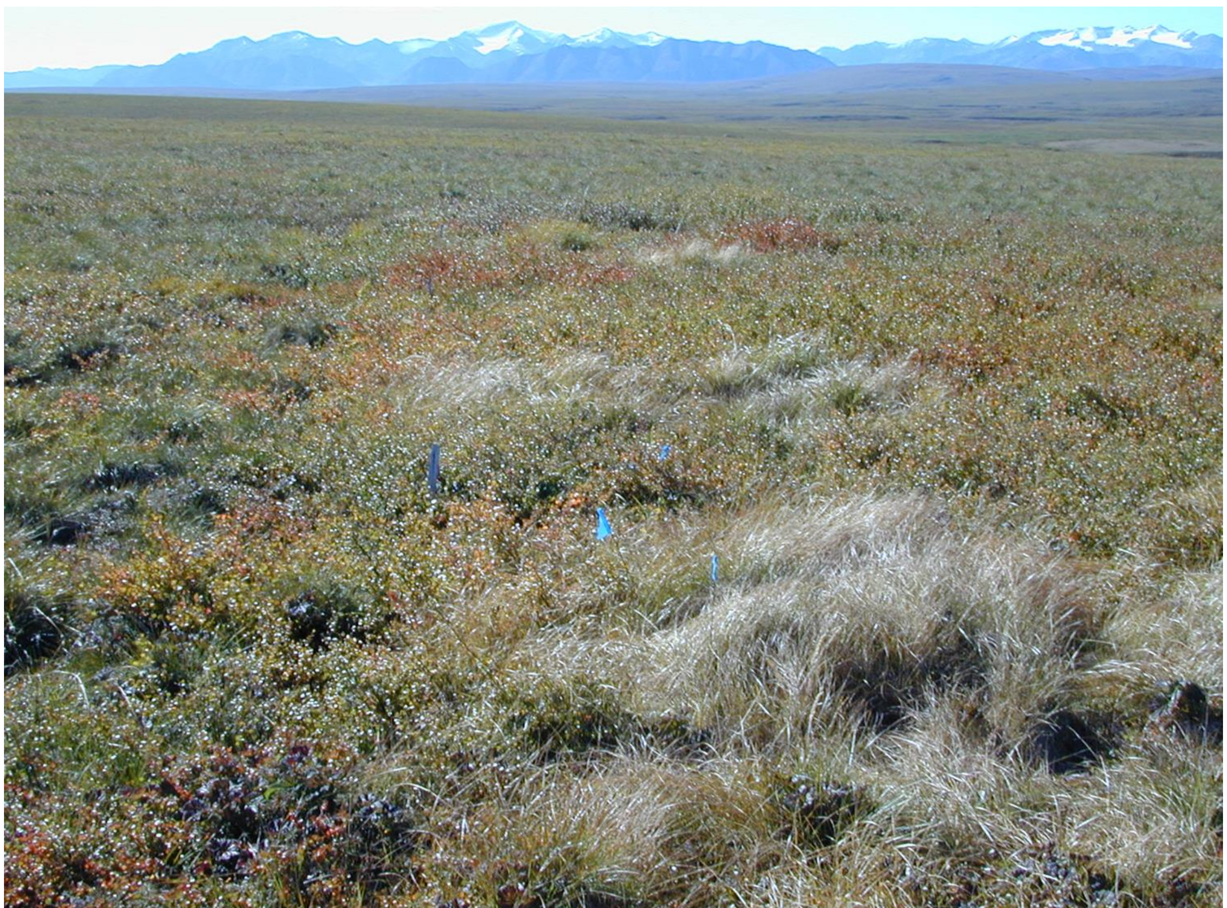
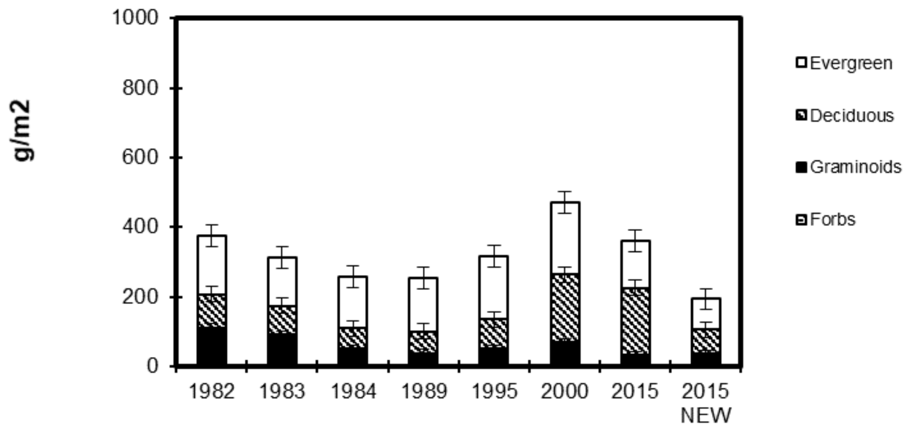
Changing species composition and biomass allocation do not change overall C-N-P stoichiometry or total plant biomass in Moist Acidic Tundra at Toolik Lake

By: G. Shaver and MANY others

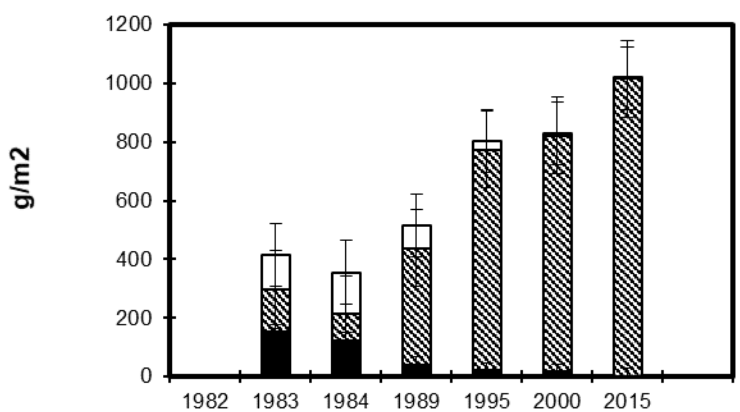


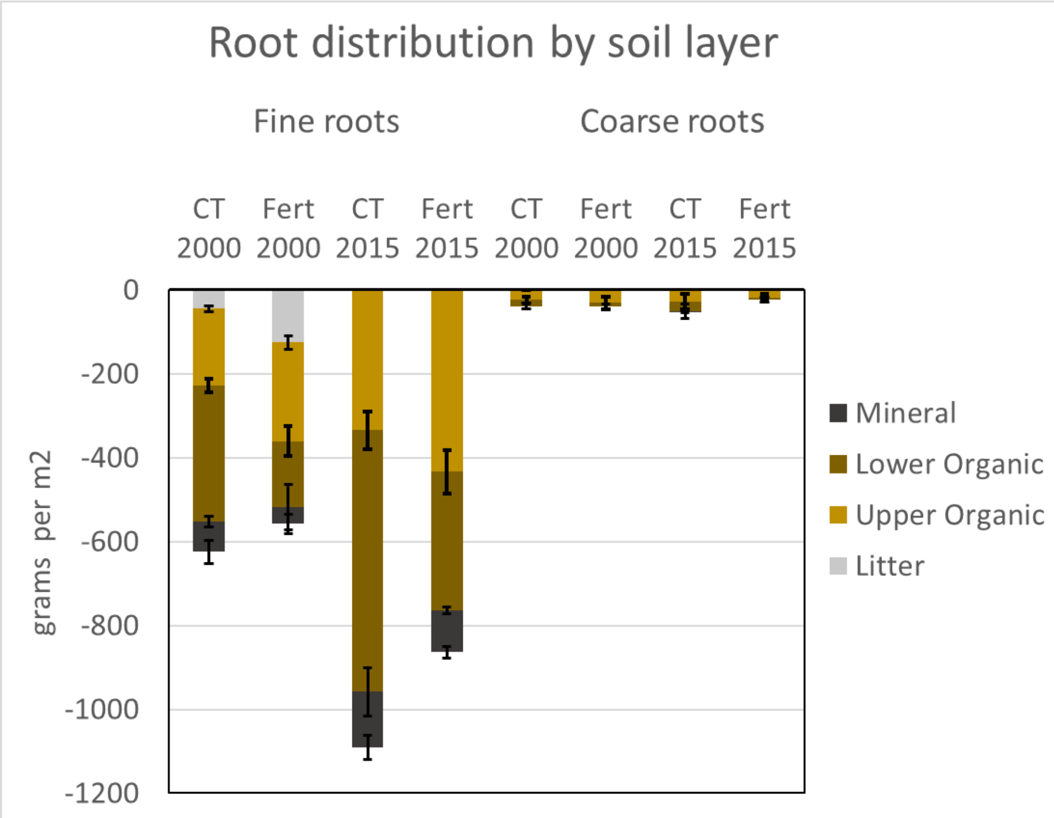
Total Aboveground biomass

A. Control plots



B. Fertilized plots





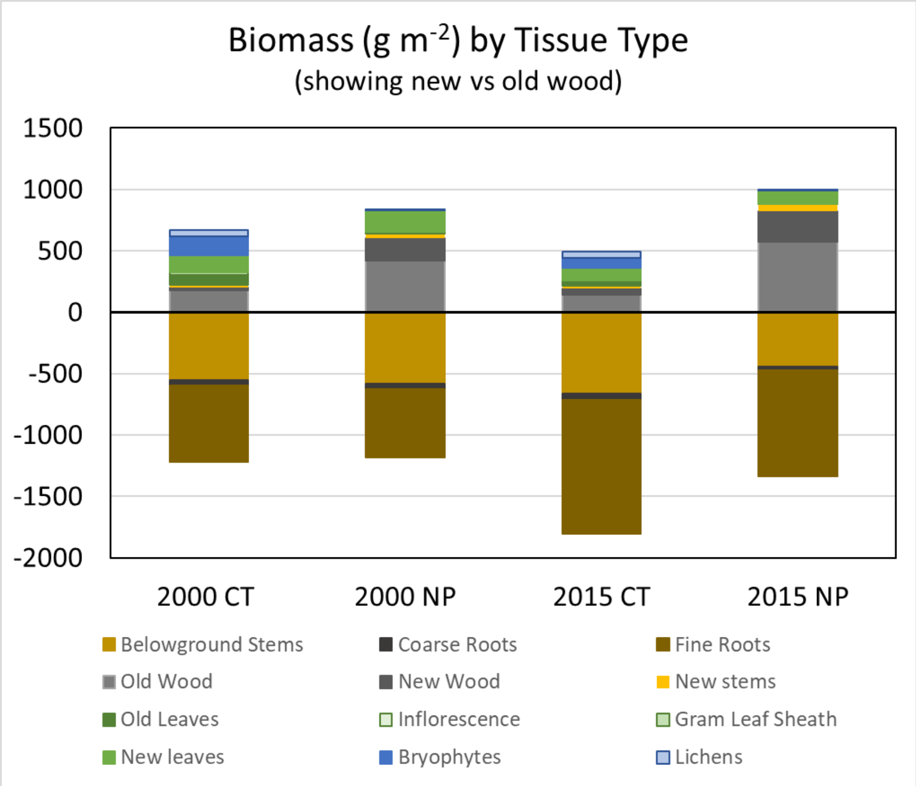
Distribution of root mass vs soil layer and as coarse (>2mm) vs fine (<2mm) roots. In 2000 we separated a Litter layer from the Upper Organic (0-5cm); in 2015 the Upper Organic layer included the Litter layer. Main points here are:

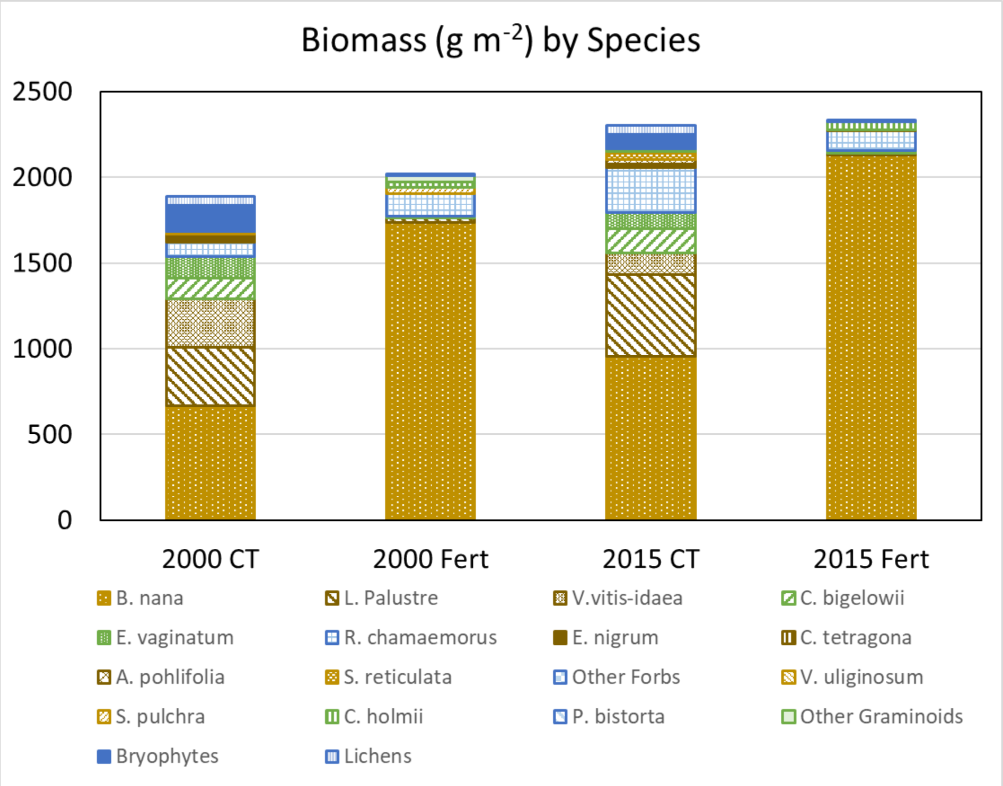
- Coarse roots were <10% of total root mass and were found mostly in the upper organic layer
- Although total fine root mass was reduced in Fert in both years, this was the result of significant decreases in lower organic and mineral layers balanced against smaller increases in fine root mass in the upper organic layer (and in litter in 2000)

Questions:

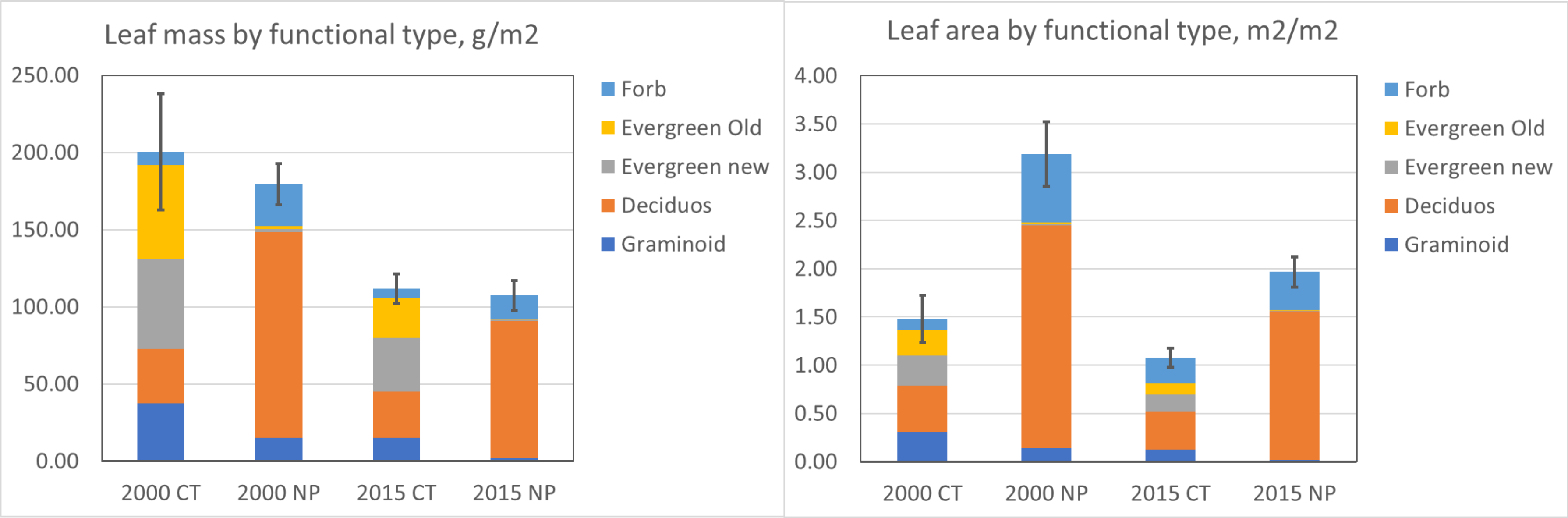
1. Does species composition make any difference to total plant biomass accumulation in N/P limited Moist Acidic Tundra (MAT)?
2. Can we scale traits of individual plant parts directly or must we consider what the whole plant is doing?





Main points here are:

- There was no significant difference in Total Live Biomass between CT and NP treatments in either 2000 or 2015
- Total Live Biomass was slightly higher ($P<0.05$) in 2015 vs 2000, in both CT and NP treatments.
- When broken down by tissue type, total aboveground biomass increased due to fertilizer treatment while belowground declined, especially in 2015. These changes almost exactly balanced each other.
- Bryophyte and lichen biomass was negligible in NP plots in both years (shown in both panels)
- New apical and intercalary growth (= new leaves + graminoid leaf sheaths + inflorescences + new stems) was NOT increased by fertilizer in either year; rather the near doubling in total ANPP in fertilized [plots was due entirely to a 7-10 fold increase in secondary growth (“New wood” shown as dark grey segments in left panel) relative to CT.



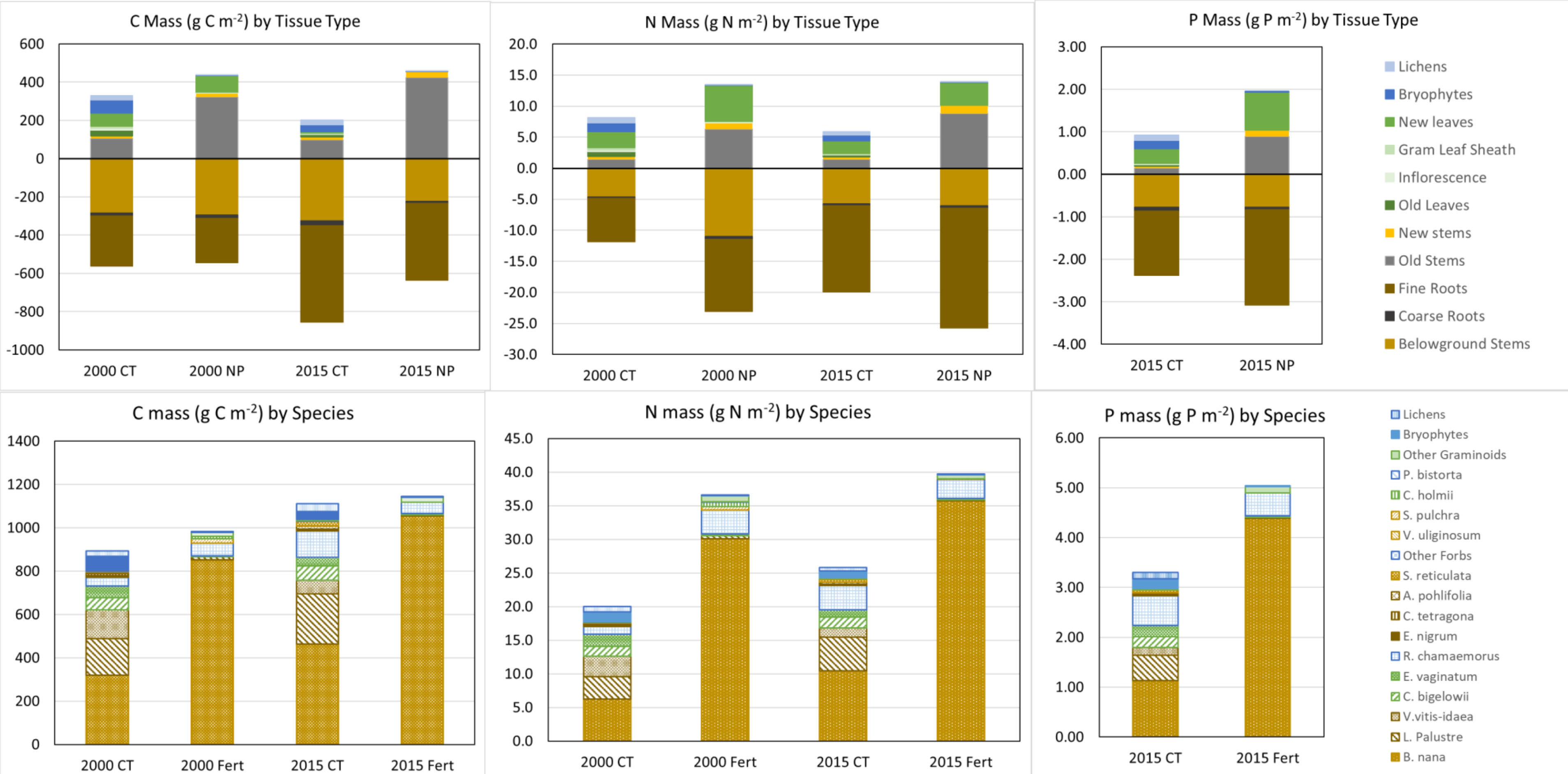
Distribution of leaf types, by leaf area or by leaf mass, is changed greatly by fertilization.

Total leaf mass is unchanged or slightly lower in fertilized plots, while total leaf area is ~doubled.

Diversity & evenness among species and among tissues

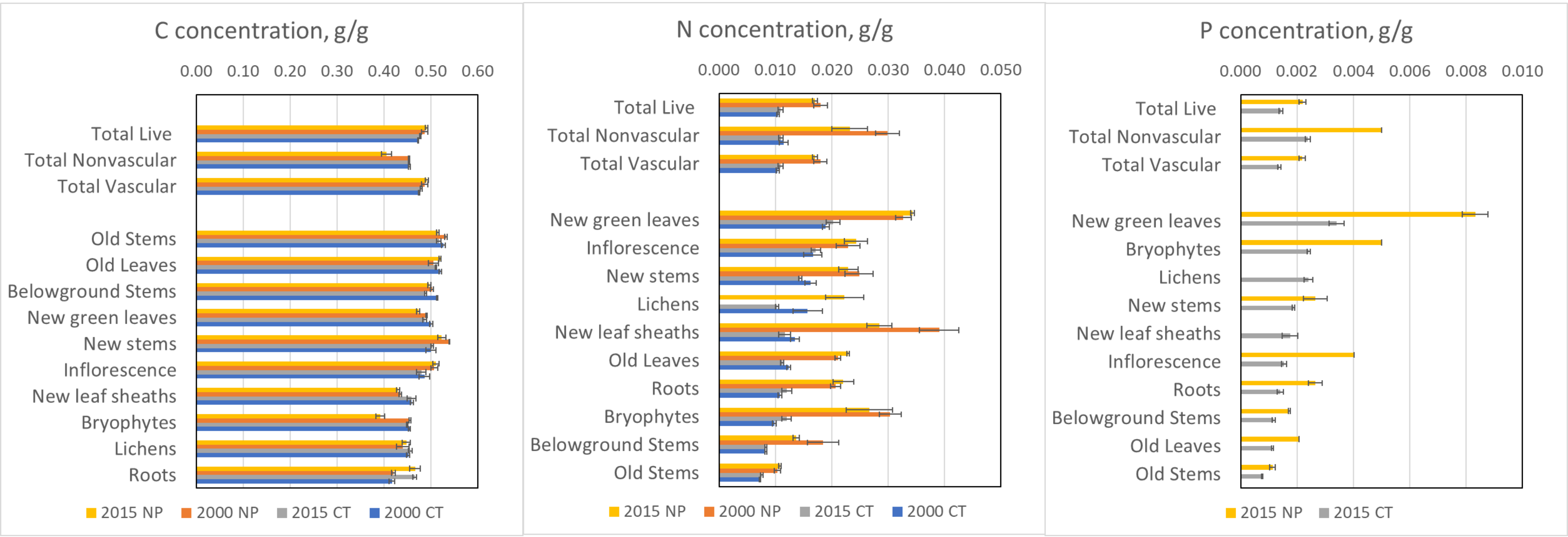
Biomass diversity and evenness are reduced by fert treatment, both among species and among tissue types. Biomass evenness is greater among tissues than among species

	2000		2015	
	CT	NP	CT	NP
Vascular species richness (# spp)	16	11	15	6
Vascular species diversity	1.713	0.610	1.669	0.377
Vascular+ Nonvascular Diversity	1.932	0.622	1.833	0.391
Vasc Spp Evenness	0.618	0.254	0.616	0.211
Vasc+ Nonvasc Spp Evenness	0.668	0.242	0.647	0.188
Vascular Tissue richness (# tissues)	8	8	8	8
Vascular Tissue diversity	1.483	1.402	1.205	1.291
Vasc+Nonvas tissue diversity (10 tissues)	1.727	1.413	1.397	1.303
Vascular Tissue evenness	0.713	0.674	0.579	0.621
Vasc plus Nonvas tissue evenness	0.750	0.614	0.607	0.566
(Diversity calculated using Shannon-Weiner index)				
(Evenness using Shannon evenness)				



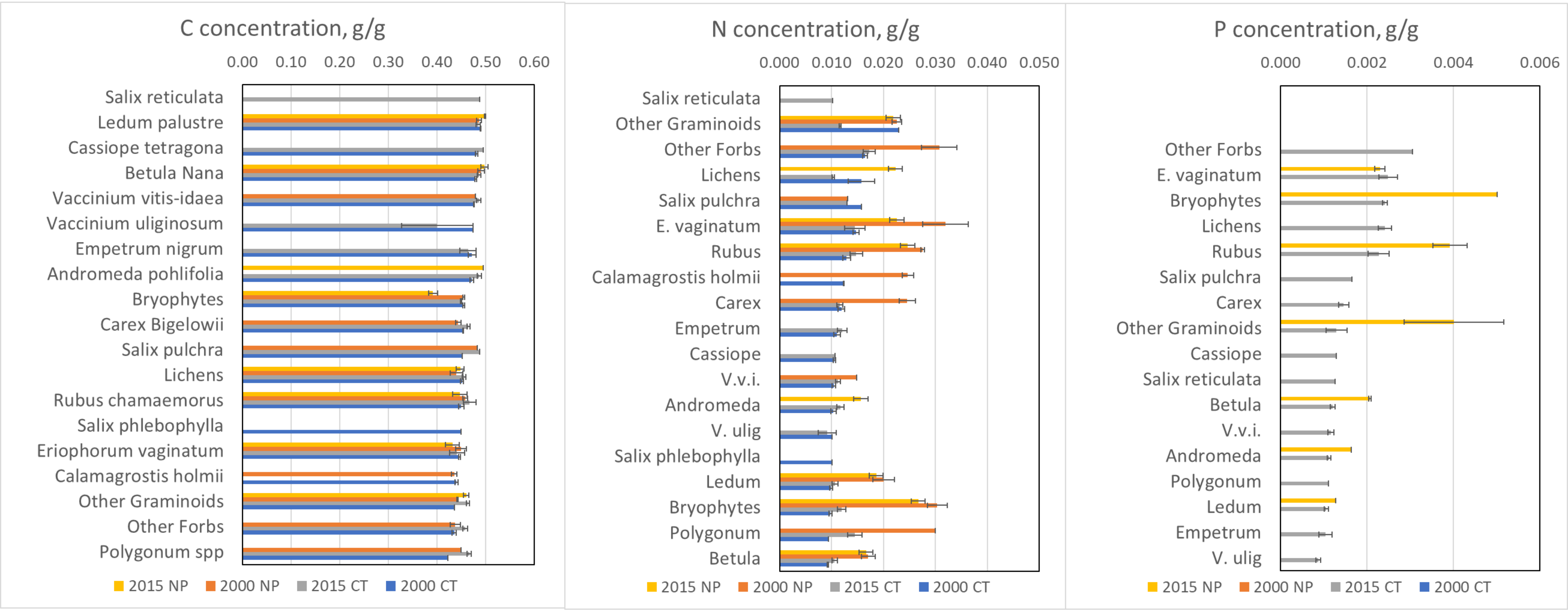
Main points are:

- Year and treatment effects on C mass were similar to effects on biomass, with no significant effect of fertilizer on Total Live C mass but a significant increase in both CT and NP from 2000 to 2015.
- Year and treatment effects on both N and P were very different, with large and significant increases in both total live N and P mass and in all individual tissue types due to fertilizer. There were also increases in total N in both CT and NP from 2000 to 2015. In the breakdown by species (lower panels), the distribution of N or P mass among species between CT and NP were similar to the distributions of species biomass and C mass.

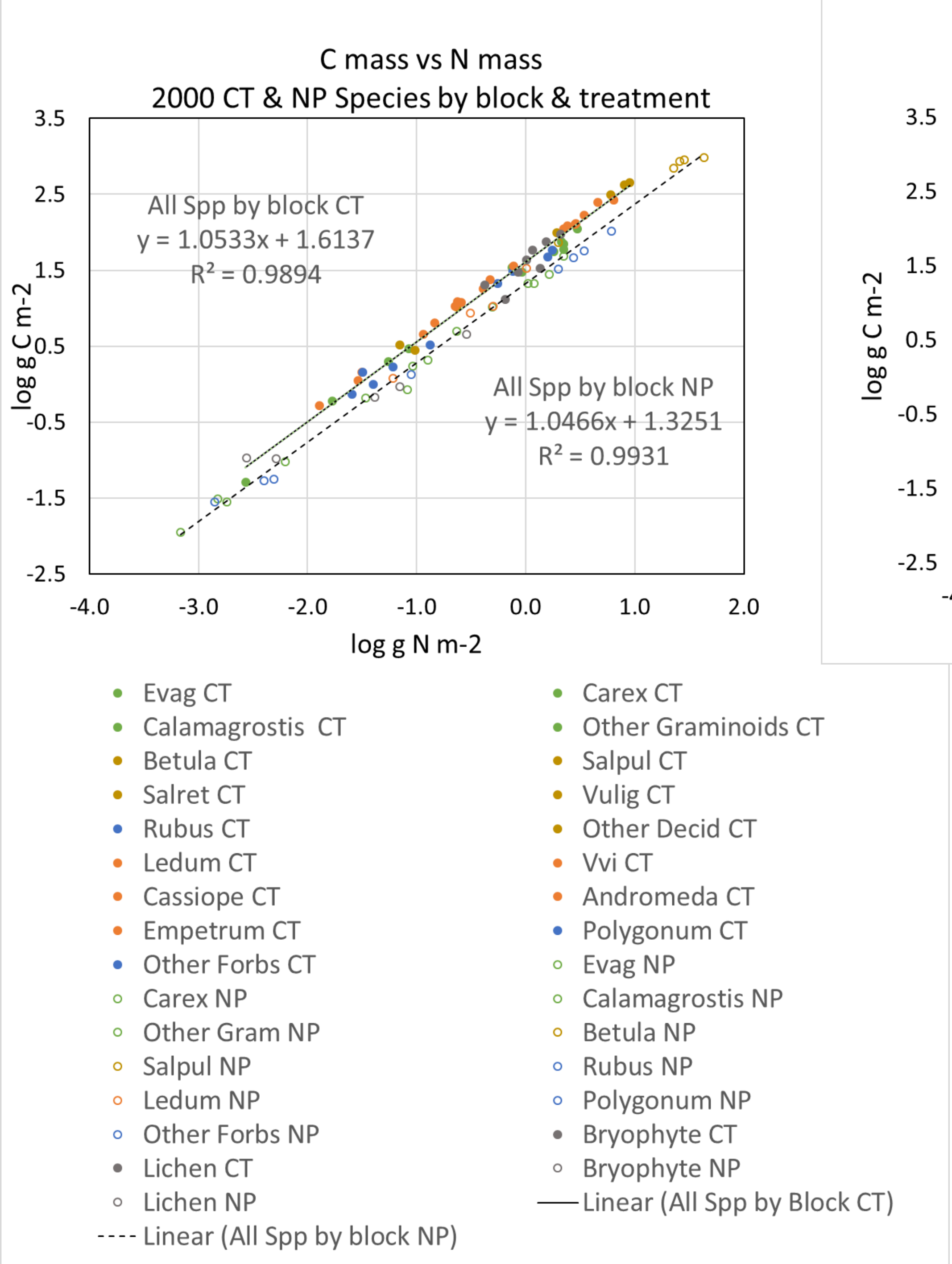


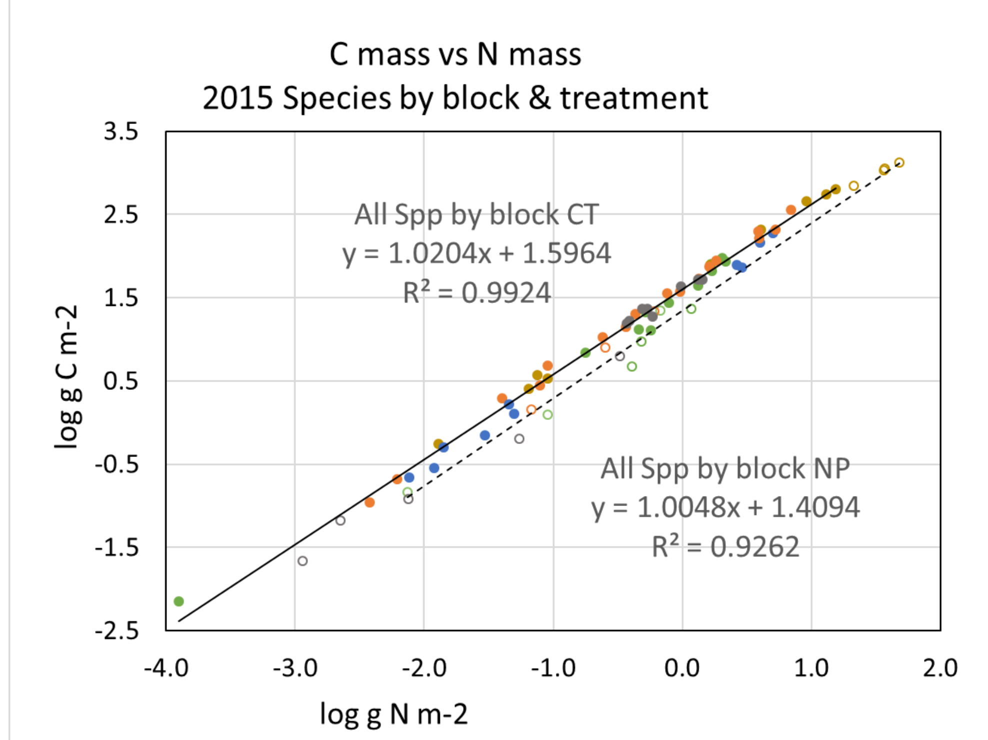
% C, N, or P when Total Live biomass is broken down by tissue types (considering bryophytes and lichens as separate tissue types)

To facilitate comparisons, individual tissue types are arranged (bottom to top) in order of increasing C, or N concentration in the CT plots in 2000, and in order of increasing P concentration in CT plots in 2015



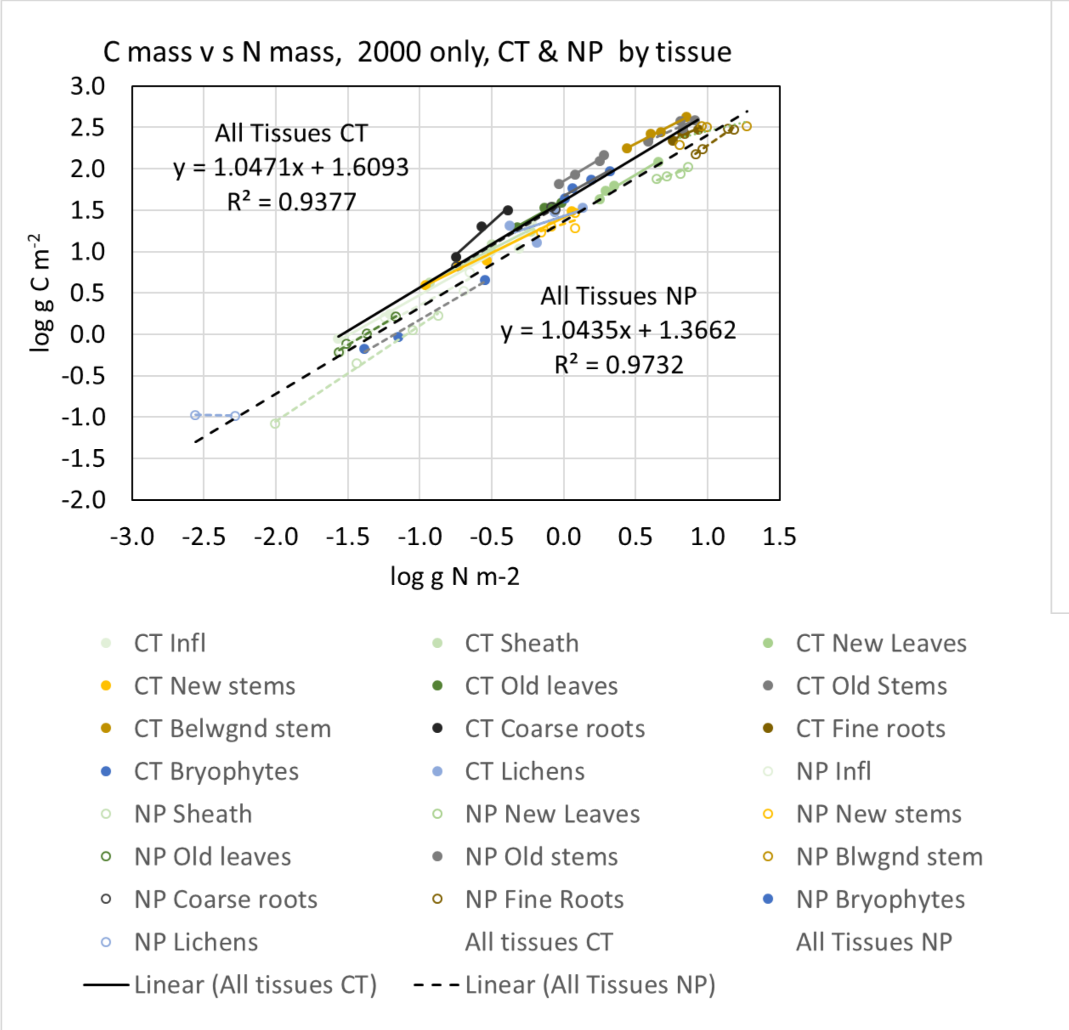
% C, N, or P when total live biomass is broken down by species or species groups. Concentrations are for whole plants of individual species or species groups. To facilitate comparisons, species are arranged in increasing order of C, or N concentrations in the CT plots in 2000 and in order of increasing P concentrations in CT in 2015

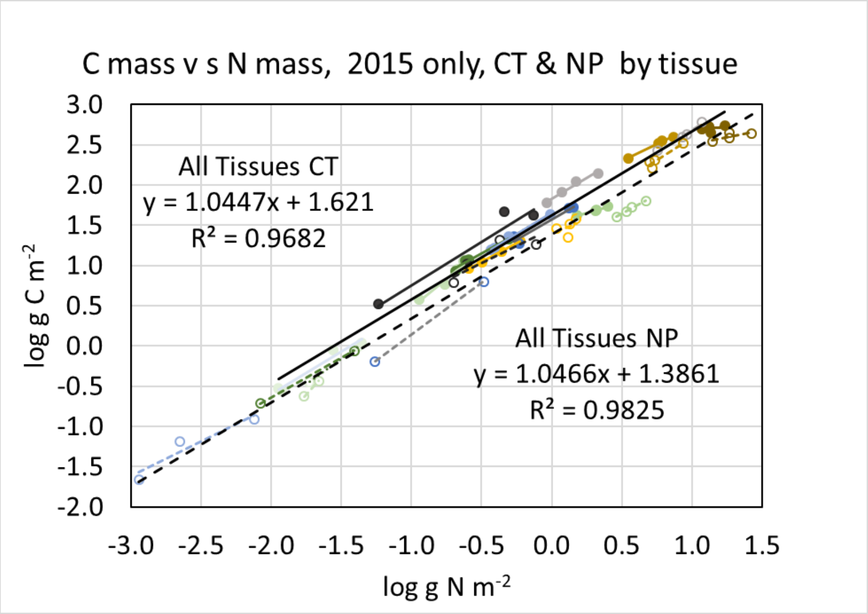




Main points:

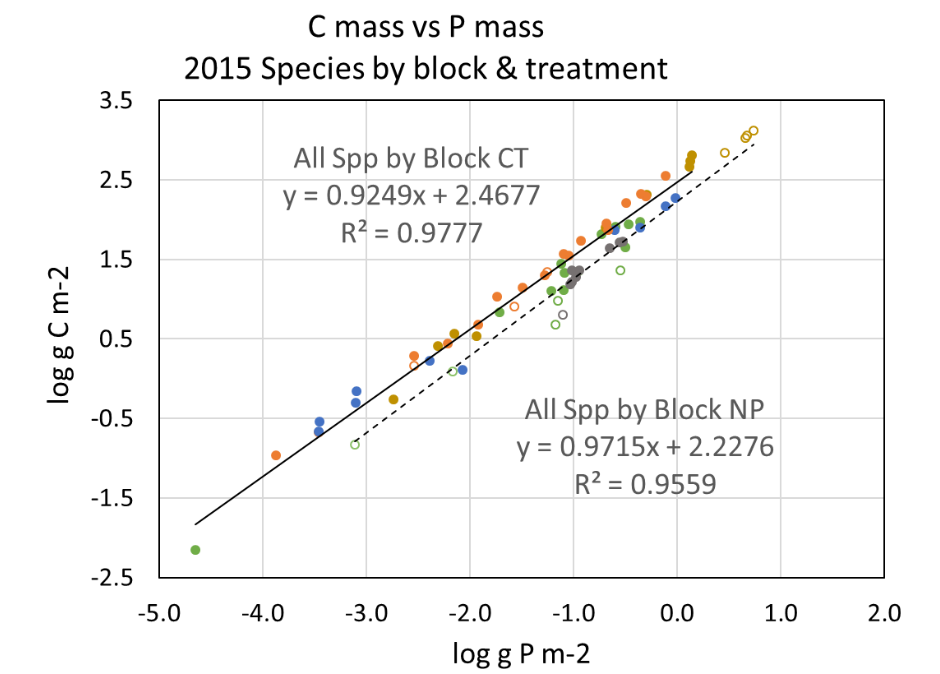
1. Over a range of 5 orders of magnitude in C mass and N mass, <u>all species follow the same stoichiometric rules of C and N allocation to total biomass</u>
2. No species are significant outliers although woody spp tend to have positive residuals and herbaceous species have negative residuals.
3. Effect of fertilizer is to shift the whole relationship down and to the right (higher %N) but there is no change in slope due to fertilizer.

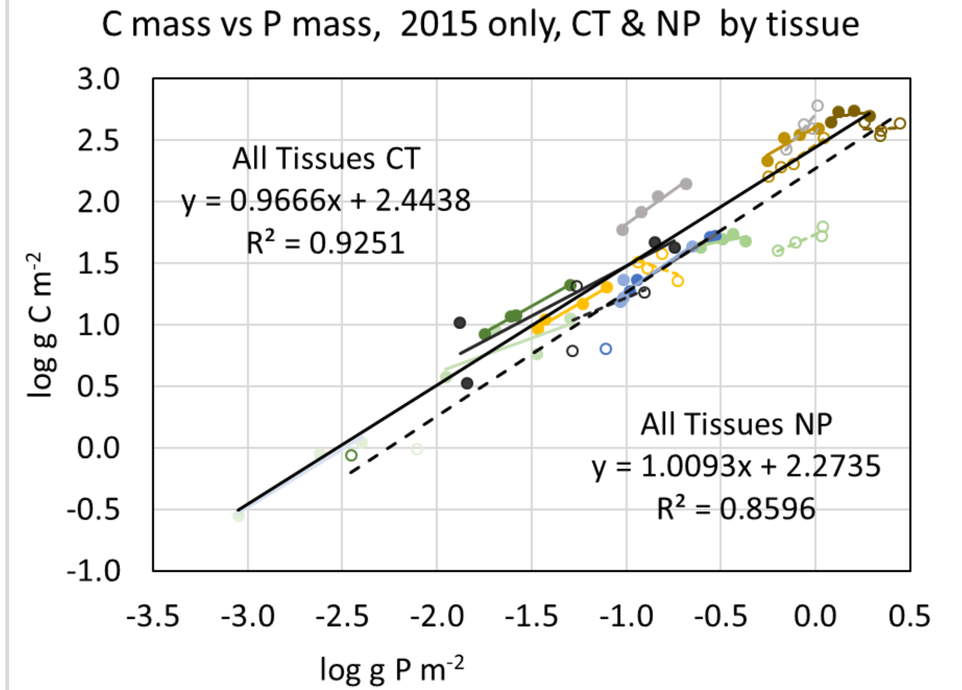


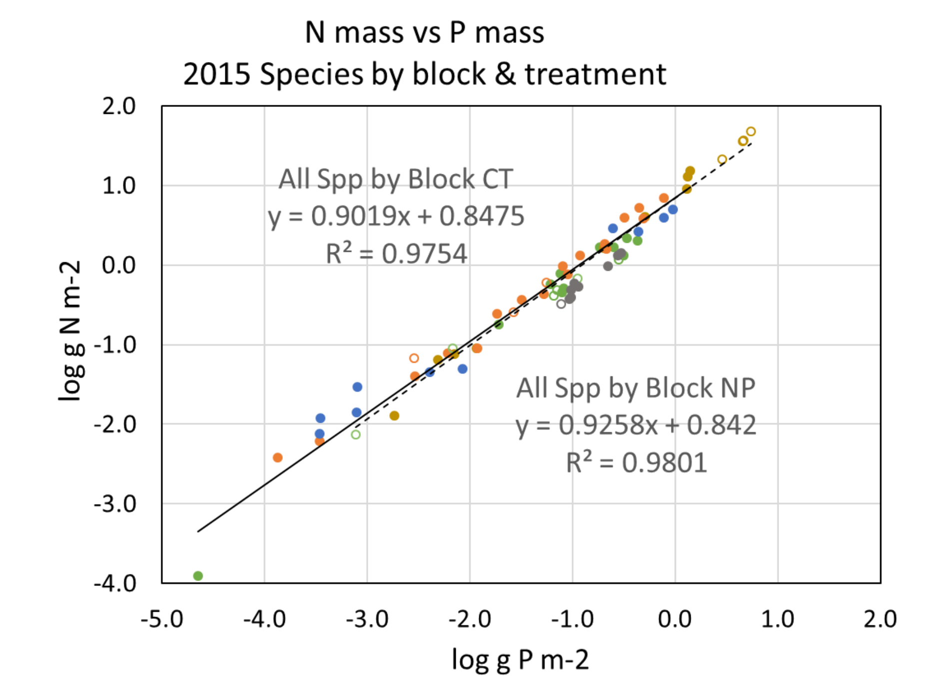


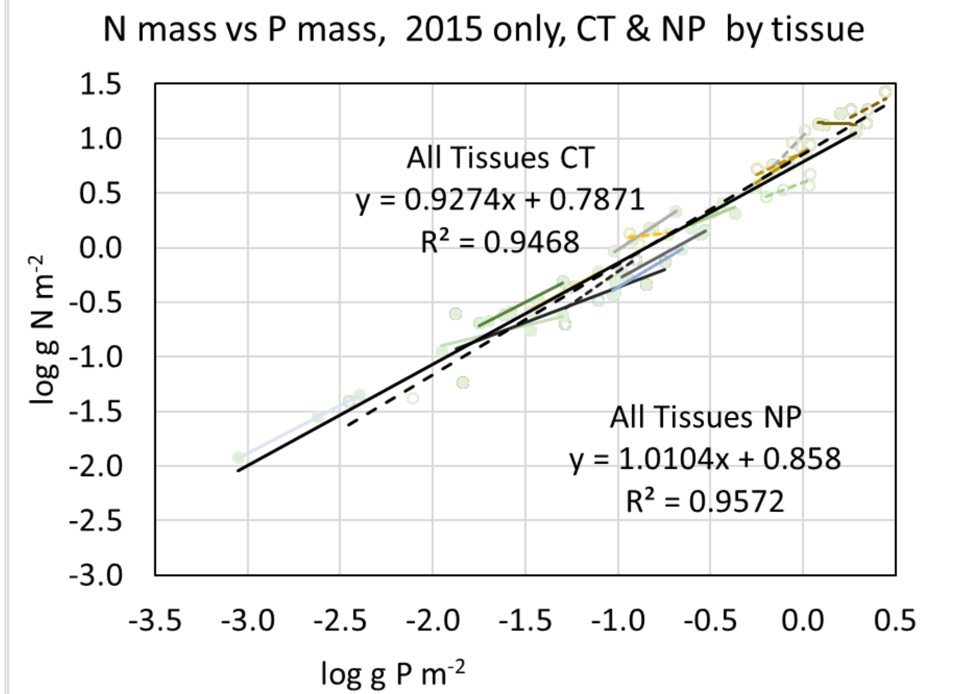
Main points:

1. Among tissue types, C and N allocation follows the same overall rules as whole plants of different species in both CT and Fert treatments
2. Individual tissues differ significantly from each other and from the overall relationship


C mass vs P mass
2015 Species by block & treatment
All Spp by Block CT
y = 0.9249x + 2.4677
R² = 0.9777
All Spp by Block NP
y = 0.9715x + 2.2276
R² = 0.9559
log g C m-2
log g P m-2
3.5
2.5
1.5
0.5
-0.5
-1.5
-2.5
-5.0
-4.0
-3.0
-2.0
-1.0
0.0
1.0
2.0

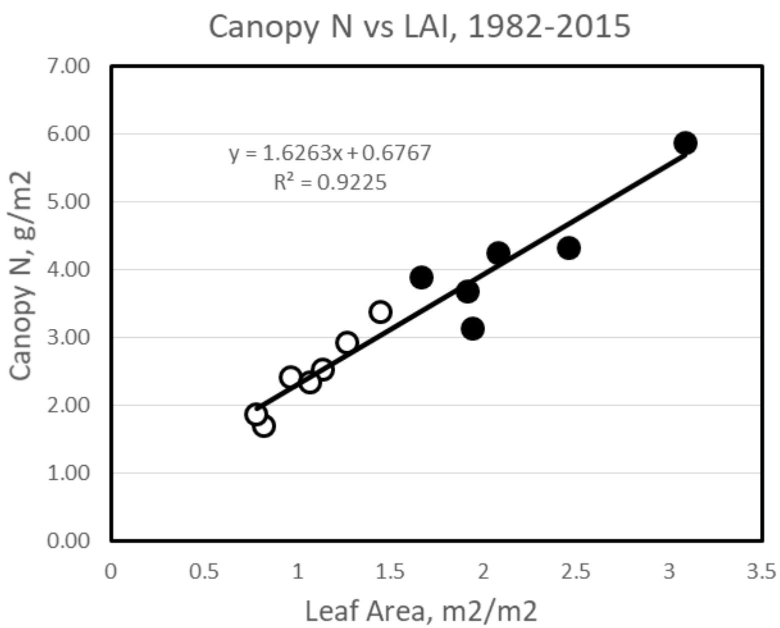

C mass vs P mass, 2015 only, CT & NP by tissue
All Tissues CT
y = 0.9666x + 2.4438
R² = 0.9251
All Tissues NP
y = 1.0093x + 2.2735
R² = 0.8596
log g C m-2
log g P m-2
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-3.5
-3.0
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5

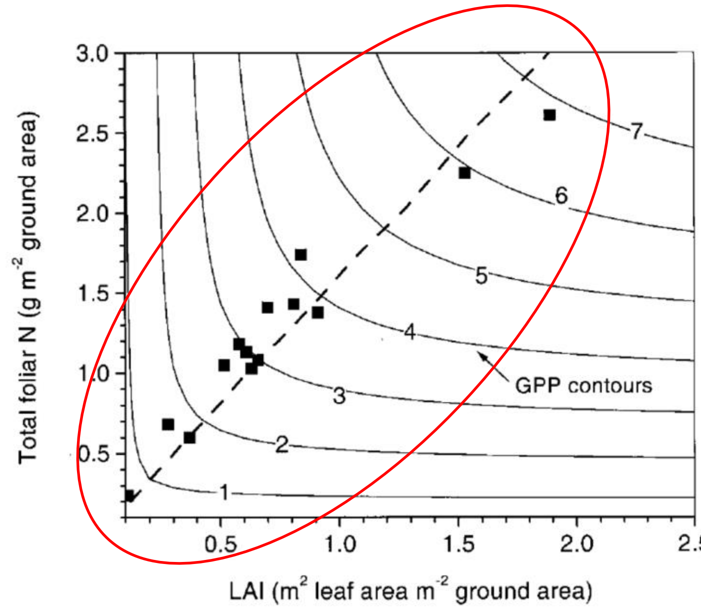

N mass vs P mass
2015 Species by block & treatment
All Spp by Block CT
y = 0.9019x + 0.8475
R² = 0.9754
All Spp by Block NP
y = 0.9258x + 0.842
R² = 0.9801
log g N m-2
log g P m-2
2.0
1.0
0.0
-1.0
-2.0
-3.0
-4.0
-5.0
-4.0
-3.0
-2.0
-1.0
0.0
1.0
2.0

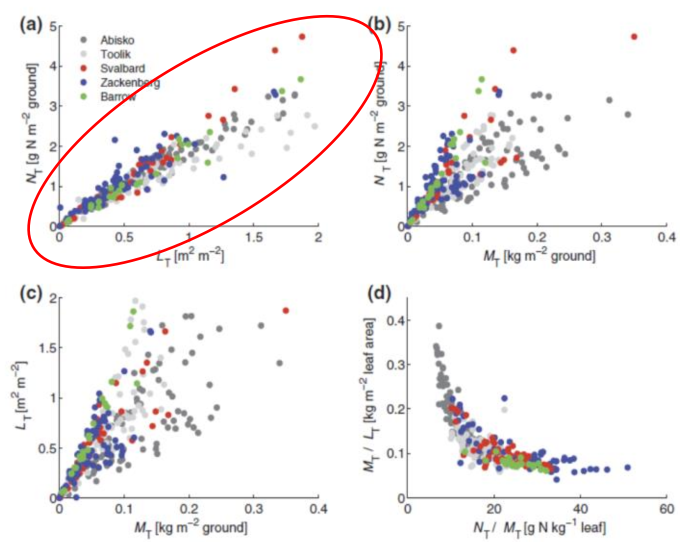

N mass vs P mass, 2015 only, CT & NP by tissue
All Tissues CT
y = 0.9274x + 0.7871
R² = 0.9468
All Tissues NP
y = 1.0104x + 0.858
R² = 0.9572
log g N m-2
log g P m-2
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
-3.0
-3.5
-3.0
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5

Conclusions:

1. Form follows function---Stoichiometry of different tissues reflects their different functions and varies widely among tissue types.
2. Form follows function—Because all whole plants must complete all of the same functions, there is no significant difference among species in C/N/P stoichiometry of whole-plant biomass
3. In N- or P-limited MAT, species composition (and species differences in whole-plant N or P concentration) has no significant impact on total biomass accumulation. Knowing species composition is less important than knowing tissue type, N mass or P mass.
4. Fertilizer changes C:N and C:P ratios of all tissues and species but has no effect on the underlying C/N/P relationships over a range of 5 orders of magnitude in biomass or C mass.
5. This is another example of how scaling of individual leaf or other tissue traits directly to the whole system doesn't work. Should be scaling whole plant (or whole canopy) properties instead.







Comparison of Leaf area/canopy N relationships in Historic Plots versus Williams and Rastetter 1995 and Street et al. 2012

Leaf traits related to photosynthesis differ with position in the canopy, both within and between species

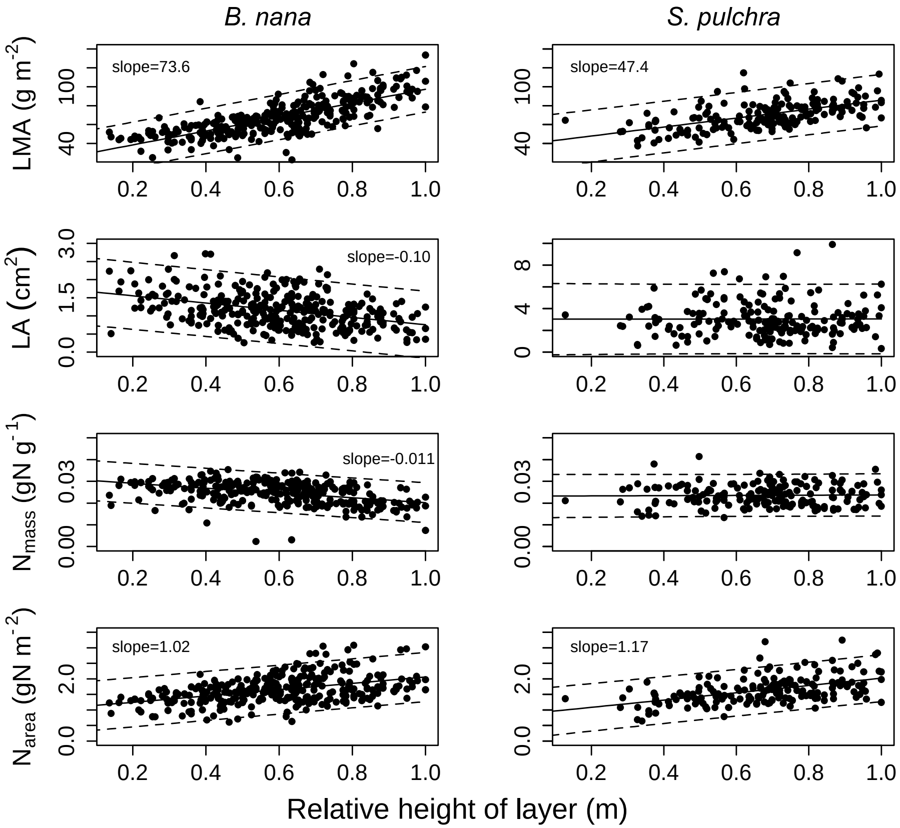
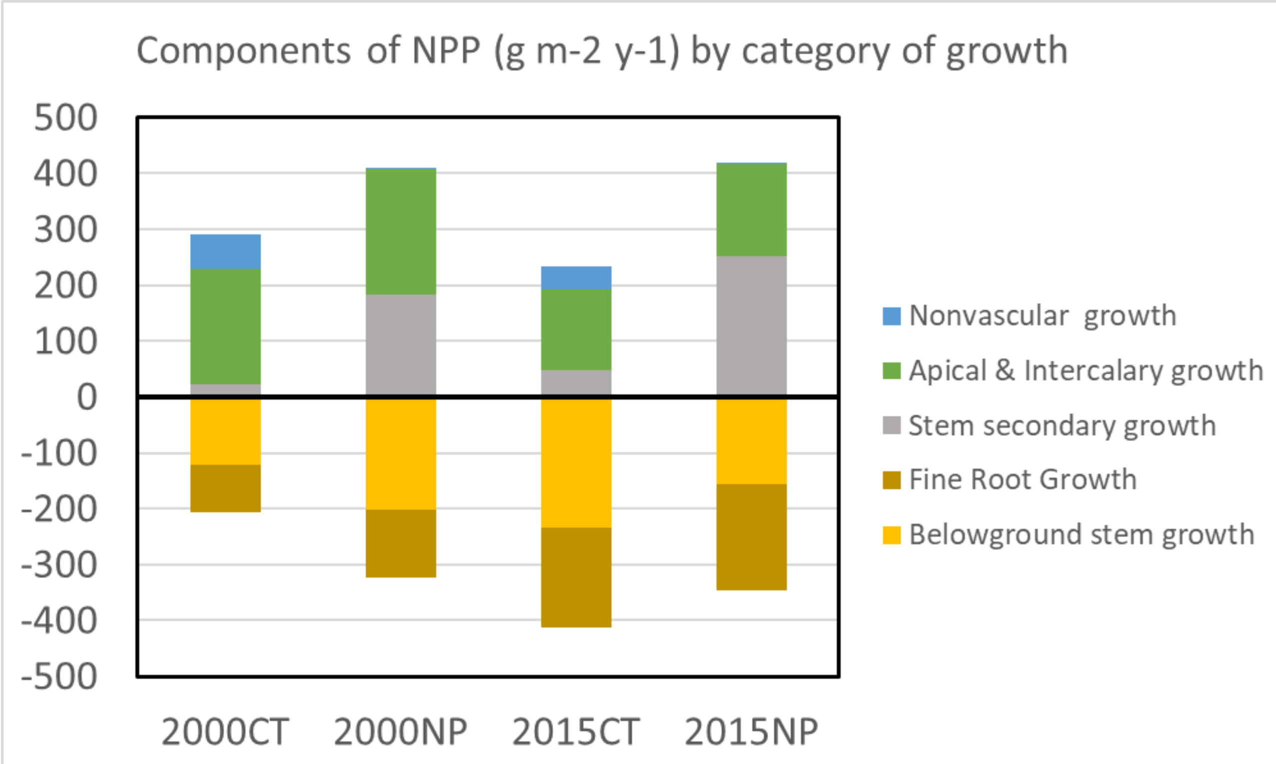


Figure 4. The variation in leaf traits with relative canopy height for *Betula nana* (left) and *Salix pulchra* (right). The regression line and 95% prediction intervals are shown, and slopes are indicated when significantly different from zero (P<0.001). LMA is leaf mass per area, LA is individual leaf area, N_{mass} is nitrogen mass per leaf mass, N_{area} is nitrogen mass per leaf area. Note the different y-axis scales for leaf area.

Z. Gratton, M. Williams et al, in prep.



Total NPP increased by 30-50% in response to fertilizer addition after 20 or 35 years. Greatest increase in woody stem production; no change in apical/intercalary growth.

Most of the NPP and its C/N/P content is not added to perennial biomass but lost as litter (or new growth is retained sufficient to balance losses of older tissues).

For comparison, the net increase in vascular biomass in both CT and NP plots from 2000-2015 amounts to a change of only 1-2% per year if annual growth rate is constant, or 32 g/m2/y in CT plots and 21 g/m2/y in NP plots (above). These net growth rates are <10% of total NPP each year, indicating high rates of biomass turnover in both CT (25-28%/y) and NP plots (32-37%/y).

Biomass & CNP turnover		Biomass Turnover (y-1)				C Turnover (y-1)				N Turnover (y-1)				P Turnover (y-1)			
(assume steady state at harvest)		CT plots		NP plots		CT plots		NP plots		CT plots		NP plots		CT plots		NP plots	
		Mean	Stderr	Mean	Stderr	Mean	Stderr	Mean	Stderr	Mean	Stderr	Mean	Stderr	Mean	Stderr	Mean	Stderr
Total Turnover																	
	2000	0.255	0.028	0.362	0.010	0.258	0.029	0.368	0.009	0.292	0.045	0.373	0.015				
	2015	0.280	0.010	0.328	0.003	0.268	0.009	0.303	0.002	0.311	0.013	0.330	0.003	0.349	0.012	0.392	0.014
Aboveground Turnover																	
	2000	0.426	0.043	0.493	0.014	0.421	0.044	0.485	0.013	0.440	0.061	0.601	0.028				
	2015	0.475	0.014	0.424	0.007	0.416	0.015	0.358	0.004	0.522	0.011	0.461	0.005	0.550	0.021	0.597	0.019
Belowground Turnover																	
	2000	0.162	0.023	0.275	0.010	0.163	0.023	0.280	0.010	0.189	0.033	0.240	0.006				
	2015	0.228	0.011	0.259	0.001	0.228	0.012	0.261	0.002	0.249	0.012	0.259	0.005	0.272	0.010	0.261	0.005
Leaf Turnover																	
	2000	0.681	0.038	0.989	0.003	0.673	0.038	0.989	0.002	0.764	0.032	0.993	0.001				
	2015	0.799	0.026	0.996	0.004	0.791	0.026	0.995	0.004	0.874	0.017	0.997	0.002	0.918	0.017	0.999	0.001
Fine Root Turnover																	
	2000	0.134	0.010	0.217	0.001	0.132	0.010	0.217	0.001	0.156	0.009	0.218	0.000				
	2015	0.166	0.007	0.219	0.001	0.164	0.007	0.219	0.001	0.186	0.005	0.219	0.001	0.198	0.005	0.220	0.000

Turnover rates vary greatly above- versus belowground and between leaves and roots. Aboveground turnover rates are much higher, particularly leaf turnover in NP plots.

PRODUCTION EFFICIENCIES				CT plots		NP plots	
				Mean	Stderr	Mean	Stderr
	NPP/g leaf mass (g/g)						
	2000			2.526	0.326	4.092	0.135
	2015			5.167	0.303	7.104	0.219
	NPP/leaf area (g/m2 leaf)						
	2000			333.962	31.797	232.506	12.159
	2015			606.686	19.651	389.695	29.384
	NPP/g leaf N (g/g)						
	2000			148.342	13.496	126.287	6.679
	2015			280.986	15.899	207.164	6.686
	NPP/g leaf P (g/g)						
	2000			nd	nd	nd	nd
	2015			518.185	341.741	2006.353	536.351
	NPP/g fine roots (g/g)						
	2000			0.777	0.112	1.470	0.303
	2015			0.599	0.057	0.879	0.033
	NPP/g fine root N (g/g)						
	2000			69.355	8.559	67.880	11.710
	2015			93.562	5.284	69.331	10.793
	NPP/g fine root P (g/g)						
	2000			nd	nd	nd	nd
	2015			2203.445	173.136	1569.109	189.710

NPP per g leaf N and per g root N unaffected by fertilizer in 2000; <u>decreased</u> in 2015

Ditto for NPP per g leaf or root P

NPP per g leaf mass increased by fertilizer; NPP per m2 leaf <u>decreased</u>

SO:

- Expression of variable “traits” among species often seems to involve tradeoffs among traits within the whole plant that lead to no net effect on ecosystem/whole vegetation properties.
- This suggests that direct scaling the effects of traits of individual tissues to functioning of whole ecosystems or whole vegetation may be misleading and that the tradeoffs among multiple traits must be considered to make useful predictions of impacts of individual traits on whole vegetation.