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 ^{13}C-enriched CO_2 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 m^2 ground) and canopy carbon gain (830 vs. 120 mg C per m^2 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 m^2 and h) in *P. dilatatum*, and high leaf area ratio (m^2 per g C) in *L. perenne*.

Key words: C3 and C4 grasses, ^{13}C-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 ^{13}C-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 (37º45'S, 58º18'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 ^{13}C-enriched CO_2 ($\delta^{13}C$=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 ºC, 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 unlabeled 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, $f_{lab} = (L - U)/(N - U)$, 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 $\alpha M^{\beta-1}$. Gross assimilation rate (GAR, mg per m^2 and h) was then estimated as f_{lab}/LAR.
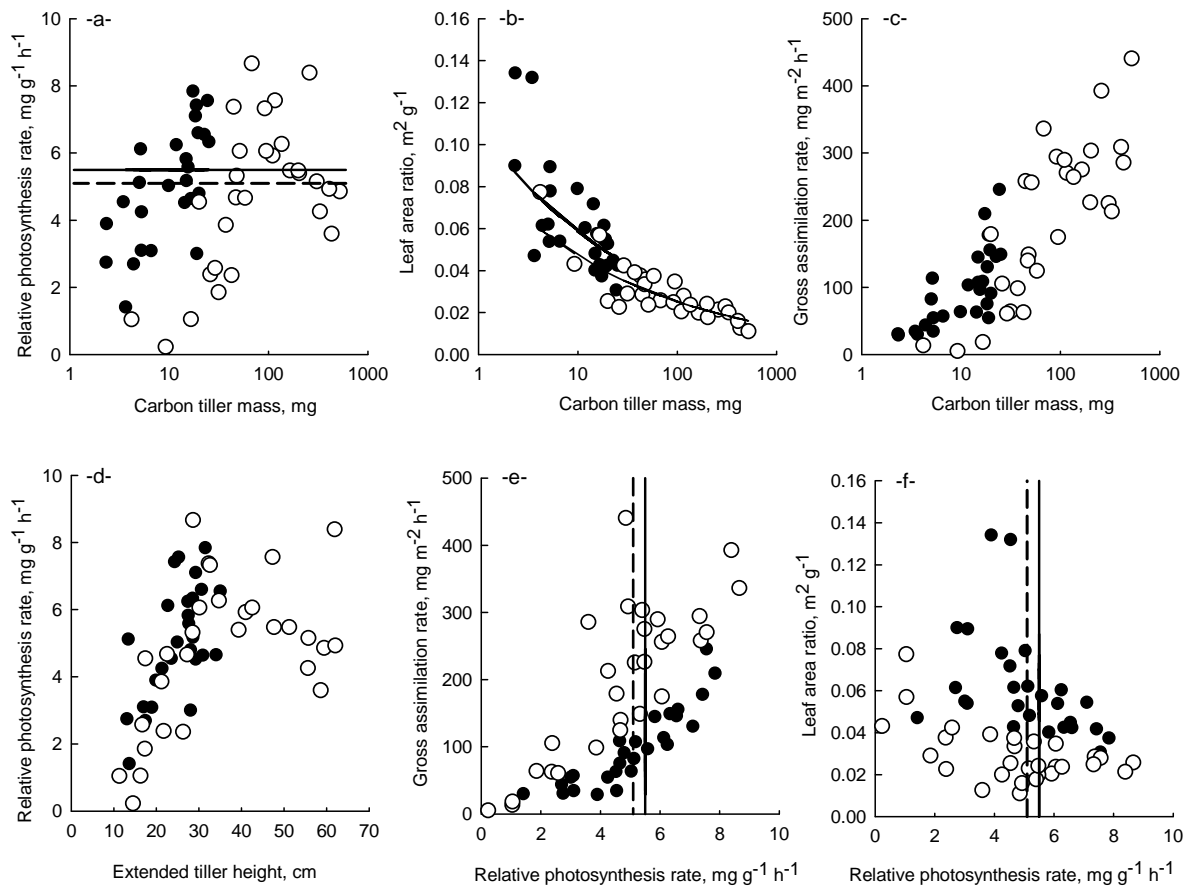

Figure 1. Relationships between tiller size and (a) relative photosynthesis rate, (b) leaf area ratio, (c) gross assimilation rate; (d) relationship between extended tiller height and relative photosynthesis rate; and relationships between relative photosynthesis rate and (e) gross assimilation rate 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 m^2 ground) and canopy carbon gain (830 vs. 120 mg C per m^2 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.

In both species, smaller tillers had 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 α = 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 β = 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

Anten N.P.R. and Hirose T. (2003) Shoot structure, leaf physiology and daily carbon gain of species in a tall-grass meadow. *Ecology* 84, 955-968.

Long S.T. (1999) Environmental Responses. In: R.F. Sage R.F., and Monson R.K.(eds) *C$_4$ Plant Biology*, Academic Press, Toronto Canada, pp. 215-249.

Schnyder H., Schäufele R., Lötscher M. and Gebbing T. (2003) Disentangling CO$_2$ fluxes: direct measurements of mesocosm-scale natural abundance $^{13}CO_2/^{12}CO_2$ gas exchange, ^{13}C discrimination, and labeling of CO$_2$ exchange flux components in controlled environments. *Plant, Cell and Environment* 26, 1863-1874.

Wedin D.A. and Tilman D. (1996) Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science* 274, 1720-1723.

Weiner J. (1990) Asymmetric competition in plants. *Trends in Ecology and Evolution* 5, 360-364.

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