Diverse Responses of Photosynthesis and Tree Growth in Competing Eucalypts Result in Niche Separation

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Dedicated to our late friend Anthony (Tony) George Swan

Abstract

In order to understand the role of productivity in competition, photosynthesis and annual carbon balances at the leaf level were investigated in the field in two montane species of *Eucalyptus*, namely *E. pauciflora* ssp. *pauciflora* Sieb. ex Spreng (snow gum) and *E. delegatensis* R. Baker (alpine ash). Furthermore, saplings of similar diameter (at breast height) were compared with respect to stem age, leaf mass and area and carbon gain per canopy.

On the leaf level, the longer-lived leaves of the lignotuberous *E. pauciflora* (average leaf age: 2.5 years) were almost twice superior to leaves of *E. delegatensis* (average leaf age: 1.5 years) concerning carbon gain. But a larger leaf area per canopy as a result of cheaper growth of leaf material and a different carbon allocation pattern led to much higher growth rates in *E. delegatensis*. Thus measurements of photosynthesis on the leaf level do not allow for conclusions on tree growth. On the other hand, different allocation patterns result in a niche separation, allowing *E. delegatensis* a rapid height gain out-shading *E. pauciflora*, whereas the lignotuber of the latter favours this species on endangered sites e.g. with respect to fire, frost and storm damage.

Since both species dominate in their stands, these species-specific features carry over to the landscape level, and they, therefore, have impacts on fire intensity, litter accumulation in the ecosystem, run-off of water, water catchment and soil erosion.

Introduction

Two montane species of *Eucalyptus* (*E. delegatensis* and *E. pauciflora* ssp. *pauciflora)* cover a similar geographical range, but they rarely form mixed stands. *Eucalyptus delegatensis* is a tall forest tree with relatively thin, short-lived leaves (1.5 years on average). *Eucalyptus pauciflora*, on the other hand, is a lignotuberous tree of more stunted growth and leaves are kept for 2.5 years on average.

Considering the obvious difference in growth forms, one would expect strong differences in carbon economy. So, in natural stands, photosynthetic characteristics and carbon balances on the leaf level were measured and related to growth parameters. Do the combined characteristics of carbon gain, within-plant carbon utilization and morphology imply niche separation of the two species? What are the implications for the use of eucalypts in plantations?

Materials and Methods

For the assessment of biomass, representative saplings of both species were harvested and analyzed in detail (concerning branching characteristics, allocation of dry matter to foliage, branches, stem, bark). From that it was possible to transfer the results to other saplings without further destructive harvesting (Küppers 1985, Küppers 1999, Stegemann 1999, Timm 1999).

Photosynthesis was measured *in situ* using a self-constructed, field portable gas exchange system (Küppers et al. 1987).

Results and Discussion

There are different levels of integration on which to approach a comparison of tree growth and partitioning of dry matter. With respect to this, figure 1 gives a general view of important factors that affect a plant´s carbon supply and within-plant utilization. Letters indicate the parameters investigated here and are the same as in table1.

Results shown here are for individuals of similar stem diameter; they were chosen since this parameter is commonly used in forestry and can be readily assessed. In table 1 parameters that favour *Eucalyptus pauciflora* in „normal" competition are marked in **bold face**, those that favour *Eucalyptus delegatensis* are labelled in *italics*. But characteristics that are unfavourable under normal conditions can be advantageous during catastrophic events, e.g. a thick bark or below ground meristems (like lignotubers) in the case of fire or short-term frost events.

Letters indicate the following results:

- **A)** *Eucalyptus pauciflora* has twice the photosynthetic capacity of *Eucalyptus delegatensis;* one would therefore expect faster growth in this species.
- **B)** But whereas annual carbon gain is rather similar (as an effect of frequent cloud cover, leaf ageing) leaf life carbon gain is twice as high in *Eucalyptus pauciflora* as compared to *Eucalyptus delegatensis*.
- **C)** Despite twice the plant age *Eucalyptus pauciflora* has less than half of *Eucalyptus delegatensis´* leaf area
- **D)** even although *Eucalyptus pauciflora* keeps its leaves on average one year longer.
- **E)** So in the end, due to the total leaf area of the canopy, *Eucalyptus delegatensis* shows nearly twice the annual canopy carbon balance per sapling.
- **F)** *Eucalyptus pauciflora* allocates a lot of resources to branch and bark biomass (and lignotuber, not shown) whereas *Eucalyptus delegatensis* grows less costly branches and uses the resources for shoot elongation and height gain instead.

Eucalyptus delegatensis, a fast growing tree, dominates fairly closed stands and out-shades shade intolerant species (like most eucalypts, e.g. snow gum). The slower growing *Eucalyptus pauciflora* on the other hand forms rather open stands but is well adapted to survive catastrophic events. Since the lignotuber is usually not affected by adverse environmental conditions, snow gum still protects the soil from erosion when the shoot is lost due to fire, windfall, frost or snow. From the carbon (and nutrients) stored in the lignotuber snow gum easily regenerates new shoots where alpine ash would fail.

Table 2 represents a summary of the comparison of the two eucalypts. From this, the following ecological consequences can be seen: While at the species and population level a clear separation of niches becomes evident, this has effects at the much larger landscape level, for large areas are covered by the two species in almost monospecific tree stands. In cases of forest fires the stands differ in intensities because of different litter productions (*E.d.* more litter in shorter time).

Similarly, soil erosion, water catchment and run off are affected by leaf area index and litter accumulation at the soil surface.

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Table 1:
Photosynthetic characteristics, annual carbon gains, canopy and growth parameters of two eucalypts under natural growth conditions in the Brindabella Ranges near Canberra, Australia (further explanation in the text).
First column: Bold face letters refer to those in Fig. 1.
Last column (Ratio of data of *E.p./E.d.*):
italics = disadvantage for *E. pauciflora* relative to *E. delegatensis* in „normal" competition**,**
bold face = advantage for *E. pauciflora* relative to *E. delegatensis* in „normal" competition,
normal print = neutral

	Eucalyptus pauciflora **Sieb. ex Spreng. ssp** ***pauciflora***	***E. delegatensis*** **R.T. Baker**	**Ratio** ***E.p./E.d.***
A) Highest observed photosynthetic capacity (µmol m^{-2} s^{-1})	26	13	**2.0**
Incident annual photon irradiance (kmol m^{-2} yr^{-1})	8.4	4.7	**1.8**
B) Annual carbon gain (mol m^{-2} yr^{-1}) (mean depending on leaf age distribution in canopy)	79	63	1.2
Leaf life carbon gain (mol m^{-2}) = annual carbon gain x mean leaf longevity	197.5	94.5	**2.1**
Basal stem diameter (cm)	11.0	9.2	1.2
Diameter at 1.5m height (cm)	5.57	5.33	1.0
Stem dry matter (kg)	4.71	4.91	0.96
Trunk volume (cm^3)	11,488	10,983	1.0
F) Bark biomass of the whole stem (g)	ca. 1,128	ca. 842	*1.3*
Specific weight of stem bark (g cm^{-3})	0.45	0.78	**0.58**
Number of leaves in canopy	930	709	1.3
C) Total leaf area in canopy (m^2)	1.93	4.35	*0.44*
Leaf mass per area (mean over canopy) (g m^{-2})	226	138	*1.6*
C) Total leaf mass (g)	436.2	600.3	*0.73*
D) Mean leaf longevity (yr)	2.5	1.5	**1.7**
Dry matter costs after 15 years of having 1 m^2 of foliage continuously in the canopy (g)	1,356	1,380	0.98
Leaf area index (individual plant) (m^2 m^{-2})	1.48	3.44	*0.53*
Leaf area index (stand, estimated) (m^2 m^{-2})	2	4	*0.5*
E) Leaf carbon balance in canopy (mol yr^{-1})	152	273	*0.56*
F) First order branch biomass (g)	666.5	174.5	*3.8*
Number of first order branches	29	34	*0.85*
No. of 1st order branches shed	ca. 39	ca. 60	*0.65*
Insertion height of lowest branch (m)	2.8	5.3	*0.53*
F) Maximum shoot elongation (cm yr^{-1})	27	70	*0.38*
Height (m)	6.01	8.20	*0.55*
Plant age (a)	20	11	*1.8*

Table 2:
Summary of the comparison of the two eucalypts and of the resultant ecological consequences.

	Eucalyptus	*Eucalyptus*	Result

	pauciflora	*delegatensis*	
Photosynthetic activity	high	low	?
Height growth	slow	fast	*E.d.* overtops *E.p.*
Leaf area index	small (≤2)	medium (4)	*E.d.* out-shades *E.p.*
Leaf longevitiy	long	medium	*E.d.* has a higher leaf turn-over rate
Lignotuber (N-, C- & H_2O storage; hypogeical protection of meristems)	yes	no	*E.p.* much better adapted to fire, to short severe frosts, snow loads and windbreaks
Distribution	exposed sites high mountains	mountainous, moister sites	no mixing of populations; differences in interception, litter production

Ecological consequences:

- Niche separation on the species and population level.
- At the landscape level with respect to
    - Fire intensity (*E.d.* more litter in shorter time)
    - Water catchment (more water from *E.d.* forests)
    - Protection from soil erosion.

Figure 1. Idealized scheme of parameters affecting a plant´s carbon supply via feedback loops at different levels of integration. Arrows indicate positive effects. Bold face letters are explained in the text and refer to those in table 1. (modified from Küppers et al. 1995)