

Assessing the photo-assimilate (^{14}C) partitioning dynamics between the source and the sink to decipher an efficient pruning practice in guava (*Psidium guajava* L.)

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Abstract

Radiotracer (^{14}C) experiments were conducted to develop a sustainable pruning strategy in guava (*Psidium guajava* L.) based on the source-sink carbon partitioning (^{14}C) dynamics. ^{14}C -photoassimilate transfer from the source leaves followed the following scheme based on the respective sink's demand i.e. fruit on the source leaf branch > shoot and foliage of the source leaf branch > fruit on the adjacent branch > shoot and foliage of the adjacent branch. This study clearly indicates that the source leaves adjacent to the developing fruit play a crucial role in governing the fruit growth and development. Thus, for an efficient canopy management and for a sustainable year to year productivity, instead of pruning an overall outer canopy, the pruning strategy in guava can be so designed to remove the branches on which the fruits are not desired, leaving intact the branches targeted to bear the fruits.

Introduction

Guava (*Psidium guajava* L.) is also known as “super fruit” belongs to family Myrtaceae. It is well known fact that guava has two distinct botanical characteristics; one is guava has more than one bearing season [1]. The second is the flowers always borne on newly emerging vegetative shoots i.e. current season shoot, irrespective of the time of year [2, 3]. This character makes guava unique, that it can be pruned as severely as temperate fruit tree Lotter [4] for high density management. Several workers reported the beneficial effects of pruning on yield and fruit quality of guava [5, 6, 7, 8]. Pruning is removal of any unwanted part of plant. But, when it is employed in high density management as a routine practice it results in the loss of plant reserves in terms of the removal of branch. This loss becomes more significant when the thick and mature branches of guava tree are pruned. It often results in the huge reduction in bearing and yield of guava in the coming years after pruning. It also results in the non-bearing of trees and/or change in the bearing time.

Now-a-days, farmers are planting guava under high density at different spacing. They end up with overcrowded and unproductive guava orchards due to lack of proper knowledge of pruning timings, severity and source-sink relationship. The dynamics of relationship between source tissue, which is a net producer of photo assimilates, and a sink tissue, which is a net importer of photosynthetic products, Ho [9] is very important among plants especially in perennials. In perennial fruit crops, the yield is not only a function of current growing season but it depends on the carbon economy over the year, and any faulty practice like overtly wrong pruning can disturb it. It is well proven in recent years that source and sink factors co-limit plant growth [10, 11, 12]. Interestingly, perennial crops have methods like pruning [13], fruit thinning [14] etc. through which the source-sink relationship can be regulated. Radiotracers and radiations were used successfully to understand the plant metabolic processes and source-sink dynamics in many crops [15, 16, 17, 18, 19, 20, 21].

The experiments related to the pruning practices for crop regulation and/or high density are primarily based on different pruning levels as treatments and their effect on canopy size and yield, and quality-based parameters. However, before deciding any pruning experiment, the knowledge of source-sink

relationship is critical to decide on what to prune and to what extent. In light of the above, radiotracer (^{14}C) study was conducted to determine the relative contribution of proximal and distant source-leaves towards the sink-fruit development when later is present on the same and adjacent branches in guava.

Materials and methods

The experiment was carried out during winter season (2024-25) in guava (*Psidium guajava* L.) variety Allahabad Safeda (15 year old) at Todapur orchard, Division of Fruits and Horticultural Technology, ICAR-IARI, New Delhi. The radiotracer (^{14}C) labelling was used to study source-sink dynamics [22].

Experimental details

The experiment comprised of two treatments (Table 1 and Fig. 1), (a) T1: adjacent leaves of fruit labelled. The treatment comprised of two branches (X1 and X2). Both branches had single fruit. In branch X1, the adjacent leaves of the fruit were labelled with ^{14}C . The branch comprised of two branches is disconnected metabolically by girdling from bottom, and (b) T2: distant leaves from the fruit labelled. T2 also had two branches (X1 and X2), but only X2 branch had fruit and leaves on X1 branch labelled. The branch comprised of two branches, is disconnected metabolically by girdling from bottom. The radiotracer (^{14}C) labelling was done under both T1 and T2, when the fruit was at the lemon size stage. Radioactivity incorporated in different parts of the experimental branches T1 and T2 was traced following a pre-decided uniform period of incubation at the fruit maturity stage.

Table 1
Details of the treatments

Treatments	Tissue labelled	Treatment details	Branch	Details of the experimental tissue	Code
T1	Adjacent leaves of fruit labelled	The study included two adjacent branches having one fruit each and leaves adjacent to fruit on one branch were labelled with ^{14}C	X1: Labelled branch	Labelled leaves	A
				Unlabelled leaves on labelled branch	B
				Shoot of labelled branch	C
				Fruit on labelled branch	D
			X2: Unlabelled branch	Leaves on unlabelled branch above the fruit at proximal end of shoot	E
				Leaves on unlabelled branch below the fruit at distal end of shoot	F
				Shoot of unlabelled branch	G
				Fruit on unlabelled branch	H
T2	Distant leaves from the fruit labelled	The study included two adjacent branches having one fruit in only one branch. The leaves of other branch (not having fruit) were labelled with ^{14}C	X1: Labelled branch	Labelled leaves	I
				Unlabelled leaves on labelled branch	J
				Shoot of labelled branch	K
			X2: Unlabelled branch	Leaves on unlabelled branch above the fruit at proximal end of shoot	L
				Leaves on unlabelled branch below the fruit at distal end of shoot	M
				Shoot of unlabelled branch	N
				Fruit on unlabelled branch	O

Radiotracer studies

Fully developed leaves on a side branch of the main experimental branches, satisfying the above criterion, were supplied with 10 µl of ^{14}C (U)-sucrose sourced from the Board of Radiation and Isotope Technology (BRIT), Mumbai, India (specific activity 180.0 mCi/mmol [666.0 MBq/ mmole]) on the top leaf surface after its gentle abrasion with a sand paper. Wax was smeared on the dorsal leaf surface, and the area of ^{14}C application was ringed on the ventral surface to avoid spillage of radioactivity and to facilitate penetration and absorption of applied radiotracer. Label was applied around late noon/evening to reduce evaporation loss [18]. Radiotracer application was made on the identified leaves in sub branch of the main axis at equidistance from the developing sink within a set of treatment replicates.

Measurement of the tissue accumulated C

After a certain period of time i.e., after 30 days of tracer application around the fruit maturity stage, the experimental branches were excised, brought to the laboratory, and were separated into different parts like leaves (labelled and unlabelled), shoot, and fruit branch-wise. The plant samples were oven dried at 80°C until complete dryness, following which the tissue dry weights were recorded and samples were ground in separate pestle and mortar taking care to avoid cross contamination. A 100 mg of the finally ground respective tissue sample was taken in glass scintillation vials and to it 50 mg of cabosil, an inert silica gel, was added followed by the addition of 10 ml of the dioxane based scintillation liquid (cocktail O). The samples were analysed for the tissue ^{14}C accumulation using liquid scintillation counter (Perkin Elmer Tri Carb, USA) against the scintillation liquid blank and were expressed as Becquerel (Bq) g^{-1} dw and ^{14}C activity (Bq) tissue^{-1} [19].

Statistical analysis

All extractions and quantifications were conducted in three ($n = 3$) replications, and data are expressed as mean $\pm$ SD.

Results and discussion

Two experimental conditions (Table 1) with tracer (^{14}C -sucrose) application made on source leaves placed on shoots adjacent and distant to the developing sinks (fruits), were enabled in the field grown 15 years old guava trees and translocation of carbon (^{14}C) assimilates from the labelled source-leaves to (a) other unlabelled source-leaves and fruit-sink on the treated branches and (b) to the source-leaves and developing fruit-sink placed on unlabelled branches were monitored to study the translocation dynamics (Fig. 1) up to the fruit harvest stage. Relative translocation of carbon to the leaves and fruits on the labelled and unlabelled branches in experiment (T1 and T2) are presented in Table 2, which reveals an overall transport of 48.14% of carbon (^{14}C) from the labelled source leaves to all other sinks present on

the same and different branches. Under T1, fruit present on the labelled branch was observed to be the most prominent site with 37.47% of carbon accumulation during its transition from the lemon-sized fruit to fully mature ripe fruit. The unlabelled leaves present on the labelled branch contributed majorly as a carbon assimilating source organ and did not act as a dominant carbon sink (0.21% accumulated ^{14}C). A similar pattern of carbon translocation was also evidenced for the distantly placed source leaves present on branch adjacent to the labelled branch. Here again, the fruit present on the distantly placed unlabelled branch showed a higher carbon accumulation (1.05%) then compared to the shoot (0.15%) and leaves (0.27%) of the same branch. It shows that the distance between source and sink affects photo assimilate accumulation [23].

Table 2

Total and relative distribution of ^{14}C metabolites in different tissue of branches X1 and X2 wherein leaves adjacent to fruit (T1) and leaves distant to the fruit (T2) on branch X1 were labelled with radiotracer (^{14}C -sucrose)

Treatments		^{14}C accumulation (Bq/tissue)	*Relative distribution of ^{14}C metabolites (%)
T1: Adjacent leaves of fruit labelled			
A	Labelled leaves	19485.9 $\pm$ 253.3a	51.86
B	Unlabelled leaves on labelled branch	80.558 $\pm$ 12.7e	0.21
C	Shoot of labelled branch	3292.15 $\pm$ 87.2c	8.76
D	Fruit on labelled branch	14076.6 $\pm$ 58.6b	37.47
E	Leaves on unlabelled branch above the fruit at proximal end of shoot	85.5758 $\pm$ 23.2e	0.23
F	Leaves on unlabelled branch below the fruit at distal end of shoot	100.045 $\pm$ 8.9e	0.27
G	Shoot of unlabelled branch	56.403 $\pm$ 3.4f	0.15
H	Fruit on unlabelled branch	394.284 $\pm$ 18.5d	1.05
*Total ^{14}C accumulation (Bq) in experimental branches (B1 and B2)		37571.48	
T2: Distant leaves from the fruit labelled			
I	Labelled leaves	28537.6 $\pm$ 721.5a	65.87
J	Unlabelled leaves on labelled branch	2249.76 $\pm$ 105.2c	5.19
K	Shoot of labelled branch	10346.3 $\pm$ 341.7b	23.88
L	Leaves on unlabelled branch above the fruit at proximal end of shoot	140.56 $\pm$ 21.6e	0.32
M	Leaves on unlabelled branch below the fruit at distal end of shoot	90.26 $\pm$ 37.2f	0.21
N	Shoot of unlabelled branch	120.78 $\pm$ 17.5e	0.28
O	Fruit on unlabelled branch	1836.1 $\pm$ 139.7c	4.23
*Total ^{14}C accumulation (Bq) in experimental branches (X1 and X2)		43321.3	

Under the treatment T2, which had a distantly placed developing sink *vis-à-vis* the ^{14}C labelled source leaves clearly showed the dominance of the fruit as a sink, however the comparison of T1 and T2 reveals that the developing fruit are majorly fed or supplied with carbon assimilates by the source leaves present on the same branch and that the source leaves of one branch do not significantly contribute towards the sink development of distantly placed fruits even when they share the vascular system. Data in Table 3 indicates the variation in total

Table 3

Total ^{14}C distribution (Bq/tissue) between the labelled (*) and the unlabelled branches in T1 and T2.

Treatments	Branch	^{14}C accumulation	% Translocation
T1	X1*	36935.21± 9085.58	98.31
	X2	636.31± 157.85	1.69
T2	X1*	41113.66± 13463.08	93.19
	X2	3006.70± 810.83	6.81
X1 represent the branch on which source leaves were labelled with ^{14}C -sucrose under both T1 and T2; T1 had one fruit sink each on both branch X1 and X2 while T2 had fruit sink only on branch X2			

^{14}C accumulation between the labelled and unlabelled branches (X1 and X2 respectively) under both T1 and T2 conditions. While only 1.69% of the total supplied radiotracer (^{14}C) was transferred to the X2 branch under the T1, the ^{14}C -translocation in the same branch (X2) under the T2 treatment was observed to be higher at 6.81% (Table 3). The higher relative ^{14}C -flow in X2 under T2 than T1 may be attributed to the presence of fruit sink in the T2.

Relative accumulation of ^{14}C radio tracer in different tissues of X1 and X2 branches under T1 and T2 treatments was recalculated following the excluding ^{14}C content of the labelled leaves. Since, the labelled leaves may not have absorbed all the ^{14}C -sucrose applied on to their leaf surface and that the ^{14}C -content of the labelled leaves may instead reflect the residual ^{14}C on the leaf surface and that absorbed by the radiotracer applied leaves (Fig. 3). The results obtained following the exclusion of ^{14}C content of the labelled leaves, reveal that almost 77.83% (Fruit on labelled branch, in T1) and 69.98% (Shoot of labelled branch, in T2) of the ^{14}C gets translocated beyond the labelled leaves in the two experimental branches. A similar pattern of carbon translocation was evidenced under both T1 and T2 when the tissue carbon (^{14}C) accumulation was derived on respective tissue dry mass basis (Fig. 2). In

both the cases, the labelled leaves retained significantly higher carbon tracer in shoot and fruit-sink present on the labelled branch followed by relatively a higher ^{14}C accumulation in the shoot of labelled branches under both T1 and T2 conditions indicates the carbon reserve or carbon flow in transit from the source to the sink organ (Fig. 2). A comparison of carbon transfer dynamics to the developing fruit in T1 (one fruit each present on labelled (X1) and unlabelled branch (X2) and T2 [fruit sink present on unlabelled distant branch (X2) only (see Fig. 1) shows a relatively higher accumulation of ^{14}C in distantly placed fruits on branch X2 in T2 ($33 \text{ Bq g}^{-1} \text{ fruit dw}$) than T1 ($93 \text{ Bq g}^{-1} \text{ fruit dw}$). A relatively lower ^{14}C translocation and accumulation in fruit-sink of X2 under the T1 than the T2 may be attributed to the presence of another fruit sink directly on the labelled branch (X1) in T1, which is absent under the T2 condition (Fig. 2). The fruit sink present in proximity to the ^{14}C -supplied source/leaves acted as the major sink for the carbon-accumulates ($3608.5 \text{ Bq g}^{-1} \text{ fruit dw}$) [24], when compared to the other developing fruit sink under the same experimental condition (T1) and accumulates in the fruit-sink of the labelled branch (X1) and in the shoot of respectively under the T1 and T2 treatments. Relative translocation and accumulation of ^{14}C in fruit-sink of X2 branch under both the T1 and the T2 treatments was 2.18 and 12.42% (Fig. 3). This indicates that the adjacent leaves play important role in the development of fruit. Herold [25] also found that the leaves closest to the fruit have a dominating photosynthetic activity.

The partitioning pattern of carbohydrate/ photoassimilate is a crop-specific subject. At the same time, it is not a genetically programmed process. It is the outcome of a combination of competing organs and their relative abilities to compete for relative carbohydrates [26]. The potential of a fruit to accumulate assimilate i.e. its sink strength depends on its size, its location and distance from the source [27]. Our group has earlier shown in Kinnow that the fruit is the most powerful sink capable of drawing maximum photo assimilates irrespective of its position [22] on the bearing branch. In some fruit crops like stone fruits, the more number of sinks altered the source-sink balance, by increasing the assimilate accumulation into the fruits and/or by inducing an intensification of competition between the fruit sinks to regulate the vegetative and reproductive growth dynamics [28, 29]. It is also evident in tropical/sub-tropical fruits like orange that the more number of fruits puts pressure on source-leaves to assimilate more carbon [30] and/or reduce the fruit size and the quality [31].

Conclusion

Evidence gathered from the radiotracer (^{14}C) study clearly indicates that leaves in proximity of the developing fruit predominantly act as the source for the C-assimilates and, thus, determine the fruit size and development. The study further reveals that the fruits irrespective of the position on the branch/tree act as major sink organ for the carbon assimilates as compared to the emerging and developed leaves. The assimilate partitioning from the source-leaves, in general, showed the following apportioning pattern i.e., fruit on the source leaf branch > shoot and foliage of the source leaf branch > fruit on the adjacent branch > shoot and foliage of the adjacent branch. Thus, the branches on which the bearing is desired should not be pruned by choice and design. However, the same can be pruned in the coming season,

when the other branches will be targeted for fruiting. This alternate strategy for fruiting-pruning of branches, rather than the overall pruning of the outer canopy, will help the growers to manage canopy structure without causing any negative effect on the photo assimilate economy of the guava tree. Further, since the foliage and shoot were found to serve as the storage reserve for the photo-assimilates, they should not severely pruned. In light of the above, the guava farmers are advised to grow varieties that are suited for high density or opt for moderate density (3 x 3 m or 4 x 4 m) planting coupled with branch-level choice pruning, rather than the overall canopy pruning, to maximize the fruit productivity in the guava orchard.

Declarations

Ethics declaration

Not applicable.

Consent for publication

All authors consent for publication.

Competing interests

The authors declare no competing interests

Author Contribution

MT, SJ and PM: conducted the experiments and radiological analysis; OPA: helped with critical analysis and discussion section; MJ and BS conceptualized the research and prepared the first draft and the final manuscript; BS did the radioactivity experimentation

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Data Availability

Data is available with first and the corresponding authors and can be shared on reasonable request

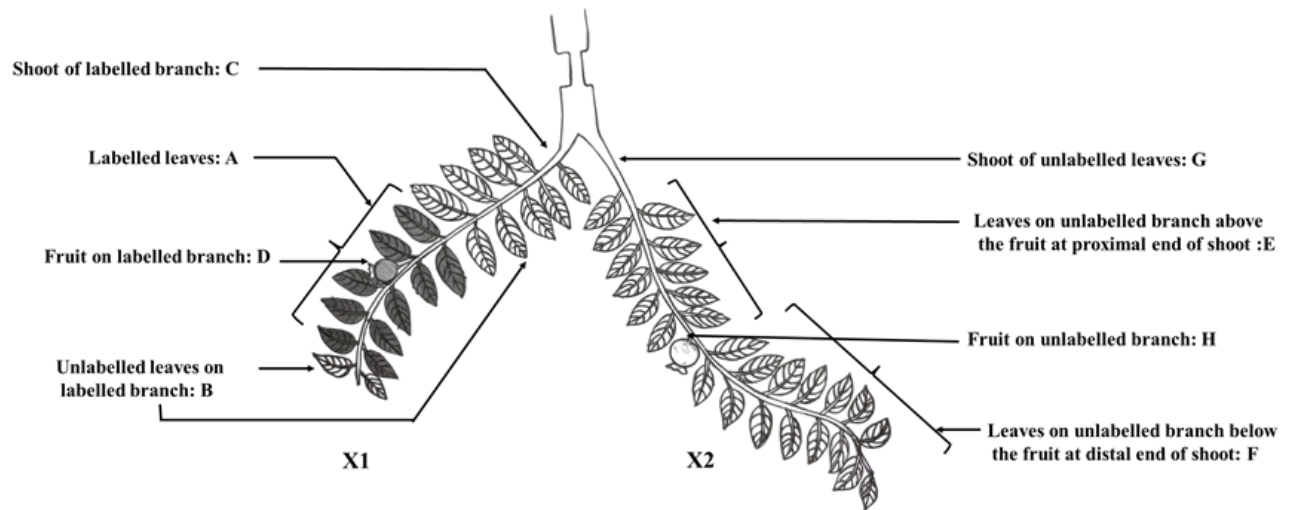
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Figures

T1



T2

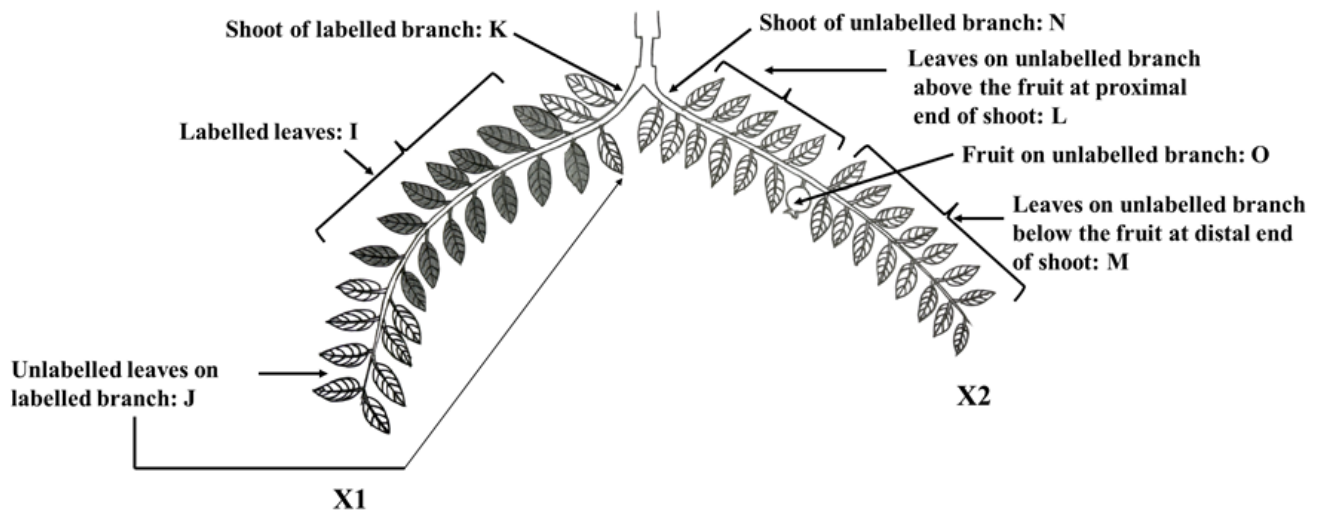


Figure 1

Diagrammatic presentation of different treatments (T1) Adjacent leaves of fruit

labelled (T2) Distant leaves from the fruit labelled used to study the partitioning of photosynthates from source organ, leaves towards the developing fruits (sink). Sample code is given in parenthesis. X1 and X2 represent respectively the labelled and unlabelled branches under the T1 and T2.

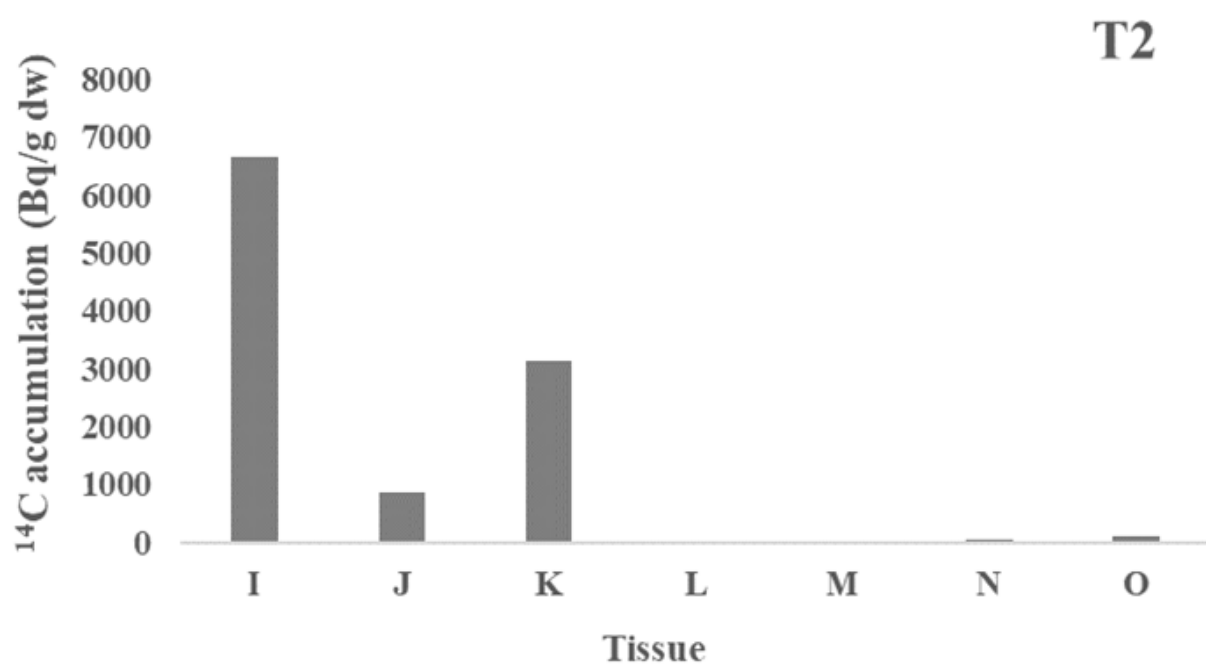
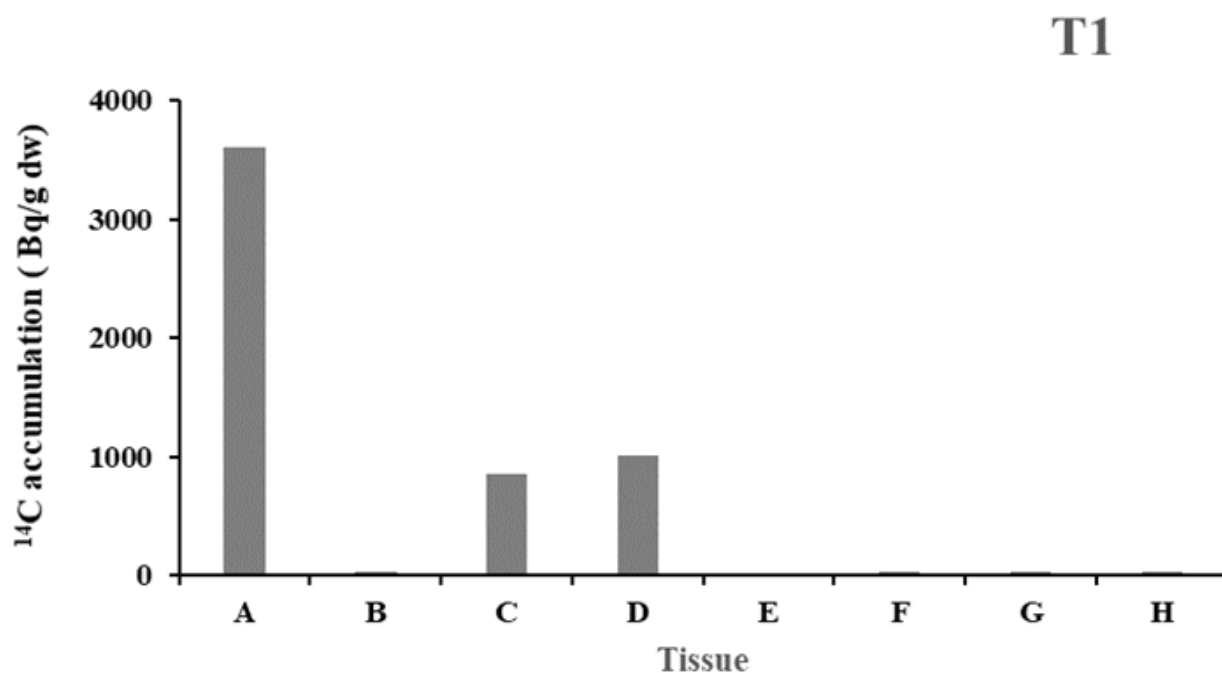
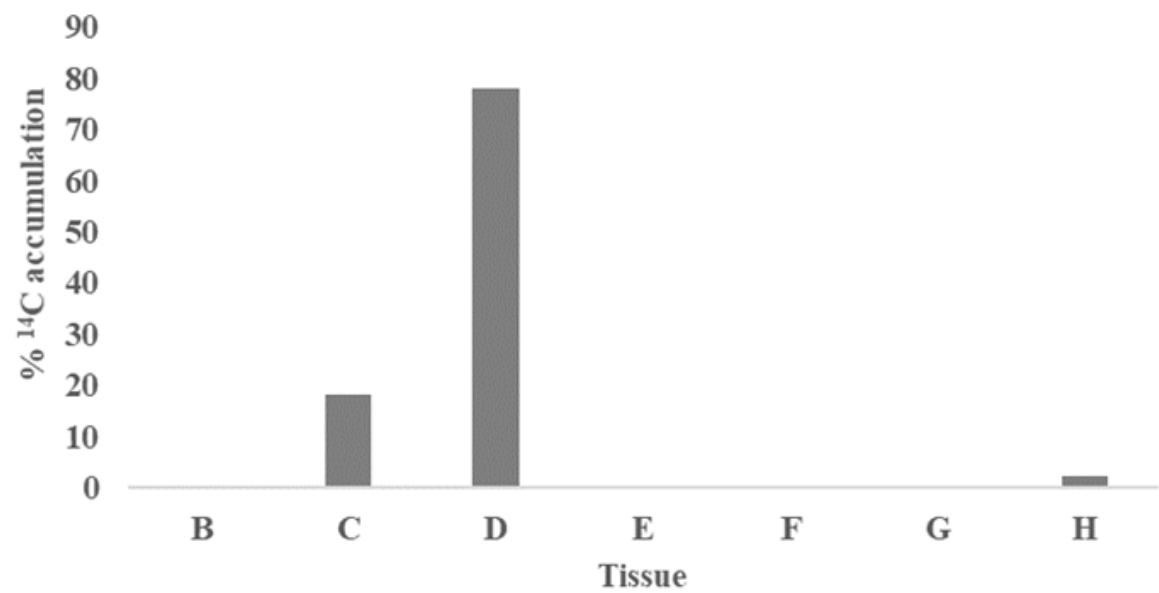


Figure 2

Partitioning of ¹⁴C tracer from the labelled source leaves on the branch X1 towards the unlabelled leaves and the fruits under the T1 (Fruits on both X1 and X2 branches) and T2 (fruit on only X2). T1: A: Labelled leaves, B: Unlabelled leaves on labelled branch, C: Shoot of labelled branch, D: Fruit on labelled branch, E: Leaves on unlabelled branch above the fruit at proximal end of shoot, F: Leaves on unlabelled branch below the fruit at distal end of shoot, G: Shoot of unlabelled branch, H: Fruit on unlabelled branch;

T2: I: Labelled leaves, J: Unlabelled leaves on labelled branch, K: Shoot of labelled branch, L: Leaves on unlabelled branch above the fruit at proximal end of shoot, M: Leaves on unlabelled branch below the fruit at distal end of shoot, N: Shoot of unlabelled branch, O: Fruit on unlabelled branch

T1



T2

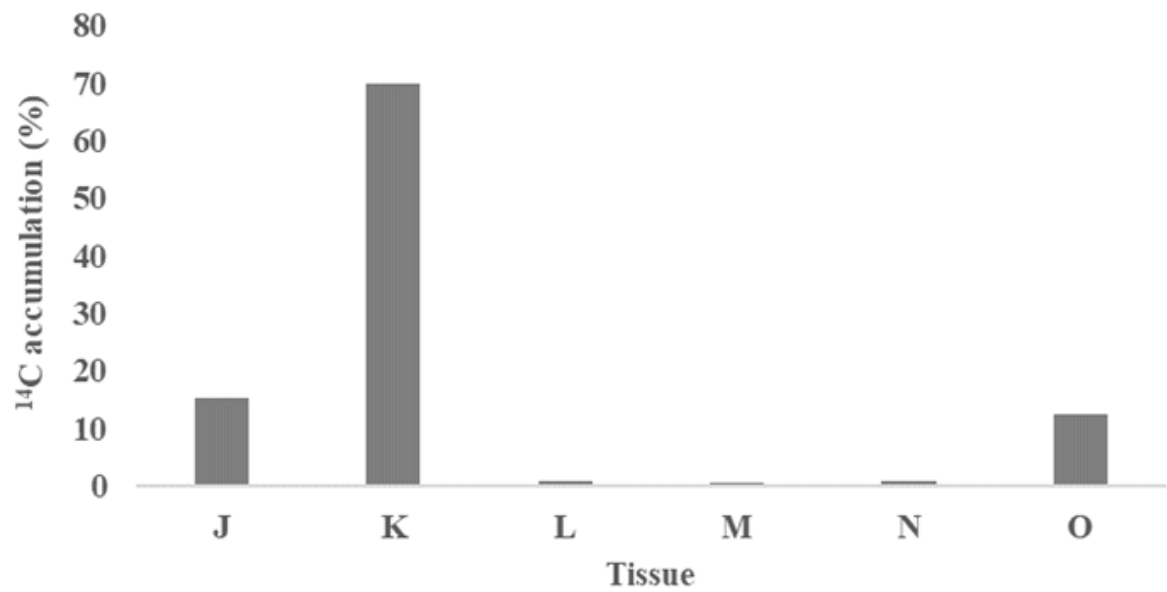


Figure 3

Relative accumulation of carbon (^{14}C) between the source (leaves) and sink tissues (Fruit and stem), excluding the amount of radioactivity accumulated in the labelled leaves on branch X1 i.e., tissue code A

and I respectively under T1 and T2. T1: B: Unlabelled leaves on labelled branch, C: Shoot of labelled branch, D: Fruit on labelled branch, E: Leaves on unlabelled branch above the fruit at proximal end of shoot, F: Leaves on unlabelled branch below the fruit at distal end of shoot, G: Shoot of unlabelled branch, H: Fruit on unlabelled branch; T2: J: Unlabelled leaves on labelled branch, K: Shoot of labelled branch, L: Leaves on unlabelled branch above the fruit at proximal end of shoot, M: Leaves on unlabelled branch below the fruit at distal end of shoot, N: Shoot of unlabelled branch, O: Fruit on unlabelled branch.