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BRIEF COMMUNICATION

Retention and allocation of ^{14}C assimilates by maintenance leaves and harvest index of tea (*Camellia sinensis* L.)

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Abstract

Partitioning of ^{14}C-labelled photosynthates to various parts of un-pruned tea clones TV1 and TV25 was assessed in *vivo* by exposing maintenance leaves to $^{14}CO_2$ at monthly intervals throughout the year. The plants from shoot apex to root tip were divided into twelve components to assess the allocation and retention of ^{14}C-photosynthates by the maintenance foliage. Out of the total photosynthates produced by the maintenance leaves, only 11.08 % was allocated to the commercially useful harvestable two and a bud shoots which is accepted as the harvest index of tea. The photosynthetically active maintenance leaves retained 19.05 % while 24.56 % was distributed to the branches. The bottom and the top parts of the trunk utilized 7.44 and 7.21 %, respectively. The thick roots at the base of the trunk, medium sized roots, pencil size roots, and feeder roots imported 7.28, 7.72, 7.65, and 8.01 % of ^{14}C assimilates, respectively. Except retention by leaves, all the plant parts of vigorous clone TV25 required higher percentage of assimilates than TV1. The mean quantities of net photosynthates utilized by the stem and the roots were 69.37 and 30.63 %, respectively.

Additional key words: clone differences; roots; shoot; translocation.

Partitioning and translocation of ^{14}C assimilates from mature leaves of plant canopy are well documented in various commercially important food species (Daie 1985, Yen and Koch 1990). Translocated saccharides are produced primarily in mature leaves and utilized in unfolded young leaves (Davis and Loescher 1990).

The photosynthetic efficiency of young expanding leaves of tea develops gradually and they do not become fully efficient until they have grown to more than half of their final size (Barua 1953, 1964). The mature leaves which are left permanently on the tea bush for the production and supply of saccharides to various sinks are known as maintenance leaves (source leaves). Saccharides manufactured by the maintenance leaves are utilized not only for the production of young harvestable shoots for making the tea of commerce but also by different organs of tea plant to keep them functional (Barua 1989).

Tea is a C_3 plant (Roberts and Keys 1978) and its photosynthetic efficiency *in vitro* has been reported by Barua (1953, 1960), Squire (1977), and Roberts and Keys (1978), and *in vivo* by Manivel and Hussain (1982), Barman *et al*. (1993), Gaic *et al*. (1993), Smith *et al*. (1994), Raj Kumar *et al*. (1998), and Mohotti and Lawlor (2002). The tea of commerce is made from the tender shoots consisting of a growing un-open apical bud with two young leaves below, *i.e*. ‘two and a bud shoot’. The young leaves of two and a bud shoots are photosynthetically less active (Barua 1953) and their growth depends on the saccharides that are translocated from the maintenance leaves (Barman *et al*. 1992). Pertaining to the nature of growth and development of various tissues, leaf photosynthates are allocated to various sinks. The actively growing buds of tea are strong sinks (Manivel and Hussain 1986, Barman *et al*. 1990). However, mature tissues of other organs also require certain quantities of photosynthates to maintain and perform the various functions. Information on quantities of assimilates partitioned towards various plant parts are lacking in a leafy beverage crop like tea.

Harvest index of tea was determined carefully in different tea growing areas by applying long and tedious techniques (Barua 1981, Murty and Sharma 1986,

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Burgess and Carr 1996). We attempted to quantify the monthly allocation and retention of ^{14}C radio-labelled assimilates by the maintenance leaves to various organs and to reassess the harvest index (HI) of tea by applying the radio-tracer technique. It is expected that this new technique will replace the traditional method of HI determination and will help the tea research institutes of other regions to determine the HI of tea easily and accurately.

Tocklai experimental station (26°47′N, 94°12′E, 96.5 m a.s.l.) is situated in the south bank of the river Brahmaputra in the state of Assam (India). The location has distinct winter and summer seasons. The monthly mean air temperature of the locality is 22.4 °C (max) and 9.4 °C (min). Around 95 % of the total rainfall of the year (2 305 mm) is received during the cropping season from March to October. Photosynthetically active radiation (PAR) in clear weather during the main cropping season from March to November is 1 430 µmol m^{-2} s^{-1} and during dormant season (winter) from December to February it is 772 µmol m^{-2} s^{-1}. Under Tocklai condition harvesting of tea begins in March and continues till November. There is practically no harvest during the winter months (December–February). The experimental area contains sandy loam soil of pH 4.9.

Distribution of ^{14}C-labelled assimilates (saccharides) from the mature maintenance leaves to various sinks was quantified monthly in twelve different parts of the plant. TV1, a standard clone, and TV25, a yield clone, both 12-years-old were selected for the trial. Planting pattern was a staggered double hedge at 110×75×60 cm spacing. After establishment in the field, the young tea plants were de-centred at the height of 20 cm from the ground to produce spreading frames. In mature tea, the trunk up to a height of 10 cm from the ground was considered as basal part and the next 10 cm above it as the top part of the trunk. The bushes were kept un-pruned during the year of experimentation and manured 100 : 50 : 100 kg(NPK) ha^{-1} y^{-1}. Three selected bushes were pulse labelled in the third week of each month with $^{14}CO_2$ and covered under a large transparent air proof polyethylene bag of 200 gauge thickness. Its bottom was tied carefully with the collar of the tea bush so that no inside air diffused out. Special arrangement was made to keep a watch glass in the middle position of the leaf canopy where 3.7 MBq of $NaH^{14}CO_3$ was kept. To evolve $^{14}CO_2$ gas, 4–5 drops of 1 M HCl was added to the $NaH^{14}CO_3$ by a syringe and the piercing point was sealed immediately with a *Scotch* tape. After one-hour pulse of $^{14}CO_2$, 5–6 drops of saturated KOH was added to the $NaH^{14}CO_3$ to stop the reaction. The piercing point was sealed as before. After one hour, the bag was removed followed by a chase period of 24 h (12/12 h light/dark) in ambient air. The exposed plants of TV1 and TV25 were then uprooted carefully. Irrespective of size, all kinds of roots were collected and soil was removed by washing in tap water. The plants were then separated into twelve different components, see Fig. 1. To stop the metabolic activities, the materials were transferred immediately to a hot air oven kept at 60 °C. After 72 h, the twelve different portions of the plants were powdered separately in a *Wiley Mill* and sieved through 40-size mesh. From each sample, 10 mg of radioactive powder was weighed out and kept in a scintillation vial to which 100 mg of *cab-o-sil* (silica powder) were added and mixed well with the radioactive sample. Scintillation cocktail (10 cm^3) was added to each vial. The cocktail was prepared by mixing 140 cm^3 2-ethoxyethanol (*Cellosolve*), 5.0 g of 2,5-diphenyloxazole (PPO), 0.5 g of 2,2-phenylene-bis-5-phenyloxazole (POPOP), and 40 g of naphthalene to 860 cm^3 of 1,4-dioxane to make 1 000 cm^3 of solution. The cocktail was shaken well to make the solution homogeneous. In the radio tracer laboratory at Tocklai, the activity of ^{14}C present in the individual sample was counted in a Liquid Scintillation Counter (model *LKB 1215 RACKBETA II*) and all counts were converted into Bq. The % of translocated assimilates were calculated monthly by applying the formula given below. Mean values of twelve months are presented. The % of assimilates recorded in the economically useful young shoots for making tea of commerce was considered as HI of tea,

$$\Delta = (\lambda/\phi) \times 100$$

where Δ = % assimilate, λ = ^{14}C activity [Bq] of the individual organs, and ϕ = total ^{14}C activity in twelve parts [Bq].

The economically useful two and a bud shoots of clone TV1 and TV25 imported 10.79 and 11.36 % of total photosynthates annually from the source leaves (Figs. 1 and 2). Partitioning of labelled assimilates towards two and a bud shoots varied significantly (p<0.001) between months while no significant variation was observed between the two clones. On an average 11.08 % of total photosynthates was allocated to the pluckable shoot (Fig. 2*B*) which was estimated as the HI of tea.

The maintenance leaves of clones TV1 and TV25 within top 10 cm depth of the bush frame retained 12.21 and 7.32 % assimilates while rest of the leaves below retained 11.47 and 7.10 %, respectively (Fig. 1). The mean retention of assimilates by the maintenance leaves as a whole were 23.68 and 14.42 % in TV1 and TV25, respectively (Fig. 2*A*). The retention by clone TV1 was significantly higher (p<0.05) as compared to TV25. The mean monthly photosynthate retention by the total maintenance foliage of the two clones was 19.05 % (Fig. 2*B*).

The ^{14}C labelled saccharide allocation to the branches of three positions was insignificant but the allocation declined gradually from tender to older branches (Fig. 1). The average allocation for the three positions of TV1 and TV25 was 7.87 and 8.46 %, respectively. The total annual allocation of saccharides to the branches of clones TV1 and TV25 was 23.72 and 24.38 %, respectively (Fig. 2*A*).

Thus mean saccharides' allocation to the branches was 24.05 % (Fig. 2*B*).

There was no significant difference in annual saccharide allocation between the top and bottom part of the trunk (Fig. 1). The monthly requirement of saccharides for this region was almost uniform throughout the year. However, TV25 being a yield clone demanded significantly more (p<0.01) assimilates than TV1. The annual saccharide allocation for the trunk of TV1 and TV25 in totality was 13.00 and 16.31 % per annum, respectively (Fig. 2*A*). Trunk bearing heavier frame (TV25) required more saccharides than the lighter one (TV1). The mean saccharide import by the tea trunk was 14.66 % (Fig. 2*B*).

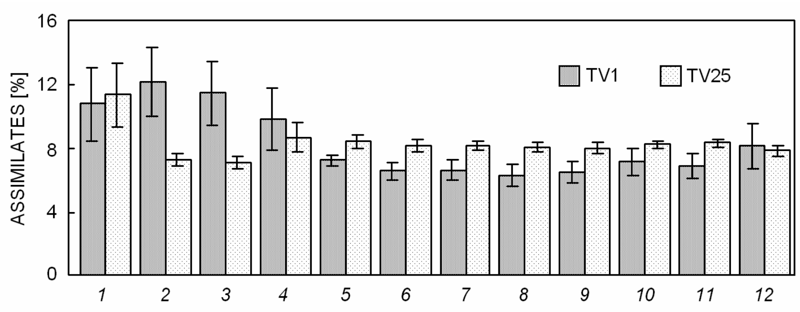

Fig. 1. Retention and allocation of ^{14}C-labelled photosynthates by leaves of different components of clones TV1 and TV25. *1* = Growing two and a bud shoots. *2* = Top 10 cm layer of the maintenance leaves. *3* = All maintenance leaves below the top 10 cm layer. *4* = Top 10 cm of the branch system. *5* = Next 10 cm of the branch system down to 20 cm. *6* = Third layer of branch above the trunk. 7 = Top part of the trunk. *8* = Basal part of the trunk. *9* = 3.60 cm diameter thick roots at the base of the trunk. *10* = 1.75 cm diameter thick medium size roots. *11* = 0.65 cm diameter thick pencil size roots. *12* = 0.15 cm diameter thick feeder roots. *Vertical bars* indicate standard error of means (n = 12).

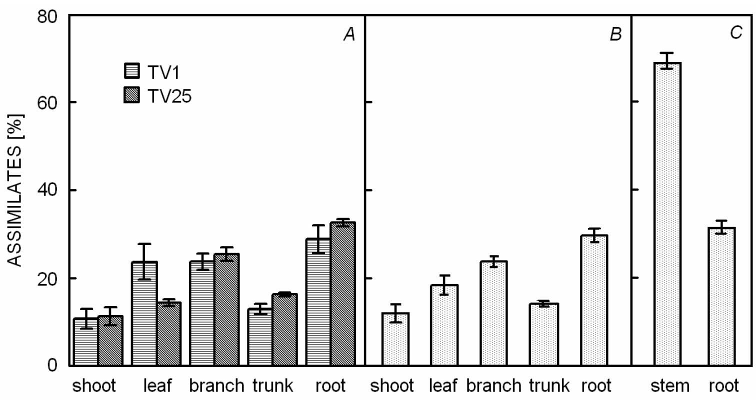

Fig. 2. Annual retention and allocation of ^{14}C-labelled assimilates by leaves to different components of (*A*) clones TV1 and TV25, (*B*) means of both clones, and (*C*) towards stem and roots. *Vertical bars* indicate standard error of means (n = 12).

Allocation of labelled saccharides towards the roots of various thickness as well as saccharide import by roots was insignificant. Except feeder roots, all other roots of TV25 consumed more saccharides than TV1 (Fig. 1). The total requirement of saccharides for root growth of TV25 (32.53 %) was higher than that of the clone TV1 (28.80 %, Fig. 2*A*). The mean allocation of saccharides for tea roots was 30.63 % (Fig. 2*C*). Thus the annual saccharide allocation towards stem and root of a tea plant was 69.37 and 30.63 %, respectively (Fig. 2*C*).

A total of 11.36 and 10.79 % ^{14}C assimilates produced by the maintenance leaves were partitioned to the pluckable shoots of the two clones TV25 and TV1. Thus, the average 11.00 % ^{14}C tagged assimilates found in the growing shoots was the HI of tea. Our results generated by this radio-tracer technique coincided with those using the traditional method of dry mass partitioning (Barua 1981, Burgess and Carr 1996). Therefore, this method can be adopted as an easy and reliable technique for determination of HI in tea. In South India, out of total saccharides fixed by the maintenance leaves 15.3 % was allocated towards the growing shoots (Rajkumar 2001) where HI of tea has been reported as high as 16 % (Murty and Sharma 1986). The loss of metabolites through respiration (Tanton 1979, Barua 1981), photorespiration (Roberts and Keys 1978), wasteful drainage of photosynthates through flowers (Barman *et al*. 1990), diversion of metabolites to other parts during winter (Squire 1977), its retention by maintenance leaves (Manivel *et al*. 1981), *etc*. are some of the key factors of low HI in tea. Partitioning of assimilates towards the growing shoots of un-pruned tea significantly (p<0.05) decreased in the back end season. Tea plants grown in North East India remained dormant during the winter season when the minimum night temperature goes below 12 °C and the day length drops below 11.15 h (Das and Barua 1987). This is one of the factors causing lower harvest index of tea in N.E. India than the other tea growing areas of the world where plucking continues throughout the year. Clone TV1 remained totally dormant from December to February but TV25 produced some growth during December when 7.81 % of photosynthates was imported by the shoots. This is an indication of genetic differences between the two clones.

The productivity of tea has a strong correlation with number and area of the maintenance leaves (Barman *et al*. 1991, 1992): the maintenance leaves retained 19.00 % of the labelled carbon in the course of year, the remaining 81.00 % was exported to the other organs, while Burgess and Carr (1996) reported in Kenya retention of 29.00 % of saccharides by the maintenance leaves. This corroborates with the findings of Jiao and Grodzinski (1996) who reported a 60–80 % export of assimilates in *Salvia splendens*. The maintenance leaves of tea retained 63.00 % of ^{14}C saccharides in N.E. India during June and December (Manivel *et al*. 1981), which was 57.00 % of that in Japan during autumn (Hakamata and Sakai 1980). In our study the 65.00 % retention was observed in December by the clone TV1 while the mean of the two clones during the month was 42.69 %. In every month, leaves of clone TV1 retained significantly higher ($p<0.05$) quantities of saccharides as compared to TV25. Hence high yielding clones retained lower amount of saccharides in the maintenance leaves and allocated higher percentage towards the pluckable shoots. It is therefore useful to develop techniques which may force higher mobilization of photosynthates from the source leaves to the pluckable shoots which contribute to the increase of HI of tea.

We found a 7.87 and 8.46 % partitioning of assimilates to branches of clone TV1 and TV25, respectively. Burgess and Carr (1996) also reported 8.00 % dry matter partition to the branches of tea in Kenya. The total requirement of saccharides for the trunk of each clone was 14.66 %. This corroborates with Wang *et al*. (1995) who reported a 15.70 % ^{14}C-assimilate translocation to the stem in *Gossypium hirsutum*. These correlations between dry matter and ^{14}C assimilate partitioning confirm the usefulness of radio-tracer technique for quick and accurate analysis of saccharide partitioning.

The mean partitioning of assimilates towards four different sizes of roots of clones TV1 and TV25 was 6.88 and 8.22 %, respectively. The requirement of photosynthates for the entire root system of a clone was 30.66 %. Burgess and Carr (1996) reported 23–29 % partitioning of dry matter towards the thick roots. Summing up, the annual budgets of photosynthates for the aerial and underground parts of tea clones were 69.37 and 30.63 % (Fig. 2*C*) and their ratio became 2.26 : 1.00. Due to variation in the agro-climatic conditions, cultural practices and geographical locations of the tea growing areas of the world, the retention and allocation of assimilates from the maintenance leaves may differ resulting in variation of HI in different countries.

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