Chapter 4

Paper:

Beerling, David J., C. P. Osborne, and W. G. Chaloner. "Evolution of leaf-form in land plants linked to atmospheric CO_2 decline in the Late Palaeozoic era."*Nature* 410, no. 6826 (2001): 352-354.

Questions:

1. **What are the morphological differences between microphylls and megaphylls? ANSWER:** Microphylls, also known as enations, are simple spine like leaves, which typically possess only one vein per leaf. Megaphylls are considered true leaves or 'euphylls'. They are flattened (planate) structures, typically with more than one vein per leaf. Microphylls are found in Zosterophyllophytes whereas meagphylls are characteristic of the majority of Euphyllophytes.

2. **Why is it so surprising to the authors that it took over 40 million years for planate megaphyll leaves to evolve? ANSWER:** The authors note that other major evolutionary developments occurred in the same interval – for example, the seed habit evolved from a homosporous habit.

3. **What is the oldest known fossil plant that evolved megaphyll leaves? ANSWER:** *Eophllophyton bellum*.

4. **What does the presence of *Eophyllophyton bellum* in the fossil record indicate about the evolution of leaves? ANSWER:** The observation that megaphyll leaves had evolved very early in *Eophyllophyton bellum* but not in any other major lineages of early land plants at the time indicates that there was likely no developmental constraint to the earlier evolution of megaphyll leaves in many more plant groups.

5. **What methodology is used to test the costs and benefits of early land plants evolving megaphyll leaves? ANSWER:** A physiological modelling approach is used to estimate photosynthetic rate, transpiration rate and leaf temperature of three hypothesized early land plants:(a) a leafless early land plant with low stomatal density (similar to that observed in the fossil record); (b) an early land plant with megaphyll leaves and low stomatal density; and (c) an early land plant with megaphyll leaves and high stomatal density. The model used includes a photosynthesis model linked to stomatal conductance and a gas diffusion resistance model linked to a leaf energy balance model to estimate leaf temperature. Initial model parameters were taken from fossil and modern observations and the model was allowed to interact in a dynamic way with the environment using an understanding of how modern plant stomata and physiology respond to key environmental parameters such as light, water availability and vapour pressure deficit.

6. **Describe the major findings of the model as illustrated in Figure 1. ANSWER:** The key model findings were as follows: an early land plant with low SD and no leaves according to the model would have had modest photosynthetic rates (~10 umol m^{-2} s^{-1}), low transpiration rates and stem (axis) temperatures well below the critical threshold where photosynthesis ceases. In contrast if the earliest land plants with low stomatal density had evolved leaves in the early Devonian (scenario b) the model suggests that the leaf temperatures would have far exceeded lethal limits due to low transpiration rates (~2 mmol m^{-2} s^{-1}) resulting in low cooling capacity of the leaf surface. Photosynthetic rates would be zero under this scenario because of protein denaturation due to exceedingly high leaf temperature. The model further suggest that true leaves could not develop widely until plants developed high stomatal densities, which would provide sufficient cooling capacities to maintain leaf temperature below lethal limits.

7. **The model is used to predict the likely size of the earliest proto-leaves at different palaeo-latitudes. What leaf size range is suggested and why are the predictions different depending on latitude? ANSWER:** 50 to 100 mm leaf widths at high latitudes and < 20 mm leaf widths at low latitudes. The difference is because of differences in heat loading on the leaf surface which is dependent on local climate – the low latitudes being hotter than the high latitudes. As leaf temperature budget is size dependent, the model suggests that larger leaf sizes would be capable of developing in plants of the cooler high latitudes without suffering negative consequences (that is, overheating).

8. **What species possessed the largest early leaves in the fossil record? ANSWER:** *Enigmophyton*, with leaves up to 160 mm long and 120 mm broad from the Middle Devonian.

9. **Why, according to the authors, did true megaphyll leaves not occur widely until the late Palaeozoic? ANSWER:** The authors argue that there was a major environmental constraint on leaf evolution which delayed their widespread origin to the late Palaeozoic. Only when atmospheric CO_2 conditions had dropped from an early Palaeozoic high of ~ 3000 ppm CO_2 and plants responded by increasing stomatal density could leaves evolve because flat webbed surfaces orientated towards the sun (e.g. leaves) could only maintain temperatures below lethal limits if they had sufficient stomata on the leaf surface to transpire effectively and cool the leaf surface via conductive cooling (similar to sweating in humans).