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THE PHOTOSYNTHESIS-FOLIAR NITROGEN RELATIONSHIP IN DECIDUOUS AND
EVERGREEN FOREST OF NEW HAMPSHIRE

BY

Conor Madison

Bachelors of Science, University of New Hampshire, 2015

THESIS

Submitted to the University of New Hampshire in Partial Fulfillment of
the Requirements for the Degree of

Master of Science

in

Natural Resources

May, 2018

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ABSTRACT

THE PHOTOSYNTHESIS-FOLIAR NITROGEN RELATIONSHIP IN DECIDUOUS AND EVERGREEN FOREST OF NEW HAMPSHIRE

By

Conor Madison

University of New Hampshire, May, 2018

Biomass production in forests is a key process in the global carbon (C) cycle that is strongly linked to photosynthesis and related leaf traits. Spatially, relationships among leaf traits can vary as a function of climate, soils and species composition. As modeling approaches to estimate C gain improve, the need to understand variability in leaf traits becomes increasingly important. Here, we characterized the relationship between photosynthetic capacity (A_{\max}), foliar nitrogen and leaf mass per area (LMA) within and across species in northern hardwood and evergreen stands of the White Mountain National Forest in New Hampshire, a region that has been underrepresented in past leaf trait studies. Results were used to parameterize a forest ecosystem model (PnET) that has been widely used in the Northeast region to predict ecosystem C fluxes. Within all species, A_{\max} was strongly and positively related to mass-based foliar percent nitrogen (%N). The observed relationship between foliar %N and A_{\max} differed significantly from the previously used model parameterization that was based on leaf trait data from forest stands in Wisconsin, and was largely a function of differences in leaf mass per area. Using site-specific foliar %N and LMA to estimate A_{\max} in PnET improved the estimation of GPP by 5.5% in comparison with GPP estimates derived from an eddy covariance tower.

Introduction

Temperate forests play a critical role in the global carbon cycle through photosynthesis, respiration and biomass accumulation (Houghton 1991, Wisniewski and Lugo 1992). In addition to abiotic factors, the assimilation and release of carbon by forests are controlled by several key leaf traits, among which are leaf mass per unit area (LMA) and the concentration of nitrogen in a leaf (Wright et al. 2004, Field and Mooney 1986, Evans 1989). The positive relationship between the concentration of nitrogen in foliage and photosynthetic capacity (Wright et al. 2004) has been integrated into many ecosystem models (PnET-II; Aber et al. 1995, GAP model; Shugart and West 1980, DOLY; Woodward et al. 1995). Studies have also shown LMA to have a significant effect on determining photosynthetic capacity (Poorter et al. 2009, Reich et al. 1998, Wright et al. 2004). Using LMA together with foliar %N to predict photosynthetic capacity is also theoretically satisfying in that it includes controls of both leaf chemistry (%N) and leaf structure (LMA) on leaf physiology. As modeling approaches advance estimation of carbon gain, it has become increasingly important to ensure that leaf trait and photosynthetic parameters accurately reflect the ecosystems being simulated (Saitoh et al. 2012; Nagai et al. 2013). However, accounting for variation among species, sites and regions represents an ongoing challenge.

In the northeastern U.S., a forest ecosystem model that has been used extensively is PnET (Aber et al. 1995, Aber and Driscoll 1997, Fahey et al. 2005), which combines the A_{\max} -N relationship with mechanisms governing carbon allocation, water availability and nitrogen cycling. Despite the number of studies in which PnET models have been applied to northeastern forests, model simulations are often parameterized with an A_{\max} -

N relationship derived using data from northern hardwood stands in Wisconsin (Reich et al. 1995). This approach assumes that parameters derived from the A_{\max} -N relationship in Wisconsin stands are similar to those in New England forests. Generalizing in this manner without accounting for regional differences may result in modeling inaccuracies that are difficult or impossible to quantify (Pan 2004).

Here, we sought to measure the relationships among leaf traits within northern hardwood and evergreen forests of New Hampshire. We examined five dominant species that are distributed among different elevations and coexist in naturally regenerated forests at two different sites in the White Mountain National Forest in New Hampshire. The results of the New Hampshire analysis were compared with the A_{\max} -N relationship observed by Reich et al. (1995) in Wisconsin. The New Hampshire measurements were used to parameterize the PnET-SOM model (Tonitto et al. 2014) and incorporate both foliar %N and LMA into the A_{\max} calculation to simulate C fluxes at well-studied stands within the Bartlett Experimental Forest (BEF). The output of the model was compared to measured estimates of C fluxes both before and after parameterization using the New Hampshire A_{\max} , N and LMA relationship to assess the accuracy of gross primary production (GPP), wood growth and foliar %N.

Methods

Foliar %N, LMA, and photosynthetic light response curves were measured in five tree species across two study sites (15 stands total) in the White Mountain National Forest (WMNF) of New Hampshire. Species were chosen to represent northern hardwood and evergreen forests, and included red maple (*Acer rubrum*), yellow birch, (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), red spruce (*Picea rubens*)

and eastern hemlock (*Tsuga canadensis*). The resulting relationships between foliar %N, A_{max} , and LMA were used to parameterize and apply an ecosystem model, PnET-SOM (Tonitto et al. 2014), results from which were then compared against previous modeling efforts to determine whether localized parameterization led to improved agreement with GPP estimated using eddy covariance.

2.1 Study sites

2.1.1 Hubbard Brook Experimental Forest

The Hubbard Brook Experimental Forest (HBEF) is located in the White Mountains of central New Hampshire, USA (43°56'N, 71°45'W).

HBEF's climate is temperate and is characterized by warm summers and cold winters (Likens 2013). HBEF receives an average of approximately 1400mm of precipitation annually (Bailey et al. 2003). Mean monthly temperatures in the forest range from -8.5°C in January to 18.8°C in July with a mean annual temperature of 5.5°C (Bailey et al. 2003). The forest is dominated by northern hardwood forest type with dominant deciduous species including American beech, red maple, sugar maple (*Acer saccharum*), yellow birch, and paper birch (*Betula papyrifera*).

Evergreens include eastern hemlock in older stands and along stream channels, and red spruce and balsam fir on upper slopes. This study was conducted within a 2.5km² area located immediately west of the

research watersheds (Siccama et al. 2007). This area was selectively logged in the late 1800s and affected by the 1938 hurricane (van Doorn 2011).

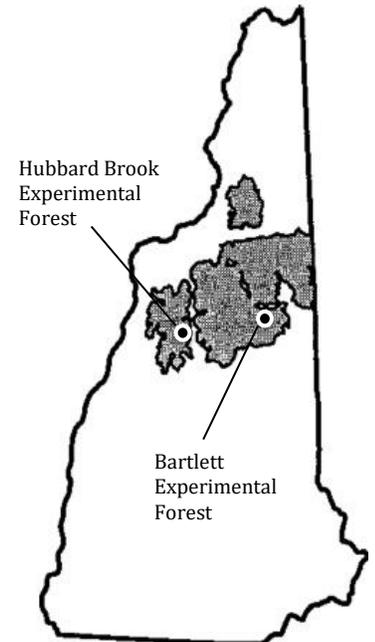


Figure 1: Location of study sites. The dark region represents WMNF, with points representing each field site as noted.

2.1.2 Bartlett Experimental Forest

The Bartlett Experimental Forest (BEF) is located in the White Mountain National Forest (WMNF) approximately 40 km to the northeast of HBEF. BEF has been used for silvicultural research to a greater extent than HBEF. The climate is similar to HBEF with cold winters and warm summers. BEF receives approximately 1300mm of precipitation, and has a mean January temperature of -9.8°C and a mean July temperature of 19.8°C (Gamel-Eldin 1998). Species composition is similar to HBEF, albeit with a different fraction of species in areas subjected to forest management research.

2.2 Tree selection

In 2016, fifteen plots (7 at BEF, 8 at HBEF) were selected from within each forest's permanent inventory plot system. Plots in this study were selected at two different elevations, 245m and 670m, and five dominant trees of each species were sampled at both elevations. Each tree was visually assessed for its health and canopy dominance before it was selected for this study.

2.3 Leaf measurements

All photosynthesis measurements were taken on sunny days within a three-week period from late July to mid-August. Shotgun sampling was used (Sweney 1975) to collect branches from the upper canopy of each sample tree. The branches were quickly submerged in water and recut to minimize stress on leaves. Photosynthetic rates were measured using a Li-Cor 6400XT portable photosynthesis system (Li-Cor, Lincoln, NE), which was calibrated between every measurement. Measurements were taken between 10:00 and 15:00 hours due to late day decline of photosynthetic capacity (Bassow and

Bazzaz 1997). One healthy sun leaf was selected from the branch and enclosed in the Li-Cor 6400XT chamber.

Inside the chamber, air temperature, relative humidity, and CO₂ were held constant at 27°C, 35% and 400 ppm, respectively, for each sample. Photosynthetic photon flux density (PPFD) was then altered in nine steps to produce one light response curve for every leaf sample. A_{max} was calculated from every light response curve by fitting a saturation curve (Equation 1) where “PAR” stands for the photosynthetically active radiation, “Hs” for the half saturation point and “Rd” for the respiration rate. Unless further noted, all analysis of A_{max} will be in mass terms (nmol m⁻² s⁻¹).

$$\frac{PAR * A_{max}}{PAR + Hs} - Rd \quad (\text{Equation 1})$$

The PPFD was initially set to 2000 μmol m⁻² s⁻¹, and after leaf stabilization PPFD was sequentially reduced to 1500, 1000, 500, 250, 120, 60, 30, 15, and 0 μmol m⁻² s⁻¹. Each light response curve began at 2000 μmol m⁻² s⁻¹ and the minimum time for stabilization for each light step was 120s. Ten light response curves were collected for each species per site (exception; nine Eastern hemlock at HBEF), with five trees at each elevation. A total of ninety-nine light response curves were produced over the course of the study.

After each light response curve was collected, the leaf was sealed in a plastic bag with a damp towel and kept out of the sun. Each leaf was then put into a scanner (HP ScanJet G4050) to measure leaf area using the ImageJ software. The leaves were then dried at 60°C for seven days and then weighed for calculating leaf mass per area (LMA, g m⁻²), which included the full leaf blade and petiole. Each dried leaf, petiole included, was

ground individually to a very fine powder using a mixer mill (SPEX Sample Prep). The nitrogen content of the ground tissue was analyzed using an elemental analyzer isotope ratio mass spectrometer (Elementar), in which standards were used between each run to correct for any error.

2.4 Data Analysis

The data collected for this study were normally distributed, although residuals showed a slight positive skew on a quantile-quantile plot where highly productive yellow birch foliage was present. Differences in mean values of A_{\max} , foliar %N and LMA between HBEF and BEF were analyzed with use of one-way ANOVAs. Differences in the slope and intercept of the A_{\max} -N relationship across sites and regions were tested with an ANCOVA involving factors A_{\max} and foliar %N, and a blocking variable for site. Least squares regression and multiple linear regression analyses were performed using the A_{\max} , foliar %N and LMA relationship with a blocking variable for site, to test for differences across sites and the prediction accuracy of A_{\max} with both foliar %N and LMA.

2.5 PnET-SOM model description

PnET-SOM (Tonitto et al. 2014) is a daily to monthly time step, canopy- to stand-level model of forest C, N, and water fluxes developed as an alternative decomposition routine for the PnET-CN model (Aber et al. 1997). The new SOM routine increased the number of soil organic matter pools from one encompassing pool of leaf and root litter as well as relatively decomposable soil humus to six litter pools and four non-litter SOM pools (Tonitto et al. 2014). A particularly important relationship in all PnET models is the A_{\max} -N relationship, which determines the maximum leaf-level carbon assimilation

rate. A_{\max} also plays a role in determining stomatal conductance resulting in water use efficiency and transpiration becoming a function of both CO_2 gain and climate (Ollinger et al. 2002). These functions are combined with light response curves and canopy light extinction to determine net carbon gain over a multi-layered canopy and to represent measurable SOM pools (Tonitto et al. 2014).

2.6 PnET-SOM model parameterization, application and comparison

For this study, PnET-SOM was run for the AmeriFlux eddy covariance tower site at BEF with site specific climate data measured from the eddy covariance tower including minimum and maximum temperature, precipitation, vapor pressure deficit and PAR. The parameters that were altered in PnET-SOM for site specification based on this study were the intercept of the A_{\max} regression ($A_{\max A}$), the foliar %N coefficient in the A_{\max} regression ($A_{\max B}$), the LMA coefficient in the A_{\max} regression ($A_{\max C}$, which was not present in earlier versions of PnET) and the half saturation point of the total average light response curve (HalfSat) (Table 5). Additional parameters were site-specified based on data from Ouimette et al. 2018 and included wood turnover rate and min foliar %N in litter (Table 5). The remainder of PnET-SOM parameters were determined from both Aber et al. 1997 and Ollinger et al. 2002. The model was run three times at a daily time step for a northern hardwood forest; one run used existing (Wisconsin-based) A_{\max} -N relationship with New Hampshire climate data, another used the New Hampshire A_{\max} -N-LMA regression accompanied with New Hampshire climate data and the third used an existing global-based A_{\max} -N-LMA regression (Wright et al. 2004) with the New Hampshire climate data. Model outputs included GPP ($\text{gC m}^{-2} \text{yr}^{-1}$), foliar %N and wood growth (gC m^{-2}), and were compared to measured site specific data

(Ouimette et al. 2018). The GPP validation value was estimated from the BEF flux tower, while values for the foliar %N and wood growth validation were estimated from adjacent plots. The GPP values were derived from flux tower NEE measurements after gap filling and partitioning. Foliar %N validation values were calculated from annual field measured data and wood growth measurements were biometrically estimated from annual measurements of DBH (Ouimette et al. 2018).

Results

3.1 Site and species specific leaf traits

Mean values for A_{\max} , foliar %N and LMA for each species and site are shown in Table 1, and their regression relationships are shown in Table 2. Mean A_{\max} (mass- and area-based) and mean foliar %N were not significantly different between the two New Hampshire sites (Table 1; ANOVA, $p=0.30$, $p=0.18$ and $p=0.10$ respectively). When looking at individual species, both red maple and red spruce had significantly different A_{\max} values across the two NH sites (Table 1; ANOVA, $p < 0.05$). In addition, yellow birch, red maple and red spruce all exhibited a significant difference of foliar %N between NH sites (Table 1; ANOVA). Red spruce also had a significantly higher half saturation rate across all species, while eastern hemlock had a significantly lower half saturation rate across all species. Across both NH sites, yellow birch exhibited the highest mass-based A_{\max} and foliar %N, and red spruce exhibited the lowest A_{\max} and foliar %N. Along with the mean A_{\max} and foliar %N values, both sites in New Hampshire showed a similar slope and intercept when A_{\max} was regressed against leaf-level %N (Table 3).

Table 1: Mean values of A_{\max} , foliar %N, LMA and half saturation rate for species sampled at the BEF and HBEF study sites. Standard errors are in parenthesis.

Species	Site	A_{\max} ($\text{nmol g}^{-1} \text{s}^{-1}$)	N (%)	A_{\max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	LMA (g m^{-2})	Half Saturation ($\text{nmol g}^{-1} \text{s}^{-1}$)
<i>Acer rubrum</i>	BEF	111. (10.)	1.44 (0.07)	10.63 (0.69)	98.23 (4.92)	131.74 (20.34)
<i>A. rubrum</i>	HBEF	137. (10.)	1.69 (0.12)	12.52 (0.74)	92.57 (4.55)	171.54 (25.79)
<i>Betula alleghaniensis</i>	BEF	165. (17.)	2.00 (0.11)	14.42 (0.96)	87.71 (5.49)	220.11 (44.79)
<i>B. alleghaniensis</i>	HBEF	201. (21.)	2.39 (0.11)	15.17 (0.93)	80.58 (6.72)	181.86 (10.42)
<i>Fagus grandifolia</i>	BEF	139. (9.6)	1.94 (0.08)	9.99 (0.80)	75.47 (6.64)	120.06 (15.08)
<i>F. grandifolia</i>	HBEF	145. (10.)	2.08 (0.09)	11.07 (1.01)	78.72 (7.28)	139.65 (19.18)
<i>Picea rubens</i>	BEF	34. (3.)	0.83 (0.02)	8.19 (0.58)	241.62 (8.05)	267.23 (23.09)
<i>P. rubens</i>	HBEF	44. (3.)	0.90 (0.10)	9.57 (0.72)	221.01 (7.82)	345.79 (17.85)
<i>Tsuga canadensis</i>	BEF	70. (8.)	1.16 (0.03)	5.84 (0.51)	92.10 (7.77)	71.17 (7.67)
<i>T. canadensis</i>	HBEF	50. (5.)	1.16 (0.03)	5.34 (0.63)	108.57 (7.85)	94.46 (8.94)

Table 2: Regression statistics for relationships between A_{\max} , foliar %N and LMA across all study areas. All relationships below are significant at $p < 0.001$ and standard errors are in parenthesis.

Site	Y Variable	X Variable	Slope	Intercept	RMSE	R ²
BEF	A_{\max}	Foliar %N	92.919 (8.972)	-33.012 (13.872)	30.03	0.69
BEF	A_{\max}	LMA	-0.608 (0.079)	176.197 (10.756)	36.23	0.55
BEF	Foliar %N	LMA	-0.005 (0.001)	2.090 (0.101)	.3413	0.50
HBEF	A_{\max}	Foliar %N	99.957 (8.787)	-48.359 (15.442)	36.73	0.73
HBEF	A_{\max}	LMA	-0.829 (0.128)	213.346 (16.645)	51.76	0.47
HBEF	Foliar %N	LMA	-0.007 (0.001)	2.524 (0.136)	.4213	0.52
WMNF	A_{\max}	Foliar %N	96.526 (6.131)	-40.482 (10.141)	33.3	0.72
WMNF	A_{\max}	LMA	-0.707 (0.074)	193.526 (9.801)	45.01	0.49
WMNF	Foliar %N	LMA	-0.006 (0.001)	2.295 (0.086)	.3943	0.49
WI	A_{\max}	Foliar %N	82.178 (9.176)	-60.025 (18.332)	26.94	0.69
WI	A_{\max}	LMA	-0.457 (0.049)	156.107 (7.380)	26.09	0.71
WI	Foliar %N	LMA	-0.004 (0.001)	2.418 (0.099)	.3479	0.49

Table 3: ANCOVA models for each site comparison with F value, MSE and p value results.

Site Comparison	Model Run	F value	MSE	p value
HBEF and BEF	$A_{\max} \sim \text{Foliar \%N} * \text{Site}$	(3,95) = 0.301	338	0.585
HBEF and BEF	$A_{\max} \sim \text{Foliar \%N} + \text{Site}$	(2,96) = 0.435	486	0.511
WI and WMNF	$A_{\max} \sim \text{Foliar \%N} * \text{Site}$	(3,133) = 1.37	1373	0.245
WI and WMNF	$A_{\max} \sim \text{Foliar \%N} + \text{Site}$	(2,134) = 52.6	53012	< 0.0001

3.2 Comparison of leaf trait relationships from New Hampshire and Wisconsin

The absence of differences in the A_{\max} -N relationship between HBEF and BEF allowed us to use a single relationship for both NH study sites. Results of this regression were compared to the results from Reich et al. 1995 (Figure 2). The relationship from the NH sites had a similar slope to the hardwood forest stands in Wisconsin (Table 3, ANCOVA; $p=0.245$, $F(3,133)=1.37$), albeit with a significant difference in intercept and a higher A_{\max} for a given foliar %N (Table 3, ANCOVA; $p<0.0001$, $F(2,134)=52.6$).

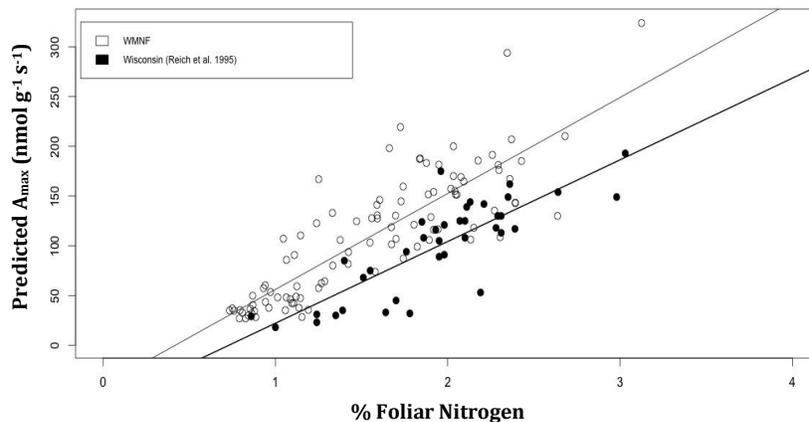


Figure 2: Relationship between A_{\max} and foliar %N in WMNF (open circles) and Wisconsin (closed circles).

In addition to using foliar %N as a predictor for A_{\max} , leaf mass per unit area (LMA) was included to determine whether it explained additional variation in A_{\max} . Including LMA decreased the differences in the A_{\max} -N relationships between New Hampshire and Wisconsin but did not eliminate them entirely (ANCOVA; $p=.032$). At each site, both the foliar %N and LMA had a significant effect on the prediction of A_{\max} . The NH and Wisconsin datasets were then combined to perform a multiple linear

regression across both sites. Again, the regression results show both foliar %N and LMA had a significant effect on the prediction of A_{\max} (Table 4). Although the F value for foliar %N in the multiple linear regression is much greater at 251, the LMA still captures a proportion of the variation with an F value of 33. Including LMA in the pooled regression also increases the R^2 from .71 to .74.

Table 4: Multiple linear regression statistics for relationships between A_{\max} , foliar %N and LMA in the WMNF, WI, and a pooled data set for both sites (***) indicates p value <0.001).

Site	Y Variable	Foliar %N	LMA	Intercept	RMSE	R^2
WMNF	A_{\max}	80.2 (8.28)***	-0.20 (0.07)*	9.37 (20.3)	32.17	0.74
WI	A_{\max}	46.7 (9.90)***	-0.28 (0.05)***	43.2 (24.6)	20.69	0.82
Both Sites	A_{\max}	57.2 (6.70)***	-0.31 (0.05)***	48.8 (16.3)	33.52	0.68

Through the use of the Global Plant Trait Network (GLOPNET), Wright et al. 2004 calculated a regression for A_{\max} using both foliar %N and LMA from data across the globe (Wright et al. 2004; $A_{\max} = 0.74*(\text{Foliar \%N}) - 0.57*(\text{LMA}) + 2.96$). The foliar %N and LMA values for both NH and WI sites were applied to the GLOPNET regression to compare both predicted and measured A_{\max} (Figure 3; RMSE= 25.46). Using an equivalence test with the two one-sided tests procedure (TOST), the samples fell outside the equivalent bounds of -.1 to 1 ($p=0.31$).

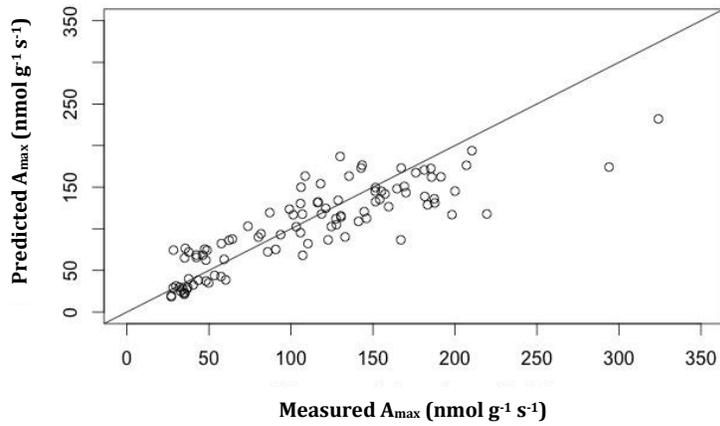


Figure 3: Predicted A_{\max} calculated a regression derived from the GLOPNET database with observed NH and WI measurements.

3.3 Model predictions

Values for several parameters used in PnET-SOM were adjusted based on field measurements collected from this study, as well as measurements from Ouimette et al. 2018 (Table 5).

Table 5: PnET-SOM model parameters that were modified for this study, with values used in prior northeastern U.S. applications and those derived using BEF specific data (Ouimette et al. 2018 and unpublished work)

Parameters	Ollinger et al. 2002 with BEF specific parameters	Wright et al. 2004 with BEF Specific parameters	BEF Specific
$A_{\max}A$ ($\mu\text{molCO}_2 \text{ g}^{-1} \text{ leaf s}^{-1}$)	-46	2.96	2.65
$A_{\max}B$ ($\mu\text{molCO}_2 \text{ g}^{-1} \text{ leaf s}^{-1}$)	71.5	0.74	1.15
$A_{\max}C$ ($\mu\text{molCO}_2 \text{ g}^{-1} \text{ leaf s}^{-1}$)	-	-0.57	-43
Half Saturation ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$)	175	175	175
Wood Turnover (year^{-1})	0.015	0.015	0.015
Minimum %N Fol. Litter (%)	0.0065	0.0065	0.0065

The model was run for the BEF tower site using the altered parameters and site specific climate data (minimum and maximum temperature, precipitation, PAR). Results are shown in Table 6. When the output of the BEF-specific model run was compared to the output of the A_{\max} regression based on WI, the agreement between predicted and field-based GPP and wood growth increased by 5.5% and 15%, respectively. The

comparison also indicated that the BEF-specific run resulted in a decreased foliar %N agreement with the measured data by an absolute difference of 1.0%. When the output of the A_{\max} regression based on global data was compared to the BEF-specific, the agreement between predicted and field based GPP and wood growth increased marginally by 0.6% and 0.46%, respectively.

Table 6: PnET modeled outputs with generalized parameters and field based parameters, along with the tower and field based estimates (Ouimette et al. 2018).

Outputs	Ollinger et al. 2002 with BEF Specific measurements	Wright et al. 2004 with BEF Specific parameters	BEF Specific	Measured Data
GPP (gC m ⁻²)	1020.8	1098.5	1090.8	1279
Foliar Nitrogen (%)	1.56	1.53	1.54	1.63
Wood growth (gC m ⁻²)	169.26	207.62	206.48	248

Discussion

The A_{\max} -N relationships observed at the two sites in NH did not exhibit significant differences from each other, but the combined relationship did differ from that observed by Reich et al. 1995 in Wisconsin. When the NH A_{\max} -N-LMA regression and other site specific parameters (Table 5) were used to run the PnET-SOM model, the agreement between predicted and observed GPP at BEF increased by 5.5%.

4.1 NH and WI comparison

The slope of the A_{\max} -N relationship in New Hampshire (Figure 2) was similar to that in other northern hardwood forests (Reich et al. 1995, Bassow and Bazzaz 1997), but the intercept in NH was significantly higher than in Wisconsin (Reich et al. 1995). There are at least two possible explanations for this. The first explanation could be that the NH sites in the WMNF are more efficient with its nitrogen use than the WI sites, possibly caused by either more efficient light absorption or by greater investment of N into

photosynthetic machinery (Poorter and Evans 1998). A forest with a higher A_{\max} to N ratio could indicate that more nitrogen is allocated towards photosynthetic material than leaf structure. Trees invest more biomass and N into leaf structure to create hardier leaves thereby increasing their survival in a more stressful environment and as a result increase their LMA (Wright et al. 2004, Villar and Merino 2001, Hikosaka 2004, Reich et al. 1998). The Wisconsin stands have approximately half the precipitation of the NH sites (700-800mm, 1400mm respectively), which may have led to higher LMA.

A second possible explanation for the regional difference in the A_{\max} -N relationship could stem from methodological differences. Both studies measured A_{\max} with ambient CO_2 concentration, however ambient CO_2 concentration have changed throughout the time in between each study. It is also unclear if the measurement of LMA in the Reich et al. study included the leaf petiole. This study included the petiole, which resulted in an increased LMA and lower mass-based foliar %N than would have been obtained if petioles were excluded. The increased LMA of the NH sites still remained lower than the LMA of the Wisconsin stands. However, as a result of this study's possible lower mass-based foliar %N, the NH A_{\max} -foliar N linear relationship shifted relative to Reich et al. 1995. Using a two variable approach in estimating A_{\max} with both foliar % N and LMA reduced this methodological source of error, but did not negate the significant site differences entirely (ANCOVA; $p=.032$).

The combination of LMA and foliar %N in the regression increased the estimation accuracy of A_{\max} across all sites (Table 4) over that obtained using foliar %N alone. Leaf structure is represented by LMA due to its strong correlations with the percent of mass constituted by the cell walls (Katabuchi et al. 2017), and sun leaf water

retention (Ashton and Berlyn 1994). The applied GLOPNET (Wright et al. 2004) two factor regression based on different LMA measurement methods (Figure 3) potentially suggests that in the absence of locally derived data, a globally derived regression including both leaf structure and chemistry could accurately predict A_{\max} . This suggestion was explored and PnET-SOM was adjusted to estimate A_{\max} from both leaf structure and chemistry based on the GLOPNET dataset ($A_{\max} = 0.74 * (\text{Foliar \%N}) - 0.57 * (\text{LMA}) + 2.96$). When the output of the GLOPNET model run was compared to the output of the A_{\max} regression based on WI, the agreement between predicted and field-based GPP increased by 6.1%. This may suggest that a globally derived equation is an acceptable alternative to a locally derived equation when A_{\max} is predicted by both leaf structural and chemical data.

4.2. Potential sources of error

During the sampling process, leaves were visually assessed for health but may have not shown visual signs of water stress. Also the shock of destructive sampling may have inhibited leaves to stabilize at full potential. After the gas exchange measurements were taken, LMA was calculated using a two-dimensional scanner thereby not accounting for any three-dimensional shape such as spruce needles. When these values were used in PnET-SOM, only select parameters listed were parameterized by NH specific measurements. Not using site-specific values for all parameters could have resulted in inaccuracies of each model run. In addition to model inaccuracies, validation values could also have introduced error, especially as GPP measurements present larger errors as estimates rely on gap filling and modeling methods (Richardson et al. 2006).

There were also differences in methods between this study and the comparison study (Reich et al. 1995). This study estimated A_{\max} with light response curves at 25°C and 35% relative humidity, while Reich et al. 1995 estimated A_{\max} as photosynthesis occurring early to late morning under ambient light, air temperature, humidity and CO₂ concentration. The trees measured in Reich et al. 1995 were also open growth trees, and this study was based in northern hardwood dominated forests.

Conclusions

By understanding regional variation and using local data in species A_{\max} -N relationships, we can improve confidence in model predictions of forest productivity. Our results illustrate the importance of comprehending relationships across forest-types and geographic regions and continually making small sequential improvements while predicting carbon fluxes. While the NH A_{\max} -N relationship shown in Figure 2 exhibits the same slope as previous studies (Reich et al. 1995), it has a significantly different intercept indicating either higher nitrogen use efficiency in NH or methodological differences between studies (Reich et al. 1995). Both explanations lead to the suggestion that measuring LMA in concert with foliar %N can improve predictions of forest carbon fluxes while also minimizing methodological differences throughout studies. As modeling approaches increasingly improve estimation of foliar %N on a broad scale, this study suggests that the predictor regression for A_{\max} be based on local data involving both leaf structure and chemistry.

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