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Translocation of ^{14}C-sucrose within the Ear in Durum and Aestivum Wheat Varieties

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With 1 figure and 2 tables

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Abstract

Excised ears of *Triticum durum* (HD 4502 and B 449) and *T. aestivum* (Kalyansona and Kundan) varieties were cultured in ^{14}C-sucrose, and the uptake and distribution of ^{14}C within the ear was examined. Species-level differences in the distribution of ^{14}C to spikelets at basal, middle and apical positions in the wheat ear (vertical distribution) were observed. *T. aestivum* var. Kalyansona and Kundan showed no limitation in vertical translocation of ^{14}C-sucrose, whereas in *T. durum* there was a decrease in the distribution of ^{14}C to apical spikelets. Within a spikelet, the distribution of ^{14}C-sucrose to distal grains was significantly less than that to proximal grains in all the genotypes.

Key words: ^{14}C-sucrose — ear — grain — spikelets — translocation — wheat species

Introduction

Large variation in the weight of grains within the ear in wheat has been observed. The grains of central spikelets are larger than the equivalent grains in basal spikelets, these in turn usually being larger than the grains in upper spikelets (Rawson and Ruwali 1972, Bremner and Rawson 1978). Within a spikelet, beyond the first two basal grains, the more distal a grain in a spikelet the lower its weight (Sunita Kumari and Ghildiyal 1997, McMaster 1997). A decrease in percentage nitrogen (N) in the distal grains of spikelets has also been observed (Bremner 1972, Bremner and Pinkerton 1974). Simmon and Moss (1978) reported that in *T. aestivum* cultivar Kitt the percentage N in distal grains does not decline and considered it to be a desirable characteristic that could contribute to a higher percentage of bulk grain protein in cultivars where those kernels make up a significant proportion of the total spike yield.

Grain growth depends on the availability of assimilates and the ability of grains to utilize assimilates for the synthesis of reserves. In *Lolium perenne*, differences in seed dry weight within the ear mainly arise from differences in growth rate, which in turn is determined by the dry weight of the ovule at anthesis (Waringa et al. 1998). In wheat, differences in grain growth within the ear have generally been attributed to the availability of assimilates on the basis of the vascular anatomy of the spike, degraining experiments and the frequently observed negative correlation between the number of grains per ear and the individual grain weight (Hanif and Langer 1972, Siddique et al. 1989, Slafer and Andrade 1993, Slafer et al. 1996). The lower availability of assimilates to distal grains than to proximal grains in spikelets of *T. aestivum* var. Kalyansona was further shown by actually determining the sugar content in those grains (Sunita Kumari and Ghildiyal 1997). Since these observations have important implications regarding the type of ear structure that is desirable, there is a need to evaluate the pattern of assimilate distribution within the ear, using ^{14}C translocation studies. The technique of culturing detached ears of wheat in ^{14}C-sucrose and examining ^{14}C translocation within the ear is a useful approach in this respect. Ugalde and Jenner (1990) cultured detached spikelets of wheat in ^{14}C-sucrose and examined the route of substrate movement into the wheat endosperm, and reported this system to be suitable for studies on transport. The present study therefore attempts to examine the pattern of assimilate distribution within the ear cultured in ^{14}C-sucrose. Four different wheat varieties, two each of durum and aestivum wheat, were used to evaluate whether genotypic differences exist in this regard.

Materials and Methods

Four wheat varieties, two of *T. durum* (HD 4502 and B 449) and two of *T. aestivum* (Kalyansona and Kundan), were used. *T. aestivum* var. Kalyansona is a small-grain type with a high number of grains per ear, whereas Kundan has larger grains but fewer grains per ear. *T. durum* var. HD 4502 has smaller grains than B 449 but a greater number of grains per ear. These wheat varieties were grown in glazed china clay pots (50 cm × 25 cm) containing sandy loam soil. Fertilizers were applied at the rates of 120, 60 and 60 p.p.m., respectively, of N, phosphorus (P) and potassium (K). N was supplied in two split doses whereas P and K were given only at the time of sowing. Four healthy plants were kept in each pot. The anthesis dates of the main shoot (MS) ear were recorded on tags placed on each plant.

In order to examine the uptake and translocation of ^{14}C-sucrose to grains at different positions within an ear, MS ears, 20 days after anthesis, coinciding with the period of maximum grain growth rate, were excised and cultured in^{14}C-sucrose (Jenner 1970, Jenner and Rathjen 1972). Ears were detached by cutting the culms under water obliquely (about 60° to the horizontal) about 5 cm from the basal spikelet. Cutting the culms under water prevents blocking of veins. The detached ears were then quickly transferred to vials (56 × 25 mm) containing a 3-ml solution of 30 mg ml^{-1} ^{14}C-sucrose (4 μCi ml^{-1}). One ear was kept in each vial and held in place with loose plugs of cotton wool. The ears were allowed to absorb^{14}C-sucrose solution at 30 ± 1 °C for 6 h in the dark, as illumination has no effect when the ears are supplied with sucrose (Jenner 1968). Three ears (three replications) were cultured for each variety.

At the end of the experimental period, the ear was removed from the vial and the culm was cut at the base of the ear and discarded. Two basal, two middle and two apical spikelets were removed from the ear. The remaining ear portion was plunged in boiling ethanol in an Erlenmeyer flask. From the two basal spikelets, the first and fourth grains were removed and plunged in boiling ethanol in separate tubes. The remaining spikelet portion was also kept in ethanol in a separate tube. Similar sampling was performed for the middle and apical spikelets of the ear. Thus, for each ear, 10 different samples were collected and plunged in boiling ethanol. Samples were then finely homogenized and extracted with different concentrations of ethanol to obtain soluble and insoluble fractions (Ghildiyal and Sirohi 1986). The insoluble component was suspended in 6 M HCl and hydrolysed in an autoclave at 6.8 kg pressure for 30 min. ^{14}C activity in this hydrolysate was considered as incorporation into the insoluble component. Radioactivity was determined in the soluble and insoluble components by a Packard liquid scintillation spectrometer (Packard Instrument Co. Inc., Downers Grove, IL, USA) with appropriate quench correction. The uptake of ^{14}C-sucrose was thus calculated as a sum of both the soluble and insoluble components.

Results

Genotypic differences were observed in the uptake of ^{14}C-sucrose by the main shoot ear (Table 1). The small-grain varieties HD 4502 (*T. durum*) and Kalyansona (*T. aestivum*) showed a greater uptake of ^{14}C-sucrose than the large-grain varieties B 449 (*T. durum*) and Kundan (*T. aestivum*). Of the total ^{14}C-sucrose uptake by the entire ear, 8.37 to 15.90 % was converted to the insoluble component. The large-grain varieties B 449 and Kundan had a greater conversion efficiency than the small-grain varieties HD 4502 and Kalyansona. The per cent incorporation into the insoluble component was, however, lower in Kalyansona than in any of the other genotypes.

The per cent distribution of the total ^{14}C-sucrose taken up by the ear to individual spikelets was significantly higher at the basal portion of the ear than in the apical spikelet in both the varieties of *T. durum* (Table 2). In *T. aestivum* var. Kalyansona, however, the per cent distribution of ^{14}C per spikelet increased from the basal to the middle to the apical spikelets. In Kundan there was no significant difference in the per cent distribution of ^{14}C-sucrose per spikelet to the basal, middle and apical spikelets.

In the ears cultured on ^{14}C-sucrose, the amount of ^{14}C received by the first and fourth grains of the

Table 1: ^{14}C-sucrose uptake and incorporation in an ear (dpm $ear^{-1} \times 10^{-5}$) of the main shoot in durum and aestivum wheat varieties

	T. durum		*T. aestivum*		LSD at 5 % P
	HD 4502	B 449	Kalyansona	Kundan	
Soluble	156.75	72.60	150.46	75.78	40.12
Insoluble	20.14	11.58	13.75	14.33	3.10
Total	176.89	84.18	164.21	90.11	56.18
Per cent incorporation into insoluble component	11.38	13.76	8.37	15.90	2.30

Table 2: Per cent distribution of total ^{14}C-sucrose taken up by the ear to one basal, one middle and one apical spikelet in durum and aestivum wheat varieties

Variety	Spikelets			LSD at 5 % P
	Basal	Middle	Apical	
T. durum				
HD 4502	5.44	5.21	2.83	1.98
B 449	7.27	5.42	4.96	2.69
T. aestivum				
Kalyansona	3.24	4.37	6.03	1.91
Kundan	5.95	5.79	4.93	ns
LSD at 5 % P	2.10	ns	1.96	

apical, middle and basal spikelets was determined. B 449 did not have a fourth grain in the apical spikelets, ans so the third grain was used. It was observed that in B 449 and Kundan, which are large-grain varieties of *T. durum* and *T. aestivum*, respectively, there was no significant difference in the amount of ^{14}C received by the first and fourth grains in the basal spikelet (Fig. 1). The amount of ^{14}C received by the fourth grain was, however, lower than that received by the first grain in *T. aestivum* var. Kalyansona and *T. durum* var. HD 4502. In the middle and apical spikelets, the amount of ^{14}C received by the fourth grain was significantly lower than that received by the first grain in all the varieties, with differences being more marked in the case of the apical spikelets.

Discussion

The present study revealed that the distribution of assimilates to different grains within an ear varies depending on the location of the grain. In a spikelet, the distribution of ^{14}C-sucrose to distal grains was significantly lower than that to proximal grain. This was true for all the genotypes. However, species-level differences in the distribution of ^{14}C to spikelets at basal, middle and apical positions in the wheat ear (vertical distribution) were observed. The *T. aestivum* varieties Kalyansona and Kundan showed no limitation in the vertical translocation of ^{14}C-sucrose, whereas in the *T. durum* varieties there was a decrease in the distribution of ^{14}C to apical spikelets.

Studies on the development of grains at different positions in the apical, middle and basal spikelets of wheat showed that, beyond the first two basal grains, the more distal a grain in a spikelet the lower its weight (Sunita Kumari and Ghildiyal 1997, McMaster 1997). The sugar concentrations measured in the grains suggested that distal grains received less assimilates than proximal grains (Sunita Kumari and Ghildiyal 1997). The lower distribution of ^{14}C-sucrose to distal grains than to proximal grains in a spikelet observed in the present radio-labelled sucrose translocation study (Fig. 1)

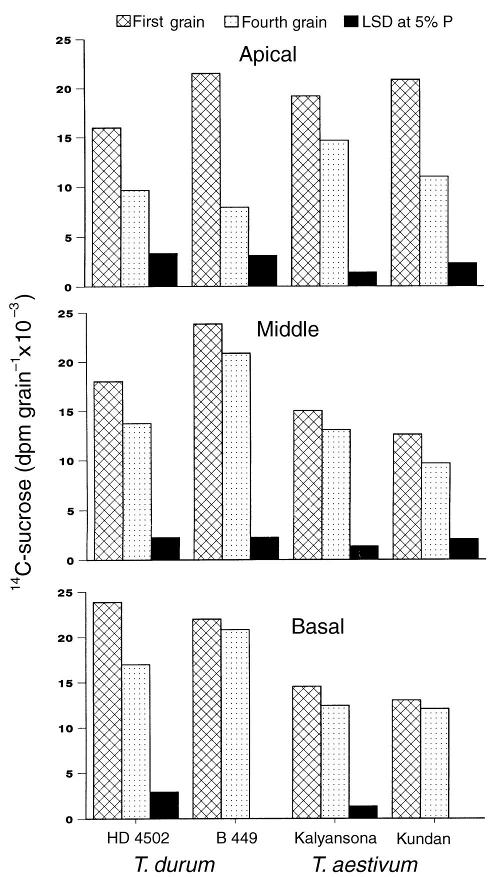

Fig. 1: Translocation of ^{14}C-sucrose to the first and fourth grains in apical, middle and basal spikelets in durum and aestivum wheat varieties

supports this finding. Moreover, the present study has shown that this result holds for both durum and aestivum wheat varieties. The lower distribution of ^{14}C-sucrose to the distal grains in a spikelet could be due to vascular limitation in the spike structure. It has been reported that, within each spikelet, the three basal grains are supplied by a separate group of vascular bundles and are therefore not in direct competition. More distal grains, however, all appeared to be linked to one series of subvascular elements arising from the bundles of the third floret, in which case the third and higher grains compete for assimilates from one poorly developed series of bundles (Hanif and Langer 1972). In the present study, the large-grain varieties B 449 and Kundan, which have a lower number of grains per spikelet, showed a smaller decline in ^{14}C translocation to distal grains, particularly in the basal spikelets (Fig. 1). The large-grain varieties also appeared to have a better efficiency of conversion of soluble precursors into insoluble reserves (Table 1). Most of this incorporation into the insoluble form must take place in the grains, as in ears 20 days after anthesis only a small amount of radioactivity was incorporated into the insoluble form in the floral parts (Ugalde and Jenner 1990).

The question arises of how the distribution of assimilates within the ear could be improved, apart from maintaining a higher grain number per ear. Solansky (1979) suggested that distal grains are smaller because they mainly depend on the amount of assimilate provided by the ear, which is smaller than the amount provided by the flag leaf, and therefore increasing the efficiency of ear assimilation in plant breeding programmes was emphasized. It should be mentioned that a higher grain number per ear could be achieved by increasing the spikelet number or by increasing the grain number per spikelet. A higher grain number per spikelet is of little consequence in increasing the grain weight per spikelet as it leads to a sharp reduction in grain growth from basal to terminal grains (Sunita Kumari and Ghildiyal 1997, Ravi 1999), as a consequence of vascular limitation in the spikelet structure, as discussed above. However, the decrease in grain weight per spikelet from the middle to the apical spikelets was less than the decrease in grain weight from the basal to the apical grains in a spikelet (Sunita Kumari and Ghildiyal 1997, Ravi 1999). Generally similar results have also been reported in *Lolium perenne* (Warringa et al. 1998). It is therefore suggested that, in order to ensure better grain uniformity while maintaining higher grain number per ear in wheat, the spikelet number per ear should be increased rather than the grain number per spikelet (Sunita Kumari and Ghildiyal 1997). Such an ear structure would also minimize the frequently observed negative association between the number of grains per ear and individual grain weight (Siddique et al. 1989, Slafer et al. 1996). Richards (1996) also suggested that, in wheat, it would be desirable to increase the number of spikelets as this is likely to result in fewer florets per spikelet.

It appears, therefore, that grain number per ear should be increased by increasing spikelet number rather than grain number per spikelet. It is in this context that genotypes in which vertical transport is not limiting would be useful. The present study revealed species-level differences in the vertical distribution of ^{14}C within the wheat ear. The *T. aestivum* varieties Kalyansona and Kundan showed no limitation in vertical translocation of ^{14}C, whereas in *T. durum* there was a decrease in the distribution of ^{14}C to apical spikelets.

Zusammenfassung

Translokation von ^{14}C-Sukrose innerhalb der Ähre von Durum-und Aestivumweizen-varietäten

Abgetrennte Ähren von *T. durum* (HD 4502 und B 449) und *T. aestivum* (Sorten: Kalyansona und Kundan) wurden in^{14}C-Sukrose kultiviert und Aufnahme und Verteilung von^{14}C innerhalb der Ähren untersucht. Die artspezifischen Differenzen in der Verteilung von^{14}C im Hinblick auf die Ährchen im basalen, mittleren und apikalen Teil der Weizenähre (vertikale Verteilung) wurden beobachtet. *Triticum aestivum* var. Kalyansona und Kundan zeigten keine Limitierung in der vertikalen Translokation von^{14}C-Sukrose, während bei *Triticum durum* eine Abnahme in der Verteilung von^{14}C zum apikalen Ährchen vorlag. Innerhalb der Ährchen war die Verteilung von^{14}C-Sukrose zu den distalen Körnern bei allen Genotypen signifikant geringer als zu den proximalen Körnern.

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