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Correlating source leaf photosynthesis and export characteristics of C_3, C_3-C_4 intermediate and C_4 *Panicum* and *Flaveria* species with whole-plant relative growth rate

ED Leonardos[1], B Grodzinski[1]

[1]*Dept. of Plant Agriculture (Hort. Sci.), Univ. of Guelph, Guelph, ON, N1G 2W1, Canada, dleonard@uoguelph.ca*

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Introduction

In spite of the obvious connection between plant growth and photosynthesis (Pn) it has been difficult to correlate whole-plant productivity with specific leaf functions such as Pn rate (Elmore 1980; Gifford and Evans 1981; Pereira 1994). There are several reasons such as mutual shading in the canopy why a maximal leaf photosynthetic rate often does not translate into an equal increase in total whole plant biomass or a proportional increase in the harvestable index of a crop (Elmore 1980). In vascular plants with many heterotrophic tissues and organs that function as transient storage sites the capacity of the source leaves to export C must be taken into account. Plant growth should be reflecting the export (Exp) capacity of the source leaves as well as their fixation rates (Leonardos and Grodzinski 2001).

It is well known that leaves of C_3 and C_4's export assimilates during the day and night (Gordon 1986; Kalt-Torres *et al.* 1987; Geiger and Servaites 1994). Transgenics with low P-translocator expression have impaired day-time Exp but still grow normally when supplied with adequate light to assimilate reserves for nighttime Exp (Heinecke *et al.* 1994). Nighttime Exp of starch reserves can be quite costly with as much as one third of the C respired to support sugar synthesis and loading (Bouma *et al.* 1995). In several C_3 and C_4's grown under ambient and CO_2 enriched conditions daytime Exp is much greater than nighttime Exp (Fondy and Geiger 1982; Kalt-Torres *et al.* 1987; Leonardos *et al.* 1996; Jiao *et al.* 1999; Grimmer and Komor 1999). Our working hypothesis is that Exp during Pn is generally more important than during nighttime periods (Leonardos *et al.* 1996; Jiao *et al.* 1999).

The primary objective in this study was to extend our earlier comparison of Pn and immediate Exp characteristics of source leaves among 17 selected C_3, C_4 and C_3-C_4 intermediate *Panicum* and *Flaveria* species (Leonardos and Grodzinski 2000). First, ^{14}C-Exp patterns from leaves were obtained during light and dark periods. Second, functions of the source leaf were correlated with each other. Finally, leaf traits such as Pn, immediate Exp, and total day/night Exp were correlated with the whole-plant growth rates.

Materials and methods

Plant material and growing conditions

Ten *Panicum* and seven *Flaveria* species (see Fig.1) were grown in a greenhouse under ambient CO_2 and a 16/8 h (day/night) photoperiod as described previously (Leonardos and Grodzinski 2000). During measurements, *Panicum* plants had 7 unfolded leaves and were flowering, whereas the *Flaveria* plants were vegetative and approximately 30- to 50-d old.

Exp during the feed and chase periods

Pn and immediate Exp during 2-h steady-state $^{14}CO_2$ feeds of the 2nd - 4th attached fully expanded leaves from the apex were measured as described previously (Leonardos and Grodzinski 2000). Immediate Exp was determined during the 90-120 min of the 2-h feed, when isotopic equilibrium existed between the $^{14}CO_2$ and the ^{14}C-translocates. Total daily ^{14}C-Exp from leaves was determined by the fate of the ^{14}C fixed during a 2-h afternoon feed (1500-1700h) and a 15-h chase (5h light/10h dark).

Whole-plant net CO_2 exchange measurements

Non-destructive estimates of whole-plant relative growth rates (i.e. daily C gain) were obtained using a whole-plant net CO_2 exchange system (Leonardos *et al.* 1994). Plants were at the same stage of development at which leaves were measured.

Results

Does Exp of ^{14}C-reserves at night compensate for low immediate Exp in the light?

Figure 1 shows that in all the *Panicum* (A) and *Flaveria* (B) C_3, C_4 and C_3-C_4 intermediates Exp in the total light period (open plus hashed bars) was greater than in the night period (dark bar).

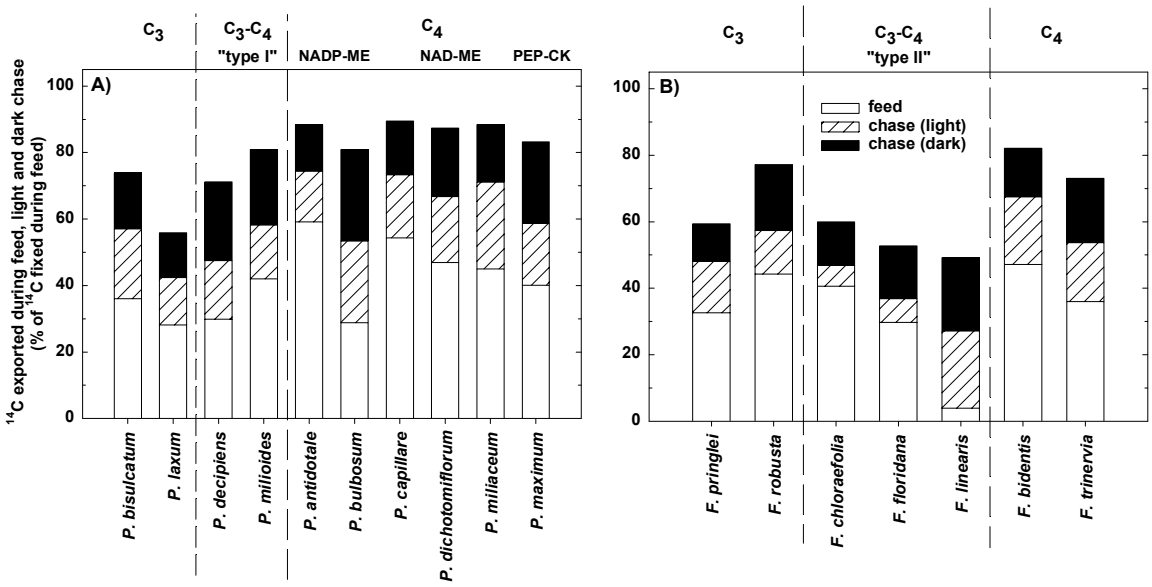

Fig.1. Patterns of ^{14}C-Exp in *Panicum* (A) and *Flaveria* (B) species during a 2-h feed (open bars) and 5-h light (hashed bars) and 10-h dark (dark bars) chase. Total ^{14}C Exp was expressed as a % of the ^{14}C fixed. Measurements were taken at saturating PPFD (1500, 1600 and 1750 µmol m^{-2} s^{-1} for the C_3, C_3-C_4 intermediate and C_4's, respectively), ambient CO_2, and at 30°C (*Panicum*) 25°C (*Flaveria*) during light and at 18°C at dark. Values are means of at least 4 leaves on different plants (SE are not shown).

Panicum C_4's exported more total ^{14}C (80 to 90% of that fixed) than did "type I" C_3-C_4 intermediates or C_3's (Fig. 1A). Two C_4's, *P. bulbosum* and *P. maximum,* seemed to compensate for their low initial ^{14}C-Exp by exporting more during the chase. The *Panicum* C_3's exported less than the C_4 relatives initially and overall (Fig. 1A). The two "type I" C_3-C_4 intermediates, appeared to have compensated better than the C_3's during the chase, but on average still exported less than the C_4's.

Among the *Flaveria*, C_4's exported more total ^{14}C than C_3's and "type II" C_3-C_4 intermediates (Fig. 1B). The C_3's, *F. robusta*, and the C_4's, *F. bidentis* and *F. trinervia*, which exported the most during the feed exported the most ^{14}C by the next morning. Although, "type II" C_3-C_4 intermediates fixed a similar amount of ^{14}C as did *Flaveria* C_4's (Leonardos and Grodzinski 2000), the "type II" C_3-C_4 intermediates exported less immediately and during the entire experiment (Fig. 1B). Notably, *F. linearis*, which had Pn approaching the fixation rates of its C_4 relatives, mobilized more ^{14}C during the chase (i.e. 8-10 times more Exp than during the feed). However, *F. linearis* exported more during the 7-h light period than during the following 10 h of darkness, which in total was the least of all *Flaveria* species.

Predicting daily Exp patterns from short-term Pn and immediate Exp rates

Table I shows that both leaf Pn and immediate Exp correlated well with total ^{14}C-Exp in both *Panicum* and *Flaveria* species.

Correlating leaf functions with whole-plant growth

When comparisons of these three main indicators of leaf source function were made with whole-plant growth (i.e. C gain) a satisfactory link could not be drawn among the *Panicum* species (Table I). However, among the *Flaveria* species a greater immediate Exp rate was the most predictive leaf function of a greater whole-plant growth rate.

Table I. Correlation analysis among leaf and whole-plant parameters of *Panicum* and *Flaveria* species. Leaf Pn and immediate Exp were measured during a 2-h feed and total ^{14}C-Exp was measured during a 17-h feed and chase. Whole-plant daily C gain was measured over a 48-h light/dark period. Values are Pearson correlation coefficients (r). *** P<0.001; ** P<0.01; * P<0.05; ns not significant.

	PANICUM		***FLAVERIA***	
Leaf	**Leaf Total ^{14}C-Exp** (mmol C m^{-2})	**Whole-plant daily C gain** (g C $plant^{-1}$ d^{-1})	**Leaf Total ^{14}C-Exp** (mmol C m^{-2})	**Whole-plant daily C gain** (g C $plant^{-1}$ d^{-1})
Pn (μmol C m^{-2} s^{-1})	0.99 ***	0.51 ns	0.85 *	0.79 *
Exp (μmol C m^{-2} s^{-1})	0.95 ***	0.54 ns	0.89 **	0.84 *
total ^{14}C-Exp (mmol C m^{-2})	-	0.52 ns	-	0.79 *

Discussion

As stated above, our working assumption is that Exp in the light is greater than in the dark in most species. Figure 1 confirms this pattern in the 17 *Panicum* and *Flaveria* species. The concentration of translocates is generally higher in the leaf during active Pn, and Exp rate is known to correlate well with sucrose concentration (Leonardos *et al.* 1996; Grodzinski *et al.* 1998).

Immediate Exp and leaf Pn are tightly correlated among C_3, C_4 and C_3-C_4 immediate species (Hofstra and Nelson 1969; Gordon 1986; Grodzinski *et al.* 1998; Leonardos and Grodzinski 2000). The correlation analyses in Table I are the first showing that immediate Exp correlates well with day and night Exp patterns in both the *Panicum* and *Flaveria* genera. Although, light and dark export patterns obtained in these study were from 2-h feeds, other studies with winter wheat plants exposed to different conditions show that similar patterns of light versus dark ^{14}C-Exp were obtained using a 2-h feed and a full photoperiod feed (S35-002).

Correlations of primary leaf functions such as Pn with whole-plant growth have been difficult to obtain (Elmore 1980; Gifford and Evans 1981; Pereira 1994). Among the *Panicum* species a satisfactory link could not be drawn. However, among the *Flaveria* species a greater leaf Pn and faster immediate Exp were predictive leaf functions of greater whole-plant growth rates (Table I). Collectively, the data indicate the value of estimating the immediate Exp rates of source leaves because its correlation to plant growth rate was the strongest at least among *Flaveria* species. Although the measurement of the immediate Exp capacity is arguably only an instantaneous estimate of one aspect of laminar function, this particular measurement may prove to be highly predictive of both the daily source leaf functions as well as the collective reducing and Exp potential of the leaf canopy as a whole.

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