Ecophysiological traits of grasses: resolving the effects of photosynthetic pathway and phylogeny

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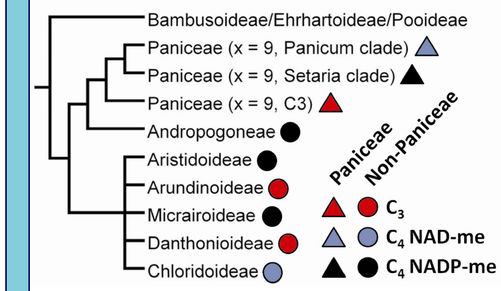
Introduction:

C_4 photosynthesis is an important example of convergent evolution in plants, having arisen in eudicots, monocots and diatoms[1]. Comparisons between such diverse groups are confounded by phylogenetic and ecological differences, so that only broad generalisations can be made about the role of C_4 photosynthesis in determining ecophysiological traits. However, 60% of C_4 species occur in the grasses (Poaceae) and molecular phylogenetic techniques confirm that there are between 8 and 17 independent origins of C_4 photosynthesis in the Poaceae[2]. In a screening experiment, we compared leaf physiology and growth traits across several major independent C_3 & C_4 groups within the Poaceae, asking 1) which traits differ consistently between photosynthetic types and 2) which traits differ consistently between clades within each photosynthetic type.



Design:

Species were picked at random from C_3, C_4 NAD-me and C_4 NADP-me clades (left). Plants were grown in 4 l. pots in a glasshouse, kept well-watered & unfertilised (right) Gas exchange and water potentials were measured. For a subset of species, sequential destructive harvests and curve-fitting were used to estimate growth traits at a common, small size.

Leaf physiology:

C_4 photosynthesis is characterised by CO_2 uptake at low concentrations (via PEPc) and saturation of Rubisco with CO_2, minimizing photorespiration and leading to improvements in Rubisco carboxylation efficiency. C_4 plants are thus expected to show higher net CO_2 assimilation rates (A), lower stomatal conductance (g_s), lower leaf nitrogen (N_{mass}, N_{area}) and improved photosynthetic nitrogen and intrinsic water use efficiencies ($PNUE$ = A/N_{area}, and $iWUE$ = A/g_s respectively) under a range of conditions[3].

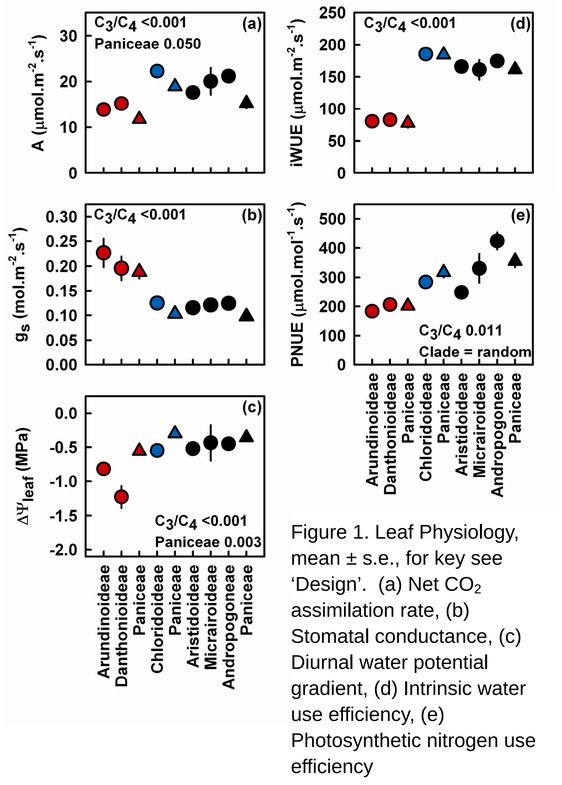


Figure 1. Leaf Physiology, mean ± s.e., for key see 'Design'. (a) Net CO_2 assimilation rate, (b) Stomatal conductance, (c) Diurnal water potential gradient, (d) Intrinsic water use efficiency, (e) Photosynthetic nitrogen use efficiency

We found

- Contrasts between C_3 and C_4 photosynthetic types in A, g_s, $\Delta\Psi_{leaf}$, $iWUE$ and $PNUE$ (Fig. 1a - e). Within either type, g_s and $iWUE$ showed strong convergence.
- $PNUE$ showed divergence between clades and $\Delta\Psi_{leaf}$ showed divergence between Paniceae and other clades.

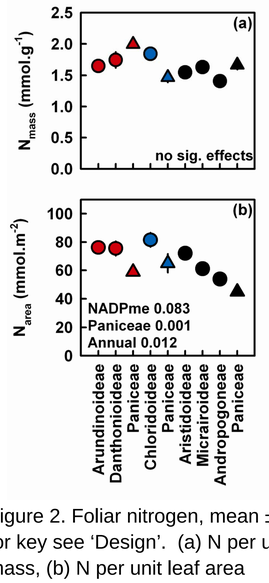


Figure 2. Foliar nitrogen, mean ± s.e., for key see 'Design'. (a) N per unit mass, (b) N per unit leaf area

- **Unexpectedly,** N_{mass} showed no significant patterns (Fig. 2a). Paniceae had lower N_{area} within each type (Fig. 2b), indicating that leaf area per unit leaf mass is high in this group. N_{area} was similar between C_3 and C_4 NAD-me.

Growth analysis:

Improved resource use efficiency is expected to correlate with differences in growth allocation between C_3 & C_4 plants[3]. If higher A is translated into improved growth rate per unit canopy area (unit leaf rate, ULR), C_4 plants may show either higher relative growth rates per unit total mass (RGR), or a greater range of allocation strategies mediated via changes in the leaf mass ratio (LMR) and root mass ratio (RMR)[3]. The resulting effect on canopy leaf area ratio (LAR) is influenced by the specific leaf area (SLA) ($LAR = SLA \times LMR$).

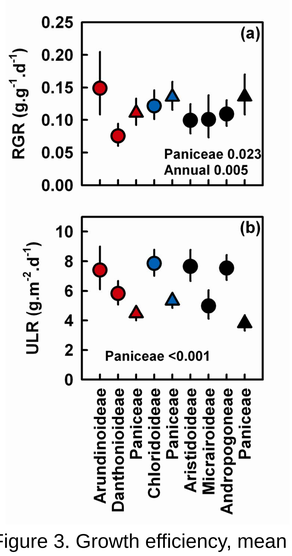


Figure 3. Growth efficiency, mean ± s.e., for key see 'Design'. (a) growth per whole plant mass, (b) growth per leaf area

We found

- No increase in ULR and RGR in C_4 types (Fig. 3a & b), despite higher A and greater resource use efficiencies at the leaf level.
- Consistent, significant effects on growth rates and biomass allocation due to:

  1) Classification as perennial vs. annual/ weak perennial (annuals showed greater SLA, LAR *and* LMR, data not shown).

  2) Paniceae, which showed increased RGR, LAR & LMR, and reduced RMR & ULR (Figs. 3 & 4).
- SLA (Fig. 4a) was the only growth trait to show a random effect of clade, indicating divergence between phylogenetic groups.
- The C_4 NADP-me subtype was associated with more extreme differences in allocation.

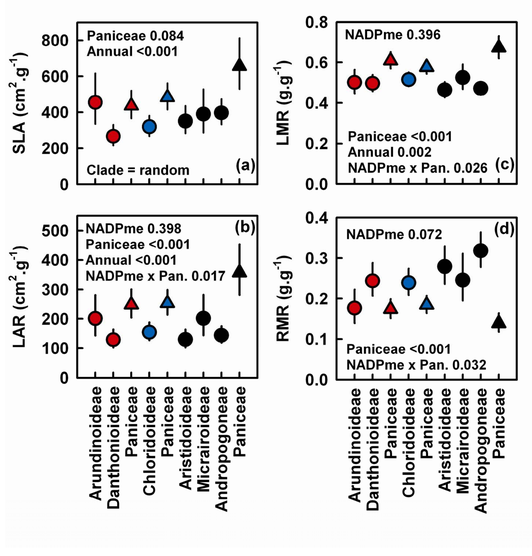


Figure 4. Whole plant allocation of growth, mean ± s.e., for key see 'Design'. (a) Specific Leaf Area, (b) Leaf Area Ratio, (c) Leaf Mass Ratio, (d) Root Mass Ratio

Conclusions:

- Some traits associated with C_3 and C_4 photosynthesis show strong convergence across independent lineages (low g_s, high $iWUE$), whilst others vary substantially between lineages (high A, high $PNUE$). C_3 and C_4 photosynthesis were not distinguished by leaf N, but low g_s in C_4 types relative to C_3 was associated with reduced diurnal water potential gradients.
- Within photosynthetic types, clades differed in allocation of resources at the leaf (SLA, $PNUE$ & N_{area}) and whole plant (LAR, LMR) levels (esp. between Paniceae and others); there was some evidence that this divergence was most extreme in the C_4 NADP-me type.
- Ecophysiological traits linked to C_4 photosynthesis in grasses are influenced by phylogeny and may show substantial divergence between independent C_4 lineages.

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