 (STEI) to 142 days (DELA) (mean across sites = 103 days). Typically 88% (range: 77-94%) of broadleaf tree leaves fall during that period. In contrast, only about 61% of needles, 37% of FWD and 43% of reproductive material fall during the same period (Figure 6).

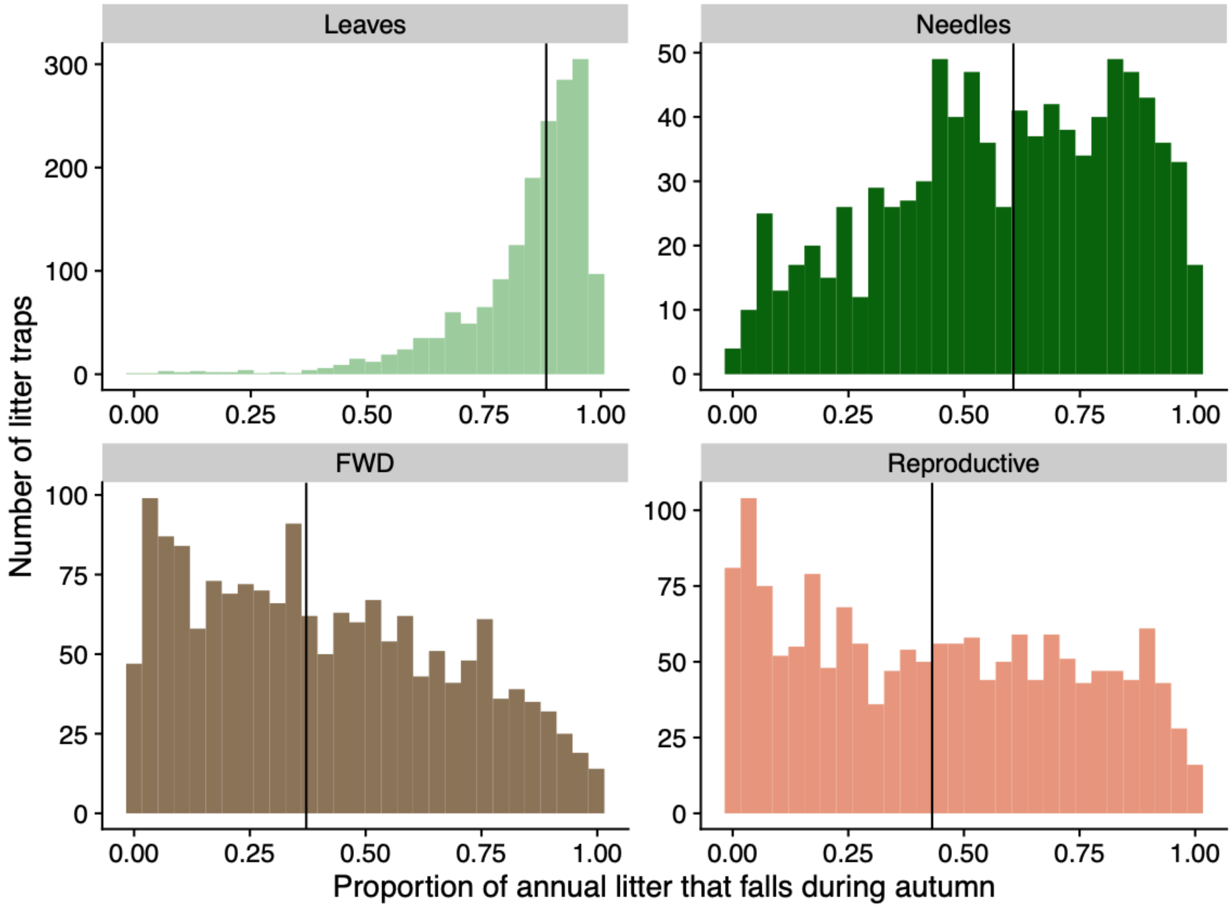

Fig. 6 Seasonality of NEON litter fall by functional group. Each observation is a single litter trap: proportions are calculated as the proportion of all litter in that type that fell during the autumn season (as defined using phenology observations- see methods section for details) relative to the total annual litter fall of that litter type. Black vertical lines indicate the median proportion of each litter type collected during autumn. Note the variable y axis ranges.

DICUSSION

We found that while foliar litter production generally increased with aboveground woody production, consistent with our first hypothesis, we also found strong evidence that this relationship is modified by plant functional group and climate (Tables 1-2). Strikingly, we found a very similar overall effect of increasing aboveground woody production on coniferous litter in our two fine-grained datasets; one of which included a regional spatial extent (NEON) and the other which included a single site (embedded in the same region) over time (HF; Fig. 2). In contrast, broadleaf litter production increased with aboveground woody production only in the temporal dataset (HF), where the overall effect was similar for broadleaf and conifer litter.

These results support the hypothesis that plant functional types have different relationships between litter production and woody production (H2): we found that deciduous broadleaf trees produce about twice as much foliar litter as conifers on average, given the same aboveground woody production and basal area. This is perhaps unsurprising, as most temperate conifers have needle lifespans of at least two years (Lusk 2010); thus, while annual foliar litter production represents the entire standing stock of foliar tissue for deciduous trees, it only represents a portion of total foliar tissue for conifers. However, assuming a relatively consistent needle retention time, litter production should be in steady state with annual production. The difference therefore suggests that coniferous forests may allocate less carbon to foliar tissue than other structures relative to deciduous forests.

We also found that basal area emerged as an important modifier of the relationship between aboveground woody and litter productivity (Fig. 3, Tables 1-2). The overall relationship between basal area and foliar and woody production is consistent with biomass allocation patterns in individual trees: as trees increase in size, they allocate relatively more biomass to wood and less to leaf tissue (Duursma and Falster 2016). At the community level, these results also suggest that as the basal-area density of forests increases, the proportion of total aboveground woody production increases more strongly than foliar production.

Although these dynamics were not part of our initial hypotheses, the findings suggest that basal area (which likely correlates with stand age) moderates carbon allocation in forests. Moreover, the finding suggests that rather than a fixed proportion of total productivity, there are tradeoffs between woody and foliar growth that vary with stand development. Stands with greater basal area are likely to exhibit canopy closure, and therefore diminishing returns on nutritionally expensive foliar biomass: as the opportunity to intercept light saturates, greater investment in leaf tissue is not useful, but greater investment in woody growth continues to help trees maintain their position in the canopy. This may help explain the steeper positive slopes for woody productivity with basal area than litter production. We note that these dynamics would not be captured in conventional terrestrial biogeochemical models, which use fixed allocation parameters, but they should emerge from demographic models (Fisher et al. 2015; Koven et al. 2020) that track time since disturbance and use allometric equations to describe changes in biomass as a function of stem diameter at breast height (Rennolls 1994).

We also found that conifer and broadleaf forests exhibit somewhat different tradeoffs between woody and foliar production with increasing basal area (Fig. 3). For both forest types litter production increases less than half as much as woody production with the same increase in basal area. However, conifers always exhibit greater woody production than foliar production, but the ratio of woody production to foliar production increases with basal area. In contrast, broadleaf forests have greater foliar litter production than woody production at low basal area, but less at higher basal area. This patterning suggests a stronger tradeoff between woody and foliar tissues in deciduous broadleaf species than in conifers.

Climate was an important control of inter-site (NEON) and inter-annual (HF) differences in broadleaf litter production (Figs. 4-5). The findings support the hypothesis (H_3) that the relationship between litter production and woody production changes with climate, as trees allocate more to their leaves in preferable climate conditions. We also found that the effect of climate differed among plant functional types: we found that spatial variation in climate had a much stronger effect on broadleaf litter production than on needle litter production (H_4). This finding contrasts with previous work on biomass allocation patterns (Reich et al. 2014), which has found a stronger effect of climate on gymnosperms than angiosperm biomass allocation; however, this may be partially due to the distribution of conifers in our dataset. Conifers were found primarily at cooler sites, so our ability to detect changes in needle litter with temperature may be restricted by the small sample size at warmer sites (Figure S4).

Although conifers appeared insensitive to spatial variation in climate, needle production was responsive to interannual variation in climate, particularly climate in the previous year. Increased autumn temperatures and winter precipitation were associated with greater needle litter production during the following year. This finding is consistent with some previous work that has found lags in the climate effect on litter production, particularly in conifers (Starr et al. 2005; Martínez-Alonso et al. 2007). Broadleaf litter production responded to spring temperatures, and also to the previous autumn-winter precipitation. As we found evidence for climate effects on litter production in both our fine-grained datasets, one which represents a regional gradient in climate and another which represents only interannual climate variability, the effects of climate may be operating at both the individual and community level. In other words, whereas individual trees may allocate more biomass to leaves in warmer, wetter years, forests in warmer, wetter locations may also typically contain species that allocate more to leaves than to woody growth. Such a potential explanation is consistent with global patterns in tree biomass allocation (Reich et al. 2014) as well as work showing individual level plasticity in allocation (Poorter et al. 2012).

Global and regional estimates of temperate forest aboveground litter inputs are largely consistent. Across sites and years, only about 80% of aboveground litter in temperate forests is composed of leaf material, with the remaining 20% split between reproductive organs and fine woody debris. This has significant ramifications for understanding litter decomposition and biogeochemical cycling in these systems, as different types of litter have very different physico-chemical traits. For example, reproductive litter is often enriched in phosphorus and micronutrients relative to foliar litter, whereas woody litter has much higher carbon to nitrogen ratios, and much lower surface area to volume ratios (Gosz et al. 1972).

A substantial proportion of litter, particularly non-foliar and needle litter, falls outside the autumn season (Fig. 6). Indeed, typically less than 50% of the fine woody and reproductive litter fell during the autumn. This observation is consistent with previous work showing that while autumn accounts for the largest proportion of aboveground litter fall, litter falling in other seasons provides quantitatively important nutrient inputs (Gosz et al. 1972; Portillo-Estrada et al. 2013; Wang et al. 2021). The varying nutrient inputs that these functional groups represent throughout the year likely have important biogeochemical effects on food webs, decomposition, and plant nutrient uptake, yet remain understudied.

The non-autumn litter patterns we report have important implications for measuring aboveground litter and interpreting datasets in which litter is only collected during the autumn: even in temperate deciduous forests, not collecting litter throughout the year would on average lead to an underestimation of leaf litter production of 12%, and an underestimation of needle, fine woody debris, and reproductive litter of 40%, 57% and 63% respectively. Thus collection during autumn only captures on average 72% of the total aboveground litter (of all types) that falls in a given year. Studies interested in capturing total carbon or nutrient inputs to soil from aboveground litter must design their sampling in a way that accounts for the seasonality of their system without excluding the litter that falls during off-peak times.

Our work reinforces the importance of including plant functional types in terrestrial ecosystem models, as is already common practice. However, our work highlights the importance of building on this representation to investigate how basal area and climate moderate allocation of NPP among plant tissues would improve the ability of terrestrial biogeochemical models to represent carbon flows within forested ecosystems. Although our synthesis of observational data does not definitively resolve climate as a causal variable that modifies biomass allocation, we believe the apparent scalability of our findings (e.g. the similarity of the climate effects across space and time), may make this low hanging fruit for model testing to improve predictions of aboveground litter production (Kyker-Snowman et al. 2022). We also suggest that a better understanding of the spatial and temporal trends in litter production is critical for connecting the rich work on litter decomposition to forest- scale carbon dynamics, as the inputs to the litter decomposition system appear modulated by climate and stand development, with potential consequences for belowground forest dynamics.

Literature Cited

Alton PB (2011) How useful are plant functional types in global simulations of the carbon, water, and energy cycles? Journal of Geophysical Research: Biogeosciences 116.: https://doi.org/10.1029/2010JG001430

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw 67:1–48

Berg B, Meentemeyer V (2001) Litter fall in some European coniferous forests as dependent on climate: a synthesis. Can J For Res 31:292–301

Boose E, Gould E (2022) Harvard Forest Climate Data since 1964. Harvard Forest Data Archive: HF300 (v.5)

Bowden RD, Deem L, Plante AF, et al (2014) Litter Input Controls on Soil Carbon in a Temperate Deciduous Forest. Soil Sci Soc Am J 78:S66–S75

Bradford MA, Veen GFC, Bonis A, et al (2017) A test of the hierarchical model of litter decomposition. Nat Ecol Evol 1:1836–1845

Bradford MA, Wood SA, Addicott ET, Fenichel EP (2021) Quantifying microbial control of soil organic matter dynamics at macrosystem scales. Biogeochemistry

Crow SE, FILLEYw TR, SWANSTONz C, et al (2009) Sources of plant-derived carbon and stability of organic matter in soil: implications for global change. Glob Chang Biol 15:2003–2019

De Kauwe MG, Medlyn BE, Zaehle S, et al (2014) Where does the carbon go? A model-data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air CO2 enrichment sites. New Phytol 203:883–899

Delucia EH, Maherali H, Carey EV (2000) Climate-driven changes in biomass allocation in pines. Glob Chang Biol 6:587–593

Duursma RA, Falster DS (2016) Leaf mass per area, not total leaf area, drives differences in above-ground biomass distribution among woody plant functional types. New Phytol 212:368–376

Fisher JB, Huntzinger DN, Schwalm CR, Sitch S (2014) Modeling the Terrestrial Biosphere. Annu Rev Environ Resour 39:91–123

Fisher RA, Koven CD, Anderegg WRL, et al (2018) Vegetation demographics in Earth System Models: A review of progress and priorities. Glob Chang Biol 24:35–54

Fisher RA, Muszala S, Verteinstein M, et al (2015) Taking off the training wheels: the properties of a dynamic vegetation model without climate envelopes, CLM4.5(ED). Geosci Model Dev 8:3593–3619

Freschet GT, Cornwell WK, Wardle DA, et al (2013) Linking litter decomposition of above- and below-ground organs to plant-soil feedbacks worldwide. J Ecol 101:943–952

Gelman A (2008) Scaling regression inputs by dividing by two standard deviations. Stat Med 27:2865–2873

Gosz JR, Likens GE, Bormann FH (1972) Nutrient content of litter fall on the Hubbard brook experimental forest, New Hampshire. Ecology 53:769–784

Harmon ME, Silver WL, Fasth B, et al (2009) Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite comparison. Glob Chang Biol 15:1320–1338

He Y, Wang X, Wang K, et al (2021) Data-driven estimates of global litter production imply slower vegetation carbon turnover. Glob Chang Biol 27:1678–1688

Holland, E. A., Post, W. M., Matthews E, Sulzman J, et al (2015) A Global Database of Litterfall Mass and Litter Pool Carbon and Nutrients. Oak Ridge National Laboratory Distributed Active Archive Center

Huang W, Spohn M (2015) Effects of long-term litter manipulation on soil carbon, nitrogen, and phosphorus in a temperate deciduous forest. Soil Biol Biochem 83:12–18

Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA (2003) National-Scale Biomass Estimators for United States Tree Species. For Sci 49:12–35

Jevon FV, Lang AK (2022) Tree biomass allocation differs by mycorrhizal association. Ecology 103:e3688

Jevšenak J, Levanič T (2018) dendroTools: R package for studying linear and nonlinear responses between tree-rings and daily environmental data. Dendrochronologia 48:32–39

Kattge J, Knorr W, Raddatz T, Wirth C (2009) Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. Glob Chang Biol 15:976–991

Koven CD, Knox RG, Fisher RA, et al (2020) Benchmarking and parameter sensitivity of physiological and vegetation dynamics using the Functionally Assembled Terrestrial Ecosystem Simulator (FATES) at Barro Colorado Island, Panama. Biogeosciences 17:3017–3044

Kyker-Snowman E, Lombardozzi DL, Bonan GB, et al (2022) Increasing the spatial and temporal impact of ecological research: A roadmap for integrating a novel terrestrial process into an Earth system model. Glob Chang Biol 28:665–684

Leff JW, Wieder WR, Taylor PG, et al (2012) Experimental litterfall manipulation drives large and rapid changes in soil carbon cycling in a wet tropical forest. Glob Chang Biol 18:2969–2979

Lehtonen A, Lindholm M, Hokkanen T, et al (2008) Testing dependence between growth and needle litterfall in Scots pine--a case study in northern Finland. Tree Physiol 28:1741–1749

Levin SA (1992) The problem of pattern and scale in ecology: The Robert H. macarthur award lecture. Ecology 73:1943–1967

Liu C, Westman CJ, Berg B, et al (2004) Variation in litterfall-climate relationships between coniferous and broadleaf forests in Eurasia. Glob Ecol Biogeogr 13:105–114

Lüdecke D (2021) sjPlot: Data Visualization for Statistics in Social Science. Version R package version 2.8.8URL https://CRAN.R-project.org/package=sjPlot

Lüdecke D (2018) Ggeffects: Tidy data frames of marginal effects from regression models. J Open Source Softw 3:772

Lusk CH (2010) Conifer–Angiosperm Interactions: Physiological Ecology and Life History.

Smithsonian Contributions to Botany

Martínez-Alonso C, Valladares F, Camarero JJ, et al (2007) The uncoupling of secondary growth, cone and litter production by intradecadal climatic variability in a mediterranean scots pine forest. For Ecol Manage 253:19–29

Matthews E (1997) Global litter production, pools, and turnover times: Estimates from measurement data and regression models. J Geophys Res 102:18771–18800

Mccarthy MC, Enquist BJ (2007) Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. Funct Ecol 21:713–720

Meentemeyer V, Box EO, Thompson R (1982) World Patterns and Amounts of Terrestrial Plant Litter Production. Bioscience 32:125–128

Mitchell S, Beven K, Freer J (2009) Multiple sources of predictive uncertainty in modeled estimates of net ecosystem CO2 exchange. Ecol Modell 220:3259–3270

Moorhead DL, Currie WS, Rastetter EB, et al (1999) Climate and litter quality controls on decomposition: An analysis of modeling approaches. Global Biogeochem Cycles 13:575–589

Munger W, Wofsy S (2022) Biomass Inventories at Harvard Forest EMS Tower since 1993 ver 37

Negrón-Juárez RI, Koven CD, Riley WJ, et al (2015) Observed allocations of productivity and biomass, and turnover times in tropical forests are not accurately represented in CMIP5 Earth system models. Environ Res Lett 10.: https://doi.org/10.1088/1748-9326/10/6/064017

NEON (National Ecological Observatory Network) (2022a) Litterfall and fine woody debris production and chemistry (DP1.10033.001)

NEON (National Ecological Observatory Network) (2022b) Plant phenology observations (DP1.10055.001)

NEON (National Ecological Observatory Network) (RELEASE-2022) Vegetation structure (DP1.10098.001)

Pan Y, Birdsey RA, Fang J, et al (2011) A large and persistent carbon sink in the world’s forests. Science 333:988–993

Poorter H, Niklas KJ, Reich PB, et al (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytol 193:30–50

Portillo-Estrada M, Korhonen JFJ, Pihlatie M, et al (2013) Inter- and intra-annual variations in canopy fine litterfall and carbon and nitrogen inputs to the forest floor in two European coniferous forests. Ann For Sci 70:367–379

Potter CS, Randerson JT, Field CB, et al (1993) Terrestrial ecosystem production: A process model based on global satellite and surface data. Global Biogeochem Cycles 7:811–841

Raich JW, Rastetter EB, Melillo JM, et al (1991) Potential Net Primary Productivity in South America: Application of a Global Model. Ecol Appl 1:399–429

Rastetter EB, Shaver GR (1992) A Model of Multiple-Element Limitation for Acclimating Vegetation. Ecology 73:1157–1174

Reich PB, Luo Y, Bradford JB, et al (2014) Temperature drives global patterns in forest biomass distribution in leaves, stems, and roots. Proc Natl Acad Sci U S A 111:13721–13726

Rennolls K (1994) Pipe-model theory of stem-profile development. For Ecol Manage 69:41–55

Ruel JJ, Ayres MP (1999) Jensen's inequality predicts effects of environmental variation. Trends Ecol Evol 14:361–366

Schimel DS, Braswell BH, Holland EA, et al (1994) Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. Global Biogeochem Cycles 8:279–293

Starr M, Saarsalmi A, Hokkanen T, et al (2005) Models of litterfall production for Scots pine (Pinus sylvestris L.) in Finland using stand, site and climate factors. For Ecol Manage 205:215–225

Thorpe AS, Barnett DT, Elmendorf SC, et al (2016) Introduction to the sampling designs of the N ational E cological O bservatory N etwork T errestrial O bservation S ystem. Ecosphere 7:e01627

Ukkola AM, De Kauwe MG, Roderick ML, et al (2021) Annual precipitation explains variability in dryland vegetation greenness globally but not locally. Glob Chang Biol. https://doi.org/10.1111/gcb.15729

Vogt KA, Grier CC, Vogt DJ (1986) Production, Turnover, and Nutrient Dynamics of Above- and Belowground Detritus of World Forests. In: MacFadyen A, Ford ED (eds) Advances in Ecological Research. Academic Press, pp 303–377

Wang CG, Zheng XB, Wang AZ, et al (2021) Temperature and precipitation diversely control seasonal and annual dynamics of litterfall in a temperate mixed mature forest, revealed by long-term data analysis. J Geophys Res Biogeosci 126.: https://doi.org/10.1029/2020jg006204

Wieder WR, Grandy AS, Kallenbach CM, et al (2015) Representing life in the Earth system with soil microbial functional traits in the MIMICS model. Geosci Model Dev 8:1789–1808

Wu Y, Zhou H, Chen W, et al (2021) Response of the soil food web to warming and litter removal in the Tibetan Plateau, China. Geoderma 401.: https://doi.org/10.1016/j.geoderma.2021.115318

Xu S, Liu LL, Sayer EJ (2013) Variability of above-ground litter inputs alters soil physicochemical and biological processes: a meta-analysis of litterfall-manipulation experiments. Biogeosciences 10:7423–7433

Statements and Declarations

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Competing Interests

The authors declare that they have no conflicting or competing interests with respect to the data, analysis and interpretation presented in this manuscript.

Data Availability

The datasets analyzed in this study are available for download from the NEON website (https://www.neonscience.org/data), the Harvard Forest Data Archive (https://harvardforest.fas.harvard.edu/harvard-forest-data-archive) and the Oak Ridge National Lab Distributed Active Archive Center website (https://daac.ornl.gov/VEGETATION/guides/Global_Litter_Carbon_Nutrients.html).

Table 1. Models of aboveground litter production (total foliar, broadleaf, and needle) as a function of aboveground woody growth (AWG), basal area, climate, and forest type (either broadleaf deciduous or coniferous/needles) at 13 forests in the Eastern US (NEON sites). Each observation is an estimate of annual litter production from a single trap within a 20 m x 20 m subplot in a given year. Values are standardized coefficients for each linear mixed model, with the associated standard error in parentheses. Fixed R^2 indicates the full model goodness-of-fit using only the fixed effects; full R^2 additionally includes the random effects of year and plot nested within site. Estimates in bold are significant at $p < 0.05$, estimates in italics. Unstandardized coefficients are in Table S1.

Predictors	Foliar aboveground litter (g m^{-2} $year^{-1}$)	Broadleaf litter (g m^{-2} $year^{-1}$)	Needle litter (g m^{-2} $year^{-1}$)
Intercept	**0.374 (0.061)**	0.016 (0.094)	0.006 (0.109)
FT [Needles]	**-1.04 (0.051)**	na	na
AWG (g m^{-2} $year^{-1}$)	0.0008 (0.028)	-0.027 (0.038)	**0.183 (0.062)**
Basal area (m^2 $hectare^{-1}$)	**0.211 (0.024)**	**0.184 (0.038)**	**0.303 (0.061)**
Mean annual temperature (C)	**0.172 (0.029)**	**0.244 (0.043)**	-0.032 (0.072)
Precipitation (mm)	**0.101 (0.026)**	**0.165 (0.039)**	0.054 (0.062)
AWG x FT	*0.075 (0.074)*	na	na
AWG x BA	**-0.082 (0.017)**	-0.08 (0.027)	-0.074 (0.035)
AWG x MAT	0.007 (0.02)	-0.011 (0.032)	-0.111 (0.062)
AWG x Precip	**0.065 (0.018)**	**0.067 (0.03)**	-0.078 (0.054)
n	1570	1096	474
Fixed R^2 /Full R^2	0.523 / 0.611	0.190 / 0.363	0.132 / 0.460

Table 2. Models of aboveground litter production (total foliar, broadleaf, and needle) as a function of aboveground woody growth (AWG), basal area, climate, and forest type (either broadleaf deciduous or coniferous/needles) across 13 years at the Harvard Forest in Central MA. Each observation is an estimate of annual production in a plot in a given year. Values are standardized coefficients for each linear mixed model, with the associated standard error in parentheses. Fixed R^2 indicates the full model goodness-of-fit using only the fixed effects; full R^2 additionally includes the random effects of plot. For the foliar litter model, mean annual temperature and precipitation are used. For the individual broadleaf and needle litter models, mean daily temperature and precipitation from the calculated climate window is used (see methods for details, and Table S6 for climate windows). Estimates in bold are significant at $p < 0.05$. Unstandardized coefficients are reported in Table S2.

Predictors	Foliar aboveground litter (g m^{-2} $year^{-1}$)	Broadleaf litter (g m^{-2} $year^{-1}$)	Needle litter (g m^{-2} $year^{-1}$)
Intercept	**0.587 (0.08)**	0.0002 (0.140)	0.002 (0.112)
Forest type [Needles]	**-0.925 (0.041)**	na	na
AWG (g m^{-2} $year^{-1}$)	**0.133 (0.043)**	0.046 (0.079)	0.088 (0.072)
Basal area (m^2 $hectare^{-1}$)	**0.403 (0.028)**	**0.344 (0.122)**	**0.742 (0.100)**
Temperature (C)	*0.023 (0.013)*	**0.088 (0.027)**	**0.069 (0.019)**
Precipitation (mm)	**0.028 (0.013)**	**0.091 (0.028)**	0.062 (0.019)
AWG x Forest type	-0.067 (0.067)	na	na
AWG x BA	**-0.205 (0.023)**	-0.002 (0.056)	0.021 (0.054)
AWG x Temp	0.006 (0.012)	0.018 (0.028)	0.035 (0.020)
AWG x Precip	**0.051 (0.012)**	-0.0130 (0.027)	**0.043 (0.020)**
n	849	441	300
Fixed R^2 /Full R^2	0.693 / 0.891	0.18 / 0.78	0.67 / 0.93

Table 3 Aboveground litter production estimates (g dry mass/m^{2}/year) in temperate forest systems from three data sources. Percentage of total aboveground litter in each category given in parentheses.

Data source	Foliar	FWD	Seed + Flower	Total
NEON (n = 13 forests, eastern US)	580 (80%)	77 (11%)	72 (9%)	728
Harvard Forest (n = 1 forest, 13 years)	324 (77%)	46 (11%)	35 (8%)	422
Holland 2015 (n = 22 forests, global)	462 (75%)	111 (15%)	70 (10%)	642