Carbon gain of C3 and C4 grasses in a dense canopy in the field

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Abstract
Daily carbon gain of a C3 (Lolium perenne L.) and a C4 (Paspalum dilatatum Poir.) species growing in a mixed dense canopy was assessed at the end of summer, in Argentina. Chambers of transparent acrylic glass received 13C-enriched CO2 continuously from 12:00 to 19:00 on a given day. Immediately after labelling, samples were harvested and carbon gain was estimated as plant carbon mass times the proportion of newly assimilated carbon. P. dilatatum contributed more than L. perenne to both canopy standing biomass (164 vs. 22 g per m² ground) and canopy carbon gain (830 vs. 120 mg C per m² and per h). Both species showed a similar ability to capture carbon per unit canopy mass (P. dilatatum=5.1; L. perenne=5.5 mg C per g C and h), which suggested that the C3/C4-grasses composition of the canopy was not changing. Tiller-level analysis revealed that in both species big tillers captured more carbon per unit mass than small tillers (asymmetric competition), and that the C3 and C4 grass species achieved a similar relative photosynthesis rate (mg C per g C and h) in different ways; high gross assimilation rate (mg C per m² and h) in P. dilatatum, and high leaf area ratio (m² per g C) in L. perenne.

Key words: C3 and C4 grasses, 13C-labelling, carbon gain, competition.

Introduction
Understanding the competition between C3 and C4 grasses is important because of the strong influence that the balance between these two functional groups has on ecosystem function (Wedin and Tilman, 1996). Understanding of the mechanisms determining the C3/C4 balance of dense canopies is emerging from studies of carbon gain based on leaf level photosynthesis models (e.g. Anten and Hirose, 2003). In this study, daily carbon gain of C3 (Lolium perenne L.) and C4 (Paspalum dilatatum Poir.) plants growing in a mixed dense canopy was measured with a novel approach based on 13C-labelling. The aim was to analyse the partitioning of canopy carbon gain between the two species, and the role of the amount of leaf area per unit mass (LAR) and of carbon gain per unit leaf area (GAR) in determining the relative photosynthesis rate (RPR) of individual tillers in the canopy.

Materials and methods
The experiment was carried out in the southeast of the Pampas region, in Argentina (37°45'S, 58°18'W), at the end of summer (15/03/08). The soil was a loam Mesic Fine Typical Argiudol, with an A horizon of 25 cm, 62 g kg⁻¹ organic matter, and pH 6.2, a textural B horizon, which presented no impediments to plant growth. Nutrients and water availability were high. Four chambers of transparent acrylic glass (0.3 x 0.6 x 0.3 m) were placed on a dense canopy (leaf area index=4.0; canopy height=28 cm) composed largely of a mixture of L. perenne (a C3 grass) and P. dilatatum (a C4 grass). The chambers received 13C-enriched CO₂ (δ¹³C=398‰) at 380 μmol mol⁻¹, during a 7-h labelling period (from 12:00 to 19:00 h). Air temperature during labelling averaged 25 °C, incident photosynthetically active photon
flux density averaged 1326 µmol m\(^{-2}\) s\(^{-1}\). Immediately after labelling, 30 individual tillers per species were harvested and photographed. Further, total aerial biomass was sampled in two quadrats (0.2 x 0.2 m) and *L. perenne* and *P. dilatatum* plants were separated. Tillers harvested outside the labelling chambers served as unlabelled reference material for \(^{13}\)C content. Immediately after harvest, samples were dried at 60 °C for 72 h, milled, weighed into tin cups and analysed by isotope ratio mass spectrometry to obtain carbon content and \(^{13}\)C/\(^{12}\)C isotope ratio. Blade area and extended height (length of the pseudostem + length of the youngest fully expanded blade) of each tiller were estimated by image analysis. The proportion of newly captured carbon per unit carbon mass \((f_{lab})\) was estimated as, 
\[
 f_{lab} = \frac{(L - U)}{(N - U)},
\]
where \(L\) and \(U\) are the \(^{13}\)C content of labelled and unlabelled plants, respectively, and \(N\) is the \(^{13}\)C content of plants grown continuously with the \(^{13}\)C-enriched CO\(_2\). The latter was estimated assuming invariant discrimination between plants growing outside and inside the chambers (Schnyder et al., 2003). \(f_{lab}\) is closely related to gross photosynthesis rate (RPR), as little tracer was respired and transferred belowground during the labelling period. Thus we equated \(f_{lab}\) with RPR. The allometric relationship between blade area (A) and tiller carbon mass (M), \(A = \alpha M^\beta\), fitted by standardised major axis regression of \(\log(A) = \log \alpha + \beta \log (M)\), served to derive leaf area ratio (LAR, m\(^2\) per g C) as \(\alpha M^{-\beta} \). Gross assimilation rate (GAR, mg per m\(^2\) and h) was then estimated as \(f_{lab}/\text{LAR}\).

![Figure 1](image-url)  

Figure 1. Relationships between tiller size and (a) relative photosynthesis rate, (b) leaf area ratio, (c) gross assimilation rate; (d) relationship between extended tiller height and relative photosynthesis rate; and relationships between relative photosynthesis rate and (e) gross assimilation rate and (f) leaf area ratio of individual *L. perenne* (filled circles) and *P. dilatatum* (open circles) tillers. Lines in (a), (e) and (f), indicate the relative photosynthesis rate of total aerial biomass of *L. perenne* (continuous) and *P. dilatatum* (dotted) in the canopy.
Results and discussion

*P. dilatatum* (C4) contributed more than *L. perenne* (C3) to both standing biomass (164 vs. 22 g C per m² ground) and canopy carbon gain (830 vs. 120 mg C per m² ground and h). However, both species showed a similar ability to capture carbon per unit mass (RPR, *P. dilatatum*=5.1; *L. perenne*=5.5 mg C per g C and per h). This relationship, referred to as symmetric competition because species accumulated resources in direct proportion to their size (Weiner, 1990), means the balance between C3 and C4 species did not change. However, both species showed a lower RPR than bigger tillers due to very low GAR not fully compensated by increased LAR (Fig. 1a,b,c). This probably resulted from their short stature and consequent subordinate (i.e. shaded) position within the canopy (Fig. 1d). This situation of asymmetric competition (cf. Weiner, 1990) implied that the difference in size among individuals was increasing, meaning that in both species the smaller tillers were being self-thinned. In agreement, in both species the canopy-level RPR was slightly higher (1.1 times) than the RPR of the average tiller (Fig. 1a).

In *P. dilatatum*, RPR increased up to a tiller size of ~70 mg C per tiller (~30 cm extended tiller height). Above that it was stable or even decreased (Fig. 1a,d). This was due to a decreasing LAR (a consequence of the increased size) and to a stabilisation, or slightly decrease, of GAR (Figs. 1b,c). The latter response may reflect a stabilisation in light interception per unit area, suggesting that increments beyond this extended height either led to minor improvements in the light environment. In fact biggest tillers of *P. dilatatum*, had an increasingly extended height, but they were not taller than canopy height (28 cm).

Contrasting mechanisms explained the similar canopy-level RPR of these two competing species: *P. dilatatum* showed higher GAR and *L. perenne* higher LAR (Figs. 1e,f). Higher GAR in the C4 species may be due to the higher photosynthetic capacity of C4 plants at 27ºC (Long, 1999). Higher LAR in *L. perenne* than in *P. dilatatum* tillers was due in part to an intrinsically higher blade area per unit mass (scaling coefficient $\alpha = 1.13$ vs. 0.91, respectively), but mainly to their smaller size, as in both species, as tillers grew bigger less blade area was produced per unit tiller carbon mass (scaling exponent $\beta = 0.721$).

In conclusion, combining carbon gain data at canopy- and at tiller-level indicated that a presumably stable C3/C4-grasses composition of the canopy can be achieved through different mechanisms: less carbon investment per unit leaf area in *L. perenne*, and higher carbon gain per unit leaf area in *P. dilatatum*.

References


