



Effect of Source-to-sink Ratio on Partitioning of Dry Matter and ¹⁴C-photoassimilates in Wheat during Grain Filling

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Increasingly, wheat (*Triticum aestivum* L.) is being grown in tropical environments, but there is inadequate information about the physiological processes limiting yield. In this investigation, the source:sink ratio was manipulated to examine the performance of source-sink interactions after anthesis and the factor(s) limiting grain filling in tropical conditions. Plants of three wheat cultivars, Cuba C-204, Candeias and IAC-60, were artificially modified to give different source:sink ratios. The treatments were: I, Control; II, all spikelets on one side of the spike removed; III, all spikelets removed except the four central spikelets of the spike; and IV, flag leaf blade removed. The distribution of dry matter between kernels and stem internodes was analysed at harvest in all three cultivars. Partitioning of ¹⁴C-photoassimilates was measured on three occasions after anthesis in the cultivar Cuba C-204. Modifications of source:sink ratio led to different patterns of allocation of dry matter between cultivars and sowing dates. The reduction in sink size in treatment II produced no significant change in the mass per grain in the January sowing, but this was enhanced in two cultivars in the November sowing. In treatment III, both mass per grain and translocation of ¹⁴C-photoassimilates declined, apparently due to feedback inhibition of photosynthesis. The participation of stem reserves in grain filling and the existence of genotypic differences in response to availability of photoassimilates were corroborated. The pattern of partitioning of dry matter observed in plants in this investigation suggests a source limitation, particularly during the November sowing. This pattern differed markedly from that in other studies, most of which have been made in temperate areas. © 1999 Annals of Botany Company

Key words: Photoassimilates, sink, source, partitioning, grain filling, wheat.

INTRODUCTION

In striving to increase the yield potential of cultivated plants it is important to determine the physiological factors limiting yield. The first step towards this is to assess whether the growth of harvested organs is limited by the availability of substrates (source limited) or by the capacity of the organ to assimilate and utilize the available substances for growth (sink limited) (Patrick, 1988). Although there is much experimental data on the effect of source:sink ratio after anthesis in wheat (Evans and Wardlaw, 1996), to our knowledge there are no such studies in tropical environments, where wheat is increasingly grown.

Attempts to identify physiological factors limiting yield must integrate source-sink interactions both spatially and temporally (Patrick, 1988). Results from the response of kernel weight and grain set to source-sink manipulations suggested yield limitation by both the sink (the number of grains m⁻²) and the source, depending on the seasons, time of day, etc (Evans and Wardlaw, 1996). However, the time courses of source and sink control have not been well documented. Some authors (Evans and Rawson, 1970; Richards, 1996) suggested that grain yield in irrigated spring wheat may not be limited by the supply of carbon at any time during grain filling. However, there are data showing

significant increases in mass per grain associated with reductions in grain number (Fischer and HilleRisLambers, 1978; Ledent and Stoy, 1985; Koshkin and Tararina, 1989), implying source limitation at least on some occasions after anthesis. Source limiting situations are more important in high temperature environments (Fischer, 1983; Blum *et al.*, 1994). This suggests that physiological processes limiting yield in temperate areas cannot be directly extrapolated to subtropical or tropical environments.

Analysis of source-sink interactions should also consider the role of alternative sinks in the plant (Schnyder, 1993; Marcelis and Koning, 1995). In wheat, particularly, special attention should be given to the stems, since competition exists between the growing upper internodes and reproductive organs in the weeks before anthesis (Wardlaw, 1968; Bingham, 1972; Patrick, 1972; Brooking and Kirby, 1981; Siddique, Kirby and Perry, 1989), the outcome of which depends on both genotype and environment. Besides, there is good evidence that temporary storage is very important under stress conditions (Bidinger, Musgrave and Fischer, 1977; Blum *et al.*, 1994; Wardlaw and Willenbrink, 1994; Seidel, 1996). Recently, genotypic differences in the patterns of allocation and mobilization of dry matter in the stem of wheat have been demonstrated (Blum *et al.*, 1994). Therefore, the inclusion of alternative carbohydrate storage

pools in the analysis of source-sink interactions should be of major importance under tropical environments.

The aims of this study were to examine the performance of source-sink interactions after anthesis, including the role of stem internodes as a source of material for grain growth and to evaluate the possible factors limiting grain filling in wheat in tropical conditions. Artificial manipulation of the source:sink ratio and evaluation of the variation in dry matter partitioning in three wheat cultivars at two sowing dates was used to assess the existence of genotypic differences in the response to availability of photoassimilates. The ^{14}C pulse-chase technique and study of ^{14}C -photoassimilate partitioning was used to examine the time course of source-sink interactions during grain filling in the cultivar Cuba C-204.

MATERIALS AND METHODS

Plant material and growth conditions

Three spring wheat (*Triticum aestivum* L.) semi-dwarf cultivars were used: Cuba C-204 from Cuba, and Candeias and IAC-60 both from Brazil. All are day length-insensitive and adapted to warm environments. The experiments were carried out at the Institute of Fundamental Investigations on Tropical Agriculture in Havana (22.8° N, 82.4° W). The sowing dates were 30 Jan. 1997 and 22 Nov. 1997. The soil was a red earth, classified as Oxisol (Academia de Ciencias de Cuba, 1979), with pH(KCl) 7.2, 28 g kg⁻¹ organic carbon and a cation exchange capacity of 18.12 cmol (+) kg⁻¹. Clay and silt formed 70.7 and 13.3% of the soil mass, respectively.

Plots were fertilized at sowing with 90 kg ha⁻¹ N as urea and 50 kg ha⁻¹ K as KCl, and 90 kg ha⁻¹ N as urea was applied 30 d after sowing. Plots were occasionally sprayed with fungicides to avoid disease and were hand weeded. The plots were irrigated when necessary to avoid water stress. Each plot consisted of seven rows, 4.0 m long, 20 cm apart and planted at a rate of 125 viable seeds m⁻². Daily maximum, minimum and mean temperatures were recorded by a meteorological station situated 200 m from the experimental site.

Treatments

Treatments consisted of a factorial combination of three cultivars and four source-sink relationships arranged in a randomized split-plot design within each sowing date. Main plots consisted of the three cultivars and the sub-plots consisted of the four source-sink relations. Main plots were arranged in blocks with four replicates.

At anthesis, 28 main shoots from the central rows of each plot were tagged and detilled to avoid the tillers becoming alternative sinks for mobilized carbohydrates (Slafer and Savin, 1994; Drecker, Grashoff and Rabbinge, 1997). In the January sowing of cultivar Cuba C-204, 37 main shoots per plot of the same height and with 16 spikelets per spike were selected within each cultivar. The plants for each treatment were selected at random from the previously tagged plants.

Six d after anthesis the plants were artificially manipulated to give different source:sink ratios according to the procedure outlined by Fischer and HilleRisLambers (1978). The treatments were: I, control; II, all spikelets from one side of the spike removed except the apical spikelet; III, all spikelets removed except the four central spikelets of the spike, two on each side (the rachis was cut off above the remaining spikelets); and IV, flag leaf blade removed. Seven plants per plot were used for each treatment.

Measurements

The date of anthesis was taken as the day when anthers were extruded in 50% of the spikes in a plot. The date of physiological maturity was recorded when 50% of the spikes in a plot had lost their green colouration (Hanft and Wych, 1982).

At anthesis, the area of the main stem leaves was measured according to Quarrie and Jones (1977) (length × maximum width × 0.78). This formula represented the actual leaf area in the cultivars used in this experiment. Leaf area duration (LAD) was estimated according to Armas, Ortega and Rodés (1988) using the following equation:

$$\text{LAD} = [(A_2 - A_1) / (\ln A_2 - \ln A_1)] (t_2 - t_1)$$

where A_2 and A_1 represent shoot leaf area at anthesis and physiological maturity, respectively, and $t_2 - t_1$ represents the time between anthesis and physiological maturity.

At maturity the number of grains per spike and the dry mass per grain from four central spikelets (two central spikelets in the case of treatment II) and from all the spikelets of the spike were recorded. All data are given for four central spikelets unless specified otherwise. Source:sink ratios were estimated as the ratios between LAD after anthesis and the number of grains per spike (Slafer and Savin, 1994).

The specific mass of the peduncle and two other uppermost internodes, with the leaf sheath removed, was determined as dry mass per length. Results for internode specific mass are taken as an indication of carbohydrate content. This is supported by the following: a positive correlation has been found between stem dry mass and total non-structural carbohydrates (Blum *et al.*, 1994); changes in stem mass of wheat after anthesis are related to changes in stem carbohydrate content (Blum *et al.*, 1994; Wardlaw and Willenbrink, 1994; Stone *et al.*, 1995); internodes reach their maximum length a few days after anthesis (Evans, Wardlaw and Fischer, 1975); and the amount of assimilates mobilized from the stems is unrelated to the culm length (Rawson and Evans, 1971).

^{14}C -supply and analysis

Studies on ^{14}C -photoassimilate partitioning were made on plants from the plots of cultivar Cuba C-204 sown on 30 Jan. 1997. Twelve uniformly-developed plants in treatments I, II and III were used for this experiment (three plants per

TABLE 1. Mean temperatures during the period from sowing to anthesis and from anthesis to physiological maturity, time to anthesis and duration of the period between anthesis and physiological maturity, flag leaf area and leaf area duration (LAD) of three wheat cultivars sown at two dates

Cultivar	Mean temperature, (°C)		Duration (d)		Flag leaf area (cm ²)	LAD (cm ² d ⁻¹)
	Sowing-anthesis	Anthesis-maturity	Sowing-anthesis	Anthesis-maturity		
30 Jan. 1997						
Cuba C-204	23.3	24.4	48	25	8.2±0.5*	260±26
Candeias	23.3	24.5	49	27	7.7±0.4	312±18
IAC-60	23.3	24.3	49	28	12.0±0.4	341±35
22 Nov. 1997						
Cuba C-204	22.8	21.5	55	35	19.7±1.7	456±14
Candeias	22.6	21.9	60	35	20.3±1.5	601±62
IAC-60	22.6	22.0	59	32	25.9±1.4	487±19

* Means ± s.e. for 28 replicates.

treatment per plot). The flag leaf of the main stem of four tagged plants was exposed to 185 kBq of ¹⁴CO₂ released from sodium [¹⁴C]carbonate (specific activity 18.5 MBq mmol⁻¹) for 15 min, 7, 14 and 21 d after anthesis. The procedure was similar to that used by Wood, Patrick and Ofler (1994). ¹⁴CO₂ was generated by the injection of excess 10% perchloric acid (approx. 0.8 ml) with a syringe into a vial connected to a transparent glass chamber which held the flag leaf blade. The chamber was carefully attached to the basal part of the flag leaf blade with two rubber bands. Labelling always took place between 0900 and 0930 h. Growth conditions were the same as for the rest of the plants. Mean temperatures on the first, second and third labelling days were 25.1, 23.4 and 24.1 °C, respectively. The leaf area of each stem was measured before the plants were removed 24 h later. Plants were dried to constant mass at 70 °C. The main stem of each plant was divided into flag leaf laminae, flag leaf sheath, upper peduncle (part of the peduncle exposed to the light), lower peduncle (part of the peduncle enclosed by the flag leaf sheath), upper and lower parts of the penultimate internode, grains of the four central spikelets, rest of the grains and chaff of the spike.

All parts were weighed and all, except the grains, cut with a scalpel into fragments of about 1 mm. The grains were ground in a mortar to powder. To assay radioactivity, each part was divided into two subsamples, weighed and placed in conical tubes. The samples were extracted three times in 5 ml 80% ethanol at 80 °C for 2 h. Washings from the final rinse and the three extractions were combined and made up to a standard volume, prior to taking an aliquot for ¹⁴C determination. In preliminary experiments only traces of ¹⁴C were found in the third extract. After extraction with ethanol the polysaccharides were separated by one extraction with boiling water and three extractions with 4 ml 30% (v/v) perchloric acid during 24 h at room temperature (Wardlaw, Moncur and Patrick, 1995). The combined extracts were made to volume prior to taking an aliquot for ¹⁴C determination in a Wallac 1409 liquid scintillation counter. The presence of starch in the residue was tested with I₂/KI following the perchloric acid extraction. This

residue contained less than 3% of the total radioactivity of the samples.

Data represent the mean of four replicates. Distribution of carbon-14 in each organ was calculated as the ratio between total radioactivity in a given organ (perchloric + ethanol fractions) and the total radioactivity in the plant. Relative radioactivity concentration (RRC) was computed as the ratio between radioactivity concentration (radioactivity per dry mass) of a given organ and radioactivity concentration of the plant. The proportion of carbon-14 in the perchloric acid fraction was determined as the ratio between radioactivity in this fraction and total extracted radioactivity (perchloric + ethanol fractions).

Data analysis

Analysis of variance and Duncan's multiple range test were used to compare the effects of source-sink manipulations on LAD, number of grains per spike, source:sink ratios, mass per grain and specific mass of the internodes. One-way Anova and Duncan's multiple range test were used to test the effects of source:sink ratios on RRC of different organs in plants of Cuba C-204.

RESULTS

In Cuba, the recommended sowing period for wheat extends from October until January; however, the January sowings generally suffer the impact of higher temperatures during grain filling (Table 1). Flag leaf area and LAD were lower in plants sown in January than in November (Table 1). This led to an increase in the source:sink ratio in plants sown in November compared with those sown in January (Table 2). The reduction in spikelet number in treatments II and III did not increase grain set in the remaining spikelets, and therefore these treatments reduced the number of grains per spike by about 50 and 75%, respectively (Table 2). Removal of spikelets did not alter the pattern of senescence of

TABLE 2. Number of grains per spike and estimated source:sink ratios of three wheat cultivars subjected to source:sink manipulations at two sowing dates

Cultivar	Treatment	Number of grains per spike	Source:sink ratio (cm ² d per grain)	Number of grains per spike	Source:sink ratio (cm ² d per grain)
		30 Jan. 1997		22 Nov. 1997	
Cuba C-204	I	30.5 ^a	8.5 ^c	27.0 ^a	16.9 ^c
	II	15.2 ^b	16.8 ^b	12.1 ^b	38.0 ^b
	III	8.2 ^c	29.6 ^a	8.1 ^c	56.3 ^a
	IV	29.6 ^a	7.5 ^d	28.2 ^a	11.4 ^d
Candeias	I	37.8 ^a	8.3 ^c	35.0 ^a	17.1 ^c
	II	18.1 ^b	17.6 ^b	15.2 ^b	40.1 ^b
	III	12.2 ^c	24.5 ^a	10.6 ^c	56.7 ^a
	IV	35.9 ^a	7.5 ^d	35.0 ^a	13.4 ^d
IAC-60	I	37.5 ^b	9.1 ^c	39.1 ^a	12.5 ^c
	II	20.8 ^c	17.3 ^b	20.2 ^b	24.4 ^b
	III	12.9 ^d	26.3 ^a	11.3 ^c	43.1 ^a
	IV	41.2 ^a	6.7 ^d	40.4 ^a	8.2 ^d

Different superscripts within cultivar and sowing date indicate statistical significance at $P < 0.05$ by Duncan's multiple-range test.

TABLE 3. Analysis of variance for grain mass and specific mass of the internodes of three wheat cultivars and four source:sink ratios (treatment)

Source of variation	d.f.	Grain mass	Peduncle specific mass	Second internode specific mass	Third internode specific mass
30 Jan. 1997					
Cultivar (A)	2	76.426**	14.66**	10.557*	13.109**
Error A	6	0.622	0.671	0.797	1.617
Treatment (B)	3	247.61**	5.690**	17.534**	24.926*
A × B	6	20.88**	0.985*	1.008	3.679
Error B	27	5.20	0.280	0.925	2.666
22 Nov. 1997					
Cultivar (A)	2	303.61**	9.139*	3.793	9.911
Error A	6	9.71	1.701	3.424	2.887
Treatment (B)	3	314.94**	1.768*	3.154	3.444
A × B	6	38.03**	0.966**	1.771	1.349
Error B	27	13.117	0.049	1.349	1.600

* $P < 0.05$, ** $P < 0.01$.
Data are mean squares.

photosynthetic tissues, and hence there were no significant differences ($P < 0.05$) in LAD between treatments I, II and III (data not shown). Therefore, we estimated the source:sink ratios as the ratio of mean LAD to the number of grains per spike. LAD in treatment IV was reduced due to lack of the flag leaf blade (data not shown) and so was the source:sink ratio (Table 2).

Cultivars differed significantly ($P < 0.05$) in grain weight at both sowing dates (Table 3). The removal of the flag leaf reduced the mass per grain, except in Cuba C-204 sown in November (Fig. 1). This reduction was greatest in IAC-60, the cultivar with the largest flag leaf area. The response of mass per grain to decreased number of spikelets differed between sowing dates in accordance with the different assimilate availability. For the January sowing, dry mass of the grains did not increase with reduction in sink size. In

treatment II (half spike), there was no significant variation ($P < 0.05$) in mass per grain relative to control plants. In treatment III (four spikelets at the centre of the spike), the mean mass per grain was reduced in Cuba C-204 and IAC-60, whereas in Candeias it decreased slightly, albeit not significantly ($P < 0.05$). For plants sown in November, the reduction in the number of spikelets in treatments II and III led to an increase in dry mass of the grains in all three cultivars relative to control plants. However, in Cuba C-204, a decrease in dry mass of the grains in treatment III compared to treatment II was observed (Fig. 1).

The effect of source-sink manipulations on specific mass of internodes varied between cultivars. Cultivars differed significantly ($P < 0.05$) in the specific weight of internodes in January (Fig. 2), whereas no differences were found in November (Fig. 3). Internodes of Candeias retained more dry matter per unit length (higher specific weight) than the other two cultivars as the availability of photoassimilates diminished (Fig. 2). On the other hand, in Candeias, an increase in specific weight of the three internodes occurred in treatments involving a reduction in spike size (Fig. 2). It is interesting to note that although the spike size of plants in treatment III was smaller than that of those in treatment II, there was no increase in the specific mass of internodes under treatment III. On the contrary, in this treatment specific mass was significantly ($P < 0.05$) reduced in the three internodes of IAC-60 (sown in January; Fig. 2) and in the peduncle of Cuba C-204 (sown in November; Fig. 3) in comparison with treatment II.

Distribution of ¹⁴C-photoassimilates in Cuba C-204, 24 h after feeding the flag leaf blade with ¹⁴CO₂, revealed that from 7–21 d after anthesis the main sink of photoassimilates was the grains. The percentage of ¹⁴C distributed to the grains ranged between 40 to 70% of the total ¹⁴C in control plants. Reduction of the number of spikelets was related to an enhancement of translocation to the penultimate internode and to the lower part of the peduncle, 7 and 14 d after anthesis (Fig. 4). After 21 d, the main sinks for the surplus photoassimilates were the flag leaf (blade + sheath) and

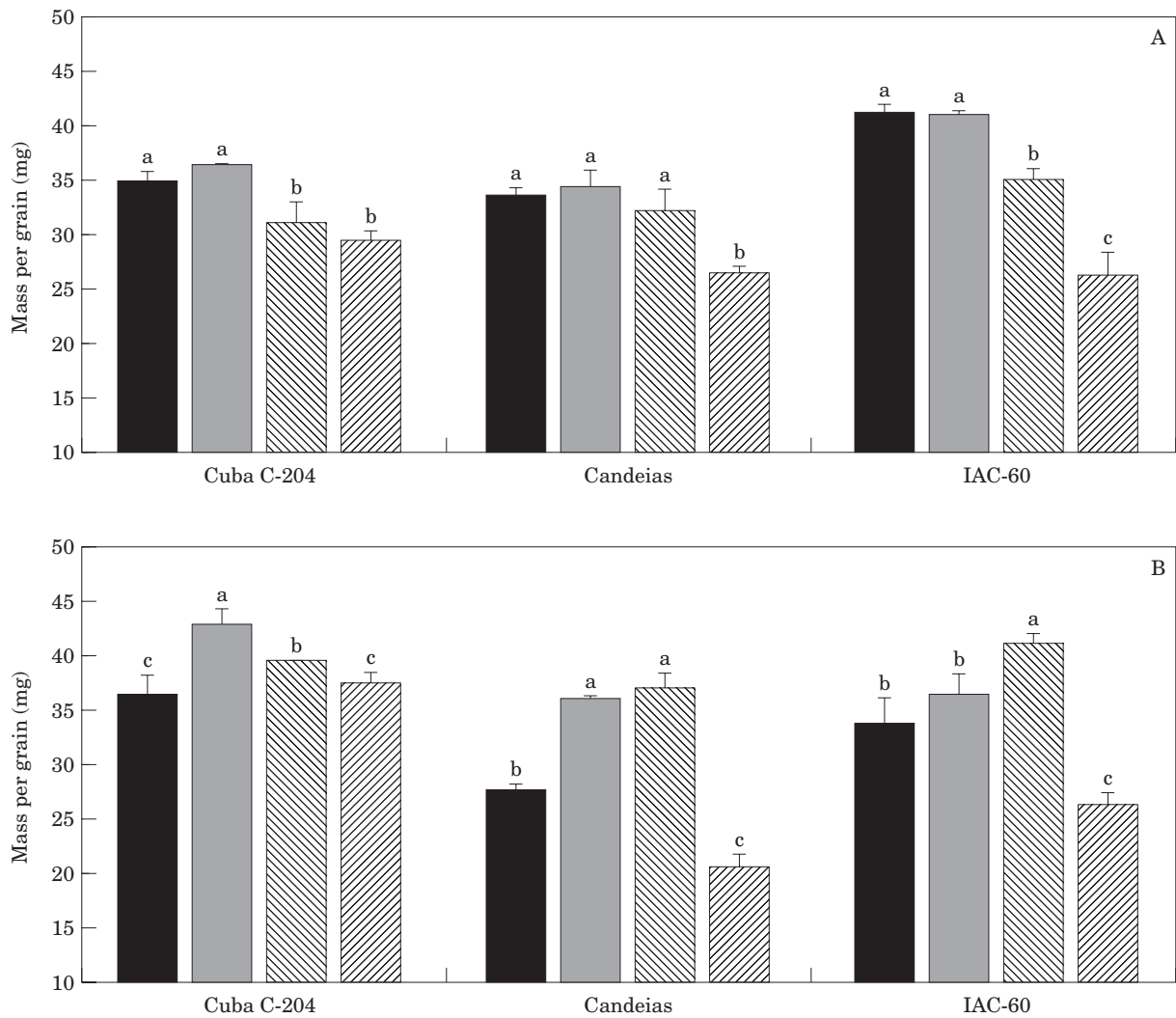


FIG. 1. Effects of source-sink modifications (Treatment I, ■; II, ▨; III, ▩; IV, ▤; see text for description) on mass per grain in plants sown on 30 Jan. (A) and 22 Nov. 1997 (B). Values within a cultivar and sowing date followed by the same letter do not differ significantly at $P < 0.05$. Vertical bars represent s.e.

penultimate internode again (Fig. 4). Reduction of the number of spikelets led to a decline in the proportion of ^{14}C -photoassimilates distributed to the grains, but this was not proportional to the reduction in sink size. The RRC of the grains in half-spike plants (treatment II) was greater 7 d and smaller 21 d after anthesis compared to control plants. The RRC of the grains in plants with four spikelets (treatment III) was always smaller than that of the control and half-spike plants. The RRC of the grains in plants of all three treatments dropped from 7 to 21 d after anthesis, whereas the RRC of the flag leaf increased during the same period.

The proportion of the ^{14}C -label incorporated into starch in the grains 24 h after feeding the flag leaf blade with $^{14}\text{CO}_2$ declined in plants with reduced sink size 21 d after anthesis (data not shown). Greater positive correlation ($r = 0.898$, $P < 0.01$) was then found between the amount of ^{14}C -photoassimilates extracted in the perchloric acid fraction and the total ^{14}C -photoassimilates translocated to the grains compared to 7 d after anthesis.

DISCUSSION

The flag leaf blade is the principal source of photoassimilates imported by grains during grain filling (Rawson, Gifford and Bremner, 1976). In spite of this, removal of the flag leaf may lead, in some circumstances, to enhancement of the photosynthetic activity of other leaves and green parts (Koch, 1996) and remobilization of stored carbohydrates (Schnyder, 1993). These mechanisms avoid the restriction of grain filling in such a manner that often no source limitation occurs (Richards, 1996). However, it has been pointed out that there is a higher degree of source limitation in warmer environments due to earlier senescence of green parts (Fischer, 1983).

Significant reduction in the dry mass per grain (Fig. 1) and the specific mass of internodes (Fig. 2) encountered in plants of treatment IV may not prove source limitation in control plants. It suggests that, with the exception of Cuba C-204 plants sown in November, storage mechanisms and

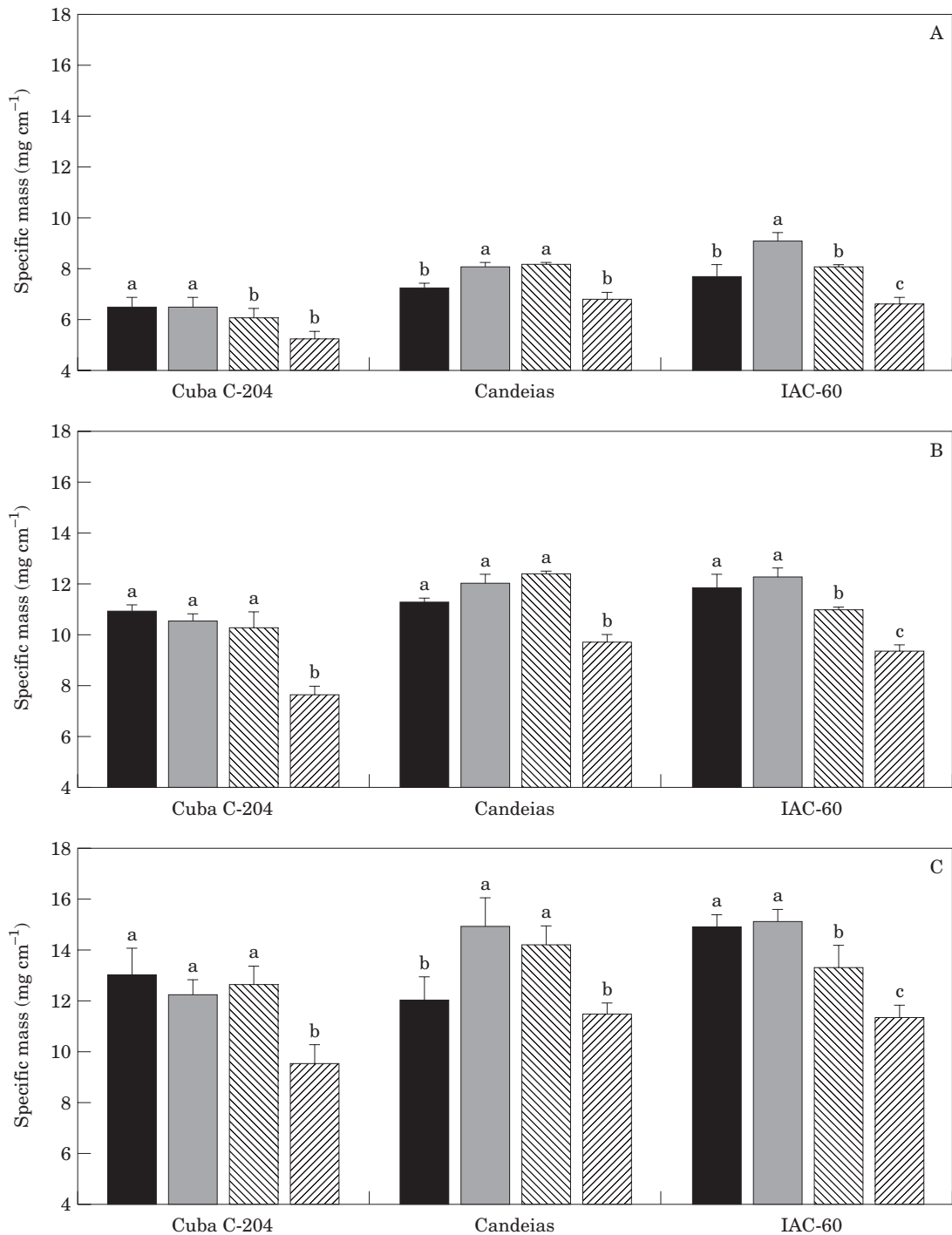


FIG. 2. Effects of source-sink modifications (Treatment I, ■; II, ▒; III, ▨; IV, ▩) on specific mass of the peduncle (A), second internode from top (B) and third internode from top (C) at maturity in plants sown on 30 Jan. 1997. Values within a cultivar and sowing date followed by the same letter do not differ significantly at $P < 0.05$. Vertical bars represent s.e.

photosynthesis of other green parts do not fulfil the requirements of grains in defoliated plants. The comparison between control and defoliated plants at both sowing dates indicates that cultivars differed in the ability to remobilize reserves from the stems to the grains.

There were differences in the source-sink interactions between cultivars. Significant cultivar \times source:sink ratio

interactions for grain mass and specific mass of the peduncle indicate that the cultivars did not respond uniformly to the availability of photoassimilates (Table 3). Sink limitation in control plants could be the cause of the significant increase in specific mass of the three internodes in the cultivar Candeias in the January sowing, as a result of removing half the spikelets (Fig. 2). On the other hand, Cuba C-204

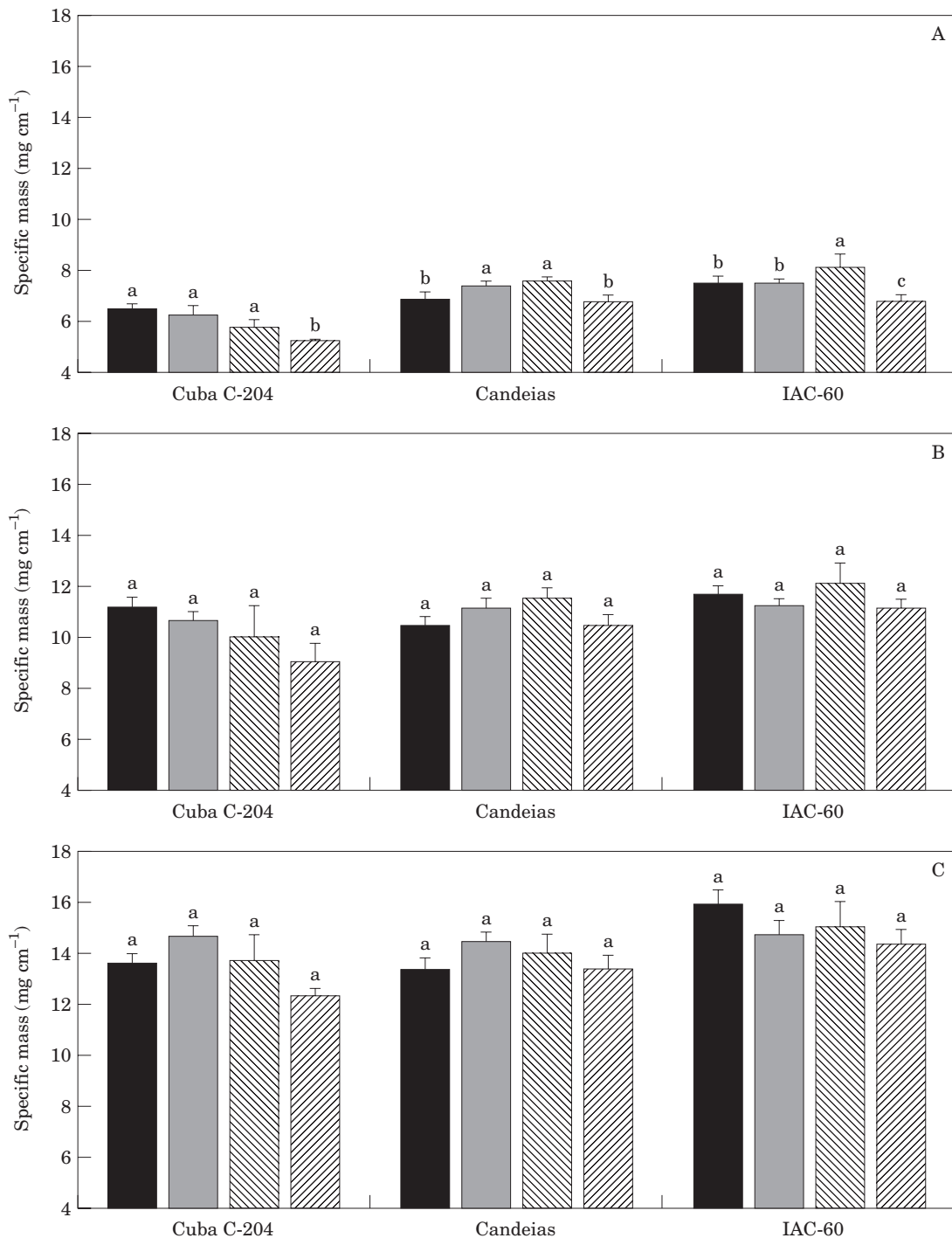


FIG. 3. Effects of source-sink modifications (Treatment I, ■; II, ▒; III, ▓; IV, ▨) on specific mass of the peduncle (A), second internode from top (B) and third internode from top (C) at maturity in plants sown on 22 Nov. 1997. Values within a cultivar and sowing date followed by the same letter do not differ significantly at $P < 0.05$. Vertical bars represent s.e.

showed a slight increase in grain mass whereas the specific mass of the internodes remain unaltered. Such differences in the response to availability of photoassimilates seem to be the consequence of different patterns of photoassimilate partitioning between cultivars with varying source:sink ratios (Evans and Wardlaw, 1996).

Sink limitation could explain the lack of growth of the central grains in half-spike plants sown in January (treatment II, Fig. 1). Analysis of the mean mass per grain for all the grains in the spikes showed no increase in mass (data not shown). Conversely, increase in dry mass of the grains with the reduction in sink size for the November sowing could be

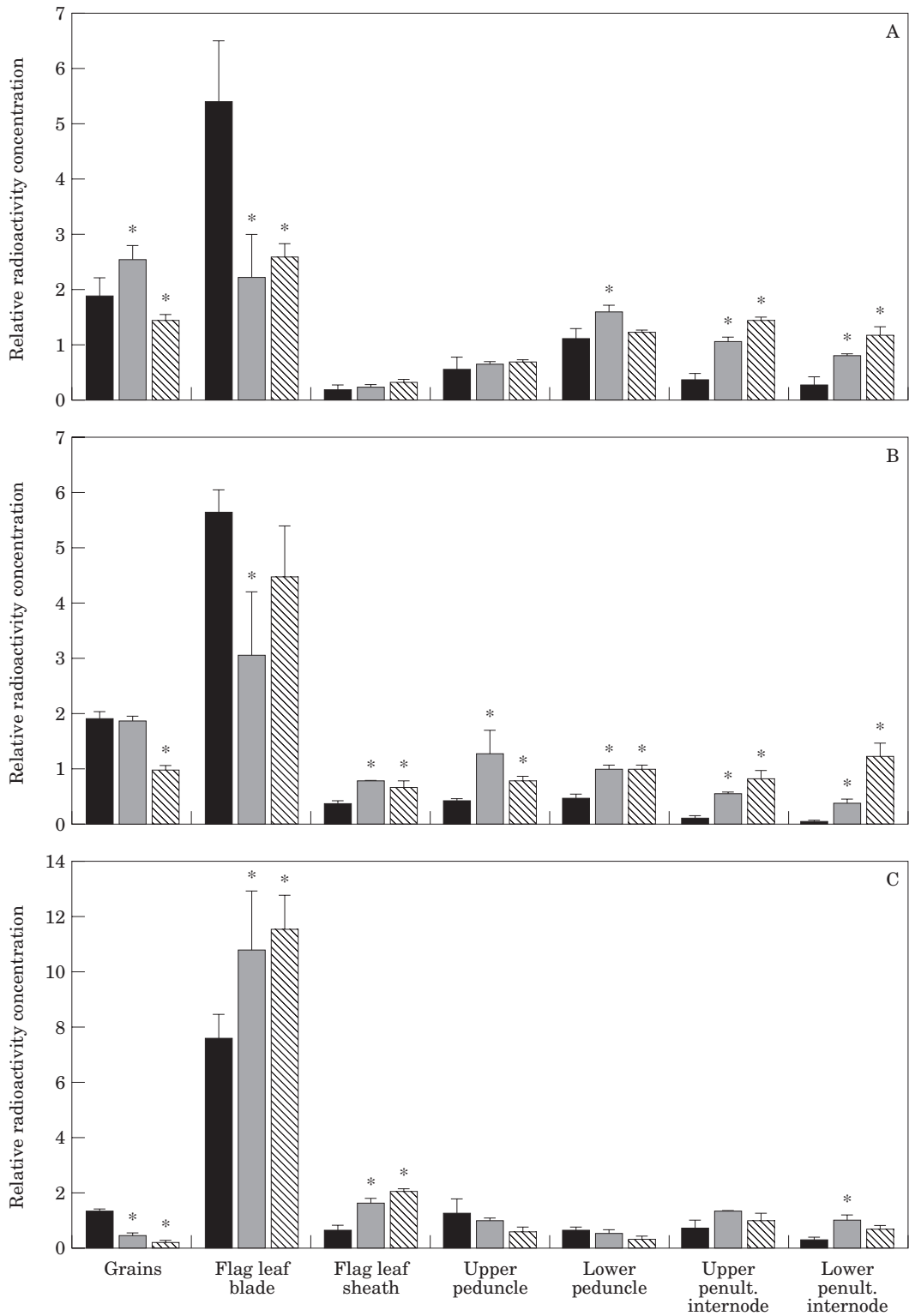


FIG. 4. Effects of source-sink modifications (Treatment I, ■; II, □; III, ▨) on relative radioactivity concentration (RRC) in wheat plants 24 h after pulse chase labelling of the flag leaf blade with $^{14}\text{CO}_2$ for 15 min. A, B and C are 7, 14 and 21 d after anthesis. Each value is the mean of four plants. Vertical bars represent s.e. *, RRC significantly different from controls at $P < 0.05$ as shown by one-way Anova followed by Duncan's multiple range test.

evidence of source limitation in control plants of this sowing (Fig. 1). In general, the source limitation for the November sowing seemed higher than that of the January sowing. This apparently contradicts the higher LAD and flag leaf area of the plants sown in November, but could be explained if the photosynthetic activity of the source organs has a pronounced effect on subsequent demand by the sink organs. Thus, the extent of the source at the time of anthesis sets an upper limit to potential sink size (Evans and Wardlaw, 1996). This supports the idea that the relative limitation of yield by source or sink is subject to both pre- and post-anthesis conditions (Wardlaw, 1994) and varies from environment to environment (Stapper and Fischer, 1990; Slater and Miralles, 1992). On the other hand, the lack of difference in grain mass between control and half-spike plants for the January sowing could be a consequence of source limitation at early stages of grain formation, when the number of endosperm cells is fixed (Brocklehurst, 1977; Wardlaw, 1994).

Surprisingly, the imposition of a more severe reduction in the number of grains per spike, by retaining only four central spikelets in the trimmed spikes (approx. 350% increase in potential assimilate availability per grain; treatment III) led to a drastic reduction (between 10 and 15%) in individual grain mass in cultivars Cuba C-204 and IAC-60 in the January sowing, compared to control and half-spike plants (Fig. 1). In IAC-60, the specific mass of the internodes was also reduced in treatment III (Fig. 2). Decreases of kernel mass between 9 and 19% were caused by a reduction in spikelet number (Lupton and Ali, 1966). Fischer and HilleRisLambers (1978) also reported small decreases in kernel mass in some tall cultivars with reduced sink size. However, no clear explanation of this behaviour was provided in either case.

We hypothesize that modification of sink size could inhibit photosynthesis in such a manner that even the filling of the remaining grains and whole plant dry matter gain could be affected by the availability of photoassimilates i.e. the rate of photosynthesis would be diminished to a greater extent than the demand. The principal cause of such inhibition of photosynthesis might be the degree of reduction in size of the sink or the position of the trimmed grains or both. These possibilities must be tested. The suggestion that modification of sink size may affect canopy photosynthesis more than proportionally is supported by the following facts: first, the mechanism of sucrose regulation is not likely to be via a mass-action effect (Pollock and Farrar, 1996), so there is no reason to expect a proportional relationship between sink reduction and photosynthesis inhibition. Secondly, significant changes in flag leaf carbon exchange rate occur in response to changing demand by the wheat ear during grain filling when alternative sinks for flag leaf assimilates are limited to such an extent that carbohydrates accumulate in the leaves (Evans and Wardlaw, 1996). This is consistent with the results of Fischer and HilleRisLambers (1978) who found a positive correlation across cultivars between grain mass in the remaining kernels of modified spikes and potential kernel weight, determined by a substantial increase in light received in intact plants. This relationship correlated well even when the mass of the

grains in modified spikes was lower than that of unmodified plants, meaning that those cultivars with a greater decrement in grain weight after reduction in the number of spikelets showed a smaller response to the increment in received light. In our study, in the cultivars where decrease of kernel mass in treatment III was more pronounced, no increase in specific mass of the internodes occurred with reduction of sink size (treatments II and III, Figs 2 and 3). Decline in the specific mass of the internodes in IAC-60 in treatment III (Fig. 2) implies that the observed effects were not a consequence of surgical disruption. Actually, inhibition of photosynthesis can also occur in intact plants although it is not always apparent (Evans and Wardlaw, 1996).

Distribution of photoassimilates between organs may change during grain filling in relation to the part of the plant, source or sink organs that exert control on the partitioning at a given moment (Marcelis and Koning, 1995). Some authors (Evans and Rawson, 1970; Richards, 1996) reported that photosynthesis of the spike and flag leaf blade alone could meet the requirements of the grains at all times during grain filling. Richards (1996) suggested that grain yield of irrigated spring wheat may not be limited by the supply of carbon. However, there are data in the literature showing a significant increase in mass of grains associated with reductions in grain number after anthesis (Fischer and HilleRisLambers, 1978; Ledent and Stoy, 1985; Koshkin and Tararina, 1989) implying source limitation, at least some time during grain filling. These conflicting results suggest a strong environmental and genotypic interaction in the response of grain mass to modifications in source-sink relationships (Ma, MacKown and VanSandford, 1990; Blade and Baker, 1991). This also underlines the importance of analysis of source-sink interactions at different times during grain filling. To test this, we investigated the distribution of ^{14}C -photoassimilates on three occasions after anthesis in plants of the cultivar Cuba C-204 (sown in January) with different degrees of reduction of the number of spikelets.

The patterns of distribution of ^{14}C -photoassimilates in control plants changed from 7 to 21 d after anthesis (Fig. 4). The increase in RRC of the flag leaf, flag leaf sheath and upper part of the peduncle from 7 to 21 d after anthesis in control plants reflects a shift from source to sink control on partitioning. This is supported by comparison with the partitioning in plants with reduced sink size. Seven d after anthesis, the grains of plants with half spikes showed a higher RRC than the control plant grains (Fig. 4). With the reduction in the number of spikelets to four, the RRC of the grains was reduced (Fig. 4), an effect that was reflected in the final grain mass as discussed earlier. The RRC of the flag leaf blade was lower in plants with modified spikes at 7 d after anthesis, perhaps as a consequence of inhibition of photosynthesis (Plaut, Mayoral and Reinhold, 1987; Koch, 1996) and the translocation of the reduced amount of ^{14}C -photoassimilates to the internodes (Fig. 4). However, it was larger than the RRC of control plant leaf blades 21 d after anthesis. The latter could be a result of a greater sink limitation in plants with reduced sink size 21 d after anthesis. At this stage the RRC of internodes did not rise with the decrement in sink size as it did at the first two samplings

(Fig. 4). This could be due to a diminished ability of the internodes to form fructans at the latter phase of grain filling (Schnyder, 1993).

At 21 d after anthesis, the RRC of the grains decreased in all three treatments, but was more pronounced in plants with reduced sink size. This could be explained by the decrease in sink strength at this stage, particularly in plants in treatments II and III. This change in the RRC of grains was closely associated with the decline in the rate of conversion of sucrose into starch in the grains. Seven d after anthesis all carbon-14 received by the grains was incorporated into the perchloric acid fraction at about the same rate by plants with different source:sink ratios. However, 21 d after anthesis, differences arose between treatments, and a close positive relationship ($r = 0.898$, $P < 0.01$) was found between translocation to the grains and transformation into starch, supporting the idea of a change from source- to sink-limited situations during grain filling. A similar relationship was found by Wardlaw *et al.* (1995) studying the incorporation of ^{14}C -sucrose into starch in wheat kernels growing in nutrient solution with an unlimited supply of substrates.

The observed change from source to sink control during grain filling was earlier and more pronounced in plants with reduced sink size in spite of possible inhibition of photosynthesis. This shift from source to sink control suggests the changes could occur under realistic field situations. Hence it emphasizes the importance of analysis of source-sink relations at different phases of growth. In general, the observed pattern of dry matter partitioning suggests that grain filling is source limited, particularly in plants sown in November. This pattern differed markedly from that in other studies (Fischer and HilleRisLambers, 1978; Blade and Baker, 1991; Evans and Wardlaw, 1996), highlighting the difference between tropical and temperate areas.

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