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Nutrient allocation and conservation mechanisms in trees: intraspecific variation, reproductive costs, and global scale comparisons

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Dissertation

NUTRIENT ALLOCATION AND CONSERVATION MECHANISMS IN TREES: INTRASPECIFIC VARIATION, REPRODUCTIVE COSTS, AND GLOBAL SCALE COMPARISONS

by

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DEDICATION

I would like to dedicate this work to my spouse Luísa and our cat Aliquot.

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ABSTRACT

Nitrogen and phosphorus have individually or jointly been demonstrated to limit primary productivity in most of Earth’s forested systems. Nutrient limitation of forest primary productivity is important because terrestrial systems currently store large amounts of carbon and partially mitigate carbon dioxide emissions from anthropogenic activities. There is also evidence that nutrient availability relative to demand is decreasing in forested systems. Trees have complex responses to nutrient availability, including changes in allocation of nutrients to different organs and mechanisms that aide in recycling of nutrients within the plant and ecosystem. In this work I provide new insight related to nutrient allocation and conservation mechanisms in trees, demonstrating that these mechanisms affect nutrient limitation of primary productivity. In Chapter 2, I provide evidence that tree reproductive organs have nutrient resorption processes that transfer nutrients from fruit to seeds and I also demonstrate that tree fruit are capable of photosynthesis – in the absence of such processes the carbon and nutrient costs of tree reproduction would likely be higher. In Chapter 3, I report on the results of a community science project through which I identified variation in biogeochemically relevant leaf

traits across much of the geographic distribution of *Acer rubrum*, one of North America's most broadly distributed tree species, demonstrating that foliar nitrogen resorption is highest in colder high latitudes and leaf litter %N is highest at warmer low latitudes. In Chapter 4, I compare leaf and reproductive litterfall nitrogen and phosphorus metrics worldwide and demonstrate that reproductive litterfall is a significant contributor to tree nutrient budgets, comprising a median of 13.0% and 16.1% of nitrogen and phosphorus fluxes, respectively, when combining leaf and reproductive litterfall. Overall, the results of my dissertation enable me to identify several understudied aspects of tree nutrient allocation and conservation processes by considering the biogeochemistry of reproductive and foliar organs and associated variation across the natural distribution of trees.

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LIST OF ABBREVIATIONS

Adj	Adjusted
AIC	Akaike Information Criterion
AICc	Corrected AIC
ANOVA	Analysis of variance
Aug	August
°C	Degrees Celsius
C	Carbon
CO_2	Carbon dioxide
cm	Centimeter
cm^2	Centimeter squared
g	Gram
Jun	June
K	Number of predictors in model
km	Kilometer
ln	Natural log
n.s.	Not significant
N	Nitrogen
n	Sample size
NIST	National Institute of Standards and Technology
nm	Nanometers
NRE	Nitrogen retranslocation efficiency

NUE	Nutrient use efficiency
m^2	Meter squared
MA	Massachusetts
MAP	Mean annual precipitation
MAT	Mean annual temperature
Max	Maximum
mg	milligram
Min	Minimum
mm	Millimeter
mol	Moles
Oct	October
PAR	Photosynthetically active radiation
P	Phosphorus
PRE	Phosphorus resorption efficiency
R^2	Coefficient of determination
RCP	Representative concentration pathway
s	Second
SE	Standard error
sec	Second
Sep	September
TASpeR	Traits Across Species’ Ranges
U.S.	United States of America

Wt	Weight
yr	Year
μ	Micro (10^{-6})
Δ	Change between two values
%	Percent

CHAPTER ONE: INTRODUCTION

Nutrient limitation of terrestrial ecosystem productivity

Both experimental and modeling studies have demonstrated that terrestrial net primary productivity (NPP) is limited by nitrogen (N), phosphorus (P), or co-limited by both (LeBauer and Treseder, 2008; Vitousek et al., 2010; Fisher et al., 2012; Wieder et al., 2015; Du et al., 2020). From an ecosystem science perspective, terrestrial NPP is important because it provides information about the rate at which biomass accrues in vegetation, thus providing insights into carbon and energy flows into ecosystems. If NPP exceeds heterotrophic respiration then the ecosystem can be considered a net sink of carbon dioxide (CO_2) from the atmosphere, whereas if heterotrophic respiration exceeds NPP the ecosystem will be a net source of carbon dioxide to the atmosphere. It has been suggested that nutrient rich sites experience higher rates of net ecosystem productivity relative to nutrient poor sites (Janssens et al., 2010; Fernández-Martínez et al., 2014).

The findings that nutrient limitation is a key driver of net ecosystem productivity is also important from a climate change perspective. It is currently estimated that from 2011-2020 land uptake of CO_2 mitigated 33% of fossil fuel derived CO_2 emissions during the same time (Friedlingstein et al., 2022). Carbon dioxide not only absorbs longwave radiation, which contributes to the greenhouse effect, but the atmospheric concentration of CO_2 also affects gross rates of photosynthesis via the CO_2 fertilization effect. Studies have found that increased NPP under elevated CO_2 experiments is contingent on adequate soil nutrients (Luo et al., 2004; Terrer et al., 2018). Despite continued increases in atmospheric CO_2 concentrations, there has been a global decline in the CO_2 fertilization effect in the years spanning 1982-2015 and this decline may be attributed to declines in nutrient availability to vegetation (Wang et al 2020).

While elevated levels of CO_2 may enhance the demand for soil nutrients, studies have found that N availability relative to demand may be concurrently decreasing in terrestrial systems (Groffman et al., 2018; Mason et al., 2022). The evidence to support decreases in relative N availability includes declines in natural abundance stable isotope values for N in leaves and wood (McLaughlan et al., 2017; Craine et al., 2018), and decreasing foliar N concentrations, net N mineralization rates, nitrous oxide (N_2O emissions), and export via streams, and rates of atmospheric N deposition (Jonard et al, 2015; Groffman et al., 2018; Mason et al., 2022). With the dual changes in both CO_2 and N availability it is important to consider plant strategies that may overcome shifts in resource availability.

Ecological and evolutionary strategies that mitigate nutrient limitation

In terrestrial ecosystems bioavailable N ultimately originates from the atmosphere via wet or dry deposition and N fixing bacteria which convert N_2 in the atmosphere to ammonia (Matson et al., 2002; Vitousek and Farrington, 1997). There is also evidence that bedrock derived N can be an important component of an ecosystem's N stock (Houlton et al., 2018). Phosphorus can also originate from the atmosphere through deposition (Eger et al., 2013), but most terrestrial P comes from the weathering of bedrock (Walker and Syers, 1976). However, on an annual basis as much as 95-100% of N and P used for new vegetation growth comes from internal recycling of these elements within ecosystems (Ryan and Bormann 1982; Yanai 1992; Likens and Bormann, 1995; Schlesinger and Bernhardt, 2011).

Trees display several different strategies that can affect their nutrient acquisition ability. Both the total amount of root allocation and root traits can influence the amount of nutrients that plants can access. For example, trees may allocate more carbon belowground to compete for soil nutrients when they are of low concentrations (Berryman et al., 2016). It has also been suggested that species with thin roots have higher absorptive capabilities compared to thicker roots (Eissenstat et al., 2015). Many tree roots also form mutualistic or symbiotic relationships with mycorrhizal fungi or N_2 fixing bacteria where both ecological relationships are commonly conceptualized as an energy – nutrient exchange between roots and fungi or bacteria (Phillips et al., 2013; Batterman et al., 2013; DeForest and Snell, 2020).

Another important aspect of tree responses to nutrient limitation is the relative allocation to different organs that may differ in their elemental ratios of C:N:P (McGroddy et al., 2004). For example, wood has high amounts of C for every molecule of N and P, but C:N and C:P for roots is lower, with leaves much lower still (Zhang et al., 2018). Both leaves and reproductive organs are among plant's most nutrient rich organs, indicating they are relatively costly to produce. Because different plant organs have different C:N:P and differing functions, the relative allocation of carbon and nutrients to different organs that maximize fitness changes in response to shifts in nutrient availability (Dybzinski et al., 2015).

As a result of nutrient limitation, there is a strong incentive for trees to retain nutrients that they acquire. Nutrient resorption prior to organ abscission is the key way in which nutrients can be reused by plants. For plant leaves, global scale resorption averages around 62 and 65% for leaf N and P, respectively (Vergutz et al., 2012). Nutrient resorption of N and P has also been observed in roots and stems but is usually less than what is observed in leaves (Freschet et al., 2010; Brant and Chen, 2015). Within ecosystems, the decomposition of tree litterfall is one of the primary ways in which nutrients are cycled between organisms and the amount of resorption directly influences the quality of the litter produced by trees and utilized by soil microbes.

Dissertation Overview

Despite the rich literature related to nutrient limitation and associated processes that plants use to navigate nutrient limitation, there are still many open questions related to plant nutrient cycles. The objective of my dissertation research is to provide new information that increases our understanding of the mechanisms by which plants navigate resource limitation by investigating tree resource conservation and allocation strategies. Specifically, I investigate the potential for nutrient resorption mechanisms in reproductive structures, how intraspecific variation influences tree foliar nutrient resorption across a broad environmental gradient, and whether litterfall derived from different plant organs display similar or distinct patterns at the global scale. In my dissertation I use a combination of field-based observations and samples collected by myself and participants in a community science project I started, and synthesis of data reported in the scientific literature.

Chapter 2. Nitrogen Retranslocation and Photosynthesis in Fruit of Samara Producing Tree Species as Mechanisms that Reduce Resource Costs of Reproduction

In Chapter 2, I describe the results of an observational field study at the Arnold Arboretum with a focus on characterizing N concentrations and amounts in the developing fruit of four different tree species along with replicating previous research that had documented photosynthesis in reproductive structures. I focused on tree species that produce samaras, which are a type of indehiscent wind dispersed fruit. Across all species I observed decreases in samara wing N content that coincided with increases in seed N content, which suggested retranslocation of N from fruit to developing seeds. The range of photosynthesis rates I measured were consistent with those reported from other studies, and about an order of magnitude lower than leaf level photosynthesis measurements for the same trees. I also found that the rate of photosynthesis was positively correlated to the N mass per unit area of samara for two out of the four species examined. Overall, these results demonstrate that the mechanisms of nutrient retranslocation from fruit to seeds, and photosynthesis in developing fruit, help to reduce the net allocation of N and carbon to reproductive organs.

Chapter 3. Macroscale Variation in Red Maple (Acer rubrum) Foliar Carbon, Nitrogen, and Nitrogen Resorption

In Chapter 3, I describe the results of a community science project with a focus on characterizing macroscale variation in N resorption across the geographic distribution of red maple (*Acer rubrum*), one of North America’s most abundant tree species. To accomplish this, I recruited volunteers throughout the eastern United States to send me green and fallen leaves from a red maple tree in their local area. I then measured leaves for surface area, mass, and carbon and N concentrations. My results show that mean annual temperatures were negatively correlated with green leaf N concentrations, fallen leaf C:N ratios, and rates of N resorption, but were positively correlated with green leaf C:N ratios and fallen leaf N concentrations. Green leaf C and N concentrations were significantly higher in open vs. closed grown sites, but leaf C:N was higher in closed grown sites. Overall, these results demonstrate that red maple may depend more on N resorption in the northern and cooler part of its range compared to the southern part of its range which is warmer and may rely more on N recycled through the soil.

Chapter 4. Global Patterns of N and P in Leaf and Reproductive Organ Litterfall

In Chapter four I report on the results of a quantitative data synthesis of leaf and reproductive litterfall N and P based on data I compiled at the global scale from the primary literature. I assessed variation in leaf and reproductive litterfall N and P concentrations, N and P fluxes, and N:P ratios in relation to mean annual temperature and precipitation, latitude, angiosperm vs. gymnosperm vs. mixed stands, canopy habit (evergreen vs. deciduous vs. mixed stands), and stand type (forest vs. plantation). Overall, the litterfall variables were only weakly related to climate and latitude, but the directionality of the relationships provided support for several biogeochemical hypotheses regarding nutrient availability at large spatial scales. Reproductive litterfall nutrient fluxes were best explained by the combination of climate, latitude, and deciduous vs. evergreen stand composition. Globally, reproductive litterfall is a non-trivial contribution to tree nutrient budgets, as it comprises a median of 13.0% and 16.1% of the combined reproductive and leaf litterfall N and P fluxes, respectively.

Chapter 5: Conclusions

In the last chapter I summarize the major findings and implications that relate to tree nutrient allocation and conservation from each of the three chapters that comprise the body of the dissertation. I also highlight future research directions to better understand the strategies trees possess to navigate a nutrient limited environment with suggestions for empirical and model-based research.

CHAPTER TWO: NITROGEN RETRANSLOCATION AND PHOTOSYNTHESIS IN FRUIT OF SAMARA PRODUCING TREE SPECIES AS MECHANISMS THAT REDUCE RESOURCE COSTS OF REPRODUCTION

ABSTRACT

Tree reproduction likely reduces the annual production of biomass per nutrient up-take from soil because resources are used in nutrient rich reproductive structures that are released from the tree, rather than vegetative growth. We investigated mechanisms within fruit that may reduce the resource costs of reproduction in trees prior to dispersal. Four species (*Acer rubrum*, *Acer platanoides*, *Ulmus americana*, and *Fraxinus angustifolia*) that produce indehiscent winged fruit (i.e., samaras) were tested for the presence of photosynthesis within samaras and nutrient retranslocation from samara wings to developing seeds. Species' maximum net photosynthesis rates in samaras were 0.7–1.6 μmol C m^{-2} sec^{-1}. For *A. rubrum* and *U. americana* photosynthetic rates were positively related to nitrogen mass per unit area of samara. Across all species, decreases in samara wing nutrients coincided with increased seed nitrogen content, and potential retranslocation of nitrogen from wings to seeds accounted for 19–57% of total seed nitrogen. The combined effects of offsetting C costs via photosynthesis in samaras and nutrient retranslocation from samara wings to seeds likely decrease the negative carbon and nutrient cost of reproduction on tree resources. Mechanisms identified here enable for better integration of reproductive processes into conceptual frameworks of plant nutrient use.

INTRODUCTION

Widespread resource limitation of forest productivity (e.g., LeBauer and Treseder, 2008; Fisher et al., 2012) selects for the efficient use of nutrients within trees (Vitousek, 1984; Aerts and Chapin, 1999). Trees also invest scarce resources towards reproduction (Obeso, 2002) and the allocated nutrients are lost from the plant during abscission (e.g., floral structures) and dispersal (e.g., pollen, fruit, seeds). Therefore, nutrients lost from trees through reproductive allocation are no longer available for vegetative growth in subsequent years, leading to a tension between the need to both maximize the efficiency of resource use and allocate resources to reproduction. Although reproduction comes at a net resource cost to trees, it does not preclude the possibility that meaningful resource acquisition and conservation mechanisms within reproductive structures exist. By considering mechanisms by which resources allocated to reproduction are also efficiently used we may gain additional insights into the ecological and evolutionary contexts of how trees successfully navigate resource limited environments.

Carbon (C) and nutrients are used in the production and maintenance of reproductive structures including seeds, fruit, flowers, and pollen. Much of the C in seeds is stored in energy rich lipids, and nitrogen (N) in seeds can be found in proteins and alkaloids which serve as reserves for the new plant and to deter granivory (McKey, 1974; Voelker and Kinney, 2001). Annual biomass estimates of reproductive output determined using litterfall traps in temperate seasonal forests have average values of 35 g m^{-2} yr^{-1}, and an associated N content of 0.7 g N m^{-2} yr^{-1} (Holland et al., 2015). This flux of nutrients in reproductive structures from trees represents 14% of total N lost in the combined amounts of tree leaf and reproductive litterfall (Holland et al., 2015). The importance of reproductive allocation to the tree resource budget is also supported by the notion that construction costs of reproductive structures tend to be higher compared to other tree organs (Poorter, 1994), and nutrients could have otherwise been used to support resource acquisitive organs. However, trees may mitigate these resource costs through several mechanisms that to date have received little attention: photosynthesis and nutrient retranslocation within reproductive structures prior to their abscission or dispersal (Obeso, 2002).

Observations of stomata and photosynthesis in tree reproductive organs suggest they support some of their own C requirements (e.g., Bazzaz et al., 1979; Ogawa and Takano, 1997; Guzmán-Delgado et al., 2017; Simkin et al., 2020). Bazzaz et al. (1979) estimated photosynthesis in reproductive structures among fifteen tree species offset 2–65% of the C costs of reproduction. Photosynthetic cones of *Picea abies* have been found to offset ~16% of C costs of reproduction (Koppel et al., 1987). Understanding the variability and extent to which photosynthesis within reproductive structures reduces the use of stored C and newly fixed C transported from leaves is likely to be important to accurately assess the C costs of reproduction.

A trait-based approach has proven to be useful in describing variation in photosynthetic capacity among leaves at the inter- and intra-specific level (Wright et al., 2004). For example, light saturated photosynthesis levels in leaves are related to leaf N levels, leaf lifespan, and specific leaf area (Reich et al., 1999). Likewise, reproductive traits such as fruit type, morphology, or nutrient concentrations may be a useful path forward to describing important variation in photosynthetic rates within reproductive structures.

In a similar way that photosynthesis in reproductive structures may reduce the C costs of reproduction, nutrient retranslocation processes within reproductive organs may help to conserve some of the nutrients in maturing fruit. Nutrient retranslocation is a process whereby nutrients are reallocated from living plant tissues to other active sinks within the plant prior to their abscission, increasing the residence time of nutrients within the plant. Nutrient retranslocation prior to leaf abscission is one of the primary ways in which trees can recycle nutrients (Kobe et al., 2005; Yuan and Chen, 2009; Zhang et al et., 2018a; Drenovsky et al., 2019), but the potential presence of similar mechanisms within reproductive structures has received much less attention.

Nutrient retranslocation between reproductive structures (e.g., from fruits to seeds) may offset some of the costs of reproduction, particularly if it preempts the need for additional nutrient allocation from elsewhere in the plant. There is little quantitative understanding of how nutrients may be retranslocated among the components of tree reproductive structures (e.g., fruit, seeds). Ashman (1994) identified the retranslocation of N and P to occur from reproductive structures prior to their abscission or dispersal from an herbaceous plant (*Sidalcea oregana*). Additionally, visual observations of tree reproductive structures reveal that many indehiscent fruit lose pigments as they approach maturation, prior to dispersal (personal observation). These lines of evidence suggest that nutrient retranslocation from fruit to seeds may be present in trees.

The objective of this study is to investigate mechanisms that may reduce the C and N costs of reproduction in four species that produce indehiscent winged fruit (i.e., samaras). We chose a polyphyletic group of species to increase the generality of our findings (Gougherty and Gougherty, 2018), yet we constrained our investigation to samara fruit that have a distinct blade like structure amenable to measurements of photosynthesis. The samara fruit type is found globally across all continents apart from Antarctica (der Weduwen and Ruxton, 2019) and around 20% of angiosperm tree species in northern temperate forests of USA produce samaras (Barnes and Wagner, 2004), including red maple (*Acer rubrum*) one of the most abundant tree species in North America (Fei and Steiner, 2007). By examining variation in photosynthetic rate relative to fruit traits, and the nutrient contents of the samara wing and seed through time, we predicted that: 1) the samaras of the four different species exhibit measurable rates of photosynthesis; 2) the photosynthetic rate of the fruit is significantly correlated with fruit traits such as N concentration, N mass per unit area, and specific samara mass; and 3) nutrient retranslocation from the samara wing to the seed may reduce the nutrient cost of reproduction by reallocating the nutrients used in the fruit to the maturing seed in these tree species.

METHODS

This study was conducted at the Arnold Arboretum of Harvard University located in Boston, MA, USA [42.30350, -71.12116]. Samaras were collected from four tree species, two with spring fruit maturation (*Acer rubrum* and *Ulmus americana*) and two with late growing season fruit maturation (*Fraxinus angustifolia* and *Acer platanoides*). The specific trees we sampled are accessioned by the Arboretum, details of which are provided with species descriptions in **Supporting Table 2.1**.

Species descriptions

A. rubrum and *U. americana* are native to North America and flowering and fruit development is typically initiated prior to full leaf expansion for both species. *A. rubrum* has paired samaras that each contain one seed and have wings that are typically 2–3 cm in length (Barnes and Wagner, 2004). *Ulmus americana* has one-seeded samaras that are found in bunches, with a typical samara length of 1–2 cm (Barnes and Wagner, 2004). *A. platanoides* is native to Europe and portions of western Asia, and it is considered an invasive species in the northeastern USA. Typically, *A. platanoides* flowers in the spring, and the 4–5 cm long fruit mature in the autumn (Barnes and Wagner, 2004). *F. angustifolia* has a native distribution over areas of northern Africa, southern Europe, and western Asia; it flowers in the spring and fruit mature in the autumn and are typically 2.5–4.5 cm long (Debussche and Lepart, 1992).

Photosynthesis measurements and samara collection

We measured gas exchange of samaras for the following species and dates in 2019: *A. rubrum* (May 15, May 22-24, May 31), *U. americana* (May 8–9, May 21, May 31–Jun 1), *F. angustifolia* (Jun 4, Jun 12), and *A. platanoides* (Jun 6, Jun 24, Jul 9) using a LI-6400 Portable Photosynthesis System (LI-COR, Lincoln, NE, USA). Carbon dioxide concentrations were set at 410 ppm, flow set at 200 µmol sec^{-1}, and photosynthetically active radiation (PAR) set at 750 µmol of photons m^{-2} sec^{-1}, a level ensuring samaras were light-saturated (**Supporting Figure 2.1**). We estimated samara respiration rates by placing one set of samaras per tree inside the chamber with the light source inactivated (PAR = 0 µmol of photons m^{-2} sec^{-1}) prior to the measurement. One set of samaras ranged between one to four samaras, depending on tree species. (*A. rubrum* = 2, *U. americana* = 4, *A. platanoides* = 1, *F. angustifolia* = 3). For each species we collected five replicate sets of samaras from each of five trees per sampling date.

One set of samaras were detached from the tree where the peduncle meets the stem and immediately placed inside the measurement cuvette on a single non-overlapping plane as a single replicate. We waited ~2 minutes until gas exchange levels stabilized inside the cuvette to conduct four measurements of net photosynthesis, each spaced 30 seconds apart. For all but *A. platanoides*, multiple samaras were placed inside the cuvette to increase the area and photosynthesis signal, which was often found to be below the detection limit in initial tests if only a single samara was used. In our calculations, we adjusted gas exchange measurements for the area occupied by the samaras in the cuvette. For all species except *A. platanoides*, the entire samara was placed in the cuvette. Due to size limitations of the cuvette (6 cm^2), only the winged portions of *A. platanoides* were placed into the cuvette which may have led to a misestimation of net photosynthetic rates of the entire samara for this species since our measurements excluded the seed component of the samara which likely have high respiratory costs.

In addition to collecting the samaras for which we measured photosynthesis, additional samples for the following species and dates to characterize nutrient dynamics in the samara wings and seeds were collected: *A. rubrum*: April 30; *U. americana*: April 25; *F. angustifolia*: July 25, Aug 20, Sep 13–14, Oct 3, Oct 24; and *A. platanoides*: July 25, Aug 20, Sep 13–14, Oct 3, Oct 24. Samara collections were made between the period of samara emergence through the point until the majority of the samara wings were dry, prior to dispersal. After dissecting into seed and wing components, samples were pooled and ~3 mg of sample was analyzed for N concentration using a NC2500 elemental analyzer (CE Elantech, Lakewood, NJ, USA).

Laboratory measurements

For every samara we determined the area of one side by using a digital camera to take photographs on a level surface and then analyzing the image using ImageJ version 1.52a. Samples were then dissected into different components: seed, wing, and peduncle and dried until constant mass at 60 °C. We noted when the seed appeared to be non-viable due to size or necrotic appearance. In total 1.0% of *A. rubrum*, 0.53% of *U. americana*, 13% of *A. platanoides,* and 47% of *F. angustifolia* has samples that contained seeds that appeared to be non-viable due to size (e.g., seed was much smaller relative to others from the same tree) or necrosis (e.g., discoloration). Samples that contained suspected non-viable seeds were included in the analysis.

To ensure adequate amount of sample material for chemical analyses we then pooled wing and seed samples by component (2 for *A. platanoides*, 3 for *F. angustifolia*, 4 for *U. americana*, 2 for *A. rubrum*). The number samaras collected from each tree was sufficient to generate five pooled samples per tree for each sampling date. Samples were weighed and then homogenized to a powder using a ceramic mortar and pestle. Due to an oversight, nineteen samples were not weighed prior to homogenization, and were thus excluded from further analysis for total or area-based nutrient metrics.

For *A. platanoides* and *F. angustifolia* there was enough remaining samara wing sample after N analysis to further analyze samples for phosphorus (P) concentration. Plant P analysis was carried out using an amended version of the method described by Cho and Nielsen (2017). Briefly, 30–50 mg of homogenized sample was weighed into acid-washed crucibles and ashed at 500 °C for three hours. After ashing, P was extracted from the ash using 2.88 M sulfuric acid and analyzed colorimetrically via the molybdate blue method at 700 nm (Cho and Neilsen, 2017). For both N and P analyses we used the NIST Apple Leaves as standard reference material. All laboratory measurements were conducted at Boston University (Boston, MA, USA).

Data analysis

We used Bayesian mixed effect models with R version 4.0.3 (R Core Team, 2020) and the R package ‘brms’, which provides a backend interface with Stan (Stan Development Team, 2020), which implements models using Markov chain Monte Carlo algorithms to assess differences in measured net photosynthesis values and respiration by sampling date within species. For gas exchange measurements fixed effects were used for sampling dates, and type of gas exchange measurement (i.e., net photosynthetic rate or respiration rate). A random effect was assigned to the individual trees. When net photosynthesis levels were significantly higher than respiration levels, we took this as evidence of gross photosynthesis occurring, even if the net photosynthesis measurement was negative. An absence of gross photosynthesis in the samara wing was inferred when net photosynthesis levels and respiration levels on a given date were not significantly different.

We investigated the relationships between the following samara wing traits and net photosynthetic rates: N concentration, specific samara mass, and N mass per unit area of samara. A natural log transformation was applied to samara traits to improve linearity with net photosynthetic rate. Linear models were fit in a Bayesian context using the ‘brms’ package in R. Samara traits as fixed effects and different trees within species were assigned random effects, repeated measures were not controlled for over different sampling dates in the photosynthesis—trait relationships. Multivariate Bayesian linear regression was explored, but this approach did not indicate the combination of multiple traits were a better fit compared to univariate regression, and thus is not presented.

We compared nutrient content of samara wings and seeds by date and species using a mixed effects model where sampling dates were fixed effects and specific trees assigned as random effects. Nutrient retranslocation from samara wings to seeds is hypothesized to occur in the interval between maximum total N in samara wings and fruit dispersal. To estimate the amount of nutrient retranslocation from the samara wing samples we compared the dates with the highest average N per unit area and total N of the samara wing to the lowest average N content dates. The lowest N was consistently found to the last sampling date for each species. Nutrient retranslocation efficiency from samara wings was calculated using the following formula:

$$Nutrient\ retranslocation\ efficiency\ (\%) = 100 \times \frac{(N\ or\ P\ mass\ or\ per\ unit\ area)\ - min\ (N\ or\ P\ mass\ or\ per\ unit\ area)}{max\ (N\ or\ P\ mass\ or\ per\ unit\ area)}$$

Models were validated using posterior predictive checks and leave-one-out cross validation in the R packages ‘bayesplot’ and ‘loo’. We used the ‘hypothesis’ function in the ‘brms’ package to perform the two-sided null hypothesis that the difference between values was zero. Results were considered significant and reported with Bayesian p-val <0.05, when the 95% credible interval did not overlap with zero. Bayesian R^2 values were computed within ‘brms’ following work from Gelman et al (2019).

RESULTS

Comparison of photosynthesis and respiration rates in samaras

Across all four species we found positive net photosynthesis rates for at least one sampling date (Figure 2.1). Maximum net photosynthesis ranged from 0.7 µmol C m^{-2}

sec^{-1} for both *U. americana* and *A. platanoides* to 1.6 μmol C m^{-2} sec^{-1} for *A. rubrum*. The maximum observed net photosynthetic rate for *F. angustifolia* was 1.2 μmol C m^{-2} sec^{-1} on Jun 4. We measured net positive photosynthesis for all sampling dates of *A. platanoides*, and *F.angustifolia*. However, for *A. rubrum* and *U. americana*, the last two dates for which we measured photosynthesis net photosynthesis levels were negative (Figure 2.1). For both *A. rubrum* and *U. americana* we observed differences between net photosynthesis and respiration for the first two photosynthesis sampling dates (Bayesian p-value<0.05), suggesting gross photosynthesis levels of 2.9 and 0.8 μmol C m^{-2} sec^{-1} for *A. rubrum* and 2.76 and 1.16 μmol C m^{-2} sec^{-1} for *U. americana* (Figure 2.1a–b). No differences between net photosynthesis and respiration on the last sampling dates for *A. rubrum* and *U. americana* were observed, suggesting gross photosynthesis has ceased by the final measurement dates. Estimates of gross photosynthesis rates for *A. platanoides* were consistent at 1.3 μmol C m^{-2} sec^{-1} across all three sampling dates (Figure 2.1c). For *F. angustifolia* estimates of gross photosynthesis were observed to be 3.3 μmol C m^{-2} sec^{-1} on Jun 4, and 2.4 μmol C m^{-2} sec^{-1} on Jun 12 (Figure 2.1d).

Samara traits in relation to net photosynthesis levels

For A. rubrum and U. americana, we observed positive relationships between net photosynthetic rate and samara N concentration, N per unit area, and specific samara mass (Bayesian p-value <0.05 for all cases; Figure 2.2 a, b, e, f, i, j). The strongest relationships with net photosynthesis for both of *A. rubrum* and *U. americana* included measurements with information related to N, such as N concentration (Bayesian R^2; *A. rubrum* = 0.30; *U. americana* = 0.46; Figure 2.2 a, b) and N mass per unit area (Bayesian R^2; *A. rubrum* = 0.37; *U. americana* = 0.49; Figure 2.2 e, f).

In contrast, there was no significant relationship between net photosynthesis and either mass- or area-based measurements of N concentration for *A. platanoides* or *F. angustifolia*. There was, however, a positive relationship between specific samara mass and net photosynthesis (Bayesian p-value<0.05) for *A. platanoides*, but the relationship was fairly weak (Bayesian R^2=0.13; Figure 2.2 k).

Changes in nutrient content of samara wings and seeds

Nitrogen

Across all species, we observed a consistent decrease in samara wing N mass per unit area through time (Figure 2.3a-d), and similar patterns were observed for N concentration and total N mass in samaras (Supporting Figure 2.2 and 2.3). Total mean (± SE) mass-based N retranslocation efficiency (NRE) for samara wings of *A. rubrum*, *U. americana*, *A. platanoides*, and *F. angustifolia* was 70% (± 21), 66% (± 16), 56% (± 23), and 31% (± 30), respectively (Supporting Table 2.2). The area-based NRE for *A. rubrum*, *U. americana*, *A. platanoides*, and *F. angustifolia* were calculated to be 83% (± 16), 67% (± 4), 45% (± 27), and 29% (± 13), respectively (Supporting Table 2.2).

In contrast to the samara wings, we found increases in the total N mass in seeds through time in all species (Figure 2.3e-h). For *A. rubrum, U. americana,* and *A. platanoides* we found that the N mass in seeds reached a peak by the second-to-last sampling date such that the last two sampling dates did not have significantly different amounts of N within the seeds (Figure 2.3e–g). *F. angustifolia* seeds reached peak total N by the third-to-last sampling date and had relatively low total N mass despite its long fruit maturation time (Figure 2.3h).

Phosphorus

For samara wings of *A. platanoides* and *F. angustifolia*, we found significant differences between the minimum and maximum values across sampling dates for total P mass and P mass per unit area (Figure 2.4). We observed a gradual decrease in samara wing P concentration from our first to last sampling date for both *A. platanoides* and *F. angustifolia* (0.34 %P ± 0.03 on 6/6 to 0.14 %P ± 0.03 on 10/24, and 0.29 %P ± 0.05 on 6/4 to 0.16 %P ± 0.02 on 10/24, respectively; Supporting Figure 2.2e–f). However, for total P mass in samara wings we observed maximum values in July or August and minimum values in October (Figure 2.4c–d). P mass per unit area of samara wing also peaked at sampling dates during the summer and decreased to a minimum by the end of October (Figure 2.4a–b).

The mass-based P retranslocation efficiency (PRE) from samara wings for *A. platanoides*, and *F. angustifolia* was found to be 63% (± 12) and 38% (± 23), whereas the area-based PRE from samara wings was found to be 60% (± 17) and 32% (± 12), respectively (Supporting Table 2.3).

DISCUSSION

In support of our first hypothesis, we found positive rates of net photosynthesis to occur in fruit of all four species we studied. These results confirm those of previous studies that have documented photosynthesis in the fruit of other temperate tree species (e.g., Bazzaz et al., 1979; Guzmán-Delgado et al., 2017). In support of our second hypothesis, we found that net photosynthesis levels in the fruit of *A. rubrum* and *U. americana* were significantly correlated with the traits of the samaras, particularly N mass per unit area and N concentration. In contrast to our second hypothesis, we did not find meaningful relationships between rates of net photosynthesis and samara traits for *A. platanoides* or *F. angustifolia*. In support of our third hypothesis, we found evidence of nutrient retranslocation from the wings of developing fruit that coincided with increased nutrient content of the seeds in all four tree species. If retranslocated N from samara wings is allocated to seeds, it would represent a substantial movement of resources at the organ level and on average it would account for 19–57% of total seed N depending on the species. Net photosynthesis and nutrient retranslocation within reproductive structures may be mechanisms by which the C and nutrient costs of reproduction are reduced particularly if they preempt the need for additional allocation of C and nutrients from other areas in the plant.

Samara photosynthetic rates and nutrient retranslocation

Across all four of the species included in our study we observed maximum net photosynthetic rates in samaras of 0.7–1.6 µmol C m^{-2} sec^{-1}. Compared to leaves measured under the same conditions at the time of samara collection, which typically had average photosynthetic rates of 5.8–8.8 µmol C m^{-2} sec^{-1}, the maximum net photosynthesis values we observed in samaras were ~4–13x lower. Our findings closely align with those of Guzmán-Delgado et al. (2017) who observed average photosynthetic rates of samaras collected from *Ulmus laevis* and *Ulmus minor* to be 1.65 and 1.07 µmol C m^{-2} sec^{-1}, respectively. Despite the relatively low rates of photosynthesis measured in the samaras, it is likely that this C uptake in fruit offsets some of the C cost of reproduction (Bazzaz et al., 1979) and is part of the broader array of organs, including leaves and stems, in which photosynthesis has been observed (Vandegehuchte et al., 2015; Simkin et al., 2020). Future studies could address how anatomical traits (e.g., number and distribution of stomata, distribution of vascular and structural tissue) are functionally related to photosynthesis rates in fruit (Onoda et al., 2017).

Overall, the average nutrient retranslocation values we observed from samara wings are similar to studies that report nutrient retranslocation efficiency for leaves of angiosperm trees (~50–60% for N ; Aerts, 1996; Yuan and Chen, 2009; Vergutz et al., 2012). Our mass-based metrics of N retranslocation from samara wings ranged from 31% (*F. angustifolia*) to 70% (*A. rubrum*), and the average across all four species was 56%. It is notable that *F. angustifolia* tended to have the lowest samara wing nutrient retranslocation efficiency because we observed that a large proportion (47%) of *F. angustifolia* fruit were either not fertilized or contained what appeared to be non-viable seeds. We speculate that this lack of seed viability within fruit may have resulted in the lower retranslocation of N from the samara wings of this species, particularly since maturing seeds are a strong sink for nutrients and may provide molecular cues for retranslocation (Tuan et al., 2019).

The highest concentrations of N in samara wings for *A. rubrum* and *U. americana* were observed on the first sample date and generally declined thereafter. It is worth noting that the significant relationships between net photosynthesis and samara N concentrations in *A. rubrum* and *U. americana* were established as N concentrations were declining in the wing and increasing in the seed. This finding suggests that the temporal variation in photosynthetic rates observed in *A. rubrum* and *U. americana* was due in part to the retranslocation of N out of samara wings. Likewise, our photosynthesis measurements for *A. platnoides* and *F. angustifolia* coincided with sampling dates for which there tended to be lower variation in N concentration and N mass per unit area of samara.

Resource fate and nutrient use efficiency

One shortcoming of our study is that we were not able to provide conclusive evidence regarding the fate of the C fixed during photosynthesis or the N observed to decrease in samara wings through time. However, it is likely that the C from photosynthesis in the fruit was used directly in the reproductive structure for tissue construction and maintenance, as the seed was an active sink, which increased in mass over the course of our sample collection. Similarly, while the fate of N remains uncertain, the concomitant decrease in nutrient content of the samara wings with increasing nutrient content within seeds suggests that the nutrients may be reallocated within reproductive structures. Nevertheless, we cannot rule out the possibility that these nutrients were lost from the samara wings through leaching during fruit maturation or reallocated to other developing non-reproductive organs. While leaching losses of nutrients may have occurred, the magnitude of leaching is not likely to account for the vast majority of the decrease in nutrient content in most plant organs (e.g., temperate forest leaves typically lose <25% of N via leaching; Berg and Staaf, 1981).

Potential retranslocation of nutrients from fruit to seeds deserves additional attention from a nutrient use efficiency (NUE) perspective. NUE is typically defined as the quantity of biomass produced divided by the amount of nutrients taken up from the soil on an annual basis. Retranslocation of nutrients from leaves prior to senescence increases NUE because it extends the residence time of nutrients within the plant (Berendse and Aerts, 1987). In fact, 31–66% of the total annual growth requirement of N may be accounted for by foliar nutrient retranslocation in forests (Finzi et al., 2002; Schlesinger and Bernhardt, 2013). Direct retranslocation of nutrients from fruit to developing seeds may operate in a similar manner. If the nutrients retranslocated from fruit to seeds preempts the need for additional nutrient allocation to seeds from other sources within the tree, both the overall nutrient costs of reproduction, and the negative impact of reproductive allocation on NUE, would be reduced. All things being equal, whole tree NUE would tend to be higher in trees that are capable of retranslocating nutrients from fruit to seeds compared to trees that lack this capability.

CONCLUSIONS

Reproductive organs are a critical component of tree resource budgets. We found evidence that positive net photosynthesis occurs in the fruits of samara-producing tree species, and that the rate of net photosynthesis is strongly related to the N content of the samara wing for two of the four species we investigated. We also identified and quantified substantial decreases of nutrients from samara wings that may have been transferred to maturing seeds. Our current understanding of these processes is limited because there are very few studies on nutrient translocation within different components of reproductive structures. Moreover, while we do not know how widespread this phenomenon is among different species or fruit types, our findings suggest the allocation of nutrients to reproduction should be more widely considered within the conceptual framework of nutrient use efficiency.

ACKNOWLEDGEMENTS

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AUTHOR CONTRIBUTIONS

Steven W. Gougherty (SWG) initiated the research idea; Adrien C. Finzi (ACF) and SWG designed the research; SWG conducted data analysis; Bailey E. Cowart (BEC) and SWG collected samples and data; ACF and SWG interpreted the data; SWG wrote the first draft; ACF, BEC, and SWG edited the manuscript and contributed to writing.

FIGURES

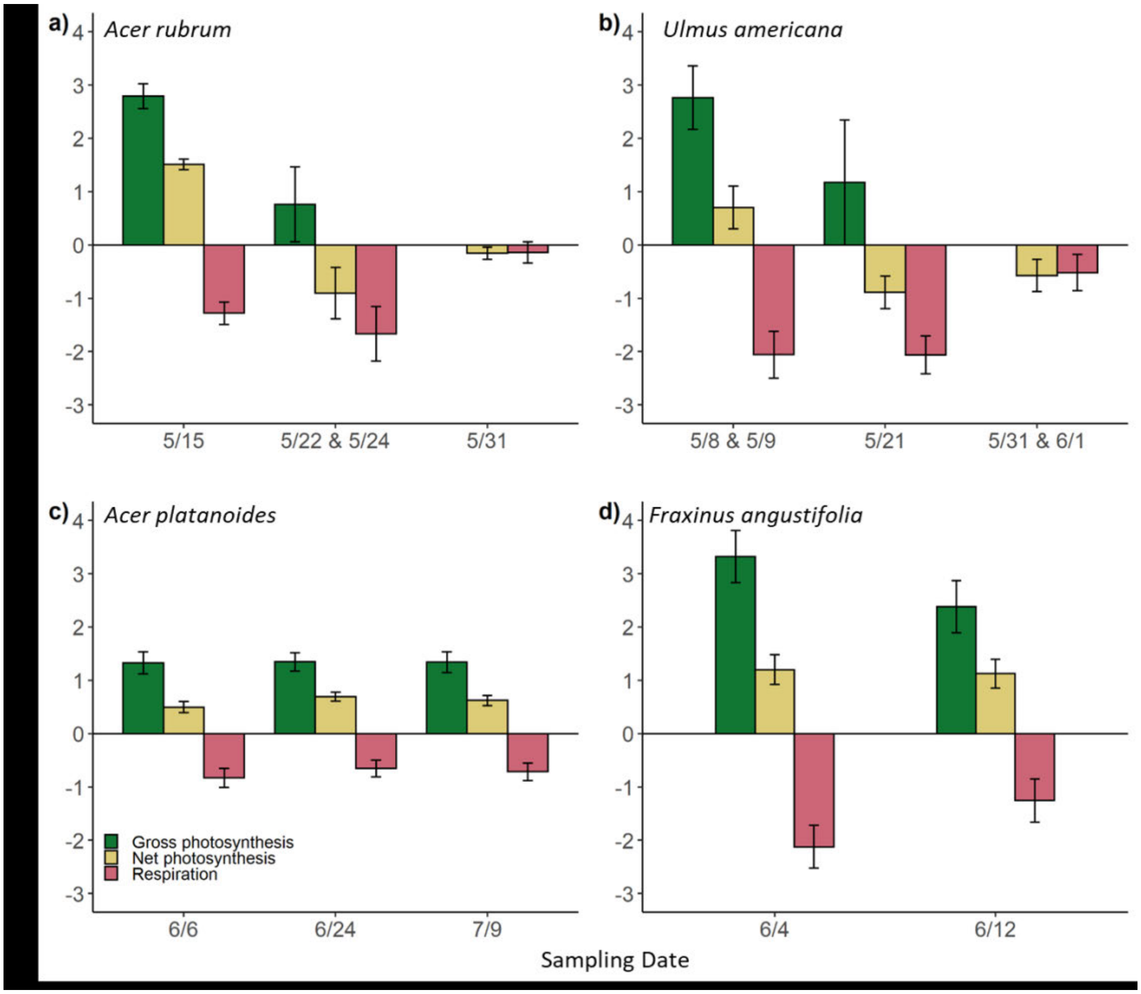


Figure 2.1. Mean (±SE) gross photosynthesis (green bars), net photosynthesis (yellow bars) and respiration (red bars) rates for samaras from a) *Acer rubrum*, b) *Ulmus americana*, c) *Acer platanoides*, and d) *Fraxinus angustifolia* collected in 2019 at Arnold Arboretum, Boston, MA. Gross photosynthesis estimates are provided only when there was a significant difference (Bayesian p-value<0.05) between net photosynthesis and respiration rates within a sampling date.

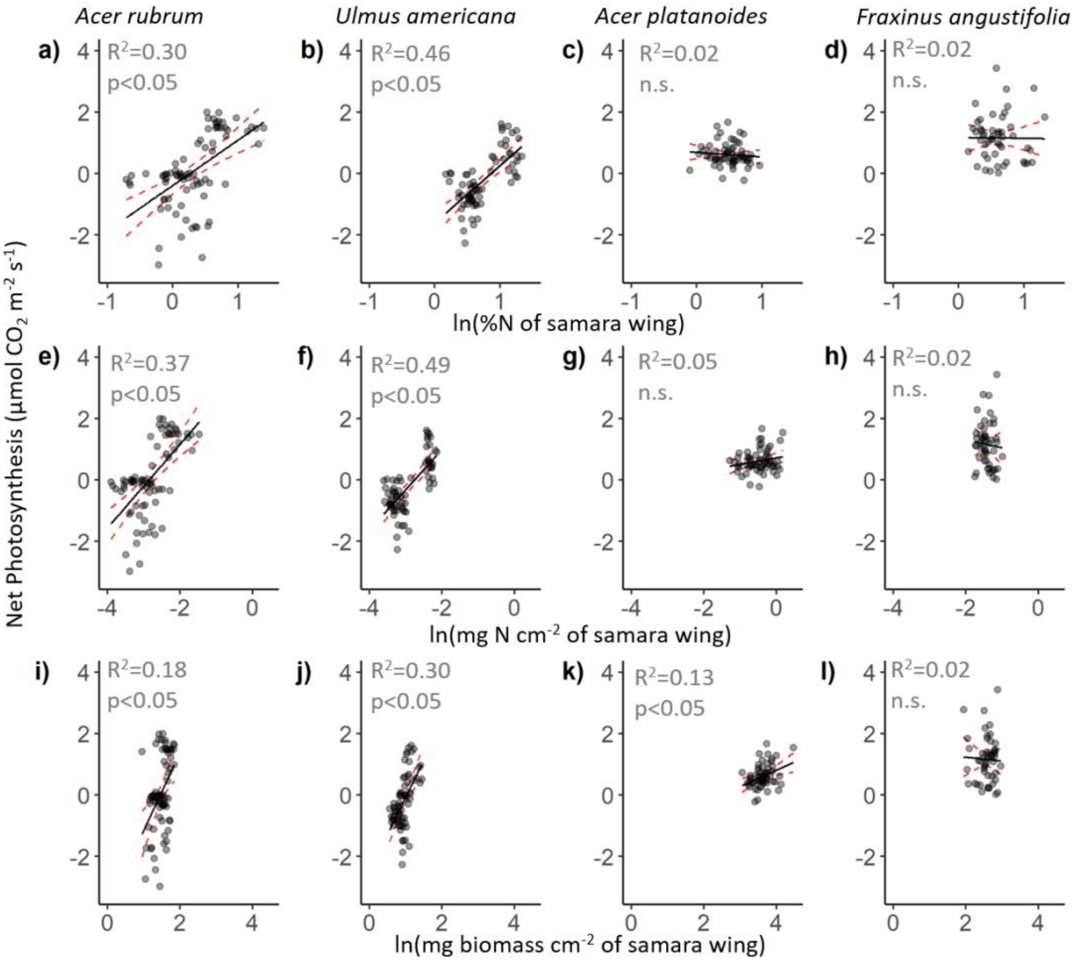


Figure 2.2. Relationships between net photosynthesis rates and samara traits: (a–d) ln(%N), (e–h) ln(mg N in samara wing/ cm^2 of samara wing), (i–l) ln(mg of samara wing/ cm^2 of samara wing). Samples were collected for *Acer rubrum*, *Ulmus americana*, *Acer platanoides*, and *Fraxinus angustifolia* in 2019 at Arnold Arboretum, Boston, MA. Black lines are the fitted means of the models and red lines are the 95% credible interval. Bayesian R^2 values are reported and a Bayesian p-value <0.05 indicates the 95% credible interval for the slope of the modelled relationship does not overlap with zero; n.s. indicates a non-significant slope.

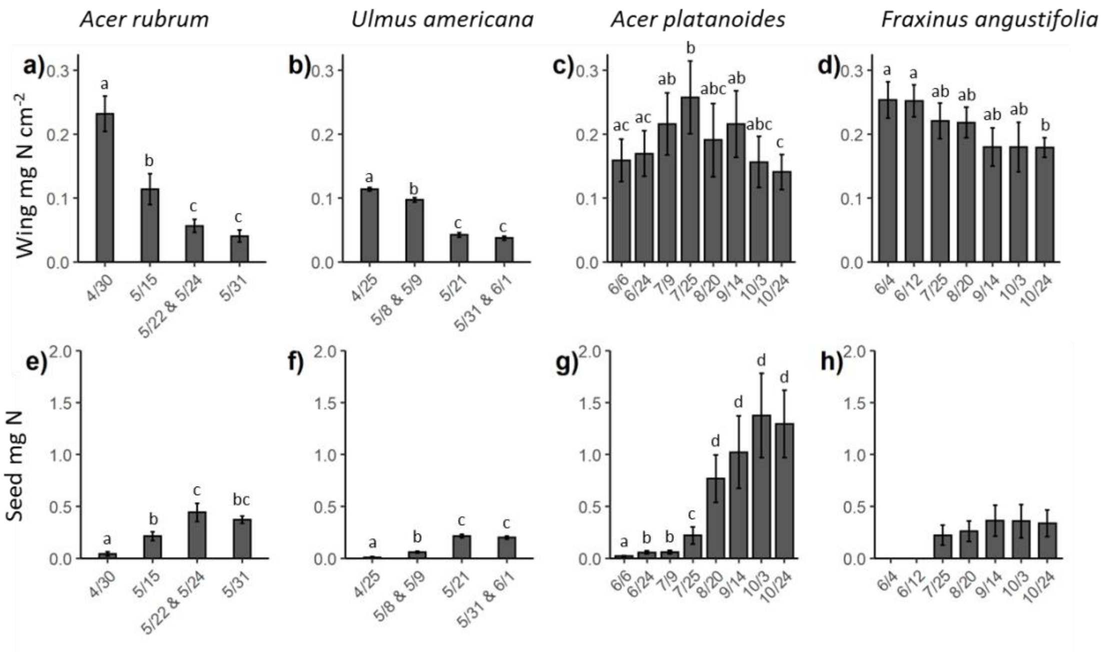


Figure 2.3. (a–d) mg N cm^{-2} in samara wings, (e-h) total N in seeds by sampling date collected in 2019 at Arnold Arboretum, Boston, MA, for *Acer rubrum, Ulmus americana, Acer platanoides,* and *Fraxinus angustifolia*. Bars represent mean values and error bars represent standard error. Distinct letters between groups within a panel indicate statistically significant differences (Bayesian p-value < 0.05). In h) no values are reported for 6/4 or 6/12 because seeds were too small to analyze.

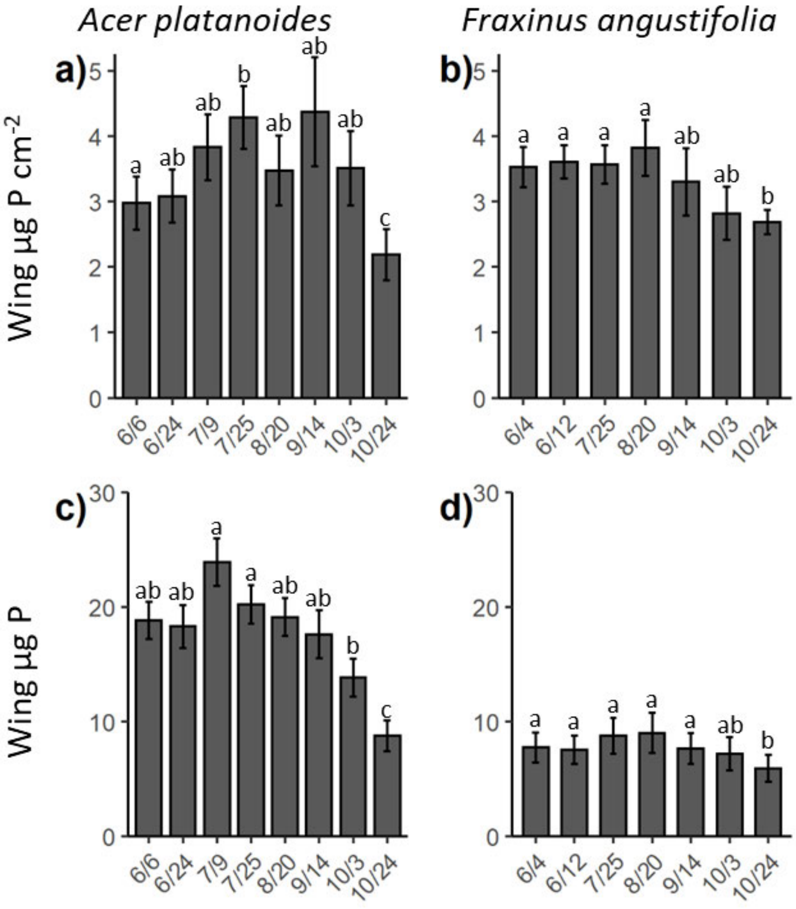


Figure 2.4. (a–b) µg P cm^{-2} in samara wings, (c–d) total P in samara wings by sampling date collected in 2019 at Arnold Arboretum, Boston, MA for *Acer platanoides* and *Fraxinus angustifolia*. Bars represent mean values and error bars represent standard error. Distinct letters between groups within a panel indicate statistically significant differences (Bayesian p-value < 0.05).

SUPPORTING INFORMATION

Supporting Table 2.1. The trees sampled as part of the study as accessioned by Arnold Arboretum.

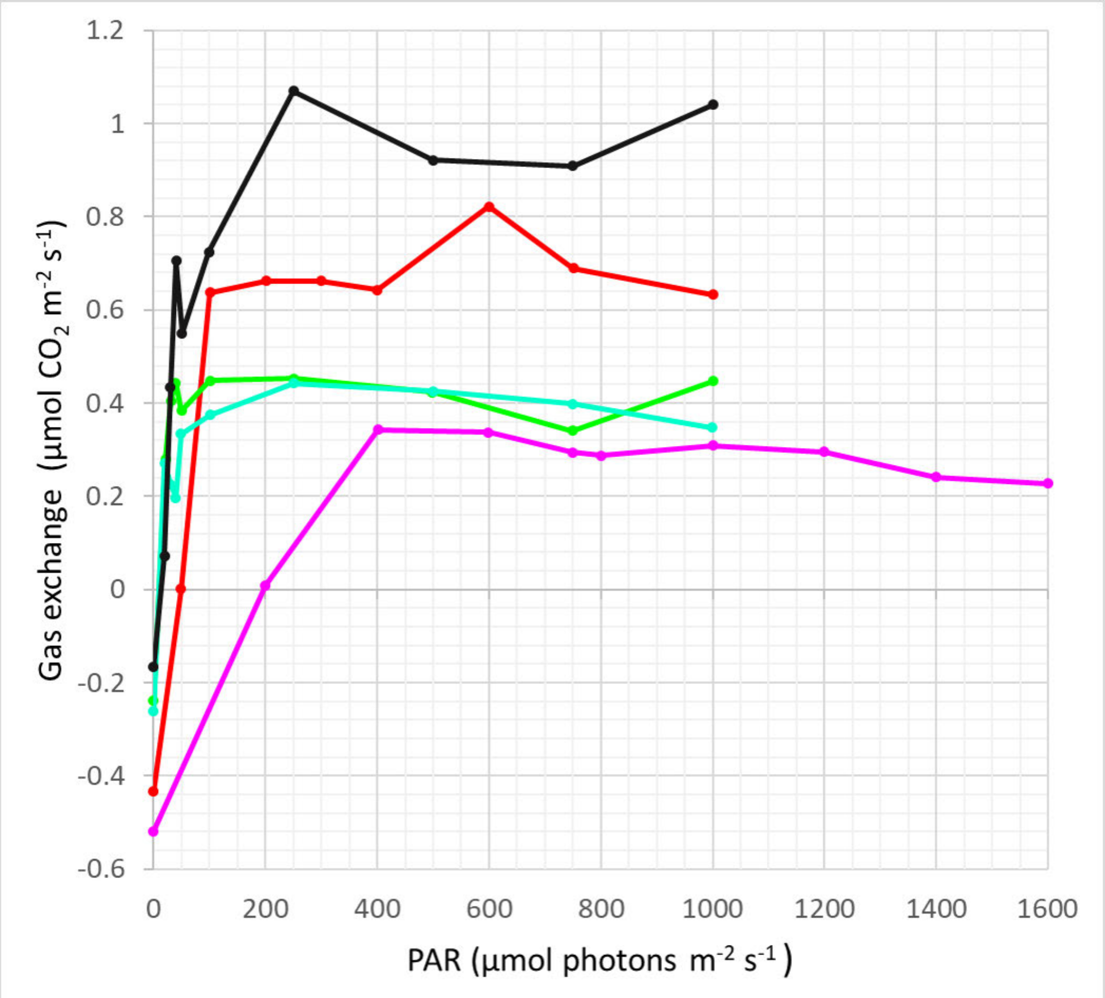
Species	**Accession identification**
Acer rubrum	875-93-B
Acer rubrum	688-39-I
Acer rubrum	1196-84-A
Acer rubrum	1196-84-C
Acer rubrum	596-39-O
Ulmus americana	352-91-A
Ulmus americana	561-89-A
Ulmus americana	180-2003-C
Ulmus americana	561-89-B
Ulmus americana	412-86-B
Acer platanoides	12549-1*A
Acer platanoides	12547*A
Acer platanoides	146-90*A
Acer platanoides	98-65*B
Acer platanoides	630-48*A
Fraxinus angustifolia	160-90-A
Fraxinus angustifolia	307-58-B
Fraxinus angustifolia	18881-A
Fraxinus angustifolia	1081-80-A
Fraxinus angustifolia	799-83-B

Supporting Table 2.2. Estimates of nitrogen resorption efficiencies (NRE) from samara wings based on maximum and minimum observed nitrogen contents in samara wings. The minimum observed nitrogen contents always occurred on the final sampling date for each species. Values represent means and numbers in parentheses are standard errors.

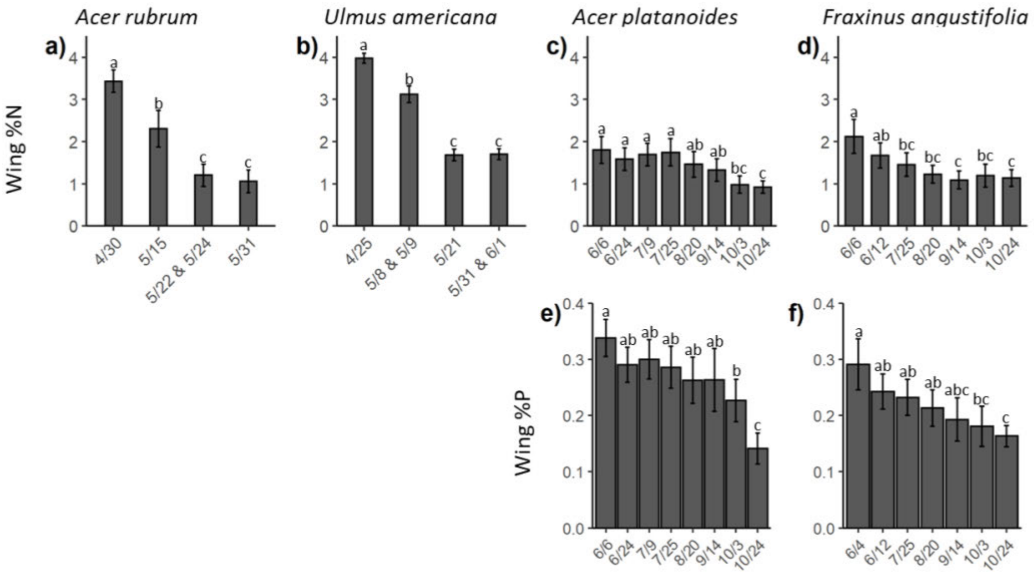
Species	**Mass-Based Nitrogen Resorption Efficiency**			**Area-Based Nitrogen Resorption Efficiency**		
	Max (mg N)	**Min (mg N)**	**NRE (%)**	**Max (mg N cm^{-2})**	**Min (mg N cm^{-2})**	**NRE (%)**
Acer rubrum	0.16 (0.03)	0.05 (0.01)	70 (21)	0.23 (0.03)	0.04 (0.01)	83 (16)
Ulmus americana	0.06 (0.01)	0.02 (0.00)	66 (16)	0.11 (0.00)	0.04 (0.01)	67 (4)
Acer platanoides	1.33 (0.25)	0.58 (0.09)	56 (23)	0.26 (0.06)	0.14 (0.03)	45 (27)
Fraxinus angustifolia	0.56 (0.14)	0.39 (0.09)	31 (30)	0.25 (0.03)	0.18 (0.02)	29 (13)

Supporting Table 2.3. Estimates of phosphorus resorption efficiencies (PRE) from samara wings based on maximum and minimum observed phosphorus contents. The minimum observed phosphorus contents always occurred on the final sampling date in October, 2019. Values represent means and numbers in parentheses are standard errors. We present data for only *A. platanoides* and *F. angustifolia* because we did not have adequate remaining sample mass for phosphorus analysis for *A. rubrum* or *U. americana*.

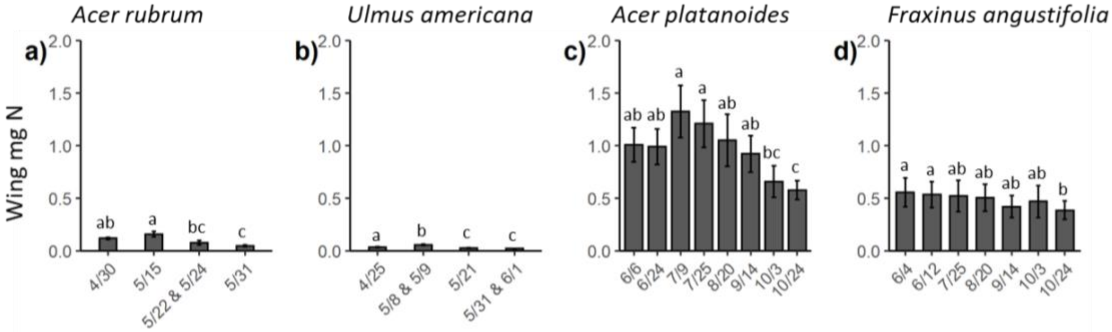
Species	**Mass-Based Phosphorus Resorption Efficiency**			**Area-Based Phosphorus Resorption Efficiency**		
	Max (μg P)	**Min (μg P)**	**PRE (%)**	**Max (μg P cm^{-2})**	**Min (μg P cm^{-2})**	**PRE (%)**
Acer platanoides	23.88	8.72	63	4.48	1.79	60
	(2.10)	(1.25)	(12)	(0.63)	(0.20)	(17)
Fraxinus angustifolia	9.08	5.60	38	3.83	2.60	32
	(1.70)	(1.05)	(23)	(0.43)	(0.18)	(12)



Supporting Figure 2.1. Relationship between light intensity and gas exchange rates for five *A. platanoides* samaras collected on Jun 10, 2019 at Arnold Arboretum of Harvard University. Data suggests that the light conditions (PAR=750 µmol m^{-2} s^{-1}) used in the photosynthesis measurements of the present study achieved the light saturation point.



Supporting Figure 2.2. (a–d) %N in samara wings, (e–f) %P in samara wings by sampling date for *Acer rubrum*, *Ulmus americana*, *Acer platanoides*, and *Fraxinus angustifolia*. Bars represent mean values and error bars represent standard error. We present %P data for only *A. platanoides* and *F. angustifoli*a because we did not have adequate remaining sample mass for phosphorus analysis for *A. rubrum* or *U. americana*. Samples were collected in 2019 at Arnold Arboretum, Boston, MA. Distinct letters between groups within a panel indicate statistically significant differences (Bayesian p-value < 0.05).



Supporting Figure 2.3. total N in samara winds by sampling date collected in 2019 at Arnold Arboretum, Boston, MA, for *Acer rubrum*, *Ulmus americana*, *Acer platanoides*, and *Fraxinus angustifolia*. Bars represent mean values and error bars represent standard error. Distinct letters between groups within a panel indicate statistically significant differences (Bayesian p-value < 0.05).

CHAPTER THREE: MACROSCALE VARIATION IN RED MAPLE (*ACER RUBRUM*) FOLIAR CARBON, NITROGEN, AND NITROGEN RESORPTION

ABSTRACT

Many tree species grow across large climatic and geographical gradients, but there is a lack of information related to intraspecific variation in leaf traits for some of the most abundant trees in temperate forests as related to these gradients. In particular, understanding intraspecific variation in carbon (C) and nitrogen (N) based traits of both plant foliage and senesced leaves is important as they provide insight into leaf physiology, tree nutrient status, and forest biogeochemical processes. We report on a community science project that focused on variation in *Acer rubrum* (red maple) foliar C and N concentrations, C:N of green and fallen leaves, and N resorption across broad mean annual temperature (MAT), precipitation (MAP), and latitudinal gradients. MAT was negatively correlated with green leaf %N and both fallen leaf C:N and N resorption, but was positively correlated with green leaf C:N and fallen leaf %N. MAP was positively related to fallen leaf %N and negatively with fallen leaf C:N and N resorption. Green leaf %C and %N was significantly higher in open than closed grown sites, but green leaf C:N was significantly higher in closed grown sites. Our results suggest red maple's leaf physiology and role in biogeochemical processes systematically varies throughout its broad geographic range. Further, our results suggest red maple's N resorption and recycling through litterfall impacts ecosystem C and N cycles differently throughout its geographic range, such that trees in warmer climates may have a greater

reliance on litter derived N on an annual basis relative to trees in cooler climates, which may be more adept at reusing N via resorption.

INTRODUCTION

Carbon- and nitrogen-based traits of both green and senesced tree leaves can provide insights into tree physiological and forest biogeochemical processes. Foliar nitrogen (N) concentrations have been found to be positively related to both net photosynthetic and respiration rates of leaves within tree species (Reich and others 1998). In fact, it has been demonstrated that leaf chlorophyll content is correlated to both foliar N concentrations and N mass per unit area of leaf (Croft and others 2017). The C:N ratio (i.e., the molar ratio of Carbon to Nitrogen in a sample) of both green leaves still on trees (hereafter referred to as “green leaves”) and leaves that have senesced and fallen from trees (hereafter referred as “fallen leaves”) is often used as a parameter to characterize decomposition of organic matter in ecosystem models. Lower C:N ratios are related to faster rates of decomposition and net mineralization, whereas higher C:N ratios are related to slower rates of decomposition and greater microbial N immobilization (Enríquez and others 1993; Alexander and Arthur 2014; Mooshammer and others 2012; Pei and others 2019).

The N concentration in fallen leaves collected as litterfall has also served as the basis of investigations into a number of processes that describe nitrogen use at the individual plant and ecosystem scale. For example, N use efficiency, the ratio of annual litterfall biomass production to N content in litterfall, has been found to be negatively correlated with soil N availability (Vitousek 1982; Birk and Vitousek 1986).

Additionally, N resorption efficiency, the ratio of the differences in N concentrations in green and fallen leaves to N concentrations in green leaves, can be used to estimate the amount of internal recycling of nutrients within trees (Aerts 1996). Resorption processes have been estimated to account for 33-66% of the nutrients needed for plant growth the following year (Finzi and others 2002; Schlesinger and Bernhardt 2013).

While the role of N and C:N ratios of both green and fallen leaves in plant physiological and microbial processes have been well characterized, relatively less is understood about whether there is systematic variation in these traits, particularly throughout the geographic range and site conditions inhabited by individual plant species. Intraspecific C and N leaf traits and N resorption variability may be especially important to understand for abundant, widely distributed tree species due to the major contribution these species make to ecosystem level processes (Grime 1998; Avolio and others 2019).

To our knowledge there have been only two studies that have examined N resorption processes within an individual tree species across broad climatic and latitudinal envelopes. Sun and others (2016) found that within *Quercus variabilis*, a broadly distributed deciduous angiosperm tree species in east Asia, N resorption efficiency was positively related to latitude, and negatively related to both mean annual temperature (MAT) and precipitation (MAP). Latitude, MAT, and MAP explained 14-17% of variation in N resorption within *Quercus variabilis*, and average N resorption ranged from ~55-70 % along the 1600 mm yr^{-1} MAP, 12 ^{o}C MAT, and 15^{o} latitude gradients in their study (Sun and others 2016). Similarly, Zhang and others (2018b) found average N resorption for *Metasequoia glyptostroboides*, a deciduous conifer, ranged from ~42-52% along a 5º latitudinal gradient in eastern China.

Studies conducted along local climate gradients that occur along elevation gradients have found that within individual tree species, the relationship between foliar N resorption and elevation can increase for some species (e.g., *Quercus variabilis*; Du and others 2017 or *Cunninghamia lanceolate*; Tong and others 2021), decrease with other species (e.g., *Broussonetia papyrifera*; Hu and others 2020), or show no change (e.g., *Betula pubescens*; Nordell and Karlsson 1995 and *Tilia rubra*; Bilgin and Güzel 2017). In a meta-analysis of intraspecific leaf traits along elevation gradients, a positive relationship between response ratio of green leaf N concentration and N mass per unit area of leaf for individual studies relative to an increase in elevation was observed (Midolo and others 2019).

While sampling across broad geographic and local elevation gradients provides strong evidence that leaf traits of individual species likely respond to changes in climate, the characterization of leaf trait variation for some of the most dominant tree species in world's forests, including *Acer rubrum* (red maple), to date remains unresolved. In this study we characterize C and N leaf traits and N resorption variability related to both climate and site conditions for red maple, one of the most abundant forest species in eastern North America, which is considered to have high adaptability and is anticipated to maintain and expand its distribution through the year 2100 under moderate and high greenhouse gas emission scenarios (RCP 4.5 and 8.5; Peters and others 2020; Iverson and others 2019; US Forest Service Tree Atlas, ver 4).

In urban and landscaped areas red maple is a popular tree to plant in all regions of the contiguous United States (Cowett and others 2017; Ma and others 2020). Urban-grown red maple trees have been shown to exhibit a degree of acclimation that is reflected in foliar traits such as higher percent N in green leaves compared to rural locations (McDermot and others 2020). Open grown red maple trees have also been observed to have higher percent N in green leaves compared to non-open grown trees (Abrams 1985).

We focus on characterizing C and N leaf traits that have been linked to ecosystem processes including percent C and N, as well as the C:N ratio, of green and fallen leaves and N resorption of red maple by sampling trees across a broad geographic climate gradient in eastern North America through a community science project. The research primarily aimed to characterize leaf trait variation with respect to MAP, MAT, and latitudinal gradients, thus we accepted leaf submissions from all habitats, ranging from street trees to forest trees and open vs. closed canopy conditions. We anticipated that broad climate and geographic variables would be of primary importance in explaining variation in leaf traits despite potential differences in site-level variables (e.g., habitat, open vs. closed canopy conditions). Nevertheless, by collecting information on site-level characteristics we were also able to examine how that variation influenced our results.

We hypothesized that across the climatic range of red maple trees grown across the eastern U.S., green leaf N concentrations, fallen leaf C:N, and N resorption are negatively related to MAP and MAT and positively related to latitude. We also hypothesized that fallen leaf N concentrations, and green leaf C:N are positively related to MAP and MAT, and negatively related to latitude. Such systematic variation in green and fallen leaf traits would indicate a greater reliance on remineralized N from leaf litter in warmer and wetter locations, where decomposition proceeds more quickly, compared to cooler and drier locations which have greater rates of foliar N resorption. Our ability to include site specific information such as open grown status, within canopy sampling location, and habitat allows us to examine potential interactions between local site conditions and climatic gradients. We expected the covariates such as open grown status, within canopy sampling location, and habitat to be important factors in explaining the intraspecific variation in C and N leaf traits, and N resorption. In particular, N concentrations of green leaves were expected to be the highest when they are open grown and are sampled from street or landscaped trees.

METHODS

Identification of sampling sites and community science participants

We conducted a community science project with volunteers who were recruited to sample green and fallen red maple leaves throughout the eastern United States. A total of ninety-four plant societies, naturalist societies, or trail clubs were contacted via email. Twenty-nine of the contacted organizations forwarded information about the community science project to their members. Additionally, posts were made on one of the author's (Gougherty) social media platforms, including Instagram (username: dissolvedeco) and Twitter (username: dissolvedeco and tasper_project). A full list of organizations contacted for this project is provided in the supporting information section (Supporting Table 3.1). Interested participants were asked to fill out a Google Form to provide contact information. Of the 144 people who responded electronically to the Google Form, 57 people sent green and fallen leaves from a total of 73 trees for this project.

Leaf collection by community scientists

To standardize the collection of leaves, each respondent to the Google Form was sent a data sheet, sampling protocol and nitrile gloves to collect leaves via the U.S. Postal Service. Examples of the datasheet and sampling protocol are included in the supporting information (Supporting Information S3.1). Participants were asked to sample both green and fallen leaves from at least one red maple tree using gloved hands. If multiple trees were sampled by a single individual, the leaves from different trees were kept separate during sample processing. We requested that ten green leaves were sampled from a variety of branches on the tree to help ensure different canopy and light conditions were represented in the sample. All but eleven of the green leaf were sampled in the requested month of August, and the inclusion of these samples in the analysis did not influence our major findings, details of which are included in the Supporting Information S3.2. Ten fallen leaves were sampled by setting out litter fall traps and collecting leaves within 2-3 days of deployment. In the sampling protocol, we suggested that litter fall traps could consist of a tarp or a plastic container such as a bucket or milk crate placed beneath the focal tree. Respondents were instructed to sample litter fall traps prior to any rainfall to avoid potential leaching from fallen leaves and to use gloves to handle all leaf material sampled for the project. Locations of the trees sampled as part of the project and histograms of the climate space sampled are found in Figure 3.1.

The red maple leaf samples included in this study came from as far south as Florida in the east and Louisiana in the west to as far north as Maine in the east and Wisconsin in the west (Figure 3.1a). Across the 67 sites, mean annual temperature ranged from 3.8 – 22.9 ^{o}C, mean annual precipitation ranged from 758 – 1786 mm yr^{-1}, and latitude ranged from 27.5^{o} – 46.5^{o} (Figure 3.1b–3.1c).

Site information

We digitized responses to questions from the datasheets that participants completed, which provided information related to several variables which we refer to as covariates in the analysis. These variables include habitat (bottomland forest, other, street tree, upland forest, or yard), location on the tree green leaf samples were collected (lower canopy, lower and mid canopy, or whole tree), whether the tree was open grown or not open grown, and dates of sample collection for green and fallen leaves. Information on location of within tree green leaf sample collection was collected because of well-established vertical canopy gradients in nutrients (e.g., higher %N of leaves in upper canopy vs lower canopy). We also obtained the latitude and longitude of the location of the trees which were sampled. Using the latitude and longitude information we extracted climate data from the WorldClim (https://www.worldclim.org/) database (WorldClim version 2.1; Fick and Hijmans, 2017) at 10-minute resolution. Mean annual temperature (MAT in ^{o}C) and precipitation (MAP in mm yr^{-1}) data are averages from 1970-2000 and represent interpolated values based on both weather station and MODIS satellite data (Fick and Hijmans, 2017).

Laboratory analysis of the green and fallen leaves

All laboratory analyses were conducted at Boston University. All paired green and fallen leaf sets received were placed inside a drying oven at 60 ^{o}C for at least 48 hours. Within each set, every green and fallen dried leaf, with petiole intact, was imaged with a flatbed scanner at 300 dpi, and weighed using a balance. Leaf area measurements were conducted using ImageJ.

To obtain a subsample of leaf material for C and N analysis, the leaf blade from each leaf was hole punched (6 mm diameter). Subsamples were homogenized to a powder using a mortar and pestle and analyzed for C and N using a NC2500 elemental analyzer (CE Elantech, Lakewood, NJ, USA). NIST apple leaves were run as standard reference material and 8% of samples were run in duplicate, average percent error was 0.5% for C and 1.2% for N. Using the C & N data we obtained the following leaf traits for both green and fallen leaves: %C, %N, C:N. N resorption was computed by the following formula:

(1) N resorption = (%N Green - % N fallen) / %N Green

One fallen leaf sample had a %N value that was greater than the green leaf %N value, which resulted in a negative N resorption. This row of data was identified as an outlier value using the Rosner test (implemented with the R function rosnerTest in the ‘EnvStats’ package) and was removed from further analysis, reducing sample size from n=73 to n=72 trees.

Results are presented on a mass basis, but we provide an analysis of the area-based metrics, including leaf mass per unit area, in Supporting Information S3.3.

Data Analysis

To account for clustering of trees that were sampled for this study, all trees sampled greater than or equal to 2 km apart were treated as independent. For trees sampled less than 2 km apart, data was averaged across trees if they shared identical covariate information (i.e., open grown status, habitat, sample location within tree, green leaf collection date, fallen leaf collection date). If trees were sampled < 2 km apart from each other, but covariate information differed between trees the samples were treated as independent. This process enabled us to identify a total of nine trees that were regrouped into four sites, reducing sample size further from n=72 to n=67 sites.

All statistical analyses were conducted in R 4.0.3 (R Core Team 2021). We used ANOVA in R to test for significant effects of each covariate on green and fallen leaf %C, %N, and C:N, and N resorption. For significant covariate models we used Tukey's honestly significant difference test implemented with the R function TukeyHSD() to account for multiple comparisons and determine which groups were significantly different from each other. Interactions between covariates were also investigated; and for significant models, pairwise comparisons were performed with TukeyHSD() to determine which groups differed from each other.

We used lm() in R to construct simple linear regressions for MAT, MAP, and latitude against the following leaf traits: green and fallen leaf %C, %N, and C:N, along with N resorption. Simple linear regression was also used to investigate potential relationships between leaf traits and collection dates. To determine whether relationships between leaf traits and MAT, MAP, or latitude were confounded by the covariates we compared the Akaike Information Criterion (AIC) values for univariate models for each covariate, and MAT, MAP, and latitude. The ANOVAs and simple linear regression models provide important insight into how single variables are related to leaf traits. However, we recognize that a model with multiple variables may better fit the data. Therefore, we also used multiple linear regression to determine if there was significant interaction between MAT, MAP, or latitude and the covariates by constructing models with a) interacting covariates or b) interactions between covariates and MAT/MAP/latitude. To determine which model best fit the data we computed AIC of models and identified those which contained significant explanatory variables. The data collected for this study can be found in Gougherty (2022).

RESULTS

MAT, MAP, and latitude were not significantly related to green or fallen leaf %C, but all other green and fallen leaf traits, and N resorption were significantly related to MAT and latitude (Figure 3.2–3.4). Fallen leaf %N, C:N, and N resorption were the only traits significantly related to MAP (Figure 3.2–3.4). MAT was negatively correlated with green leaf %N (R^2=0.09; p<0.01) and positively correlated with green leaf C:N (R^2= 0.12; p<0.01) (Figure 3.2b–c). MAT was also positively correlated with fallen leaf %N (R^2=0.15; p<0.001) and negatively correlated with both fallen leaf C:N (R^2=0.18; p<0.001) and N resorption (R^2=0.41; p<0.001) (Figure 3.2e–3.2g). There was a positive relationship between MAP and fallen leaf %N (R^2=0.16; p<0.001) and negative relationships between MAP and both fallen leaf C:N (R^2=0.22; p<0.001) and N resorption (R^2=0.33; p<0.001), but we found no significantly relationships between MAP and green leaf %C, %N, C:N, nor fallen leaf %C (Figure 3.3a–g). Latitude was positively related to green leaf %N (R^2=0.06; p=0.022) and both fallen leaf C:N (R^2=0.19; p<0.001) and N resorption (R^2=0.38; p<0.001), but negatively related to green leaf C:N (R^2=0.09; p<0.01) and fallen leaf %N (R^2 = 0.15; p<0.001; Figure 3.4).

We found a significant relationship between green leaf collection date and green leaf %N, and green leaf C:N was driven by a single data point with high leverage (collected October 15, 2019), suggesting green leaf traits were not largely influence by green leaf collection date. Fallen leaf collection date was negatively related to N resorption (R^2 =0.18; p<0.001) and latitude (R^2=0.32; p<0.001), but positively related to MAT (R^2=0.36; p<0.001; Figure 3.5 a–c). We checked to determine whether removing a single fallen leaf collection date in January influenced interpretation of the relationships and found the same directionality of trends and levels of significance, with marginal changes in R^2. N resorption relationship shifted from R^2 = 0.18 to R^2 = 0.25, Latitude relationship shifted from R^2=0.32 to R^2 = 0.25, MAT relationship shifted from R^2=0.36 to 0.30 when the January data point was removed.

Green leaf %C and %N was significantly higher in open than closed grown sites, but green leaf C:N was significantly higher in closed grown sites (Figure 3.6a–c). For fallen leaf traits, %C was significantly higher in open than closed grown sites, but %N and C:N did not differ significantly with tree location (Figure 3.6d–f). Foliar N resorption did not differ between open and closed grown sites (Figure 3.6g).

Street and yard trees trended towards having higher %C, %N and lower C:N for both green and fallen leaves compared to other habitats, but the results were not always statistically significant (Figure 3.7). While tree habitat did not significantly affect green leaf %C (Figure 3.7a) or foliar N resorption (Figure 3.7g), bottomland grown trees had significantly lower green leaf %N and higher green leaf C:N compared to either street or yard grown trees (Figure 3.7b–c). For fallen leaves, bottomland grown trees had significantly lower %C values than yard trees (Figure 3.7a). Street trees had higher %N and lower C:N in fallen leaves than upland grown trees (Figure 3.7e–f).

The sampling location within the canopy did not significantly affect green leaf %C, %N, or C:N (Figure 3.8a–c). However, leaves collected throughout the entire canopy (i.e. "whole" in Figure 3.8d) had lower amounts of N resorption compared to leaves collected only from the "lower & middle" (i.e., leaves accessible by hand and a tool such as a telescoping vegetation pruner, but upper canopy was not sampled because it remained out of reach) parts of the canopy (Figure 3.8d). N resorption from trees where green leaves collected from the "lower" (i.e., leaves that were accessible by hand) were not statistically different from those collected from the "whole canopy".

Models with interactions between habitat and tree location (open vs. closed grown) were significant for green leaf %N, green leaf C:N, fallen leaf %N, fallen leaf C:N, and N resorption (see Supporting Table 3.2). The habitat–within tree foliar sample location interaction was significant for fallen leaf %N (see Supporting Table 3.2). The tree location (open vs. closed grown) within tree foliar sampling location was significant for green leaf %N and N resorption (see Supporting Table 3.2).

Among all the potential explanatory variables to explain variation in green leaf %C and green leaf %N we consistently found that the models with tree location (open vs.

closed grown) as the only predictor resulted in the lowest AIC scores while retaining significance among all the predictors (Supporting Table 3.3). For green leaf C:N we found that a model that included green leaf collection date and latitude had the lowest AIC score among models that retained significance among all predictors (AIC= 425.97; R^2=0.16; p<0.01), however the tree location model was still significant despite having a higher AIC (AIC= 432.61; R^2=0.18; p<0.001). Models with the lowest AIC score for fallen leaf traits (i.e., fallen leaf %C, fallen leaf %N, and fallen leaf C:N) and N resorption consistently contained either latitude or a climate variable (MAT or MAP) and interactions with fallen leaf collection date (Supporting Table 3.3) (Figure 3.2-3.5).

DISCUSSION

In this study, we document significant variation in red maple leaf traits that were sampled by participants in a community science project throughout the eastern U.S. To our knowledge, this study is among the first to document relationships between leaf-traits (i.e. green and fallen leaf N, C, C:N, and N resorption) and both broad climate and latitudinal gradients for a dominant tree species in North America. The climate- and latitude- associated changes in leaf traits we observed suggest red maple's physiology and role in biogeochemical processes varies throughout its geographic range, which may have implications for tree C acquisition and N retention, and decomposition processes that make nutrients available to trees and soil microbes.

Green Leaf Trends and Implications

While the negative relationship between green leaf N concentrations and temperature was fairly weak, it suggests that red maples in cooler climates may have higher rates of N allocated to leaves and a higher photosynthetic capacity (Wilson and others 2000). In our dataset we observed that MAT, MAP, and latitude were correlated with each other, nevertheless the data suggests that green leaf N concentrations are greater in systems with shorter growing seasons. In practice, any carbon benefit that may result from increased photosynthetic capacity due to higher green leaf N concentration in cooler climates could be counteracted by constraints on photosynthesis imposed by relatively lower temperatures and shorter growing seasons (Sage and Kubien 2007).

For green leaf N concentration, the negative relationship with MAT, and positive relationship with latitude, combined with the finding of no significant relationships between green leaf C concentration and MAT or latitude, suggest the positive MAT—green leaf C:N relationship and negative latitude—green leaf C:N relationship is driven by changes in green leaf N concentrations. Overall, we found a lack of significant relationships between any green leaf trait (C, N and C:N) and precipitation, which suggests temperature or day length (latitude) play a larger role than precipitation in green leaf traits. However, the relationships between green leaf traits and MAT and latitude are not particularly strong (i.e., both $R^2 < 0.09$), suggesting that climate or day and growing season length (latitude) are not key determinants by themselves of green leaf traits. Another possibility is that green leaf trait – climate and latitude relationships are obscured by site-level covariates, for example irrigation in more managed settings such as those experienced by yard and street trees.

Rather than MAT, MAP, or latitude being the primary driver of green leaf traits, our analyses suggest site specific conditions, particularly whether the sampled trees were open vs closed grown, and habitat, had notable influence on green leaf N concentrations. Open grown trees had significantly higher N concentrations in green leaves, suggesting such trees have higher rates of N uptake and higher photosynthetic capacity compared to closed grown trees (Abrams 1985). Habitat influenced green leaf N concentrations as well, specifically, more human influenced areas such as those in “yard” and “street” habitats had higher N concentrations compared to “bottomland forest” habitats, which may indicate higher photosynthetic potential in human influenced areas compared to forest grown trees, and may be a result of greater sun exposure or greater soil nutrient availability (e.g., fertilizer application or higher N deposition) (Decina and others 2019 ; Polsky and others 2014). The pattern of higher green leaf N concentrations in “street” and “yard” habitats relative to forests supports previous research that found red maples growing in urban areas have higher photosynthetic capacity and green leaf N concentrations compared to less urbanized counterparts (McDermot and others 2020).

Fallen Leaf Trends and Implications

The negative relationships we observed between fallen leaf C:N and both MAT and MAP, and positive relationships with latitude indicate that the quality of the red maple leaf litter produced in warm and moist climates, and lower latitudes is likely higher (i.e. more labile) than litter produced in cooler and drier climates (Coûteaux and others 1995). The variation in fallen leaf C:N appears to be a result of changes in N concentration rather than changes in C concentrations, as we found no significant relationship between fallen leaf C concentrations and MAT, MAP, or latitude. In contrast, fallen leaf N concentration was positively related to MAT and MAP, and negatively related to latitude.

Briefly setting aside the influence of temperature and moisture on decomposition rates, the higher quality (low C:N) litter produced in warm and moist climates would likely result in higher rates of decomposition compared to the lower quality (high C:N) litter produced in cooler and drier climates because lower C:N litter has been shown to decompose faster than high C:N litter (Nicolardot and others 2001; Keller and Phillips 2019). Additionally, when temperature and moisture are considered, cooler and drier climates often exhibit suppressed decomposition rates relative to warmer and moister climates because decomposer activity tends to be greater in warmer environments with adequate moisture (Coûteaux and others 1995; Keller and Phillips 2019). As a result, in warmer and moister climates, the higher litter quality likely results in greater amounts of N returned to the soil via litterfall and the suitable environmental conditions would be expected to yield higher decomposition rates of red maple litter compared to the lower quality litter produced in cooler and drier climates.

“Upland forest” fallen leaf N concentrations were lower compared to “street” trees, and “yard” fallen leaf C concentrations were higher than “bottomland” forest trees. The differences in “street” vs. “upland forest” fallen leaf N concentrations were also evident by lower fallen leaf C:N in “street” trees compared to “upland forest” trees. The fallen leaf C concentration differences between “bottomland” and “yard” did not manifest as differences in the fallen leaf C:N data. The overall quality of the litter produced by “street” trees may be higher compared to trees produced in “upland forests”, but our analysis suggests that the habitat effect on fallen leaf traits is smaller than the effect of latitude and fallen leaf collection date. Overall, our analyses indicate that fallen leaf N concentration and C:N were best explained with models that included interactions between latitude and fallen leaf collection date.

Foliar N Resorption Trends and Implications

The negative relationships between N resorption and both MAT and MAP indicate that average red maple N resorption is greatest in relatively cooler and drier climates, suggesting trees in cooler and drier climates exhibit higher amounts of internal N recycling compared to warmer moister climates. Likewise, N resorption was also positively related to latitude, suggesting shortening photoperiods may be linked with greater rates of N resorption. The higher amounts of N recycling within trees in cool and dry climates could be a response to lower soil N availability because of suppressed rates of decomposition due to limitations imposed by the physical environment relative to warmer moister climates (Aerts 1996; Yuan and Chen 2015).

Notably, the higher levels of N resorption in cool and dry climates, and higher latitudes appears to be directly linked with higher fallen leaf C:N (i.e. lower quality litter) compared to warmer more moist climates at lower latitudes.

The climate-litter quality relationship could reinforce a positive feedback loop imposed by physical environment constraints, whereby red maple trees in cool dry climates release litter with higher C:N, which leads to slower rates of decomposition, and lower levels of soil N availability. In turn, the lower soil N availability leads to an incentive for trees to resorb more N in Autumn, again resulting in higher C:N litterfall.

Similar positive feedback loops between environmental changes like rising atmospheric CO_2 concentrations and growing season temperatures, have been proposed to explain decreasing soil N availability to trees relative to their demands in rural forests around the globe (Groffman and others 2018; Craine and others 2018).

Our analyses show that N resorption in red maple was best explained by models that included MAT and fallen leaf collection date or latitude and fallen leaf collection date. Interestingly, N resorption was negatively related to fallen leaf collection date and we suggest fallen leaf collection date captures information related to growing conditions at the individual sites which is less likely to be captured with the coarser MAT, MAP, or latitude metrics. These results suggest that climate and/or latitude exerts a strong control on red maple N use and retention throughout the geographic range and climate space sampled in our study.

Comparison to past studies

Our results show similar relationships to what has been found in other studies that sampled individual species' leaf C, N, and N resorption traits across broad climate and latitudinal gradients (Sun and others 2016; Zhang and others 2018b). Sun and others (2016) sampled *Quercus variabilis* throughout a large geographic range in China and found negative correlations between N resorption and MAT/MAP and positive correlation with latitude. Zhang and others (2018b) sampled *Metasequoia glyptostroboides* and found N resorption to be positively related to latitude.

The directionality of the relationship between leaf traits we examined and MAT is supported by some studies based on elevation gradients. Our results of finding higher N concentrations in cooler climates is consistent with findings of a meta-analysis of intraspecific variation in leaf traits which found N concentrations in green leaves generally increases with elevation (Midolo and others 2019). While the directionality of the elevation–N resorption relationship in trees appears to be species or site specific (Du and others 2017; Tong and others 2021; Hu and others 2020; Bilgin and Güzel 2017; and Nordell and Karlsson 1995), our findings are consistent with N resorption being greater in cooler climates (Du and others 2017 ; Tong and others 2021).

Our results are also similar to those revealed in literature syntheses that compile leaf trait data across different species along climate and latitudinal gradients (Yuan and Chen 2009a; Yuan and Chen 2009b ; Zhang and others 2018b ; Reich and others 2004), specifically the directionality of the relationship between leaf traits and MAT, MAP, and latitude are the same in inter- and intra-specific studies. Based on our study and existing literature we suggest there is strong evidence that physiologically and biogeochemically important leaf traits within species can be sensitive to climate and latitudinal variation (Sun and others 2016; Zhang and others 2018b). Data syntheses that look at leaf traits along climate/latitude gradients across species therefore likely reflect not-only the turnover of species (and higher taxonomic levels) and associated changes in leaf traits, but also have an intra-specific variation component embedded within the data because individual species’ traits likely vary throughout their climate and geographic ranges. The large variation of leaf traits within species in response to climate observed in some studies (Sun and others 2016; Zhang and others 2018b), including the present study, suggest that intraspecific variation should be considered when information is aggregated to characterize species, such as generating species level mean trait values.

Shortcomings of the present study

One shortcoming of our work is that we are not able to identify the ultimate driver of the climate and latitudinal variation in leaf traits we observed, and we only sampled red maple trees throughout the eastern U.S. Much caution is needed in extrapolating results from the present study to potential changes in leaf traits with climate change and in regions we did not study. Particularly, latitude directly correlates with photoperiod, such that shortening day length appears to play a physiological role in triggering senescence and resorption cues in some species (Gill and others 2015; Lang and others 2019). Climate change is modifying MAP and MAT (Crowley 2000; Trenberth 2011; Vose and others 2014), but latitude and day-length at fixed locations are not influenced by climate change. Therefore, it is possible that the strong negative relationships we observed between fallen leaf C:N and N resorption and both MAT and MAP are wholly or partially physiologically driven by differences in photoperiod along the same gradient.

With this study, we are also not able to disentangle the degree to which the climate- and latitude-associated variation in leaf traits was a result of genetic structuring along the gradient and/or phenotypic plasticity in response to environmental gradients. Reciprocal transplant studies and experiments could help to elucidate whether the variation in plant traits we observed was predominantly a result of genetics vs. phenotypic plasticity (Nooten and Hughes 2017), which could also help disentangle climate vs. photoperiod effects on the plant traits we observed (Ettinger and others 2021).

While a formal population genetics investigation could also be conducted to help address this shortcoming, it was beyond the scope of this study. We also note an additional complexity related to genotypes such that they may interact with habitat and influence results in unexpected ways, particularly if street and yard trees originate from nursery stock and the forest trees were naturally recruited.

CONCLUSIONS

Understanding how tree species will respond to continued changes in climate is important for predicting future ecosystem function**.** We documented meaningful variation in C and N concentration, and N resorption in both green and fallen leaves of red maple trees that was related to site conditions and broad climatic and latitudinal gradients. Notably, we found that latitude and climate were both strongly related to N resorption and fallen leaf C:N. These findings suggest red maple may participate in ecosystem N cycles differently throughout its geographic range such that red maple trees in warmer climates may have a greater reliance on litter derived N on an annual basis relative to trees in cooler climates which may be more adept at recycling N via resorption.

ACKNOWLEDGEMENTS

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AUTHOR CONTRIBUTIONS

Steven W. Gougherty (SWG) initiated the research idea; SWG designed the research; SWG conducted data analysis; Bailey E. Cowart (BEC) and SWG performed laboratory analysis; SWG and Pamela H. Templer (PHT) interpreted the data; SWG wrote the first manuscript draft; BEC, SWG, and PHT edited the manuscript and contributed to writing.

FIGURES

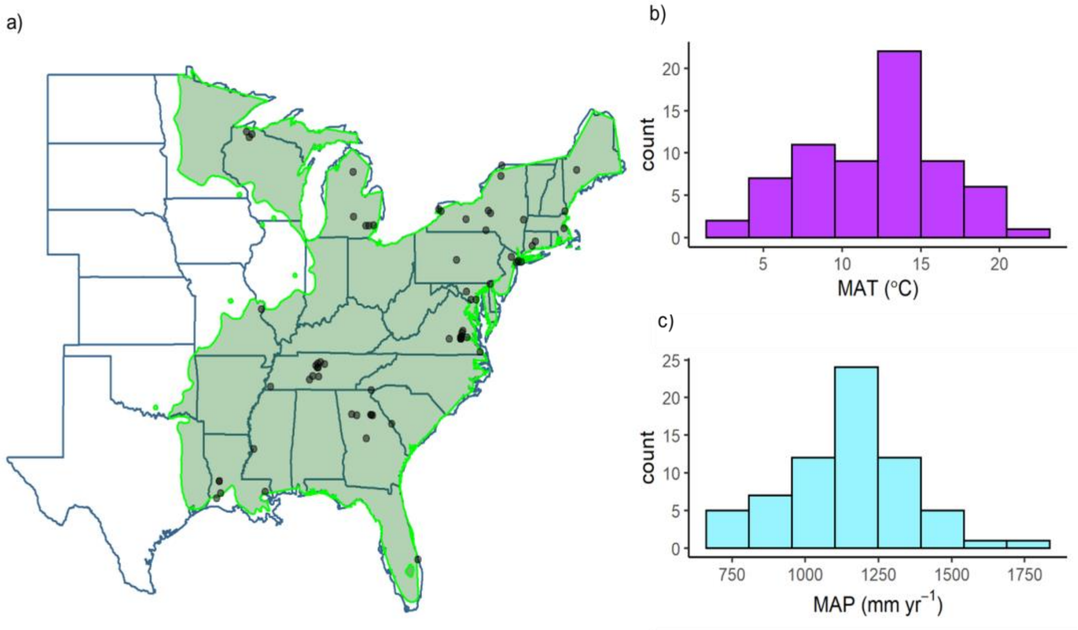

Figure 3.1. a) Map of natural geographic distribution of red maple (*Acer rubrum*) within USA shaded in green. Points indicate the location of trees sampled as part of the study. b) Histogram of the mean annual temperature (MAT) at the sample locations in degrees Celsius. c) Histogram of the mean annual precipitation (MAP) at the sample locations in mm yr^{-1}.

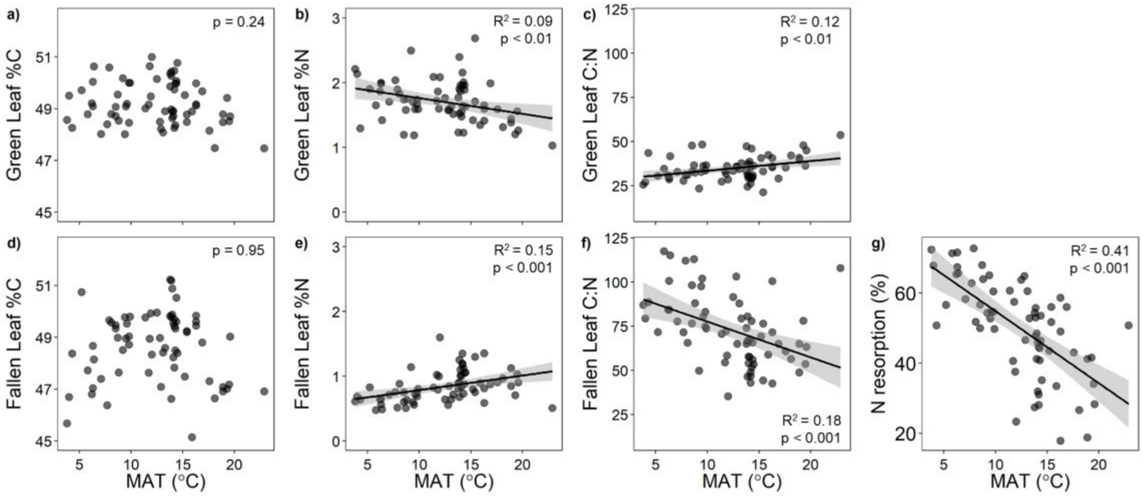

Figure 3.2. Mean annual temperature (MAT) plotted against a) %C, b) %N, and c) C:N of green leaves; d) %C, e) %N, and f) C:N of fallen leaves; and g) foliar N resorption. Lines indicate results from significant simple linear regressions. Areas with overlapping data points appear darker because dots are partially transparent. n = 67 for all regressions.

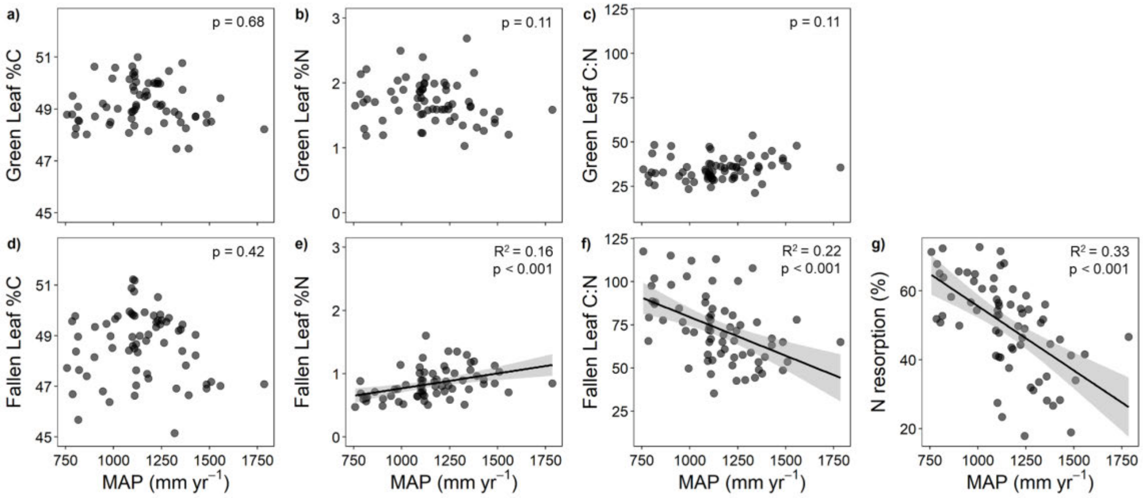

Figure 3.3. Mean annual precipitation (MAP) plotted against a) %C, b) %N, and c) C:N of green leaves; d) %C, e) %N, and f) C:N of fallen leaves; and g) foliar N resorption. Lines indicate results from significant simple linear regressions. Areas with overlapping data points appear darker because dots are partially transparent. n = 67 for all regressions.

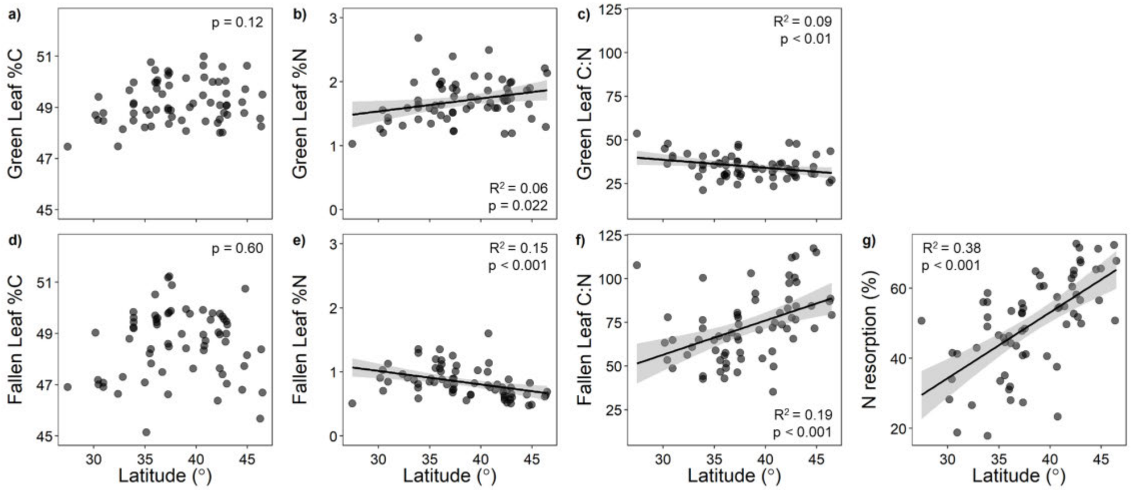

Figure 3.4. Latitude plotted against a) %C, b) %N, and c) C:N of green leaves); d) %C, e) %N, and f) C:N of fallen leaves; and g) foliar N resorption. Lines indicate results from significant simple linear regressions. Areas with overlapping data points appear darker because dots are partially transparent. n = 67 for all regressions.

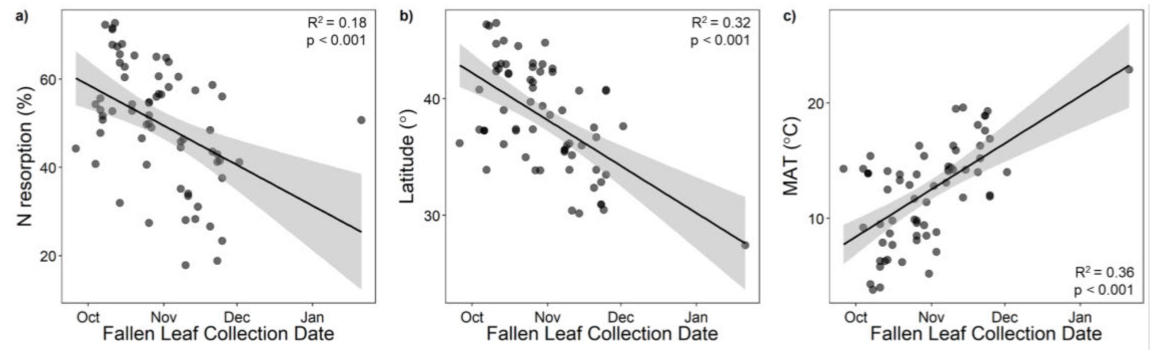

Figure 3.5. Relationships between fallen leaf collection date and a) foliar N resorption, b) latitude, and c) mean annual temperature. Lines represent results from simple linear regression. Areas with overlapping data points appear darker because dots are partially transparent. n = 66 in all regressions due to one missing value for fallen leaf collection date.

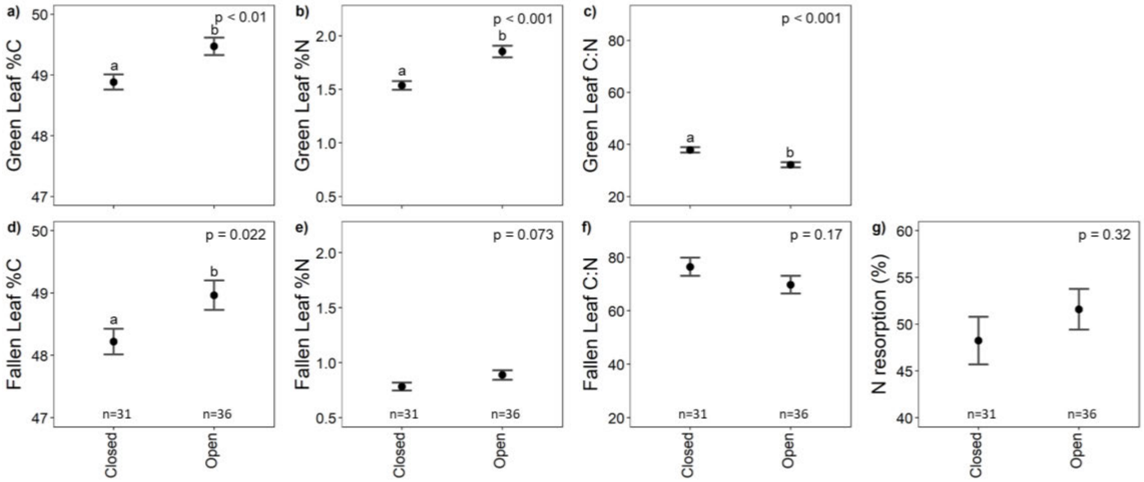

Figure 3.6. Effect of tree location (open grown vs. closed grown) on a) %C, b) %N, and c) C:N green of green leaves; d) %C, e) %N, and f) C:N of fallen leaves; and g) foliar N resorption. Distinct letters between groups within a leaf trait indicate statistically significant differences (α = 0.05) based on TukeyHSD test. Points and error bars represent mean ± 1 SE. Sample sizes for green and fallen leaves are identical.

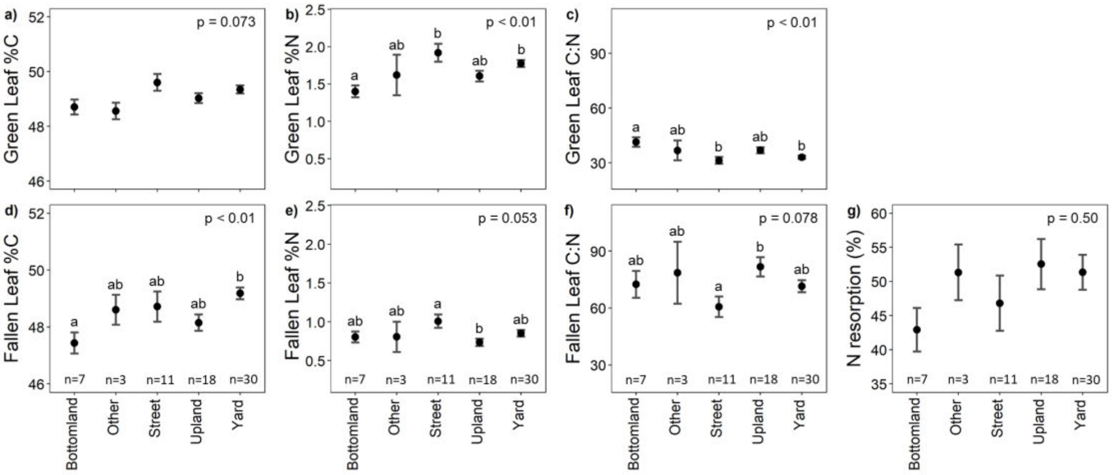

Figure 3.7. Effect of habitat on a) %C, b) %N, and c) C:N green of green leaves; d) %C, e) %N, and f) C:N of fallen leaves; and g) foliar N resorption. Distinct letters between groups within a leaf trait indicate statistically significant differences (α = 0.05) based on TukeyHSD test. p-value is reported for the overall model. Points and error bars represent mean ± 1 SE. "Bottomland" refers to bottomland forest, "Street" refers to street tree, "Upland" refers to upland forest. Sample sizes for green and fallen leaves are identical.

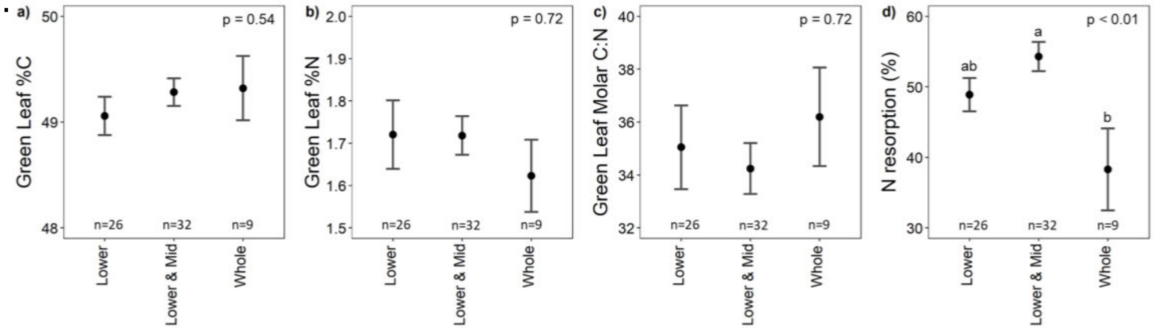

Figure 3.8. Effect of foliar sampling location on a) %C, b) %N, and c) C:N green of green leaves; and d) foliar N resorption. Distinct letters between groups within a leaf trait indicate statistically significant differences ($\alpha = 0.05$) based on TukeyHSD test. p-value is reported for the overall model. Points and error bars represent mean ± 1 SE. “Lower” indicates samples were collected from lower canopy, “Lower & Mid” indicates samples were collected from the lower and middle canopy, “Whole” indicates samples were collected from the entire tree canopy. Sample sizes for green and fallen leaves are identical.

SUPPORTING INFORMATION

Supporting Information S3.1—Datasheet and sampling protocol provided to all project participants

TASpeR Data Sheet

Please fill out this data sheet and send it back with the fallen leaves you collect in the autumn. If you sample from more than one tree, additional Data Sheets are available on our website: sites.bu.edu/tasper. Alternatively, the responses for the additional trees can be written on another sheet of paper and returned to us.

For individuals sampling multiple trees, make sure that the leaves are separated and labelled by tree (write Tree 1, Tree 2, etc. on the white paper separating the leaves of different trees) so we can keep track of the leaves from different trees in the lab. Make sure that you use the same names for the trees you sample when the leaves are green and when you collect fallen leaves, otherwise we won't know which green leaves correspond to which fallen leaves.

Please email Steve Gougherty if you run in to any problems or questions: gougher@bu.edu

Collector, Location, and Sampling Dates

1) Collector's Name:
____

2) Collector's
Email:____

3) City and state of
collection:____

4) Latitude and longitude of tree*:
____

*Go to the website: google.com/maps, click 'Satellite' in the lower left hand corner and then navigate to your tree using the satellite imagery. To extract the lat/long, right click on your tree and select 'What's Here?'. This will open a small dialogue box that gives the lat/long coordinates in decimal notation.

5) Sampling date of green leaves:
____

6) Date litter trap deployed to collect fallen leaves*:
____

* You may deploy the trap early in the season, but it needs to be emptied 2-3 days prior to leaf collection. The date you list here should be the date you initially empty the trap before you collect fallen leaves.

7) Date fallen leaves collected:
____

8) Total number of trees sampled:
____

9) Which tree are you filling out the data sheet for*:__________________________________

*If you are sampling only one tree, write 'Tree 1'. If you are sampling more than one tree for this project start with 'Tree 1', then for your second tree write 'Tree 2', etc.

Site and Tree Descriptions

10) Check all the landscape attributes that apply to where your red maple (*Acer rubrum*) tree is located:

- ☐ Upland forest
- ☐ Bottomland or riparian (stream side) forest
- ☐ Wetland
- ☐ Street or sidewalk tree*

☐ Yard or landscaping tree*

☐ Other (please list):

____

*If you know other information about your tree such as subspecies or cultivar, whether it is from wild origin or a nursery, please describe in greater detail in the comments / notes section at the end of the data sheet.

11) What other vegetation is dominant in the area surrounding your tree?

☐ Trees (list species, if known):____

☐ Grass (list species, if known):____

☐ Wetland plants (list species, if known):__________________________________

☐ None

12) Is tree 'open grown'? An open grown tree is generally not next to other trees and thus does not experience shading or great competition for light.

☐ Yes ☐ No

13) Circumference of the tree at height of 1.3 m (130 cm, 4 ft 3 inches). See sampling protocol on how to do this. Please report to at least the nearest centimeter.

Circumference: __________ cm

14) For the green leaf samples, where on the tree did you sample leaves from?

☐ Sampled only the lower portion of the tree that was accessible by hand.

☐ Sampled the lower portion of the tree that was accessible by hand and at a higher height using a tool such as a telescoping vegetation pruner. However, **the upper canopy was not sampled** because it was out of reach.

☐ Sampled the lower portion of the tree accessible by hand and at a higher height by using a tool such as a telescoping vegetation pruner. **The upper canopy was sampled** because it was within reach.

Other relevant details: ______________________________

15) Comments / notes: ______________________________

16) Did you take pictures of your specimen, submit them to iNaturalist and include the tag ‘tasper’ in your submission?

☐ Yes ☐ No

17) In 2020, we will expand this project to include more tree species. Would you be interested in remaining involved with the TASpeR project by joining our email list (note: your email address will not be shared, sold, or otherwise distributed to a third party)?

☐ Yes ☐ No

18) We would like to acknowledge your contribution to this project by posting your name on our website in a section that thanks the Citizen Scientists for making this project possible (note: mailing and email addresses will not be posted). We are also happy to link to your iNaturalist profile if you would like. If you would like us to acknowledge you on our website please list your preferred name. Please leave this section blank if you wish to remain anonymous.

Name:____________________________________

iNaturalist username: ________________________

TASpeR Sampling Protocol

Supplies needed:

Included in sampling kit:

- Sampling data sheet
- Gloves
- White printer paper to place samples between (if sampling more than one tree place a labelled piece of paper between sets of leaves from each tree)
- Cardboard

User provided:

- Telescoping vegetation pruner (if available, but not mandatory)
- Measuring tape (for circumference)
- String or rope (for circumference)
- Litter trap (see below)

Site access and permissions

Prior to sampling, please make sure you have received appropriate permissions to sample. If you plan to sample in a park you will likely need permission from the park's office or administration. Sampling permission can take some time, so it is a good idea to request permission ahead of the first sampling dates in August.

If you are sampling on private property make sure you have received permission from the property owner prior to sampling. For private property sampling we recommend sampling on your own land or that of a friend or family member.

Identification of a red maple to sample

Before sampling leaves you will need to identify a red maple tree to sample. *Acer rubrum* is very widely distributed throughout the eastern United States and is also fairly common. In the landscape it can be found in wetlands and riparian forests along with upland systems. In wetter sites it can be found in stands or in association with black ash, cottonwood, and black gum (https://plants.usda.gov/factsheet/pdf/fs_acru.pdf). In more upland sites it is known to associate with sugar maple, beech, black cherry and birch trees. Cultivars of red maple are also commonly planted as ‘street trees’ for landscaping trees in residential yards.

Confirm you have identified a red maple by consulting a field guide that includes *Acer rubrum*. Links to red maple descriptions are available on our website: www.sites.bu.edu/tasper

Measuring tree circumference

By knowing the circumference of the tree we are able to estimate its total size using published allometry equations. These equations relate easily measurable tree metrics, such as circumference, to the biomass of the tree.

Wrap a rope or piece of string at a height of 1.3 meters (130 cm, or 51 inches) above the ground surface around the tree you are sampling. For multi-trunked trees, report multiple circumferences and note in the comments section of the datasheet that the tree was multi-trunked. Make sure you are not stretching the rope or string and note the ‘start’ and ‘end’ points of the circumference on your string (a marker works well). Then laying the string out measure its distance using your measuring tape.

Sampling Green Leaves

Prepping for leaf collection. It is important that you do not touch the leaves you are going to sampling with your bare hands - the naturally occurring oils on your hands can contaminate the sample. For this reason, we have included several pairs of gloves to wear while handling the leaves.

Green leaves should be collected from a single tree. You should collect a total of ten leaves from your tree. Select leaves from a variety of locations and branches on the tree - this ensures we will document the within tree variability that is caused by different light environments and locations in the canopy. Select only leaves that are not damaged by insects and that look healthy. You need to collect both the leaf blade and petiole. The petiole is the botanical term commonly referred to as the 'stem' of the leaf.

Storing leaves - Immediately after collection place the leaves between the included sheets of paper and then 'sandwich' the leaves between the two pieces of cardboard and tape around the edges to secure the sample. Make sure that the leaves are not folded during this process. The taped cardboard should then be mailed back to Boston University in one of the yellow mailers included in the sampling kit.

Sampling Fallen Leaves

Sampling fallen leaves from your tree will require you to set out a receptacle under your tree and return within 2-3 days to collect the fallen leaves. You will need to keep track of leaf fall in your local area in order to time this correctly. Note that red maples are among the first trees to lose their leaves in the autumn. Similar to the green leaf samples, a total of 10 leaves should be collected. If your trap contains more than 10 leaves, make a representative selection of leaves to sample.

It is important to keep an eye on the weather when getting ready to sample fallen leaves. Leaves that have fallen and have been exposed to standing water due to rain are not suitable for this study, so make sure to clear your leaf litter trap prior to rainfall.

Building the litter trap:
Idea 1: Place and secure a 'tarp' under the tree you are sampling. You can improvise a tarp by using a trash bag cut open to increase surface area or a shower curtain. Basically any plastic sheeting can be used as a tarp.
Idea 2: Bucket, milk crate, or plastic container placed under the tree you are sampling.

The leaves should be handled with gloves and pressed between white paper and cardboard and shipped within several days of collection as with the green leaves.

Sending leaves and processing at Boston University

Leaves should be returned to Boston University sandwiched between the pieces of cardboard and paper provided, inside the included mailer. The mailing address is:

Finzi Lab (TASpeR Project)
Department of Biology
Boston University
5 Cummington Mall
Boston, MA
02215

At Boston University we will weigh the leaves, determine their areas, and analyze their carbon and nitrogen concentrations. The resulting data will be shared on the TASpeR website. Analyses and interpretation of the data will be written up and published in peer reviewed scientific journals.

Submitting pictures on iNaturalist and connecting on social media

We highly encourage you to submit photos of your tree(s) and leaves to iNaturalist (www.inaturalist.org) and add the Tag ‘tasper’ to your observations. This will not only provide independent confirmation that the tree you sampled is *Acer rubrum*, but will also help out another Citizen Science project. By including the Tag ‘tasper’ everyone that uses iNaturalist (including other TASpeR participants) will be able to look at the tree specimens sampled for the TASpeR project.

Note, our project does not have any formal affiliation with iNaturalist.org

The TASpeR project is active on Twitter (@tasper_project). We post updates about the project and share information about red maple and plant traits. Give us a follow and include @tasper_project in your tweets to post some pictures (we will retweet) – we’d love to see some shots of you sampling leaves for the project!

Thank you for your contributions to the TASpeR project !!!

Supporting Information S3.2. Comparison of model results with all green leaf samples included vs. green leaf samples collected only in the month of August. For ANOVA results we indicate overall model p-value and which pairwise comparisons are significantly different based on TukeyHSD test.

Relationship	Results when excluding 11 green leaf samples collected outside August	Results when including 11 green leaf samples collected outside August	Shift in significance between including/excluding non-August collected green leaf samples
Green %C ~ MAT	n.s.	n.s.	No
Green %N ~ MAT	p<0.05; R2=0.06	p<0.01; R2=0.09	No
Green C:N ~ MAT	p<0.05; R2=0.07	p<0.01; R2=0.12	No
N resorption ~ MAT	p<0.001; R2=0.44	p<0.001; R2=0.41	No
Green %C ~ MAP	n.s.	n.s.	No
Green %N ~ MAP	n.s.	n.s.	No
Green C:N ~ MAP	n.s.	n.s.	No
N resorption ~ MAP	p<0.001; R2=0.33	p<0.001; R2=0.33	No
Green %C ~ Latitude	n.s.	n.s.	No
Green %N ~ Latitude	p=0.08; R2=0.04	p=0.022; R2=0.06	Yes
Green C:N ~ Latitude	p=0.06; R2=0.04	p<0.01; R2=0.09	Yes
N resorption ~ Latitude	p<0.001; R2=0.37	p<0.001: R2=0.38	No
Green %C ~ open.grown	p<0.001	p<0.01	No
Green %N ~ open.grown	p<0.001	p<0.001	No
Green C:N ~ open.grown	p<0.001	p<0.001	No
N resorption ~ open.grown	n.s.	n.s.	No
Green %C ~ habitat	n.s.	n.s.	No
Green %N ~ habitat	p<0.05 [street-bottomland]	p<0.01 [street-bottomland]&[yard-bottomland]	Yes
Green C:N ~ habitat	p<0.05 [no pairwise comparisons are	p<0.01 [street-bottomland]&[yard-bottomland])	Yes

	significantly different]		
N resorption ~ habitat	n.s.	n.s.	No
Green %C ~ within.tree.sample.location	n.s.	n.s.	No
Green %N ~ within.tree.sample.location	n.s.	n.s.	No
Green C:N ~ within.tree.sample.location	n.s.	n.s.	No
N resorption ~ within.tree.sample.location	p<0.01 [lower.mid - whole]	p<0.01 [lower.mid - whole]	No

Supporting Information S3.3. Area based leaf trait metrics. Results from regression (MAT, MAP, latitude) and ANOVA (open.grown, habitat, within tree sample location) for area-based leaf traits. For the habitat category overall model and R2 results are presented followed by a description of which categories differed from each other based on TukeyHSD test. Cell shading is used to compare results with the mass based data reported in the original manuscript submission (green shading: indicates the area based metrics agree in directionality and test of significance with the mass based metrics, red cells: indicate mass and area based metrics do not agree with respect to tests of significance, orange cells: are overall models that are significant in both mass and area based metrics but have different significant pairwise comparisons in mass vs area based trait metrics, no shading: indicates a similar comparison was not reported in original manuscript.

	MAT	MAP	Latitude	Open grown status	habitat	Within tree sample location
Green leaf mass per unit area	p=0.096	p=0.066	p=0.144	p<0.001 R2=0.33	p<0.001; R2=0.28 [upland-street] [upland-yard]	p=0.89
Fallen leaf mass per unit area	p=0.076	p=0.18	p=0.138	p<0.01 R2=0.10	p<0.01; R2=0.17 [upland-yard]	–
Green leaf C mass per unit area	p=0.141	p=0.085	p=0.211	p<0.001 R2=0.34	p<0.001; R2=0.28 [upland-street] [upland-yard]	p=0.86
Fallen leaf C mass per unit area	p=0.101	p=0.25	p=0.185	p<0.01 R2=0.11	p<0.01; R2=0.18 [upland-yard]	–
Green leaf N mass per unit area	p=0.454	p=0.932	p=0.512	p<0.001 R2=0.47	p<0.001; R2=0.30 [street-bottomland] [yard-bottomland] [upland-street] [upland-yard]	p=0.85
Fallen leaf N mass per unit area	p<0.01; R2=0.12	p<0.01; R2=0.11	p<0.01; R2=0.11	p<0.01 R2=0.12	p<0.01; R2=0.14 [upland-street] [upland-yard]	–
N resorption area based	p<0.001; R2=0.27	p<0.001 R2=0.18	p<0.001 R2=0.25	p=0.17	p=0.75	p=0.19

Supporting Table 3.1. List of organizations contacted to participate in the community science project. A contact was considered successful if the organization sent information about the community project to their members.

Date Contacted	Organization	Contact successful?
6/11/2019	Minnesota Waters and Prairie Chapter of North Country Trail Association	No
6/11/2019	Laurentian Lakes Chapter of North Country Trail Association	No
6/11/2019	Itasca Moraine Chapter of North Country Trail Association	No
6/11/2019	Star of the North Chapter of North Country Trail Association	No
6/11/2019	Arrowhead Chapter of North Country Trail Association	No
6/11/2019	Kekekabic Trail Chapter of North Country Trail Association	No
6/11/2019	Brule - St. Croix Chapter of North Country Trail Association	No
6/11/2019	Heritage Chapter of North Country Trail Association	No
6/11/2019	Ni-Miikanaake Chapter of North Country Trail Association	No
6/11/2019	Peter Wolfe Chapter of North Country Trail Association	No
6/11/2019	North Country Trail Hikers Chapter of North Country Trail Association	No
6/11/2019	Superior Shoreline Chapter of North Country Trail Association	No
6/11/2019	Hiawatha Shore-to-Shore Chapter of North Country Trail Association	No
6/11/2019	Harbor Springs Chapter of North Country Trail Association	No
6/11/2019	Grand Traverse Hiking Club Chapter of North Country Trail Association	No
6/11/2019	Spirit of the Woods Chapter of North Country Trail Association	No
6/11/2019	Chief Noonday Chapter of North Country Trail Association	No
6/11/2019	Wampum Chapter of North Country Trail Association	No
6/11/2019	Butler County Chapter of North Country Trail Association	No
6/11/2019	Clarion County Chapter of North Country Trail Association	No
6/11/2019	Allegheny National Forest Chapter of North Country Trail Association	No
6/11/2019	Central New York Chapter of North Country Trail Association	No
6/17/2019	Maine Appalachian Trail Club	No
6/17/2019	Appalachian Mountain Club	No
6/17/2019	Randolph Mountain Club	No
6/17/2019	Dartmouth Outing Club	No
6/17/2019	Wilmington Trail Club	No
6/17/2019	BATONA Hiking Club	No
6/17/2019	Allentown Hiking Club	No
6/17/2019	York Hiking Club	No

6/17/2019	Cumberland Valley Appalachian Trail Club	No
6/17/2019	Mountain Club of Maryland	No
6/17/2019	Potomac Appalachian Trail Club	No
6/17/2019	Outdoor Club at Virginia Tech	No
6/17/2019	Piedmont Appalachian Trail Hikers	No
6/17/2019	Tennessee Eastman Hiking & Canoeing Club	No
6/17/2019	Smoky Mountains Hiking Club	No
6/17/2019	Nantahala Hiking Club	No
6/17/2019	Georgia Appalachian Trail Club	No
6/25/2019	Alabama Wildflower Society	No
6/25/2019	Arkansas Native Plant Society	No
6/25/2019	Delaware Native Plant Society	No
6/25/2019	The Botanical Society of Washington	No
6/25/2019	Illinois Native Plant Society Members	No
6/25/2019	Indiana Native Plant Society	No
6/25/2019	Minnesota Native Plant Society	No
6/25/2019	Mississippi Native Plant Society	No
6/25/2019	The Native Plant Society of New Jersey	No
6/25/2019	Pennsylvania Native Plant Society	No
6/25/2019	Vermont Botanical & Bird Club	No
6/25/2019	West Virginia Native Plant Society	No
6/25/2019	Botanical Club of Wisconsin	No
7/3/2019	Arkansas Master Naturalists	No
7/3/2019	The Florida Master Naturalist Program	No
7/4/2019	Illinois Master Naturalists	No
7/4/2019	Acadiana Chapter of the Louisiana Master Naturalist Association	No
7/4/2019	Great Baton Rouge Chapter of the Louisiana Master Naturalist Association	No
7/4/2019	Northeast Chapter of the Louisiana Master Naturalist Association	No
7/4/2019	Northwest Chapter of the Louisiana Master Naturalist Association	No
7/4/2019	Central Carolinas Master Naturalist Program	No
7/4/2019	Ohio Certified Volunteer Naturalist Program	No
7/4/2019	Pennsylvania Master Naturalist Program	No
7/4/2019	South Carolina Master Naturalist Program	No
7/4/2019	Vermont Master Naturalist Program	No
6/17/2019	Mt. Rogers Appalachian Trail Club	No
6/11/2019	Western Michigan Chapter of North Country Trail Association	Yes

6/11/2019	Great Trail - Sandy Beaver Canal Chapter of North Country Trail Association	Yes
6/11/2019	Chief Baw Beese Chapter of North Country Trail Association	Yes
6/17/2019	Blue Mountain Eagle Climbing Club	Yes
6/17/2019	Roanoke Appalachian Trail Club	Yes
6/17/2019	Green Mountain Club	Yes
6/17/2019	Carolina Mountain Club	Yes
6/17/2019	Natural Bridge Appalachian Trail Club	Yes
6/17/2019	CMC President	Yes
6/11/2019	Jordan Valley 45 Chapter of North Country Trail Association	Yes
6/17/2019	Susquehanna Appalachian Trail Club	Yes
6/17/2019	Tidewater Appalachian Trail Club	Yes
6/17/2019	Chequamegon Chapter of North Country Trail Association	Yes
6/25/2019	Georgia Botanical Society	Yes
6/25/2019	Maryland Native Plant Society	Yes
7/4/2019	New York Master Naturalist Program	Yes
7/4/2019	Tennessee Naturalist Program	Yes
7/4/2019	Southwest Chapter of the Louisiana Master Naturalist Association	Yes
7/4/2019	Maine Master Naturalist Program	Yes
7/4/2019	Greater New Orleans Chapter of the Louisiana Master Naturalist Association	Yes
7/4/2019	Mississippi Master Naturalist Program	Yes
6/25/2019	Michigan Botanical Club	Yes
6/25/2019	Florida Native Plant Society	Yes
7/4/2019	Minnesota Master Naturalist	Yes
6/25/2019	Connecticut Botanical Society	Yes
7/11/2019	Cheshire Land Trust	Yes
7/11/2019	Missouri Master Naturalist Program	Yes
7/18/2019	New Hampshire Citizen Science program	Yes
7/16/2019	Texas Master Naturalist	Yes

Supporting Table 3.2. List of models for leaf traits that have significant interactions among categorical covariates. P-values and adjusted-R^2 values reported for the overall model. Pairwise significant differences were determined using the TukeyHSD() test in R.

Model	Model p-val	Adj. R^2	Pairwise significant differences ($p<0.05$)
open.grown * habitat			
%N Green Leaf ~ open.grown * habitat	$p < 0.0001$	0.34	street—bottomland yard—bottomland upland—street street:y—bottomland:n street:y—upland:n
C:N Green Leaf ~ open.grown * habitat	$p < 0.0001$	0.35	street—bottomland yard—bottomland street:y—upland:n yard:y—upland:n bottomland:y—yard:n other:y—bottomland:y street:y—bottomland:y upland:y—bottomland:y yard:y—bottomland:y
%N Fallen Leaf ~ open.grown * habitat	$p < 0.01$	0.15	upland—street upland:y—street:y
C:N Fallen Leaf ~ open.grown * habitat	$p < 0.0001$	0.35	upland—street upland:y—bottomland:n upland:y—street:y yard:y—upland:y
N resorption ~ open.grown * habitat	$p = 0.39$	0.14	upland:y—bottomland:n
open.grown * sample location within tree			
%N Green Leaf ~ open.grown * sample location within tree	$p < 0.01$	0.19	y—n one:y—one:n
N resorption ~ open.grown * sample location within tree	$p = 0.016$	0.13	two—three two:n—three:n two:y—three:n
habitat * sample location within tree			
%N Fallen Leaf ~ habitat * sample location within tree	$p = 0.022$	0.19	two—three upland—street two:upland—one:street

Supporting Table 3.3 List of five model summaries for each leaf traits that had the lowest AIC scores. Blue highlighting indicates the model within each leaf trait with the lowest AIC scores that retain significance for all predictors included in the model. For C:N Green Leaf an additional sixth model summary is provided (C:N~open.grown) for comparison given the importance of the open.grown variable in other green leaf models.

Model	K	AICc	Δ AICc	AICc Wt	Cum. Wt	LL	Model p-val	Adj. R^2	Significant predictors in model
%C Green Leaf ~ open.grown * green leaf collection date	5	162.30	0	0.18	0.51	-75.65	p<0.01	0.13	None
%C Green Leaf ~ open.grown	3	162.63	0.33	0.15	0.67	-78.12	p<0.01	0.11	Intercept, open.grown
%C Green Leaf ~ open.grown * latitude	5	164.89	2.59	0.05	0.72	-76.95	p<0.05	0.12	Intercept
%C Green Leaf ~ open.grown * MAT	5	165.93	3.63	0.03	0.79	-77.47	p<0.05	0.10	Intercept
%C Green Leaf ~ open.grown * MAP	5	166.74	4.43	0.02	0.83	-77.88	p<0.05	0.09	Intercept
%N Green Leaf ~ open.grown * MAT	5	21.97	0	0.06	0.95	-5.49	p<0.0001	0.30	Intercept, open.grown
%N Green Leaf ~ open.grown * latitude	5	24.36	2.38	0.02	0.97	-6.69	p<0.0001	0.28	Intercept
%N Green Leaf ~ open.grown * green leaf collection date	5	24.36	2.39	0.02	0.98	-6.68	p<0.0001	0.26	None
%N Green Leaf ~ open.grown	3	26.34	4.36	0.01	0.99	-9.98	p<0.0001	0.23	Intercept, open.grown
%N Green Leaf ~ open.grown * MAP	5	27.31	5.34	0	0.99	-8.16	p<0.001	0.25	Intercept
C:N Green Leaf ~ open.grown *	5	420.81	0	0.08	0.93	-204.91	p<0.001	0.24	None

green leaf collection date									
C:N Green Leaf ~ MAT + green leaf collection date	4	424.45	3.64	0.01	0.94	-207.9	p<0.001	0.18	MAT (intercept and green collection date are p<0.06)
C:N Green Leaf ~ MAT * green leaf collection date	5	424.84	4.03	0.01	0.95	-206.92	p<0.001	0.19	None
C:N Green Leaf ~ open.grown * MAT	5	425.09	4.28	0.01	0.97	-207.05	p<0.001	0.30	Intercept, open.grown
C:N Green Leaf ~ latitude + green leaf collection date	4	425.97	5.16	0.01	0.98	-208.66	p<0.01	0.16	Intercept, latitude, green leaf collection date
C:N Green Leaf ~ open.grown	3	432.61	11.8	0	1	-213.12	p<0.001	0.18	Intercept, open.grown
%C Fallen Leaf ~ MAP * fallen leaf collection date	5	220.30	0	0.76	0.76	-104.65	p<0.01	0.18	Intercept, MAP, fallen leaf collection date, MAP and date interaction
%C Fallen Leaf ~ MAT * fallen leaf collection date	5	224.54	4.24	0.09	0.85	-106.77	p<0.05	0.12	Intercept, MAT, fallen leaf collection date, MAT and date interaction
%C Fallen Leaf ~ latitude * fallen leaf collection date	5	225.31	5.01	0.06	0.91	-107.15	p<0.05	0.11	Intercept, latitude, fallen leaf collection date, latitude and date interaction
%C Fallen Leaf ~ habitat	6	227.44	7.14	0.02	0.93	-107.02	p<0.01	0.14	Intercept, habitat
%C Fallen Leaf ~ open.grown	3	229.20	8.9	0.01	0.96	-111.41	p<0.05	0.06	Intercept, open.grown
%N Fallen Leaf ~ latitude * fallen leaf collection date	5	-20.66	0	0.88	0.88	15.83	p<0.0001	0.34	Intercept, latitude, fallen leaf collection date, latitude fallen collection date interaction

%N Fallen Leaf ~ MAT * fallen leaf collection date	5	-16.13	4.53	0.09	0.98	13.57	p<0.0001	0.29	Intercept, MAT, fallen leaf collection date, MAT fallen leaf collection date interaction
%N Fallen Leaf ~ MAP * open.grown	5	-9.71	10.95	0	0.98	10.35	p<0.001	0.20	MAP
%N Fallen Leaf ~ MAP * fallen leaf collection date	5	-8.88	11.78	0	0.98	9.94	p<0.001	0.21	Intercept, MAP, fallen leaf collection date, MAP fallen leaf collection date interactions
%N Fallen Leaf ~ MAP	3	-8.56	12.1	0	0.99	7.47	p<0.001	0.16	Intercept, MAP
C:N Fallen Leaf ~ latitude * fallen leaf collection date	5	554.17	0	0.95	0.95	-271.59	p<0.0001	0.41	Intercept, latitude, fallen leaf collection date, Latitude fallen leaf collection date interaction
C:N Fallen Leaf ~ MAT * fallen leaf collection date	5	560.43	6.26	0.04	1	-274.72	p<0.0001	0.35	Intercept, MAT, fallen leaf collection date, MAT fallen leaf collection date interaction
C:N Fallen Leaf ~ latitude * open.grown * habitat	18	567.36	13.19	0	1	-258.56	p<0.0001	0.55	Open.grown, open grown habitat interaction
C:N Fallen Leaf ~ MAP * fallen leaf collection date	5	568.02	13.84	0	1	-278.51	p<0.0001	0.27	Intercept, MAP, fallen leaf collection date, MAP fallen leaf collection date interaction.
C:N Fallen Leaf ~ MAT * open.grown * habitat	18	570.9	16.72	0	1	-260.32	p<0.0001	0.52	Intercept, open.grown habitat interaction
N resorption ~ MAT * fallen leaf collection date	5	497.45	0	0.52	0.52	-243.23	p<0.0001	0.47	Intercept, MAT, fallen date, MAT fallen leaf collection date interaction

N resorption ~ latitude * fallen leaf collection date	5	498.10	0.65	0.37	0.89	-243.55	p<0.0001	0.46	Intercept, latitude, fallen date, latitude fallen leaf collection date interaction
N resorption ~ MAT + fallen leaf collection date	4	502.94	5.48	0.03	0.92	-247.14	p<0.0001	0.41	MAT
N resorption ~ MAT + green leaf collection date	4	503.03	5.57	0.03	0.96	-247.19	p<0.0001	0.41	MAT
N resorption ~ MAT * green leaf collection date	5	504.94	7.49	0.01	0.97	-246.97	p<0.0001	0.40	None

CHAPTER FOUR: GLOBAL SCALE PATTERNS OF N AND P IN LEAF AND REPRODUCTIVE LITTERFALL

ABSTRACT

Several different hypotheses have been developed to explain variation in nutrient availability across broad environmental scales including the temperature/precipitation hypothesis which suggests net mineralization of nitrogen (N) and phosphorus (P) is highest in warmer wetter climates relative to cooler drier climates, and the substrate age hypothesis that suggests in young soils of high latitudes N is more limiting compared to old highly weathered soils of the tropics where P is more limiting. Many studies have suggested N and P concentrations and N:P of foliar and senesced leaves reflect constraints of nutrient availability on productivity. However, the biogeochemistry of reproduction is rarely explicitly considered across broad geographic and environmental gradients. In this paper we compiled site level leaf and reproductive litterfall N and P concentrations, fluxes, and N:P in order to examine global scale trends against established biogeochemical hypotheses and investigate whether angiosperm vs. gymnosperm, deciduousness (i.e., evergreen vs. deciduous), or stand type (i.e., forest vs. plantation) interact with environmental gradients to influence the results. We found weak support for the substrate age hypothesis that leaf litterfall %P was lowest near the tropics and increased with increasing latitude, whereas %N was highest near the tropics and decreased with increasing latitude. However, reproductive litterfall %N and %P were both weakly negatively related to latitude providing some support for the temperature/precipitation hypothesis. Both leaf and reproductive litterfall fluxes of N and

P tended to increase towards more tropical latitudes and warmer climates, which supports established trends in both productivity and fecundity. Leaf litterfall N:P was significantly higher in low latitudes compared to higher latitudes. Our global median (interquartile range) estimates of the percent contribution of reproductive litterfall to leaf plus reproductive litterfall for N was 13.0% (4.6% - 20.0%) and for P was 16.1% (6.8% - 25.9%). Our results demonstrate that reproductive litterfall fluxes of N and P are important components of litterfall, biogeochemical cycling, and plant nutrient limitation.

INTRODUCTION

The biogeochemical cycling of nitrogen (N) and phosphorus (P) are of principal interest in ecosystem ecology because primary productivity in forests is commonly limited by one or both elements (Elser et al., 2007; Du et al, 2020; Hou et al. 2020). Forest primary productivity under continued climate change is also expected to be constrained by nutrient availability (Wieder et al., 2015).

The availability of N and P within forest soils is mediated by interactions between ecosystem state factors such as climate, parent material, time, and plant functional type (Chapin et al., 2011). Warm and wet climates are associated with enhanced rates of decomposition and net mineralization rates of N and P (Davidson and Janssens, 2006; Li et al, 2019). Young soils formed from glacial till, which are present in temperate and common in boreal biomes are often more fertile compared to older soils developed directly from bedrock (Anders et al, 2018). Additionally, compared to young soils, very old soils experience more chemical and physical weathering that can deplete P availability (Walker and Syers, 1976), likewise acidic soils may render P insoluble due to sorption with iron and aluminum oxides at low pH (Brady and Weil, 2008). Young soils can be limited by N due to low levels in rock and it takes considerable time for biological N fixation and N deposition to accrue (Vitousek and Farrington, 1997; Menge et al, 2012). In addition to physical environmental controls on ecosystem nutrient dynamics, different plant functional types differ in senesced foliage nutrient concentrations. (e.g., angiosperm trees have higher leaf litter N and P concentrations compared to gymnosperms; McGroddy et al., 2004; Vergutz et al., 2012).

The interaction between ecosystem state factors has led to several hypotheses related to nutrient limitation at the global scale. The temperature-moisture hypothesis posits that warm-wet climates such as those in the tropics experience the highest rates of nutrient net mineralization (Reich and Oleksyn, 2004). The substrate-age hypothesis posits that the highly weathered nature of tropical soils has led to depleted P availability in the tropics relative to temperate ecosystems and has thus led to higher P limitation in tropical latitudes and higher N limitation in more temperate latitudes (Walker and Syers, 1976; Reich and Oleksyn, 2004).

It has also been suggested that leaf litterfall reflects aspects of nutrient availability and limitation in global scale studies (Killingbeck, 1996; Yuan and Chen, 2009; Vallicrosa et al 2022; McGroddy et al 2004). Foliar P resorption proficiency has been suggested to be greatest in tropical latitudes and lowest in boreal and temperate latitudes, whereas N resorption proficiency is lowest in tropical latitudes and greatest in boreal and temperate latitudes (Yuan and Chen, 2009). However, Vergutz et al (2012) found that foliar N and P resorption efficiencies are both lowest in tropical latitudes and greatest in temperate and boreal latitudes. Leaf litterfall N:P ratios are highest in tropics and decrease with latitude to temperate systems for both green and senesced leaves (McGroddy et al, 2004), which has been suggested to reflect higher P limitation in tropics relative to temperate systems (Marklein et al., 2016). Litterfall N:P ratios influence N and P release from litter during decomposition, whereby high N:P leaf litter tends to be associated with elevated rates of net N mineralization during decomposition and low N:P leaf litter tends to be associated with elevated rates of net P mineralization during decomposition (Güsewell and Gessner, 2009).

Evergreen trees have higher N and P proficiency of resorption in senesced leaves compared to deciduous trees (Killingbeck et al., 1996), but this pattern does not necessarily translate to differences in leaf litterfall N:P between evergreen and deciduous (McGroddy et al., 2004). Canopy traits, such as leaf area index (LAI) and specific leaf area are critical to understanding leaf litterfall nutrient fluxes because the flux of N and P from the canopy in leaf litterfall depends not only on the concentration N and P, but also on the biomass of leaves in the canopy. LAI tends to be lower in immature compared to mature forests where it reaches a saturation point based on soil resources and light extinction through the canopy (Jagodzinsky and Kalucka, 2008; Chang et al., 2020). Additionally, LAI saturates at higher levels from boreal to tropical systems (Rasul et al, 2020) and previous studies have demonstrated increases in annual leaf litterfall fluxes moving from boreal to tropical latitudes (Shen et al., 2019). While there has been a great deal of research investigating changes in biogeochemical patterns of leaf litterfall along geographic and environmental gradients, much less attention has been given to biogeochemical patterns of reproductive allocation despite its importance for plant fitness.

From boreal to tropical latitudes previous research shows that seed mass increases 320 fold (Moles et al., 2007) and seed production increases 100-250 fold (Journé et al., 2022), suggesting that reproductive allocation is highest in low latitudes. Trees also have minimum size and age requirements before reproductive allocation initiates (Minor and

Kobe, 2019), and at old age reproductive allocation has been shown to decline (Qiu et al., 2021). Although reproductive litterfall is subject to florivory, granivory, and frugivory and rarely includes pollen it has been used as an estimate of stand level allocation to reproduction in forested systems (Kitayama et al., 2015). Reproductive allocation has also been shown to respond positively to N additions and elevated CO_2 (LaDeau and Clark, 2001; Kaspari et al., 2008), suggesting allocation to reproductive tissues in forests is also resource limited.

While there are known gradients in rates of primary productivity, fluxes of leaf litterfall N and P, and plant fecundity across different climates, and latitudinal gradients, there is a need to better understand patterns of N and P reproductive allocation because unlike foliage where resorption prior to abscission increases plant nutrient use efficiency, there could be a fitness cost if reproductive tissues have low N and P concentrations that negatively affect seed quality or protection. Reproductive tissues may require special consideration related to their contribution to litterfall fluxes and relative to global scale plant biogeochemical patterns.

There remains to be a characterization of reproductive litterfall N and P concentrations, N:P, N flux and P flux across gradients in mean annual temperature, precipitation and latitude. There is also for an opportunity to assess how reproductive litterfall N and P biogeochemistry relates to that of foliar litterfall, and general biogeochemical theory (e.g., temperature moisture hypothesis and substrate-age hypothesis).

In this paper we seek to address four questions and related hypotheses related to global scale patterns in leaf and reproductive litterfall: (1) How do N and P leaf and reproductive litterfall concentrations, (2) fluxes and (3) N:P ratios vary along latitudinal, MAT, and MAP gradients? (4) What additional covariates affect patterns of leaf and reproductive N and P concentrations, rates of litterfall N and P fluxes, and N:P? To address these questions, we conducted a data synthesis of peer-reviewed publications that reported N and P fluxes, concentrations, and N:P of leaf and reproductive litterfall.

We tested the following hypotheses:

(1) Following the temperature/moisture hypothesis for litterfall, leaf and reproductive litterfall N and P concentrations increase from boreal to tropical latitudes and from low to high gradients in MAT/MAP.

(2) Following the substrate-age hypothesis for litterfall, leaf and reproductive litterfall N concentrations are highest in tropical latitudes and lowest in temperate and boreal latitudes. Whereas leaf and reproductive litterfall P concentrations and N:P are highest in tropical latitudes and increase towards temperate and boreal latitudes.

(3) There is no difference in N or P concentration in reproductive litterfall across MAT, MAP, or latitude.

(4) Following the productivity and fecundity gradient hypothesis, leaf and reproductive litterfall fluxes of N and P are highest in tropical latitudes and decrease at higher latitudes.

(5) Gymnosperm, evergreen, and forest stands produce litter with lower N and P concentrations and N and P fluxes compared to their angiosperm, deciduous, and plantation stand counterparts.

METHODS

Data collection

We conducted a Web of Science search of "All Databases" on July 18, 2022 to identify papers that reported leaf or reproductive litterfall fluxes of N or P from forested systems. The exact keyword search used is provided in Supporting Information 4.1. This search resulted in 911 publications, which were accessed from publicly available online resources, Boston University libraries, or requested through inter-library loan services.

From the initial 911 papers we only included publications that reported N and/or P for leaf or reproductive litterfall. We excluded: (1) studies reporting only the results of data syntheses, (2) studies that did not report litterfall over at least one annual cycle, (3) studies that were not written in English, (4) studies where the study system did not contain trees, forest, or a plantation, (5) studies that sub-sampled litterfall from individual trees and excluded litterfall from non-target tree species, (6) studies where litterfall fluxes were not reported on a per area basis.

After applying our selection criteria, it resulted in 178 publications included in our study (Supporting Table 4.1). Different sites reported in the same paper were retained as different sites within our study, except when the original study reported results from individual replicate plots. Replicate plots as identified by the original authors were averaged prior to inclusion in our analysis. In cases where authors reported on the same site over multiple years we averaged site data over years prior to inclusion in our analysis. By including different sites within publications, a total of 449 sites were included in our study, however, not every study reported every variable examined in our analysis.

For each paper included in our study leaf and reproductive litterfall biomass, N, and P fluxes were recorded using the paper's original units and converted to g m^{-2} yr^{-1} prior to analysis. Our preference was to extract data from values reported in tables or manuscript text, but some studies reported data solely in figures. In cases where data was reported only in figures, we used WebPlotDigitizer 4.6 (Rohatgi, 2022) to extract values from the figures. WebPlotDigitizer has been reported to yield good estimates of the true values based on calibration data (Labonte et al., 2016).

We recorded whether each site was a forest or plantation (hereafter variable referred to as 'site type') and used reported species data as the basis of determining angiosperm vs. gymnosperm vs. mixed and evergreen vs. deciduous vs. mixed (hereafter variable referred to as 'deciduousness') stand traits, if not otherwise reported in the methods. Mean annual precipitation (MAP) and temperature (MAT) were also recorded for each site, and if the original paper did not report MAT or MAP we used the latitude and longitude of the site to estimate MAP and MAT from the WorldClim 2.1 database (Fick and Hijmans., 2017). Climate space and geographic location of sites can be found in Figure 4.1.

Data Analysis

From the values reported by authors for N and P fluxes of leaf and reproductive litterfall, we calculated N and P concentrations, and molar ratios for N:P . N and P concentrations were computed by dividing the N or P flux by the biomass flux and multiplying by 100. We also calculated the relative N and P fluxes in reproductive litterfall compared to leaf plus reproductive litterfall. In total this resulted in 12 different response variables. Inspection of the leaf litterfall N and P fluxes, leaf and reproductive litterfall N concentrations, P concentrations, and N:P generally indicated linear relationships with climate and latitudinal variables, but demonstrated heteroskedasticity that was not always corrected with log() transformations. Additionally, the reproductive litterfall N and P fluxes are undefined with log() transformations because of zeros present in the dataset, and the log + n transformation changes the relationship with the explanatory variables.

Therefore, we used a rank-based estimation of linear models, a type of nonparametric analyses that is robust to assumptions of least squares-based regression and was implemented in the R package 'Rfit' (Kloke and McKean, 2012). The weighting scheme we used to assign ranks accounts for right skewness in the response variables (scores="bentscores1" as implemented in 'Rfit' for right skewed data). 'Rfit' models are compatible with the base R summary() function, which provided estimates of the slopes, intercepts, R^2, and overall model and predictor level significance. In order to assess hypotheses 1-5 we performed univariate rank-based regression analyses between the response variables and the explanatory variables of mean annual temperature (MAT), precipitation (MAP), and latitude, phylogenetic group (classified here as angiosperm, deciduous, and mixed stands), deciduousness (classified here as deciduous, evergreen, and mixed stands), and stand type (classified here as forest or plantation).

To gain insight into multivariate drivers of reproductive litterfall nutrient concentrations and fluxes we conducted variable selection based on backwards elimination of variables. For each response variable (reproductive %N, %P, N:P, N flux, P flux, and relative reproductive contribution to leaf + reproductive N and P fluxes) we started with a full model that consisted of additive terms: MAT + MAP + Latitude + Deciduousness + Phylogenetic category + Plantation vs. Forest and sequentially removed non-significant variables based on the lowest t-scores until all variables in the model were significant. From there we added all pair-wise comparisons for the remaining explanatory variables in the model and again performed sequential backwards elimination of non-significant interaction terms based on lowest t-scores. The package ‘ggplot’ (Wickham et al., 2016) was used for data visualization, and all data analyses were conducted in R 4.2.2. (R Core Team, 2022)

RESULTS

Leaf and Reproductive Litterfall N and P Concentrations

Leaf litterfall N concentrations were weakly positively related to MAT and negatively related with latitude ($p<0.01$; $R^2=0.02$ for both) (Table 4.1; Figure 4.2d and 4.4d). Leaf litterfall P concentrations were weakly negatively related to MAP ($p<0.001$; $R^2=0.05$; and positively to latitude ($p<0.001$; $R^2=0.04$) (Table 4.1; Figure 4.3e and 4.4e).

Deciduousness was significantly related to leaf litterfall N concentrations whereby deciduous and evergreen stands had lower N concentrations compared to mixed stands ($p<0.001$; $R^2=0.06$). Deciduous stands had significantly higher leaf litterfall P concentrations compared to evergreen and ‘undesignated’ stands. Also, undesignated stands were lower than evergreen and mixed stands for leaf litterfall P concentrations ($p<0.001$; $R^2=0.07$, respectively). Reproductive litterfall N concentrations were higher in deciduous compared to evergreen stands ($p<0.01$; $R^2=0.09$).

Angiosperms had higher reproductive litterfall N and P concentrations compared to gymnosperms ($p<0.001$; $R^2=0.24$; $p<0.01$; $R^2=0.10$, respectively). Angiosperm stands also had higher leaf litterfall N concentrations compared to gymnosperm stands ($p<0.001$; $R^2=0.13$). Stand type tended not to be an important factor for leaf litterfall nutrient concentrations apart from P concentrations of leaf litterfall where we found plantations to exhibit greater leaf litterfall P concentrations compared to forested systems ($p<0.001$; $R^2=0.07$).

Backwards elimination of variables for multivariate analysis of reproductive N concentrations indicated that the best model contained angiosperm vs. gymnosperm vs. mixed stand categorization as the only explanatory variable ($p<0.001$; $R^2=0.24$; Table 4.2; Supporting Table 4.2). For reproductive P concentration the model best based on backward elimination of variables included additive variables of latitude (negative relationship) and deciduousness (deciduous > evergreen & unknown stands) ($p<0.001$; $R^2=0.15$) (Table 4.2; Supporting Table 4.2).

Nitrogen fluxes

Leaf litterfall

MAT and MAP were positively related to leaf litterfall N fluxes (both $p<0.001$; $R^2= 0.20$ and 0.12, respectively) (Table 4.1; Figure 4.2a and 4.3a). Latitude was negatively related to leaf litterfall N fluxes ($p<0.001$; $R^2=0.19$) (Table 4.1; Figure 4.4a).

Angiosperm stands and had higher leaf litterfall N fluxes compared to gymnosperm stands and stands with a 'mixed' contribution of angiosperm and gymnosperms ($p<0.001$; $R^2=0.13$). Stand type alone indicated plantations had higher leaf litter fall N fluxes compared to forests ($p<0.01$; $R^2=0.02$).

Reproductive Litterfall

MAT and MAP were positively related to reproductive litterfall N flux ($p<0.001$; $R^2=0.06$ and $p<0.001$; $R^2=0.09$, respectively; Table 4.1; Figure 4.2a and 4.3a). Latitude was negatively related to reproductive litterfall N flux ($p<0.001$; $R^2=0.09$) (Table 4.1; Figure 4.4a).

For models with individual categorical covariates, angiosperm reproductive litterfall N fluxes were higher than gymnosperms ($p<0.001$; $R^2=0.09$). Deciduousness and forest vs. plantation alone were not significant predictors of reproductive litterfall N fluxes. Backwards variable selection for reproductive litterfall N flux indicated that the best fit model included additive terms for MAP, latitude, deciduousness and an interaction between latitude and deciduousness ($p<0.001$; $R^2=0.25$) (Table 4.2; Supporting Table 4.2).

Comparing reproductive and leaf litterfall N fluxes

MAT, MAP, and latitude alone were not significantly related to the proportion of reproductive litterfall N fluxes to the combined reproductive and leaf litterfall N fluxes (Figures 4.2f, 4.3f, and 4.4f). The global median percent (IQR) of the reproductive litterfall N fluxes to leaf litterfall N fluxes was 13.0% (4.6% - 20.0%), which was not significantly different from the relative biomass contribution of reproductive litterfall to the combined reproductive plus leaf litterfall of 11.0 (4.7% - 18.2%).

Backwards variable selection for the proportion of reproductive litterfall N fluxes to the sum of reproductive and leaf litterfall N fluxes indicated the model with additive components of latitude and deciduousness and an interaction between latitude and deciduousness best fit the data ($p<0.001$; $R^2=0.18$) (Table 4.2; Supporting Table 4.2). For the interaction between deciduousness and latitude, not only are there differences in slope, but deciduous stands have opposite directionality compared to evergreen and ‘mixed’ stands. For deciduous stands there is positive relationship with latitude whereas evergreen and ‘mixed’ stands negative relationship with latitude).

Phosphorus fluxes

Leaf litterfall

All univariate categorical models were significantly related to leaf litterfall P flux, but had low explanatory power ($R^2 \leq 0.04$). The deciduousness model was significant, but the only individual pairwise comparisons that were different was that ‘unknown’ category was lower than all others (deciduous, evergreen, and mixed; $p<0.01$; $R^2=0.04$).

Angiosperm stands had significantly higher leaf litterfall P fluxes compared to gymnosperm, ‘mixed’, and unknown stands ($p<0.001$; $R^2=0.04$). Plantations had higher leaf litterfall P fluxes compared to forest stands ($p<0.001$; $R^2=0.04$). MAT was positively related to leaf litterfall P flux ($p<0.01$; $R^2=0.03$), whereas MAP and latitude were not significantly related to leaf litterfall P flux (Table 4.1; Figures 4.2b, 4.3b, and 4.4b).

Reproductive Litterfall

MAT and MAP were positively related to reproductive litterfall P flux ($p<0.001$; $R^2=0.09$) and ($p<0.001$; $R^2=0.09$), respectively (Table 4.1; Figures 4.2b and 4.3b). Latitude was negatively related to reproductive litterfall P flux ($p<0.001$; $R^2=0.09$) (Table 4.1; Figure 4.4b).

No univariate models with just categorical variables for reproductive litterfall P flux were significant apart from angiosperm vs. gymnosperm vs. mixed stand categorization ($p<0.05$; $R^2=0.05$) which indicated angiosperms had higher reproductive P flux compared to gymnosperms. Backwards variable elimination indicated reproductive litterfall P flux was best explained by additive components of MAP, latitude, deciduousness and the interaction between latitude and deciduousness ($p<0.001$; $R^2=0.23$; Table 4.2; Supporting Table 4.2).

Comparing reproductive and leaf litterfall P fluxes

The proportion of reproductive to reproductive plus leaf litterfall P flux increased with precipitation ($p<0.001$; $R^2=0.11$; Table 4.1; Figure 4.3f) and decreased with latitude ($p<0.001$; $R^2=0.10$) (Table 4.1; Figure 4.4f) but was not related to MAT (Table 4.1;

Figure 4.2f). The global median percent (IQR) of the reproductive litterfall P fluxes to reproductive plus leaf litterfall P fluxes was 16.1% (6.8% - 25.9%), which was significantly higher than global biomass-based proportion of 11.0 % (4.7% - 18.1%). No univariate categorical model was significantly related to the proportion of reproductive litterfall P fluxes to reproductive plus leaf litterfall P fluxes apart from stand type, but only the intercept was significant, and the forest and plantation were not significantly different from each other ($p<0.05$; $R^2=0.02$).

Backwards variable selection for the reproductive litterfall P proportion realtive to reproductive plus leaf litterfall P fluxes indicated the best fit model included additive components for MAT, MAP, and latitude, and the interactions between MAT and latitude, and MAP and latitude ($p<0.001$; $R^2=0.29$) (Table 4.2; Supporting Table 4.2).

N:P of Leaf and Reproductive Litterfall

MAP had a positive relationship with leaf litterfall N:P ($p<0.001$; $R^2=0.08$) (Table 4.1; Figure 4.3c), whereas latitude had a negative relationship with leaf litterfall N:P ($p<0.001$; $R^2=0.05$; Table 4.1; Figure 4.4c). Alone, deciduousness ($p<0.01$; $R^2=0.04$), angiosperm vs. gymnosperm vs. mixed stand categorization ($p<0.05$; $R^2=0.03$), and stand type ($p<0.01$; $R^2=0.02$) were all significant, but weak predictors of leaf litterfall N:P.

Reproductive N:P was positively related to MAP ($p<0.05$; $R^2=0.04$) (Table 4.1; Figure 4.3c), but was not related to MAT or latitude (Table 4.1; Figures 2c and 4c). Angiosperm vs. gymnosperm vs. mixed stand categorization was a weak significant predictor of reproductive N:P ($p<0.01$; $R^2=0.10$) where gymnosperm stand reproductive

N:P was lower than ‘unknown’ stands. Deciduousness was also weakly related to reproductive N:P ($p<0.05$; $R^2=0.05$) where ‘unknown’ stands had higher N:P compared to deciduous stands. Backwards variable selection suggests a model with additive components of angiosperm vs. gymnosperm vs. mixed stand categorization, deciduousness, and latitude best fit the data ($p<0.001$; $R^2=0.21$) (Table 4.2; Supporting Table 4.2).

DISCUSSION

Overall, our analyses demonstrated that leaf and reproductive litterfall N and P fluxes, N and P concentrations, and N:P were only weakly related to MAT, MAP, and latitude when statistical results were significant. Many of the relationships in the analysis that had low p-values (e.g., $p<0.01$) were accompanied by very low R^2 values (e.g., $R^2<0.05$) indicating the variables in the model were significant (e.g., a non-zero slope, or a non-zero difference between groups) but the model had low explanatory power. Because low p-values do not necessarily indicate large effect sizes it is recommended that effect sizes such as coefficient of determination (R^2) be reported along with p-values, additionally low R^2 values are not incompatible with low p-values (Sullivan and Feinn, 2012). Low p-values accompanied by low R^2 are not uncommon and have been observed in a number of other published ecological studies (e.g. Reich et al., 2014; Yuan and Chen 2015; He et al., 2020). While these findings suggest there is much site-specific variation unaccounted for in our analyses we can still weigh the evidence of support for the initial hypotheses outlined in this study.

Litterfall N and P concentration

Leaf and reproductive litterfall N concentrations were positively related to MAT and negatively related to latitude. Although the positive and negative relationships were weak, the directionality is consistent with hypothesis 1 where environmental factors such as higher temperatures result in greater N availability (Guntiñas et al., 2012; Liu et al., 2016), and hypothesis 2 where N availability is higher in lower latitudes rather than higher latitudes, potentially as a result of differences in soil age and weathering. Leaf litterfall P concentrations were negatively related to MAP and positively related to latitude, but only weakly. The lower P concentrations in leaf litterfall at lower latitudes are consistent with hypothesis 2, that suggests tropical soils (e.g., oxisols) may be depleted in P due to age and weathering (Walker and Syers, 1976; Yang et al., 2013). It is notable that reproductive litterfall P concentrations were positively related to MAT and negatively related to latitude, thus following a different pattern than leaf litterfall P concentrations, suggesting that hypotheses 3 is invalid because we did observe relationships between reproductive litterfall N and P concentrations with climate and latitude. In fact, reproductive litterfall N and P concentrations most closely align with hypothesis 1, tracking N and P mineralization rates (Gill and Finzi, 2016; Liu et al., 2016).

Our findings for leaf litterfall N and P concentrations align with Yuan and Chen (2009) who observed similar directionally in relationships with climate variables. The relationships between observed in Yuan and Chen (2009) tended to be stronger compared to what we observed for foliar litterfall and may have resulted from their exclusive use of senesced leaf material whereas our analysis accounts for all leaf litterfall whether it was senescent or not. If the cause of the difference in strength of the relationships between our results and those of Yuan and Chen (2009) is due to the use of litterfall vs. exclusive use of senesced leaf material, it suggests differences in litterfall quality along climate and latitudinal gradients is muted compared to what might be anticipated by senesced foliage nutrient concentrations because of the potential inclusion of non-senesced foliage in litterfall.

Litterfall N and P fluxes

Overall leaf and reproductive litterfall N and P fluxes were positively related to MAT and MAP, and negatively related to latitude apart from leaf litterfall P flux which was not related to latitude or MAP. These relationships are largely consistent with hypothesis 4 and track changes in productivity, LAI, and fecundity across these gradients (Rasul et al., 2020; Journé et al., 2022).

We found evidence to suggest that the proportion of reproductive litterfall N and P flux changed across gradients in MAT and latitude. Specifically, we found that proportional reproductive litterfall N fluxes to leaf plus reproductive litterfall fluxes for deciduous stands increased with latitude. This is different from evergreen and mixed stands for which we found proportional reproductive litterfall N fluxes to leaf plus reproductive litterfall fluxes to decrease with latitude. We also found that the proportion of reproductive litterfall P flux to leaf plus reproductive litterfall flux was best explained by a model with a positive relationship with MAT and negative interactions between MAT and latitude and positive interaction between MAP and latitude.

Our global median (interquartile range) estimates of the percent contribution of reproductive litterfall to leaf plus reproductive litterfall for N was 13.0% (4.6% - 20.0%) and for P was 16.1% (6.8% - 25.9%) and the finding that reproductive litterfall N and P fluxes can reach or exceed parity with leaf litterfall demonstrates the need to better include the biogeochemical implications of reproductive allocation in ecosystem studies to develop predictions related to when and how reproduction meaningfully contributed to ecosystem elemental cycling. Further our finding that relative P fluxes in reproductive litterfall were higher compared to relative biomass fluxes indicates that reproductive organs are particularly P rich and that the metric used to assess reproductive costs (e.g., biomass, N, or P) also matters (Obeso, 2002)

Litterfall N:P

We found positive relationships in leaf litterfall N:P with MAP, and a negative relationship with latitude. We also found a positive relationship between MAP and reproductive litterfall N:P. Overall our analyses are consistent with hypothesis 2 that leaf litterfall N:P was greatest in tropical latitudes and decreased at higher latitudes (McGroddy et al., 2004; Marklein et al., 2016). We found that the best fit model to explain reproductive litterfall N:P had a positive coefficient for latitude, and angiosperm and evergreen stands had greater N:P than gymnosperms and deciduous stands. As alluded to previously, our ability to explain variation in litterfall N:P was limited and might have been improved with the inclusion of additional site information.

Future directions

In the dataset we compiled reported values for N fluxes for leaf litterfall was the greatest (n=440 sites), followed by P fluxes for leaf litterfall (n=340 sites). Reproductive litterfall N (n=196 sites) and P (n=168 sites) fluxes were much less commonly reported. The separation of reproductive components of litterfall is a time-consuming task, but we recommend more studies report such data. We also note that boreal sites were underrepresented in our dataset so additional collection efforts for both leaf and reproductive nutrient litterfall would be of high value. Additionally, with reproductive data, ‘zero’ measurements can be informative for analyzing trends in the reproductive biogeochemistry and we recommend that future studies report when reproductive litterfall was ’zero’ and differentiate that finding from the non-measurement of reproductive litterfall.

Out of the 196 reproductive litterfall N values we compiled, only twelve studies reported “zero” values. If many studies have failed to report a zero value or to make a statement in the methods that reproductive litterfall is zero, it likely means that the values reported in this manuscript overestimate reproductive contributions to litterfall. Capturing good estimates of reproductive allocation based on reproductive litterfall can also be problematic because studies very rarely consider the nutrient rich contributions of pollen (but see Doskey and Ugoagwu, 1989 and Cho et al., 2003) and florivores, frugivores, and granivores may consume and excrete reproductive structures in the canopy prior to abscission (Donoso et al., 2004; Chung et al., 2011; Fleming and Kress, 2011).

Given that primary productivity is nutrient limited and dynamic global vegetation models have started to implement nutrient allocation rules, the data presented in this manuscript may serve as an empirical basis to assign N and P to not only leaf litterfall, but also reproductive allocation. Previous researchers have suggested that the reproductive litterfall biomass could be used to better constrain fecundity in vegetation models (Hanbury-Brown et al., 2022), and the data we present will allow for implementing a nutrient cost of reproduction in such models because as we document, reproductive N and P are non-trivial components of litterfall and tree nutrient budgets.

CONCLUSIONS

In summary, we conclude that leaf and reproductive litterfall N and P concentrations, N:P, and N and P fluxes tended to only be weakly related to broad climate and latitudinal gradients, but the relationships were consistent with hypotheses we tested. Categorical variables such as angiosperm vs. gymnosperm or deciduousness tended to improve relationships between nutrient litterfall and climate and latitudinal gradients. Overall we show reproductive litterfall fluxes of N and P are important components of litterfall and should be continued to be studied in the context of biogeochemical cycling and plant nutrient limitation.

TABLES

Table 4.1 Summary of univariate regression models for N & P fluxes, concentrations, N:P for leaf and reproductive litterfall and the proportion of N and P in reproductive litterfall relative to the sum of reproductive and leaf litterfall fluxes.

Response variable	Explanatory variable	Equation	p-value	R^2
Leaf				
Nitrogen Flux (g N m^{-2} yr^{-1})	MAT	0.17 * MAT + 1.98	$p<0.001$	0.20
	MAP	1.1 E-3 * MAP + 2.85	$p<0.001$	0.12
	Latitude	-8.12 E-2 * Lat + 7.01	$p<0.001$	0.19
Phosphorus Flux (g P m^{-2} yr^{-1})	MAT	3.1 E-3 * MAT + 0.17	$p<0.01$	0.03
	MAP	1.1 E-5 * MAP + 0.20	n.s.	-
	Latitude	-6.7 E-4 * Lat + 0.23	n.s.	-
N:P	MAT	0.16 * MAT + 38	n.s.	-
	MAP	5.3 E-3 * MAP + 32	$p<0.001$	0.08
	Latitude	-0.30 * Lat + 40	$p<0.001$	0.05
%N	MAT	7.2 E-3 * MAT + 0.95	$p<0.01$	0.02
	MAP	2.2 E-5 * MAP + 1.0	n.s.	-
	Latitude	-3.5 E-3 * Lat + 1.17	$p<0.01$	0.02
%P	MAT	4.9 E-4 * MAT + 0.072	n.s.	-
	MAP	-8.0 E-6 * MAP + 7.4E-2	$p<0.001$	0.05
	Latitude	4.4 E-4 * Lat + 5.0 E-2	$p<0.001$	0.04
Reproductive				
Nitrogen Flux (g N m^{-2} yr^{-1})	MAT	0.02 * MAT + 0.32	$p<0.001$	0.06
	MAP	1.2 E-4 * MAP + 0.38	$p<0.001$	0.09
	Latitude	-9.5 E-3 * Lat + 0.82	$p<0.001$	0.09
Phosphorus Flux (g P m^{-2} yr^{-1})	MAT	7.2 E-4 * MAT + 1.9 E-2	$p<0.01$	0.04
	MAP	8.0 E-6 * MAP + 2.0 E-2	$p<0.001$	0.09
	Latitude	-4.9 E-4 * Lat + 4.4 E-2	$p<0.001$	0.09

N:P	MAT	0.13 * MAT + 0.27	n.s.	-
	MAP	2.2 E-3 * MAP + 25	p<0.05	0.04
	Latitude	2.6 E-2 * Lat	n.s.	-
%N	MAT	2.6 E-2 * MAT +0.71	p<0.001	0.11
	MAP	5.9 E-5 * MAP + 1.1	n.s.	-
	Latitude	-1.3 E-2 * Lat + 1.48	p<0.001	0.11
%P	MAT	1.7 E-3 * MAT + 5.8 E-2	p<0.01	0.07
	MAP	1.5 E-6 * MAP + 8.4 E-2	n.s.	-
	Latitude	-7.9 E-4 * Lat + 0.10	p<0.01	0.06
Reproductive / Leaf + Reproductive				
Nitrogen	MAT	-2.8 E-6 * MAT + 0.13	n.s.	-
	MAP	1.2 E-5 * MAP + 0.11	n.s.	-
	Latitude	-9.7 E-4 * Lat + 0.16	n.s.	-
Phosphorus	MAT	-7.7 E-4 * MAT + 0.15	n.s.	-
	MAP	4.2 E-5 * MAP + 9.8 E-2	p<0.001	0.11
	Latitude	-3.3 E-3 * Lat + 0.24	p<0.001	0.10

Table 4.2 Summary of best fit models based on backwards variable selection for reproductive litterfall nitrogen and phosphorus fluxes and concentrations, N:P , and the proportion of N and P in reproductive litterfall relative to the sum of reproductive and leaf litterfall fluxes.

Reproductive N flux ~ MAP + Latitude + Deciduousness + Latitude:Deciduousness					
	Coefficients	Std. Error	t-value	p-value	Significance
(Intercept)	-3.28E-02	2.14E-01	-0.1536	0.8781135	
MAP	8.05E-05	3.73E-05	2.1593	0.0320993	*
Latitude	1.79E-02	4.96E-03	3.6007	0.0004065	***
Deciduous (Evergreen)	7.96E-01	2.11E-01	3.7742	0.0002154	***
Deciduous (Mixed)	1.00E+00	2.53E-01	3.9569	0.0001077	***
Deciduous (Unknown)	2.10E-01	2.90E-01	0.7267	0.4682945	
Latitude:Deciduous (Evergreen)	-3.12E-02	5.63E-03	-5.5395	1.02E-07	***
Latitude:Deciduous (Mixed)	-3.67E-02	7.30E-03	-5.0318	1.14E-06	***
Latitude:Deciduous (Unknown)	5.91E-03	1.94E-02	0.3051	0.7606152	
Signif. Codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1					
Multiple R-squared (Robust): 0.2541064					
Reduction in Dispersion Test: 7.96325 p-value: 0					
Reproductive P flux ~ MAP + Latitude + Deciduousness + Latitude:Deciduousness					
	Coefficients	Std. Error	t-value	p-value	Significance
(Intercept)	8.10E-03	1.29E-02	0.6273	0.5313373	
MAP	6.06E-06	2.25E-06	2.69	0.0079073	**
Latitude	6.96E-04	3.04E-04	2.2892	0.0233837	*
Deciduous (Evergreen)	3.17E-02	1.24E-02	2.5537	0.0115973	*
Deciduous (Mixed)	3.97E-02	1.50E-02	2.6523	0.0088047	**
Deciduous (Unknown)	-2.94E-03	1.59E-02	-0.1851	0.853403	
Latitude:Deciduous (Evergreen)	-1.37E-03	3.49E-04	-3.924	0.0001294	***
Latitude:Deciduous (Mixed)	-1.60E-03	4.45E-04	-3.5884	0.0004425	***

Latitude:Deciduous (Unknown)	7.09E-04	1.07E-03	0.665	0.506997	
Signif. Codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1					
Multiple R-squared (Robust): 0.2322694					
Reduction in Dispersion Test: 6.01299 p-value: 0					
Reproductive %N ~ Phylogeny					
	Coefficients	Std. Error	t-value	p-value	Significance
(Intercept)	1.3	0.053475	24.3104	< 2.2e-16	***
Phylogeny (Gymnosperm)	-0.593796	0.09307	-6.3801	1.56E-09	***
Phylogeny (Mixed)	-0.114637	0.151567	-0.7563	0.4505	
Phylogeny (Unknown)	0.063275	0.228592	0.2768	0.7823	
Signif. Codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1					
Multiple R-squared (Robust): 0.2354016					
Reduction in Dispersion Test: 17.75419 p-value: 0					
Reproductive %P ~ Latitude + Deciduousness					
	Coefficients	Std. Error	t-value	p-value	Significance
(Intercept)	0.13858637	0.01343249	10.3172	< 2.2e-16	***
Latitude	-0.00106509	0.00026844	-3.9676	0.0001134	***
Deciduous (Evergreen)	-0.03389741	0.0096115	-3.5268	0.0005626	***
Deciduous (Mixed)	-0.02264614	0.01260786	-1.7962	0.0745318	.
Deciduous (Unknown)	-0.05491957	0.01908777	-2.8772	0.0046142	**
Signif. Codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1					
Multiple R-squared (Robust): 0.1525719					
Reduction in Dispersion Test: 6.5715 p-value: 7e-05					
Repro N:P ~ Latitude + Phylogeny + Deciduousness					
	Coefficients	Std. Error	t-value	p-value	Significance
(Intercept)	14.731365	2.972604	4.9557	2.00E-06	***
Phylogeny (Gymnosperm)	-11.272223	2.235283	-5.0429	1.36E-06	***
Phylogeny (Mixed)	1.789202	3.380173	0.5293	0.5973967	
Phylogeny (Unknown)	10.943857	4.252435	2.5736	0.0110765	*

Latitude	0.284852	0.067706	4.2072	4.53E-05	***
Deciduous (Evergreen)	8.835968	2.215214	3.9888	0.0001053	***
Deciduous (Mixed)	3.363893	3.111862	1.081	0.2815084	
Deciduous (Unknown)	13.250961	4.390291	3.0182	0.0030077	**
Signif. Codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1					
Multiple R-squared (Robust): 0.2079525					
Reduction in Dispersion Test: 5.40104 p-value: 2e-05					
Relative Reproductive N Flux to Reproductive and Leaf ~ Latitude * Deciduousness					
	Coefficients	Std. Error	t-value	p-value	Significance
(Intercept)	-0.00610673	0.03903019	-0.1565	0.875843	
Latitude	0.00435005	0.00097581	4.4579	1.45E-05	***
Deciduous (Evergreen)	0.17557884	0.04143762	4.2372	3.60E-05	***
Deciduous (Mixed)	0.18388414	0.05004585	3.6743	0.000314	***
Deciduous (Unknown)	0.13952855	0.05492876	2.5402	0.01192	*
Latitude:Deciduous (Evergreen)	-0.00660038	0.00111425	-5.9236	1.55E-08	***
Latitude:Deciduous (Mixed)	-0.00717222	0.0014464	-4.9587	1.63E-06	***
Latitude:Deciduous (Unknown)	-0.00375516	0.00372009	-1.0094	0.314117	
Signif. Codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1					
Multiple R-squared (Robust): 0.1773667					
Reduction in Dispersion Test: 5.57502 p-value: 1e-05					
Relative Reproductive P Flux to Reproductive and Leaf ~ MAT + MAP + Latitude + MAT:Latitude + MAP:Latitude					
	Coefficients	Std. Error	t-value	p-value	Significance
(Intercept)	1.24E-01	6.20E-02	1.9975	0.0475165	*
MAT	7.78E-03	2.61E-03	2.9813	0.0033346	**
MAP	-1.47E-05	1.47E-05	-0.9997	0.3190251	
Latitude	7.08E-04	1.57E-03	0.4501	0.6532723	
MAT:Latitude	-4.73E-04	8.61E-05	-5.4992	1.54E-07	***
MAP: Latitude	2.24E-06	6.03E-07	3.709	0.0002894	***

Signif. Codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Multiple R-squared (Robust): 0.2893428
Reduction in Dispersion Test: 12.62159 p-value: 0

FIGURES

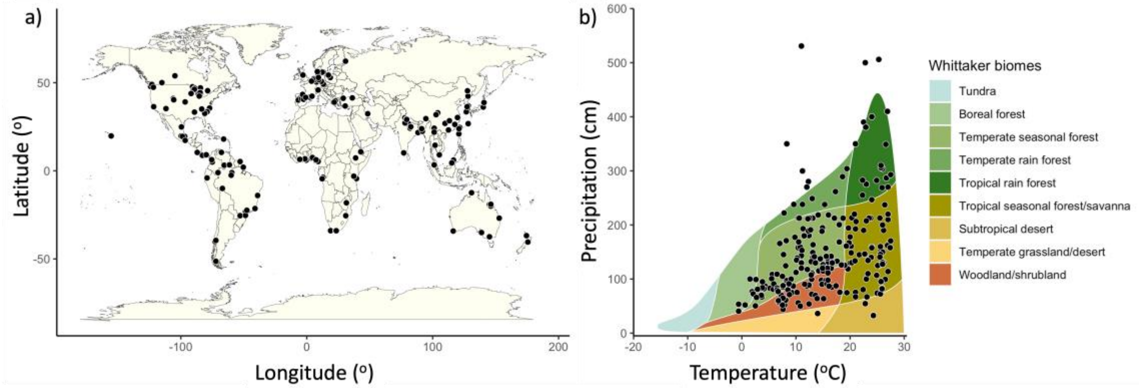

Figure 4.1. a) Map showing geographic location of sites included in analysis b) Site mean annual temperature and precipitation plotted on top of Whittaker classification of Earth's biomes.

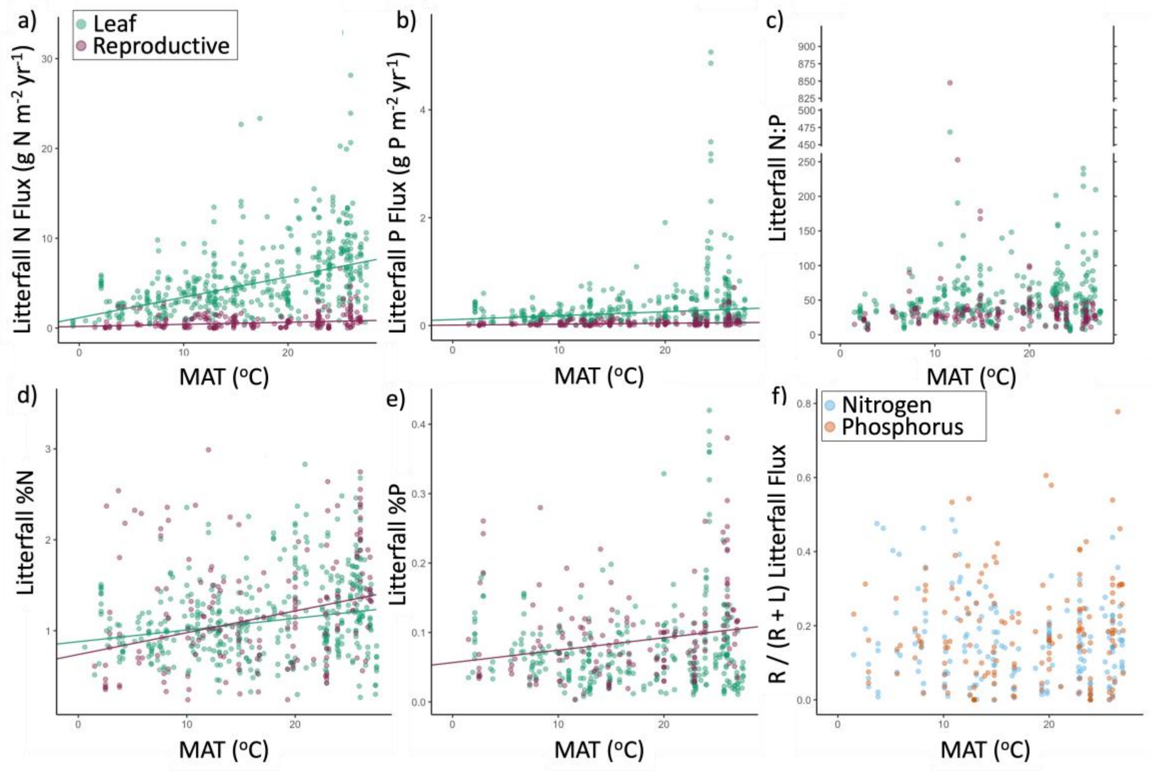

Figure 4.2. Scatter plots of mean annual temperature (°C) plotted against a) litterfall N flux, b) litterfall P flux, c) litterfall N:P, d) litterfall %N, e) litterfall %P, and f) reproductive / (reproductive + leaf) litterfall N and P fluxes. In (a-e) green symbols represent leaf litterfall, red symbols represent reproductive litterfall. In (f) blue symbols represent nitrogen and orange symbols represent phosphorus. Significant relationships indicated by inclusion of rank-based regression line, model equations are provided in Table 4.1.

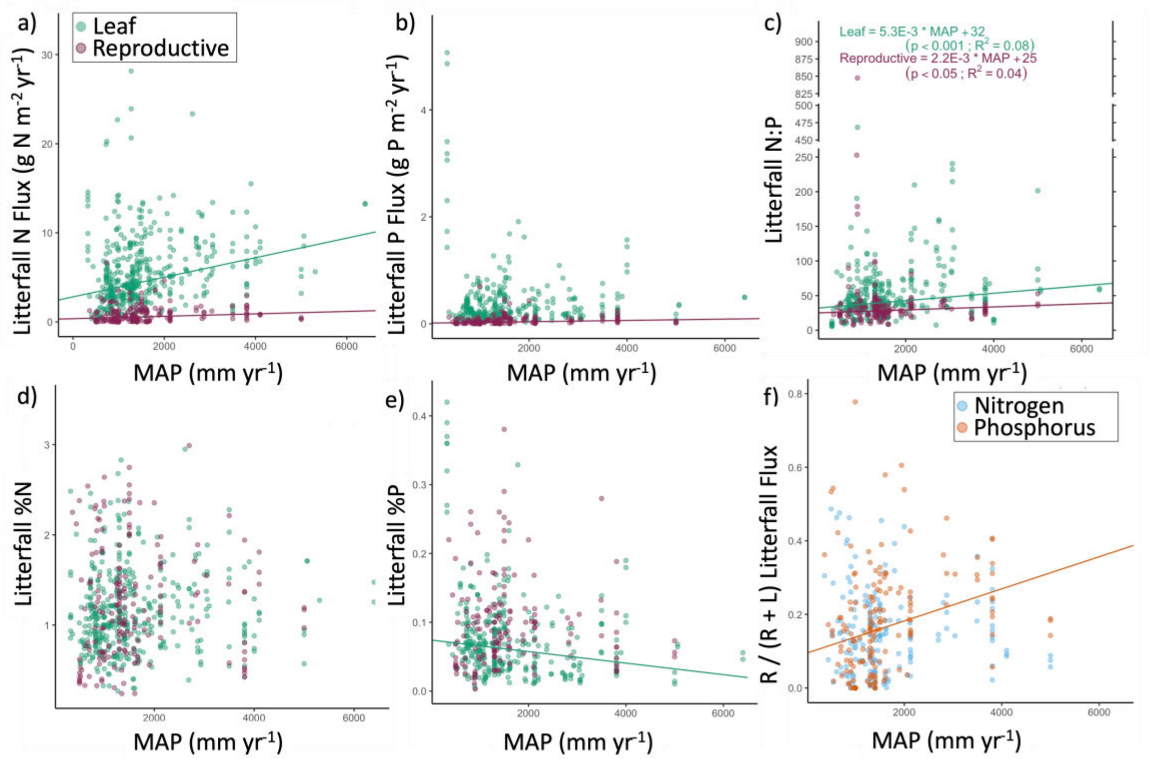

Figure 4.3. Scatter plots of mean annual precipitation (mm yr^{-1}) plotted against a) litterfall N flux, b) litterfall P flux, c) litterfall N:P, d) litterfall %N, e) litterfall %P, and f) reproductive / (reproductive + leaf) litterfall N and P fluxes. In (a-e) green symbols represent leaf litterfall, red symbols represent reproductive litterfall. In (f) blue symbols represent nitrogen and orange symbols represent phosphorus. Significant relationships indicated by inclusion of rank-based regression line, model equations are provided in Table 4.1.

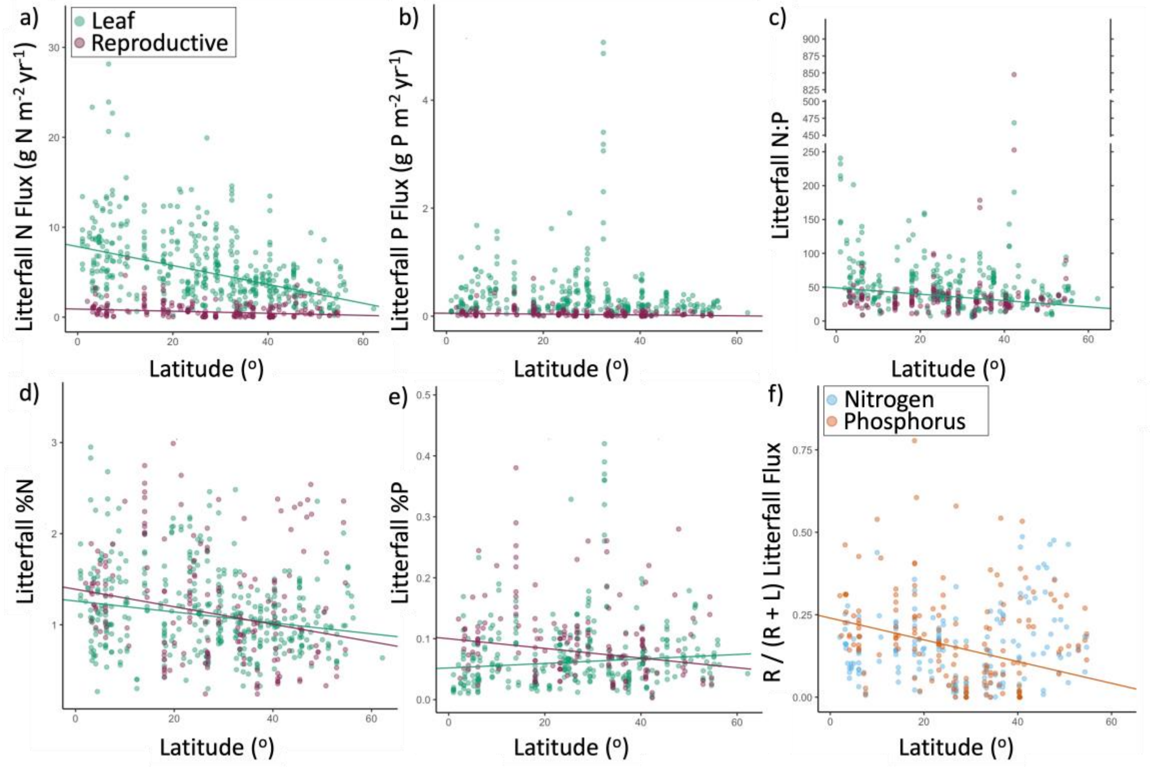

Figure 4.4. Scatter plots of the absolute value of latitude (º) plotted against a) litterfall N flux, b) litterfall P flux, c) litterfall N:P, d) litterfall %N, e) litterfall %P, and f) reproductive / (reproductive + leaf) litterfall N and P fluxes. In (a-e) green symbols represent leaf litterfall, red symbols represent reproductive litterfall. In (f) blue symbols represent nitrogen and orange symbols represent phosphorus. Significant relationships indicated by inclusion of rank-based regression line, model equations are provided in Table 4.1.

SUPPORTING INFORMATION

Supporting Information 4.1

We conducted a Web of Science search of “All Databases" on July 18, 2022 for the following search terms: litterfall AND (reproduct* OR seed* OR flower* OR cone*) AND (nitrogen OR phosphorus OR nutrien* OR element*)) OR TS=(litter-fall AND (reproduct* OR seed* OR flower* OR cone*) AND (nitrogen OR phosphorus OR nutrien* OR element*)) OR TS=("litter fall" AND (reproduct* OR seed* OR flower* OR cone*) AND (nitrogen OR phosphorus OR nutrien* OR element*)) OR TS=("annual litterfall" AND (nitrogen OR phosphorus OR nutrien* OR element*)) OR TS=("annual litter fall" AND (nitrogen OR phosphorus OR nutrien*OR element*)) OR TS=("annual litter-fall" AND (nitrogen OR phosphorus OR nutrien* OR element*)) OR TS=("annual production" litterfall AND (nitrogen OR phosphorus OR nutrien* OR element*)) OR TS=("annual production" litter fall AND (nitrogen OR phosphorus OR nutrien* OR element*)) OR TS=("annual production" litter-fall AND (nitrogen OR phosphorus OR nutrien* OR element*)) OR TS=("leaf litter fall" AND (nitrogen OR phosphorus OR nutrien*OR element*)) OR TS=("leaf litter-fall" AND (nitrogen OR phosphorus OR nutrien* OR element*)) OR TS=("leaf litterfall" AND (nitrogen OR phosphorus OR nutrien* OR element*)) OR TS=("foliar litter fall" AND (nitrogen OR phosphorus OR nutrien*OR element*)) OR TS=("foliar litter-fall" AND (nitrogen OR phosphorus OR nutrien* OR element*)) OR TS=("foliar litterfall" AND (nitrogen OR phosphorus OR nutrien* OR element*))

Supporting Table 4.1. List of papers used in the data synthesis, including the number of sites reported in each paper, latitude, longitude, MAT, and MAP. For variables reported LN and RN represent leaf and reproductive litterfall nitrogen, respectively. LP and RP represent leaf and reproductive phosphorus, respectively.

Authors	Year	Number of sites	Variables Reported	Latitude (°)	Longitude (°)	MAT (°C)	MAP (mm/yr)
Achilles et al	2021	2	LN RN	50.76	11.61	8.1	611
Aranguren	1982	1	LN RN	10.46	-67.76	25	740
Arthur and Fahey	1991	1	LN LP RN RP	40.30	-105.64	1.5	1000
Ashton	1975	2	LN LP	-37.40	145.20	12.1	1177
Asigbaase et al	2021	2	LN LP	6.04	-0.46	25.7	1527
Astel et al	2009	2	LN LP RN RP	54.68	17.30	7.3	700
Baek et al	2019	1	LN LP RN RP	35.21	128.17	13.1	1490
Bahamonde et al	2015	4	LN LP	-51.22	-72.25	6.75	600
				-51.32	-72.16		
Becker et al	2015	6	LN LP	-3.06	37.35	17.3	2616
						20.9	1336
						20.2	1485
						15.3	2378
						11.2	2998
						9.8	1773
Bernal et al	2003	1	LN	41.70	-2.40	10.4	561
Bernhard-Reversat	1993	5	LN RN	-3.72	12.98	25.3	1250
Brechet	2009	1	LN LP	5.30	-52.88	26	3041
Brinson et al	1980	1	LN LP RN RP	35.58	-77.17	15	1266
Brumme et al	2021	1	LN LP RN RP	50.40	7.72	8.3	971
Bubb et al	1998	3	LN	-26.52	152.60	19.6	1188
Bunyavejchewin et al	1997	2	LN LP RN RP	14.52	101.92	26.2	1305
Bussotti et al	2003	2	LN LP RN RP	10.45	43.51	14.7	978
				10.80	42.86	15.1	637
Cakir and Akburak	2017	3	LN LP	41.17	28.97	13	1121
Callaway and Nadkarni	1991	1	LN LP RN RP	36.38	-121.56	12.4	540
Cantu Silva et al	2013	2	LN LP RP	24.72	-99.86	13.9	639
				24.74	-99.74	21	755

Carlisle et al	1966	1	LN LP RN RP	54.33	-3.02	8.2	1710
Celentano et al	2011	4	LN LP	8.77	-82.94	21	3500
Chaturvedi and Singh	1987	1	LN LP	29.37	79.58	14.1	2185
Chuyong et al	2000	2	LN LP	5.00	9.00	25.3	5060
Coomes	1997	3	LN LP RN RP	3.17	-65.55	26.7	2869
Cormier et al	2013	6	LN	33.49	-79.16	17.6	1330
				32.16	-81.13	19	1255
Cragg et al	1977	1	LN LP	50.03	-115.05	2.7	660
Cuevas and Lugo	1998	10	LN LP RN RP	18.00	-66.00	22.9	3807
Dawoe et al	2010	4	LN	6.81	-1.42	25.6	1454
Demessie et al	2012	7	LN	7.30	38.80	15.5	973
Dziadowiec and Pichta	1985	1	LN LP	53.67	18.25	6.8	574
Edmonds and Murray	2002	2	LN LP RN RP	47.83	-124.00	8.3	3500
Egunjobi	1974	1	LN LP RN RP	7.16	3.86	27	1140
Enright	2001	1	LN LP RN RP	-36.94	174.52	14.5	1375
Erkan et al	2020	1	LN LP RN RP	36.78	30.54	16.6	849
Fahey	1983	6	RN RP	41.00	-106.00	2.5	504
Fassnacht and Gower	1999	6	LN	45.86	-90.06	4.1	822
Ferrari et al	1999	1	LN RN	46.25	-89.25	3.8	840
Finer	1996	1	LN LP	62.20	30.80	1.9	766
Fontes et al	2014	9	LN LP RN RP	-14.00	-39.03	26	1500
Frangi and Lugo	1985	1	LP RP	18.40	-65.75	19.7	1943
Gallardo et al	1998	5	LN LP RN RP	40.32	-6.72	12.9	720
						12.5	872
						8.1	1245
						10.4	1580
						14.2	1152
Garg	1992	4	LN LP RN RP	26.70	80.80	25.7	954
Ghosh et al	1990	1	LN LP RN RP	21.68	88.33	26.2	1900
Goma-Tchimbakala and Bernhard-Reversat	2006	4	LN	-4.50	12.23	25.1	1250

Gonzalez	2012	1	LN LP RN RP	41.65	-0.86	14	363
Gonzalez-Rodriquez et al	2011, 2018, 2019	4	LN LP RP	24.72	-99.86	13.9	639
				24.74	-99.74	21	755
				24.78	-99.53	22.4	805
				24.90	-99.53	21	672
Gordon et al	2000	3	LN LP RN	45.47	-78.72	3.8	950
Gower and Son	1992	5	LN	43.86	-91.85	6.5	835
Guo and Sims	1999	8	LN LP RN RP	-40.40	175.60	12.9	995
Guo et al	2022	1	LN	29.60	94.60	0.6	521
Haines	1978	1	LN LP	9.15	-79.70	26.4	2373
Hansen et al	2009	3	LN LP	55.95	12.35	7.6	648
				55.16	8.88	7.6	890
				56.28	8.42	7.6	878
Hemati et al	2017	2	LN	3.66	100.96	27.5	1705.5
				3.33	101.23		
Herbohn and Congdon	1998	3	LN LP RN RP	-19.00	146.20	23.3	1344
Hinesley et al	1991	4	LN LP RN RP	33.30	-89.16	16.7	1300
Hojjati et al	2009	2	LN LP	51.78	9.62	6.5	1090
Inagaki et al	2012	2	LN RN	36.17	140.17	13.1	1400
Jasinska et al	2020	2	LN LP RN RP	52.92	18.70	7.9	522.5
Jha et al	2010	4	LN LP	27.16	78.03	25.6	725
Jonczak et al	2016	1	LN LP RN RP	54.32	17.17	7.6	440
Joshi et al	1997	9	LN LP RN RP	29.00	79.55	23.9	1400
Kaspari et al	2008	1	LN LP	9.10	-79.83	26.4	2373
Killingbeck	1986	1	LN LP RN RP	39.08	-96.58	12.1	866
Kim et al	2011	1	LN	35.44	127.63	12.8	1322
Kim et al	1996	2	LN LP	44.52	-84.75	6.7	770
Kitayama et al	2015	9	LN LP RN RP	6.08	116.55	23.8	2126
						18.7	2126
						13.1	2126
						10.4	2126
						23.5	2126
						17.1	2126

						12.5	2126
						10.6	2126
						17.1	2126
Klemmedson et al	1990	1	LN LP	35.30	-111.80	7.5	520
Knoepp et al	2018	4	LN	35.06	-83.43	12.3	1890
						12.7	1910
						11.2	2380
						9.6	2380
Koopmans et al	1998	2	LN	52.22	5.65	9.25	750
				51.50	5.92	9.25	750
Kopacek et al	2010	4	LN LP RN RP	48.78	13.87	5.6	1085
				48.77	13.86	5.6	1085
				49.16	13.20	5.5	1007
				49.17	13.19	5.9	910
Kulmann et al	2021	2	LN LP	-25.46	-52.91	20	1780
Kusumoto and Enoki	2008	1	LN	26.73	128.23	22.3	2550
Kutbay et al	2001	1	LN LP RN RP	41.38	36.18	13.6	698
Lavery et al	2004	2	LN LP	49.00	-123.00	10	1123
Lee and Correll	1978	1	LN LP	-35.02	138.77	12.8	1077
Liao et al	2006	4	LN LP	20.96	120.80	23	2753
Lin et al	2015	1	LN	51.76	9.56	7.6	877
Lin et al	2003	1	LN LP	24.56	121.56	18.6	2893
Lips et al	1996	5	LN LP	-1.00	-70.50	25.7	3060
Liu et al	2003	1	LN LP RN RP	24.16	101.20	11.3	1931
Lodge et al	1991	3	LN LP	18.28	-65.78	24	2467
Lodhiyal and Lodhiyal	1997	1	LN LP	29.13	79.36	24	1577
Lodhiyal et al	1994	2	LN LP	29.13	79.35	24	1593
Lu and Liu	2012	3	LN LP RN RP	24.07	121.13	12.3	2802.5
				24.08	121.03	19.4	3041.1
				23.93	120.89	20.3	2132.5
Lucas et al	1993	1	LP RP	-2.39	-60.00	27	2100
Lugo et al	2007	1	LN LP RN RP	17.96	-66.22	26.5	994
Macinnis-Ng and Schwendenmann	2015	1	LN RN	-36.78	174.48	14.9	1200
Maggs	1985	1	LN LP RN RP	-26.83	153.03	20.2	1609

Martin et al	1996	1	LN LP RN RP	40.96	-5.82	10.8	500
Martinez-Alonso et al	2007	1	LN LP	40.82	-4.01	9.1	1000
Masuda et al	2021	3	LN	38.75	140.75	10.5	1687
Mayor and Roda	1992	1	LN LP	41.77	2.35	9.5	870
McGrath et al	2000	1	LN LP RN RP	-10.00	-67.00	26	2000
McIvor	2001	2	LN LP RN RP	-19.12	145.13	22.8	546
				-20.03	146.12	23.1	670
Mehra et al	1985	6	LN LP	29.12	79.72	23	2076
				29.35	79.48	18	2005
				29.38	79.47	16	2185
				29.63	79.45	16	1313
				29.42	79.45	13	2488
				29.42	79.45	13	2488
Michopoulos et al	2020	2	LN LP	39.70	22.65	12.4	1804
Michopoulos et al	2021	2	LN LP	38.86	21.17	15.1	1213
				38.94	21.83	11	1433
Mo et al	1995	1	LN LP	23.17	112.55	21	1927
Molinero and Pozo	2004	2	LN LP RN RP	43.34	-3.31	13.4	1414
Montagnini	1993	4	LN LP	10.43	-86.98	24	4000
Morrison	1990	1	LN LP RN RP	47.05	-84.42	2.6	992
Mtambanengwe	1999	1	LN	-18.16	31.50	17.4	875
Mun et al	2007	3	LN LP RN RP	36.85	128.00	10.1	1349.8
				36.00	128.00		
				36.85	128.20		
Muoghalu et al	1993	2	LN LP RN RP	7.53	4.53	26	1305
Muqaddas and Lewis	2020	3	LN RN	-26.87	152.85	19.8	1670
Murbach et al	2003	1	LN LP	-22.40	-47.55	20.3	1304
Murovhi et al	2012	3	LN LP	-25.45	30.96	19.4	748
Newbery et al	1997	2	LN LP	5.28	9.04	24.9	2824
Nga et al	2005	4	LN LP	9.06	105.28	27.5	2930
Ni et al	2021	3	LN LP RN RP	26.32	117.58	19.3	1610
Nilsson	1978	1	LN LP	55.98	13.17	6.5	800
O’Connell and Manage	1982	5	LN LP RN RP	-34.18	116.30	14.8	903

Okeke and Omaliku	1994	1	LN LP RN RP	6.25	7.40	25.6	1600
Osman et al	1997	1	LN LP	22.39	91.84	25.9	2690
Park et al	2019	1	LN RN	35.21	128.17	13.15	1635
Park et al	2020	4	LN LP RN RP	33.30	126.26	15.5	1569
				33.50	126.71	14.8	1883
				36.36	127.35	13.6	1299
Pedersen and Billie-Hansen	1999	3	LN LP	55.21	8.96	8.5	800
Pendry and Proctor	1996	3	LN RN	4.50	115.17	26.9	4100
Pereira et al	2016	2	LN LP	-1.04	-59.50	27	2200
Polglase and Attiwill	1992	7	LN LP	-37.50	145.60	11	1300
Polglase et al	1986	4	LN LP	-37.40	145.10	13	1100
Pregitzer and Burton	1991	5	LN RN	47.68	-90.73	3.7	670
				46.87	-88.88	4.3	870
				45.55	-84.85	5.2	830
				44.38	-85.83	5.8	810
				43.67	-86.15	7.6	850
Proctor et al	1983	3	LN LP RN RP	4.10	114.91	22.8	5000
Quichimbo et al	2020	2	LN LP	-4.05	-79.18	15.7	912
Ramirez et al	2014	3	LN LP	6.30	-75.50	14.9	1948
Robles et al	2011	2	LN LP	17.27	-96.55	18.1	756
Rode	1993	2	LN LP	52.96	9.25	8.8	712
Russell et al	2004	1	LN	42.40	-85.40	8.7	912
Salazar and Santa Regina	2005	2	LN LP RN RP	40.57	-2.50	10.8	1590
						11.1	1530
Santa Regina	2000	1	LN LP RN RP	40.13	-6.71	15	1150
Santa-Regina and Tarazona	2000	2	LN LP RN RP	42.33	4.16	12.4	890
						11.6	905
Sayad et al	2012	8	LN LP	32.40	48.42	24.3	325.8
Scott et al	1993	1	LN LP RN RP	2.04	-50.40	26.6	3490
Shin et al	2011	1	LN LP RN RP	36.86	128.21	10.1	1349.8
Shure and Gottschalk	1985	4	LN	32.60	-81.00	18.4	1261
Singh	1992	3	LN LP	25.00	82.64	25.9	821
Singh et al	1999	4	LN LP	24.19	82.00	24.9	1069

Singh et al	1994	2	LN LP	30.10	77.90	23.3	1100
Singh et al	1994	4	LN LP	29.40	79.15	22.7	1464
Slim	1996	1	LN	-4.42	39.50	26	1271
Sloboda et al	2017	1	LN LP RN RP	-25.30	-48.67	21.1	2063
Staelens et al	2011	1	LN LP RN RP	50.87	3.76	10.2	754
Staelens et al	2005	2	LN	-40.12	-72.85	7	1658
				-39.50	-72.15	11	5308
Suo et al	2016	1	LN LP	42.38	128.08	3.6	700
Swamy and Proctor	1994	4	LN LP	10.19	77.00	22.5	6400
						22.5	3900
						22.5	1900
						22.5	6400
Torres-Duque	2022	2	LN LP	19.74	-99.76	7.5	1050
				19.49	-98.73		
Tripathi and Singh	1995	2	LN LP	25.04	82.63	25.9	830
Turner and Olson	1976	1	LN	47.40	-121.80	7.8	2221
Van Langenhove et al.	2020	1	LN LP	5.25	-52.92	25.7	3100
Vargas et al	2019	9	LN LP RN RP	-23.17	-48.67	20	1300
Vasconcelos and Luizao	2004	2	LN LP	-2.50	-60.00	27	2700
Veneklaas	1991	2	LN LP RN RP	5.00	-75.00	12.2	2115
						7.7	1453
Verghese et al	2001	1	LN LP	23.88	91.25	25.5	2128
Versfeld	1991	1	LN LP RN RP	-33.96	18.93	15.8	1390
Villela and Proctor	1999	3	LN LP RN RP	3.37	-61.43	26.9	1622
Villela et al	2006	2	LN RN	-21.40	-41.10	23	1000
Vogel and Gower	1998	4	LN	53.90	-104.68	-0.6	536
Wang et al	2010	2	LN LP RN RP	26.75	109.50	16.5	1200
Wang et al	2008	2	LN LP	26.90	109.80	15.8	1200
Wang et al	2022	9	LN LP	45.40	127.66	2.1	726
Wang et al	2013	1	LN LP	23.90	120.90	20.8	2200
Weinand and Stock	1995	3	LN LP	-33.90	23.03	15.9	1113
				-33.98	23.10	15.9	980
				-33.98	23.42	16.1	868

Williams-Linera et al	2021	4	LN	19.50	-96.93	18	1685
Won et al	2018	1	LN LP RN RP	36.85	128.20	10.2	1387.8
Woodroffe et al	1988	3	LN LP	-12.43	130.86	27.4	1580
Wu et al	2021	1	LN LP	31.85	102.68	8	913
Xu et al	2004	1	RN RP	26.75	128.16	22.3	2827
Yamashita et al	2010	1	LN RN	14.50	101.92	25.5	1407
Yang et al	2006	3	LN LP RN RP	32.90	104.00	2.9	813
Yao et al	2021	3	LN LP	6.50	-5.52	26	1275
Yelenik et al	2022	2	LN RN	19.79	-155.32	12	2700
Zeng et al	2017	1	LN LP	28.40	113.30	16.5	1420
Zhang et al	2017	2	LN LP	30.23	119.70	15.6	1420
Zheng et al	2006	1	LN LP RN RP	21.93	101.18	21.7	1450
Zimmerman et al	2002	2	LN RN	46.15 45.86	9.00 9.03	11.5	1800

Supporting Table 4.2 Details of the backwards variable selection for reproductive litterfall nitrogen and phosphorus fluxes and concentrations, N:P , and the proportion of N and P in reproductive litterfall relative to the sum of reproductive and leaf litterfall fluxes.

Reproductive N flux			
Model	p-val	R^2	Step
Reproductive N flux ~ MAT + MAP + Latitude + Phylogeny + Deciduousness + Forest vs. Plantation	$p<0.001$	0.15	Remove MAT
Reproductive N flux ~ MAP + Latitude + Phylogeny + Deciduousness + Forest vs. Plantation	$p<0.001$	0.15	Remove Forest vs. Plantation
Reproductive N flux ~ MAP + Latitude + Phylogeny + Deciduousness	$p<0.001$	0.15	Remove Phylogeny
Reproductive N flux ~ MAP + Latitude + Deciduousness	$p<0.001$	0.14	Add pairwise
Reproductive N flux ~ MAP + Latitude + Deciduousness + MAP:Latitude + MAP:Deciduousness + Latitude:Deciduousness	$p<0.001$	0.27	Remove MAP:Latitude
Reproductive N flux ~ MAP + Latitude + Deciduousness + MAP:Deciduousness + Latitude:Deciduousness	$p<0.001$	0.27	Remove MAP:Deciduousness
Reproductive N flux ~ MAP + Latitude + Deciduousness + Latitude:Deciduousness	$p<0.001$	0.25	Stop
Reproductive P flux			
Model	p-val	R^2	Step
Reproductive P flux ~ MAT + MAP + Latitude + Phylogeny + Deciduousness + Forest vs. Plantation	$p<0.01$	0.14	Remove MAT
Reproductive P flux ~ MAP + Latitude + Phylogeny + Deciduousness + Forest vs. Plantation	$p<0.01$	0.14	Remove Forest vs. Plantation
Reproductive P flux ~ MAP + Latitude + Phylogeny + Deciduousness	$p<0.01$	0.13	Remove Phylogeny
Reproductive P flux ~ MAP + Latitude + Deciduousness	$p<0.001$	0.13	Add pairwise

Reproductive P flux ~ MAP + Latitude + Deciduousness + MAP: Latitude + MAP:Deciduousness + Latitude:Deciduousness	$p<0.001$	0.27	Remove MAP:Lat
Reproductive P flux ~ MAP + Latitude + Deciduousness + MAP:Deciduousness + Latitude:Deciduousness	$p<0.001$	0.27	Remove MAP:Deciduousness
Reproductive P flux ~ MAP + Latitude + Deciduousness + Latitude:Deciduousness	$p<0.001$	0.23	Stop
Reproductive %N			
Model	p-val	R^2	Step
Reproductive %N ~ MAT + MAP + Latitude + Phylogeny + Deciduousness + Forest vs. Plantation	$p<0.001$	0.29	Remove MAT
Reproductive %N ~ MAP + Latitude + Phylogeny + Deciduousness + Forest vs. Plantation	$p<0.001$	0.29	Remove Forest vs. Plantation
Reproductive %N ~ MAP + Latitude + Phylogeny + Deciduousness	$p<0.001$	0.28	Remove MAP
Reproductive %N ~ Latitude + Phylogeny + Deciduousness	$p<0.001$	0.27	Remove Deciduousness
Reproductive %N ~ Latitude + Phylogeny	$p<0.001$	0.24	Remove Latitude
Reproductive %N ~ Phylogeny	$p<0.001$	0.24	Stop
Reproductive %P			
Model	p-val	R^2	Step
Reproductive %P ~ MAT + MAP + Latitude + Phylogeny + Deciduousness + Forest vs. Plantation	$p<0.001$	0.19	Remove Forest vs. Plantation
Reproductive %P ~ MAT + MAP + Latitude + Phylogeny + Deciduousness	$p<0.001$	0.19	Remove Phylogeny
Reproductive %P ~ MAT + MAP + Latitude + Deciduousness	$p<0.001$	0.18	Remove MAP
Reproductive %P ~ MAT + Latitude + Deciduousness	$p<0.001$	0.15	Remove MAT
Reproductive %P ~ Latitude + Deciduousness	$p<0.001$	0.15	Stop, pairwise not significant
Reproductive N:P			
Model	p-val	R^2	Step

Repro N:P ~ MAT + MAP + Latitude + Phylogeny + Deciduousness + Forest vs. Plantation	p<0.001	0.23	Remove Forest vs. Plantation
Repro N:P ~ MAT + MAP + Latitude + Phylogeny + Deciduousness	p<0.001	0.23	Remove MAT
Repro N:P ~ MAP + Latitude + Phylogeny + Deciduousness	p<0.001	0.22	Remove MAP
Repro N:P ~ Latitude + Phylogeny + Deciduousness	p<0.001	0.21	Stop, pairwise not significant
Relative Reproductive N Flux to Reproductive and Leaf			
Model	p-val	R^2	Step
Relative Reproductive N Flux to Reproductive and Leaf ~ MAT + MAP + Latitude + Phylogeny + Deciduousness + Forest vs. Plantation	n.s.	0.06	Remove Forest vs. Plantation
Relative Reproductive N Flux to Reproductive and Leaf ~ MAT + MAP + Latitude + Phylogeny + Deciduousness	n.s.	0.06	Remove Phylogeny
Relative Reproductive N Flux to Reproductive and Leaf ~ MAT + MAP + Latitude + Deciduousness	n.s.	0.06	Remove MAP
Relative Reproductive N Flux to Reproductive and Leaf ~ MAT + Latitude + Deciduousness	n.s.	0.05	Remove MAT
Relative Reproductive N Flux to Reproductive and Leaf ~ Latitude + Deciduousness	n.s.	0.04	Add pairwise
Relative Reproductive N Flux to Reproductive and Leaf ~ Latitude * Deciduousness	p<0.001	0.18	Stop
Relative Reproductive P Flux to Reproductive and Leaf			
Model	p-val	R^2	Step
Relative Reproductive P Flux to Reproductive and Leaf ~ MAT + MAP + Latitude + Phylogeny + Deciduousness + Forest vs. Plantation	p<0.01	0.17	Remove Phylogeny
Relative Reproductive P Flux to Reproductive and Leaf ~ MAT + MAP + Latitude + Deciduousness + Forest vs. Plantation	p<0.001	0.17	Remove Deciduousness
Relative Reproductive P Flux to Reproductive and Leaf ~ MAT + MAP + Latitude + Forest vs. Plantation	p<0.001	0.17	Remove Forest vs. Plantation

Relative Reproductive P Flux to Reproductive and Leaf ~ MAT + MAP + Latitude	p<0.001	0.18	Add pairwise
Relative Reproductive P Flux to Reproductive and Leaf ~ MAT + MAP + Latitude + MAT:MAP + MAT:Latitude + MAP:Latitude	p<0.001	0.30	Remove MAT:MAP
Relative Reproductive P Flux to Reproductive and Leaf ~ MAT + MAP + Latitude + MAT:Latitude + MAP:Latitude	p<0.001	0.29	Stop

CHAPTER FIVE: CONCLUSIONS

My dissertation focused on portions of the nitrogen (N) and phosphorus (P) cycles that trees exert direct control over, specifically nutrient resorption processes and allocation to different organs. The approach I used during my dissertation included data collection via field work I personally conducted, a community science network I constructed, and a data synthesis project. Using these varied approaches, my research spanned scales ranging from the individual plant organ level in chapter 1, the geographic range of an entire species in chapter 2, all the way up to the global scale in chapter 3.

In chapter two, to my best of my knowledge, I provided some of the first evidence of nutrient retranslocation from fruit to developing seeds in trees. Depending on species, the retranslocation from fruit to seed accounts for 19-57% of the amount of N in seeds. I also demonstrated that fruit traits, such as N mass per unit area of fruit are significantly correlated to their photosynthetic rates. These results are particularly important because it extends nutrient resorption phenomena from the leaf to other tree organs and can for the basis of a way to reframe reproductive allocation from just being a resource sink for trees to a process that efficiently uses tree nutrients.

Next, in Chapter 3, I documented leaf trait variation in red maple along a latitudinal gradient of ~20° and demonstrated that red maple leaf traits respond to environmental gradients either through plasticity or environmental filtering. I observed that N resorption rates were the highest at higher latitudes, and that the specific habitat such as being open or closed grown also influenced %N in green leaves. These results are particularly important because the range of trait values we observed for individual species rivals that of variation observed between species. In addition, the results suggest that red maple relies on different N sources for its annual requirement throughout its geographic range—with northernly distributed red maple relying more on nutrient resorption processes compared to more southernly distributed red maple potentially relying more on uptake of N from the soil.

Finally, I conducted a global scale analysis that compared N and P concentrations, N and P fluxes, and N:P ratios of leaf and reproductive litterfall. Overall, the litterfall traits were only weakly related to mean annual temperature, precipitation, and latitude. However, the directionality of the litterfall flux relationships did lend support to the temperature biogeochemistry hypothesis for reproductive litterfall because the litterfall N and P concentrations tended to be higher in warmer, lower latitude ecosystems. I also found some support for the substrate-age hypothesis for leaf litterfall N and P concentrations, which suggests old weathered soils in the tropics may be more P limited compared to more northernly distributed soils. Further, I demonstrate reproductive litterfall comprises median of 13.0% and 16.1% of the combined reproductive and leaf litterfall N and P fluxes, respectively.

Conclusions, Implications, and Future Directions

Changes in nutrient availability and the constraint nutrient availability places on primary productivity and responses to elevated carbon dioxide are vitally important to understanding the potential for a continued terrestrial carbon sink. In my dissertation I highlight the importance of reproductive structures in the nutrient economies of trees where nitrogen retranslocation within reproductive organs accounts for 19-57% of seed

N, and I also provide some of the first global scale comparisons of leaf and reproductive litterfall demonstrating it is an important component of tree resource allocation and litterfall N and P fluxes. I also demonstrate large and meaningful variation within species' biogeochemically relevant leaf traits across environmental gradients. By investigating the biogeochemical components of reproduction and the within species variation of leaf traits my research identifies effects and responses to nutrient limitation that could not be uncovered by solely investigating leaf and productivity at a single location.

My dissertation results point to numerous important paths for future research directions. In chapter two, I identified that there is a lot of work to be done related to the physiology and nutrient dynamics of reproduction in the fruit and other reproductive structures of forest tree species. While my work focused on the samara fruit type, there is the potential to expand to different fruit types. Another research path is to examine drivers of photosynthesis in fruit based on traits including differentiating conductive vs. support tissues, along with quantifying other traits such as transpiration rates. Scaling results of within reproductive nutrient transfer up from organ to tree level would make my findings more immediately applicable to ecosystem scale relevance. Future experimental work related to reproductive nutrient retranslocation may be useful in identifying exactly where nutrients are going as they decrease in concentration of the fruit, along with determining whether the fruit nutrient retranslocation process influences fitness either by influencing seed quality or parent tree survival.

In chapter three, I highlighted red maple leaf trait variation across broad environmental gradients. One key open question is whether the observed leaf trait variation was a result of phenotypic plasticity or genetic structuring in response to the climate and latitudinal gradients. Future work to address the mechanism as under the control of plasticity vs. genetics could involve common garden experiments and population genomics studies. While I demonstrated variation in leaf N traits, another path forward would be to examine other nutrients such as P, which might be anticipated to display similar or opposing trends to those found for N. Further, while this study was conducted at the leaf level, future work could simultaneously collect data to scale up to the canopy level and assess soils nutrient mineralization rates because both would be informative in placing the results into an ecosystem context. Finally, while I found meaningful variation in red maple leaf traits across its geographic distribution that aligned with environmental gradients, another important path forward is to investigate intraspecific trait variation for a range of other species.

In chapter three, I used previously published litterfall values to examine the stand level biogeochemical consequences of reproductive N and P allocation and compared it to that of leaves. There are opportunities to integrate the biogeochemistry of reproductive allocation into dynamic global vegetation models which often have only simple allocation rules for reproduction implemented and rarely include nutrient components. In my analysis reproductive N and P allocation ranged from zero to more than 50% of the combined leaf and reproductive litterfall flux. Understanding and identifying the underpinnings of this variation is likely important for accurately understanding nutrient cycling and limitation within terrestrial ecosystems. I also found that reproductive litterfall was less commonly reported than leaf litter fall, and N fluxes were more commonly reported than P fluxes, which presents opportunities for future data collection. Additionally, ‘zero’ values for reproductive litterfall N and P are also informative and if not reported could bias global scale reproductive litterfall estimates in the direction of being too large.

Through the work in my dissertation and the proposed future research directions we will better understand how plants navigate nutrient limitation and further integrate reproduction into the general frameworks of biogeochemistry.

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