**Notes on photosynthetic apparatus response to light environment:**

Nitrogen concentrations per unit leaf mass were constant between the two light treatments, but plants grown in low light partitioned a larger fraction of leaf nitrogen into light harvesting. (Evans & Poorter PCE 2001)

Niinemets 2007 review: (this is really good stuff for discussion – contextualises things in whole canopy setting)

*Plants can acclimate to varying light conditions by changing leaf angle, canopy leaf density, leaf construction (e.g. SLA) and leaf light harvesting ability*

“Acclimation of Amax to high light availability involves accumulation of rate- limiting photosynthetic proteins per unit leaf area as the result of increases in leaf thickness in broad-leaved species and volume : total area ratio and mesophyll thickness in species with complex geometry of leaf cross-section.”

“In particular, both temperature and water vapour pressure deficit scale posi- tively with canopy light availability (Baldocchi et al. 2002; Niinemets &Valladares 2004), implying that foliage can be exposed to simultaneous heat, water and high light stresses.”

“These possible trade-offs mean that individual foliage acclimation responses must be assessed in the context of specific canopy light availabilities and from the perspective of maximizing whole canopy per- formance. Species” (good reason for measuring new mid and old leaves and aggregating)”

“Because of the large nitrogen cost of chlorophyll and chlorophyll-binding pro- teins, within-canopy modifications in light interception efficiency depend on variations in nitrogen investments in light harvesting” – more stuff here about chlorophyll but its complicated. Can use this to just introduce the idea

6.25 is the nitrogen content of Rubisco protein (Niinemets &Tenhunen 1997).

Jmax can be revealed analogously, with FB characterizing the fraction of nitrogen in proteins limiting Jmax & (Niinemets Tenhunen 1997)

Fractional allocation of nitrogen in Rubisco and in pro- teins limiting photosynthetic electron transport (Eqn 4) increases or is relatively constant with increasing light avail- ability (Niinemets&Tenhunen 1997; Niinemets et al. 1998b; Evans & Poorter 2001; Grassi & Bagnaresi 2001; Le Roux et al. 2001b;Warren et al. 2003)

“photosynthetic capacity [fraction of nitrogen in ribulose 1·5-bisphosphate carboxylase/ oxygenase (Rubisco)” (i.e. photosynthetic capacity is on a mass basis – although can scale to area if N scales with LMA, which it does)

As nitrogen contents per dry mass (NM) vary hardly along canopy light gradients, an increase in MA results also in a strong positive scaling of nitrogen content per area (NA=MA NM) with light

Even if leaf nitrogen allo- cation were invariable along the light gradient, scaling of bulk nitrogen content per area would already mean accu- mulation of limiting photosynthetic enzymes per unit area, and positive scaling of maximum foliage photosynthetic rates (Amax) and its partial determinants Vcmax and Jmax (Fig. 4c).

**We actually found no strong scaling of LMA along light gradient. This might be because we weren’t just measuring within-canopy variation – tavg and precip were correlated with light environment and are known to affect LMA too\*. Photosystems did go down on a per area basis though as light increased.**

**\***To produce tough leaves, plants need to allocate more biomass and nitrogen to make thick cell walls, leading to a reduction in the mesophyll conductance and in nitrogen allocation to the photosynthetic apparatus. Allocation of biomass and nitrogen to cell walls may cause the negative relationship between PNUE and LMA. Since plants cannot maximise both PNUE and leaf toughness, there is a trade-off between photosynthesis and persistence, which enables the existence of species with various leaf characteristics on the earth.- Hikosaka 2004 “Interspecific difference in the photosynthesis–nitrogen relationship: patterns, physiological causes, and ecological importance”

Overall, it seems that in woody species, the structural adjustment through light-dependent modifications inMA is responsible for most of the variation in Vcmax and Jmax ,while alteration in nitrogen partitioning plays a secondary role (Niinemets et al. 1998b; Evans & Poorter 2001) (but see Niinemets & Tenhunen 1997; Grassi & Bagnaresi 2001).

acclimation to high light was dominated by adjustments in leaf anatomy (Aamax=AmmaxMA) rather than in foliar biochemistry. This differed from adaptation to low light, where the alterations in foliar biochemistry were predicted to be at least as important as anatomical modifications.

**Thus, we conclude that analyses of the effects of nitrogen investments on potential carbon acquisition should use mass-based rather than area-based expressions.**

* **Niinemets and tenhueusen 1997**

**Notes on photosynthetic apparatus response to temperature:**

Hikosaka et al. give 2006 minireview “Temperature acclimation of photosynthesis: Mechanisms involved in the changes in temperature dependence of photosynthetic rate”:

“In the biochemical model of C3 photosynthesis, the photo- synthetic rate is limited either by the RuBP (ribulose-1,5- bisphosphate) carboxylation or by the RuBP regeneration (Farquhar et al., 1980).”

I’m assuming RuBP regeneration involves various Calvin cycle enzymes as well as input of NADPH & ATP from light reactions.

Both of these processes should be temperature dependent, although at high temperatures there is inactivation (for carboxylation likely via rubisco activase, and empirically for RuBP regen via some undescribed mechanism)

**Carboxylation limitation of photosynthesis:**

Under dry conditions? – see Wright et al. 2005 ‘Modulation of leaf economic traits and trait relationships by climate’

“Nmass showed no trend with rainfall, but decreased with increasing MAT, VPD, PET or irradiance (Table 2). Narea tended to show the opposite pattern, being higher at higher MAT, VPD, PET or irradiance, and higher at lower rainfall. Narea is the product of Nmass and LMA. Therefore, it must have been the underlying trends in LMA rather than Nmass that led to higher Narea at hotter/drier/higher irradiance sites. Narea increased with irradiance with rainfall held constant, and increased with decreasing rainfall at any given level of irradiance (Fig. 2). That is, the rainfall and irradiance effects were independent of each other”

**A lot of what has been demonstrated apparently is structural adaptation to light environment – or that the structural component is more important. In our data light capture and carboxylation capacity scale with LMA and leaf N but we can also show adaptation at the molecular level using proportional amounts.**

From Dong Ning paper leaf N from first principles

“the hypothesis that photosynthetic capacity is optimized at the leaf level as a function of irradiance, leaf-internal CO2 concentration (ci) and temperature (Haxeltine and Prentice 1996, Dewar 1996) – as assumed in the widely used LPJ DGVM (Sitch et al. 2003) and other models derived from it, including LPJ-GUESS (Smith et al. 2001) and LPX (Prentice et al. 2011a; Stocker et al. 2013). This ‘plant-centred’ approach is based on the idea 20 that plant allocation processes determine leaf-level traits. More specifically it is derived from a long-standing concept, the ‘co-ordination hypothesis’, which states that the Rubisco- and electron transport-limited rates of photosynthesis tend to be co-limiting under average daytime conditions (Chen et al. 1993; Haxeltine and Prentice 1996; Maire et al. 2012). Co-limitation is optimal – even though mechanistically, it may be an inevitable outcome of leaf metabolism (Chen et al. 1993) – in the sense 25 that it provides the right balance of investments in the biochemical machineries for carboxylation and electron transport. It implies that enzyme activities adjust, over relatively long periods (weeks or longer), so that co-limitation holds. An important consequence is that the predicted responses of photosynthetic traits and rates to environmental variables observed in the field (whether temporally, comparing different seasons or spatially, comparing different environments) are substantially different from those 30 seen in short-term laboratory experiments.”