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Effect of Sector (Position in Canopy) on Allocation of ^{13}C-photosynthates in Mangosteen

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ABSTRACT

We investigated the effect of sector (position in canopy) on translocation and distribution of ^{13}C-photosynthates in mangosteen trees and related the findings to previous analyses of fruit quality. Our experiment was conducted on three 25-year-old mangosteen trees. Tree canopies were divided into 9 sectors based on height (bottom, middle, top) and width (inner, center, outer). One branch from each sector was labeled with $^{13}CO_2$ in December 2003. Immediately after labeling, ^{13}C concentration in leaves from middle sectors was higher than that in leaves from other positions. ^{13}C concentration in all leaves decreased rapidly for 24 h after ^{13}C feeding, followed by a gradual decrease. In contrast, ^{13}C concentration increased over time in the pericarp and aril of fruits. Translocation of ^{13}C-photosynthates into fruit was high in Sectors 4 and 5, and in top positions (Sectors 7 to 9). At 96 h after ^{13}C feeding, the highest distribution ratio of ^{13}C-photosynthates was observed in stems, followed in descending order by pericarp, leaf, and aril. ^{13}C distribution ratio in the aril was generally highest in fruits from inner and center positions. The relationship between partitioning of photosynthates and quality of mangosteen fruit, which differs among sectors, has been discussed.

Keywords: fruiting positions, Garcinia mangostana L., photosynthate partitioning, ^{13}C, tree branches

ABSTRAK

Tujuan penelitian adalah mengetahui pengaruh dari sektor (posisi buah pada kanopi) pada translokasi dan distribusi ^{13}C-fotosintat pada tanaman manggis, terkait dengan temuan sebelumnya tentang analisis kualitas buah. Penelitian dilakukan dengan menggunakan tiga pohon manggis umur 25-tahun. Kanopi pohon dibagi menjadi 9 sektor berdasarkan tinggi (bawah, tengah, dan atas) dan lebar (bagian dalam, tengah, dan luar). Setiap cabang dari masing-masing sektor diberi label dengan $^{13}CO_2$ pada Desember 2003. Sesaat setelah pelabelan, konsentrasi ^{13}C pada daun dari sektor tengah lebih tinggi daripada sektor lainnya. Konsentrasi ^{13}C pada semua daun menurun dengan cepat dalam 24 jam setelah diberi ^{13}C, diikuti oleh penurunan bertahap. Sebaliknya, konsentrasi ^{13}C pada buah (pericarp dan aril) meningkat dari waktu ke waktu. Translokasi ^{13}C-fotosintat tertinggi ke buah terjadi pada Sektor 4 dan 5, serta pada posisi atas (Sektor 7 sampai 9). Pada 96 jam setelah diberi ^{13}C, rasio distribusi ^{13}C-fotosintat tertinggi terjadi pada batang, diikuti oleh pericarp, daun, dan aril. Distribusi rasio ^{13}C ke aril itu umumnya tertinggi dalam buah-buahan yang berasal dari sektor dalam dan tengah. Hubungan antara pembagian fotosintat dan kualitas buah manggis yang berbeda antar sektor, telah dibahas.

Kata kunci: cabang pohon, Garcinia mangostana L., pembagian fotosintat, posisi berbuah, ^{13}C

INTRODUCTION

The quality of fruit produced by mangosteen trees (*Garcinia mangostana* L.) varies markedly among individual trees, and according to season and growing conditions (Nakasone and Paull, 1998; Malip and Masri, 2006; Apiratikorn *et al.,* 2012). The commercial quality of mangosteen fruit is evaluated according to the following criteria: size and weight (Diczbalis, 2009), scarring of skin surface due to thrip infestation or other damage (Affandi and Emilda, 2010), and sugar and acid content of the aril (Chaisrichonlathan and Noomhorm, 2011). Some researchers report that the highest quality mangosteen fruit is borne on branches close to the trunk, or on internal branches that are not exposed to direct sunlight (Yaacob and Subhadrabandhu, 1995; Nakasone and Paull, 1998; Setiawan and Poerwanto, 2008). We have previously reported that the quality of mangosteen fruit varies substantially among bearing positions in tree canopy (Setiawan *et al.,* 2006). Moreover, we found that the quality of mangosteen fruit borne on Sectors 1, 2, 4, and 5 was higher than that of fruit in Sectors 3, 6, 7, and 8, in terms of size, occurrence of scars, and sugar content of the aril (unpublished data).

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For many species of fruit trees, size and sugar content of fruit are largely affected by partitioning of photosynthates (Kubota *et al.,* 1990; Teng *et al.,* 1999; Yamamoto, 2001). Numerous studies have examined the translocation and distribution of ^{13}C-photosynthates in temperate fruit trees, including peach, grape, and pear (Kubota *et al.,* 1990; Teng *et al.,* 1998; Ono *et al.*, 2000). Carbon assimilation and allocation in different plant organs varies with plant species, phenology, and growing conditions (Ge *et al.*, 2012). An important outcome of understanding photosynthate allocation within fruit tree species would be improved pruning practices that could lead to increased fruit yield (Yamamoto, 2001). Judging from the facts mentioned above, different fruit quality of mangosteen among sectors (fruiting positions in canopy) may be caused by different allocation of photosynthates. The objectives of this study were to determine how partitioning of ^{13}C-photosynthates in branches of mangosteen varied by sector, and how this partitioning related to fruit quality.

MATERIALS AND METHODS

Plant Materials

Our experiment was conducted on three 25-year-old mangosteen trees (*Garcinia mangostana* L.) grown in a commercial orchard in Bogor, Indonesia. The canopy of each tree was divided into 9 sectors based on tree height (bottom, middle, top) and width (inner, center, outer), as follows: Sector 1 = inner bottom, Sector 2 = center bottom, Sector 3 = outer bottom, Sector 4 = inner middle, Sector 5 = center middle, Sector 6 = outer middle, Sector 7 = inner top, Sector 8 = center top, and Sector 9 = outer top (Figure 1). A lateral branch of moderate size (ca. 120 cm in length) bearing approximately 5 fruits was selected from each sector for $^{13}CO_2$ feeding. The experimental was set up a randomized complete block design (RCBD) in three replications with one tree per replicate.

Feeding and Analysis of ^{13}C

Pulse-labeling was conducted by enclosing each branch in a transparent plastic bag (120 cm × 120 cm), and exposing it to $^{13}CO_2$ for 1 h. The $^{13}CO_2$ label was made by reacting 1.5 g $Ba^{13}CO_3$ (99 atom % ^{13}C) with 50% lactic acid. $^{13}CO_2$ feeding was repeated 2 times for each branch and was carried out on the mornings of December 12 or 13, 2003, which corresponded to approximately 1 month before harvesting stage. At 0 and 48 h after $^{13}CO_2$ feeding, 2 leaves and 1 fruit were collected from each branch and washed with tap water, and the fruits were separated into pericarp and aril. At 96 h after feeding, all lateral branches fed with $^{13}CO_2$ were removed from the secondary scaffold limb and were separated into stem, leaf, and fruit (receptacle and pedicel, pericarp, and aril). All samples were dried in an oven at 70°C for 4 days, and ground to a fine powder with a mill. Concentration of ^{13}C in each sample was determined using CN Corder (MT-700MC; Yanaco, Tokyo), attached mass spectrometry (MSI-150-MT-600NC; Yanaco). ^{13}C atom % excess was calculated using a previously published

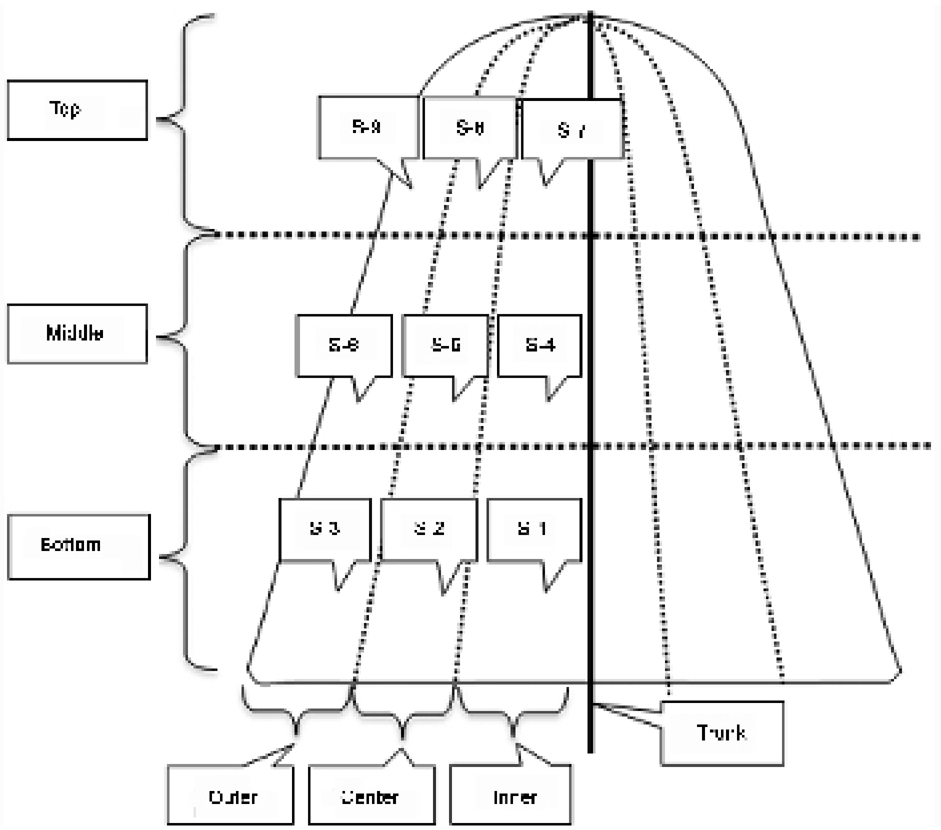

Figure 1. Illustration of the sectors (positions in the canopy, S-1 to S-9) defined for study of mangosteen trees

Table 1. Translocation of ^{13}C-photosynthates in mangosteen trees as affected by sectors (position in canopy)

Organ / Tissue	Sector	C (%)	Dry weight (g)	^{13}C % of total amount of ^{13}C applied	Amount of ^{13}C (mg)
Aril	1	27.9	3.6	0.129	1.3
	2	28.6	2.5	0.105	0.8
	3	29.2	3.5	0.118	1.2
	4	31.7	4.5	0.122	1.8
	5	30.3	4.5	0.118	1.6
	6	32.2	2.5	0.110	0.9
	7	33.4	3.7	0.103	1.3
	8	28.3	4.4	0.113	1.4
	9	28.8	4.2	0.118	1.4
Pericarp	1	25.6	30.6	0.093	7.3
	2	26.3	36.3	0.069	6.6
	3	26.3	57.3	0.097	14.6
	4	24.4	61.4	0.110	16.4
	5	24.9	51.3	0.139	17.8
	6	25.3	59.3	0.095	14.2
	7	24.4	45.7	0.156	17.4
	8	25.3	55.8	0.138	19.5
	9	23.1	58.3	0.130	17.4
Receptacle and pedicel	1	29.0	3.2	0.091	0.9
	2	28.2	3.0	0.071	0.6
	3	29.2	5.2	0.060	0.9
	4	28.7	3.8	0.063	0.7
	5	28.4	3.8	0.040	0.4
	6	27.5	4.3	0.040	0.5
	7	29.2	3.8	0.064	0.7
	8	29.3	4.1	0.064	0.8
	9	29.4	5.0	0.061	0.9
Leaf	1	29.6	21.7	0.076	4.9
	2	29.7	18.5	0.085	4.7
	3	29.9	19.8	0.065	3.9
	4	28.3	21.4	0.132	8.0
	5	28.7	19.2	0.079	4.3
	6	28.8	22.5	0.055	3.6
	7	28.4	21.2	0.037	2.2
	8	28.8	22.5	0.070	4.5
	9	28.3	21.9	0.059	3.7
Stem	1	29.5	55.5	0.093	15.2
	2	30.7	45.3	0.097	13.5
	3	30.4	98.6	0.101	30.2
	4	30.2	67.3	0.126	25.5
	5	29.8	65.7	0.138	27.1
	6	30.4	74.6	0.068	15.4
	7	30.1	57.0	0.128	21.9
	8	29.9	86.5	0.119	30.9
	9	29.4	99.4	0.131	38.4

Note: Samples were taken at 96 h after $^{13}CO_2$ feeding method (Kubota *et al.,* 1990). Translocation and distribution of ^{13}C-photosynthates to lateral branches and fruits were compared among sectors.

Statistical Analysis

A one-way analysis of variance was performed to examine whether there were significant differences in photosynthate allocation among sectors. Means were compared using Duncan's multiple range test. All statistical tests were carried out using SPSS version 16.0 (IBM SPSS Inc., Chicago) and differences with p-values less than 0.05 were considered significant.

RESULTS AND DISCUSSION

Changes in ^{13}C concentration of leaf, pericarp, and aril in each sector of mangosteen are shown in Figure 2. At the end of $^{13}CO_2$ feeding, leaves in Sectors 4 and 5 contained more labeled ^{13}C than leaves of other sectors. This may suggest that photosynthetic activity of leaves in Sectors 4 and 5 is higher than that of other sectors; however, we do not have an explanation for this phenomenon. In all sectors, ^{13}C concentration in leaves decreased rapidly within 24 h after feeding, followed by a gradual decrease. Leaves in the upper part of the canopy (e.g., Sectors 5 to 9) showed a larger decline of ^{13}C concentration than did leaves lower in the canopy (e.g., Sectors 1 to 4). At 0 and 48 h after feeding, ^{13}C atom % excess in leaves was higher in Sectors 4 and 5 than in leaves of other sectors. ^{13}C concentration in fruit (pericarp and aril) increased with time after ^{13}C feeding, but there was no significant difference among sectors. Our results coincide with the findings for peach and grape plants, in which ^{13}C concentration decreases in leaves and increases in fruits with time after $^{13}CO_2$ labeling (Kubota *et al.,* 1990; Ono *et al.,* 2000). It is apparent that ^{13}C-photosynthates exported from leaves of mangosteen were translocated into fruits. ^{13}C concentration in the aril was higher than that of the pericarp in Sectors 1, 2, 3, 4, and 6, while in Sectors 5, 7, 8, and 9 the opposite was true. Teng *et al.* (1999) reported that the highest concentration of ^{13}C in Japanese pear one week after labeling was found in folded leaves, followed in descending order by the upper parts of extension shoots, unfolded leaves, fruits, and lower parts of extension shoots.

In this experiment, a greater amount of ^{13}C-photosynthates was translocated into fruits (pericarp and aril) in Sectors 8, 5, 9, 7 and 4 than in Sectors 2 and 1 (Table 1). This may suggest that translocation of photosynthates is reduced in lower, inner positions of mangosteen tree, possibly because of shading or competition with another strong sink organs such as the shoot apex. We have previously reported that carbohydrate levels (in terms of dry weight) in leaves of old mangosteen trees increased at one month before harvesting (Setiawan *et al.*, 2012). Moon *et al.*

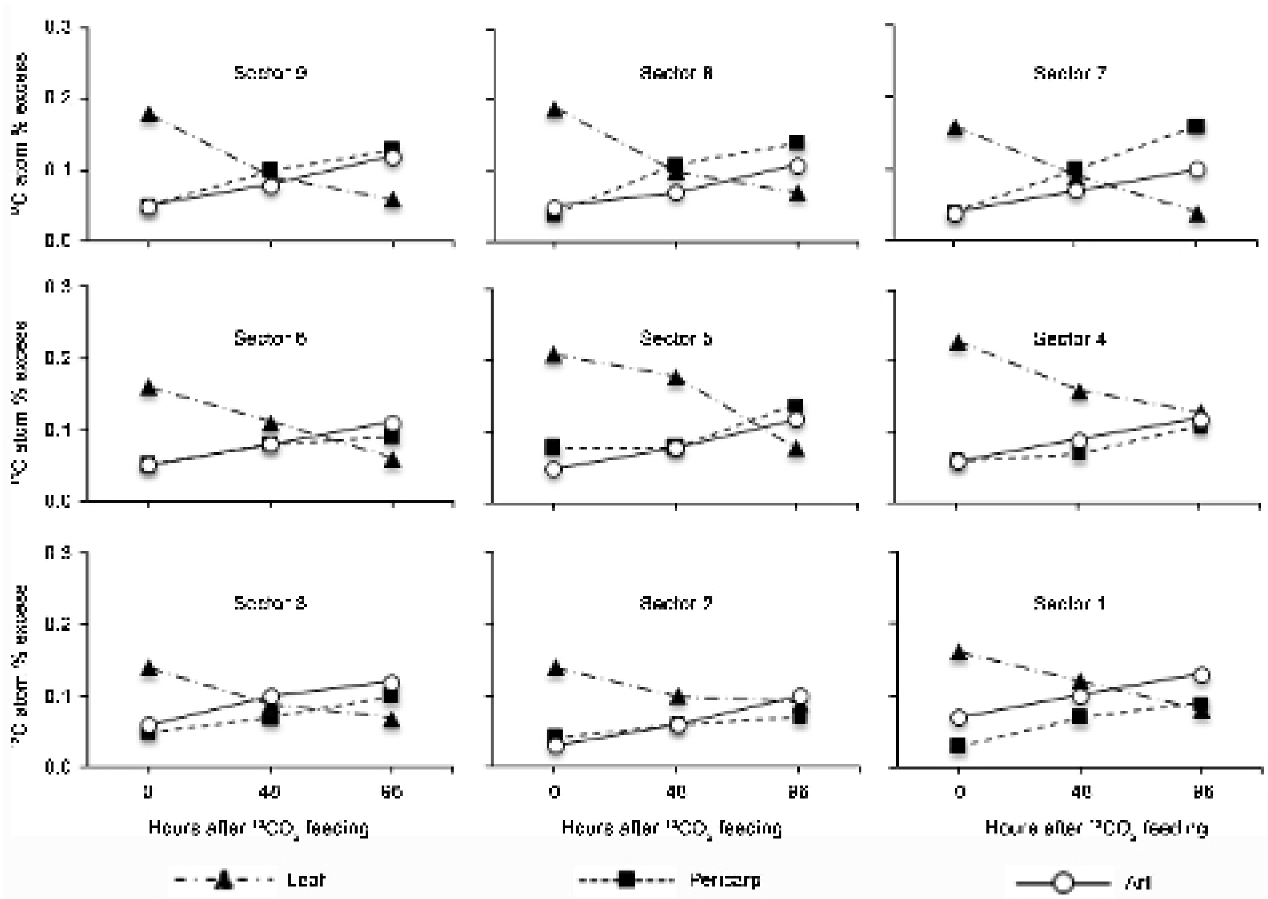

Figure 2. Changes in ^{13}C concentration of leaves, pericarp, and aril of mangosteen as affected by sectors (positions in canopy). Error bars indicate ± SE (n = 3)

(2011) have reported that the diameter and weight of fruit and weight and thickness of pulp in citrus were higher in fruits harvested from upper parts of the tree canopy than in the middle and lower portions.

The partitioning calculated from ^{13}C measurements indicates the ratio of carbon translocated to each organ to total carbon fixed by photosynthesis (Sasaki *et al.*, 2005). At 96 h after $^{13}CO_2$ feeding, the highest distribution ratio of ^{13}C-photosynthates was observed in stems, followed in descending order by pericarp, leaf, aril, and receptacle and pedicel for all sectors (Table 2). This is in contrast to the results observed in peach (Kubota *et al.,* 1990) and grape (Ono *et al.,* 2000) plants, in which more than half of the measured photosynthate was allocated to fruits or berries. These differences in experimental results may be due to the different xylem volumes of stems, limbs, and trunks in tropical and temperate fruit trees. Although the distribution ratio in arils was small (<5% for all sectors), the highest ratio was observed in Sector 1, followed in order by Sectors 4, 2, 5, and 7 with minimal $^{13}CO_2$ translocated to arils in Sectors 3, 9, 8, and 6 (Table 2 and Figure 3). We previously found that the quality of mangosteen fruit in terms of size and sugar content was higher in Sectors 1, 2, 4, and 5 than in Sectors 3, 6, 7, and 8 (unpublished data). The results presented here suggest that higher quality of mangosteen fruit in Sectors 1, 2, 4, and 5 could be due to greater allocation of photosynthate into fruits. It has been reported that the highest quality fruits of mangosteen are produced on branches close to the trunk or hidden below the canopy (Yaacob and Subhadrabandhu, 1995; Nakasone and Paull, 1998). Amano *et al.* (1998) showed that shoot elongation during growth of kiwi fruit adversely affects the distribution of photosynthates into fruit. Exported assimilates are partitioned among sink organs, including shoots, stems, and fruits, and can be accumulated in the aril as sugar, starch, or proteins (Gifford and Evans, 1981). Teng *et al.* (1998)

Table 2. Distribution ratio of ^{13}C-photosynthates in mangosteen branches as affected by sectors (positions in canopy)

Sector	Distribution ratio of ^{13}C-photosynthates (%)					
	Aril	Pericarp	Receptacle and pedicel	Leaf	Stem	Total
1	4.4a^{z}	24.7d	2.9a	16.7a	51.3bcd	100
2	3.0ab	25.3d	2.3b	18.0a	51.5bcd	100
3	2.4b	28.8cd	1.8bc	7.7bc	59.4ab	100
4	3.4ab	31.4bc	1.3cd	15.3a	48.6cd	100
5	3.2ab	34.7b	0.8d	8.5bc	52.8bcd	100
6	2.5b	41.5a	1.4c	10.4b	44.2d	100
7	3.0ab	40.1a	1.6c	5.2c	50.1cd	100
8	2.5b	34.2b	1.3cd	8.0bc	54.0bc	100
9	2.3b	28.3cd	1.5c	5.9c	62.0a	100

Note: ^{z} value with different letters in each column indicate significant difference among sectors by Duncan's Multiple Range Test, $p<0.05$

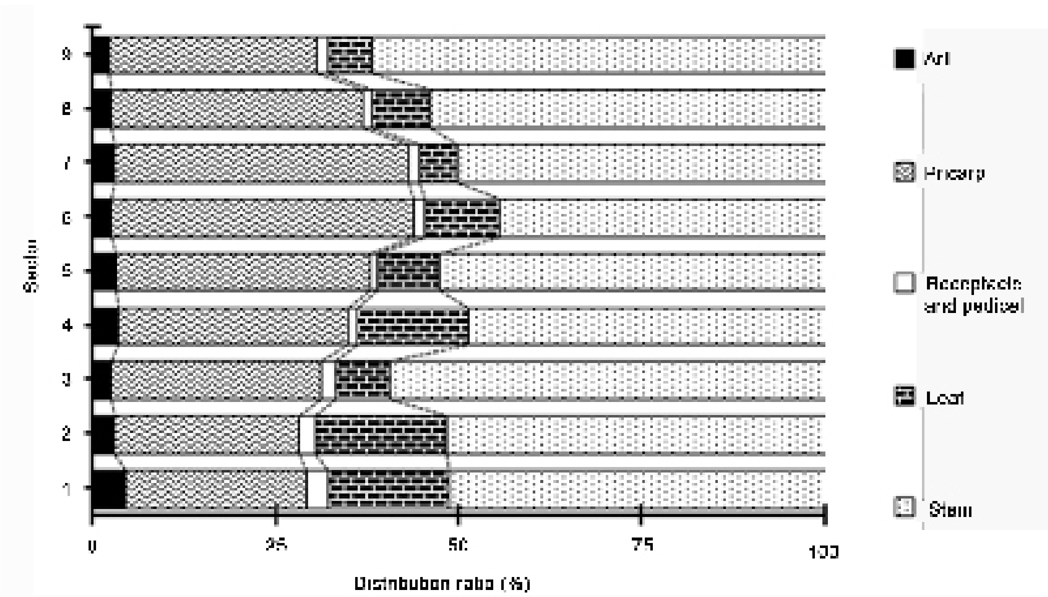

Figure 3. Distribution ratio of ^{13}C-photosynthates in mangosteen branches based on Table 2

reported that ^{13}C-photosynthates in Japanese pear were exported from spur leaves within 24 h of feeding, but that translocation into fruit decreased with age of spur leaves.

Compared to other organs and tissues, receptacles and pedicels of mangosteen fruit displayed low ^{13}C-photosynthate distribution ratios (Table 2). Receptacles and pedicels from Sectors 1 and 2 produced the highest distribution ratio of ^{13}C-photosynthates for these tissues; this was consistent with the greater aril size in Sectors 1 and 2. Zhang *et al.* (2005*a*) reported that the application of growth hormone GA_{3+4} to Japanese pear during the period of rapid fruit growth resulted in a marked increase in pedicel diameter and fruit size at harvest. These researchers maintained that fruit growth in Japanese pear is dependent upon the supply of assimilates from leaves (leaf area and photosynthetic ability) and the sink capacity of fruit (number, size, and duration of growth) (Zhang *et al.,* 2005*b*).

CONCLUSION

Regardless of sector, ^{13}C concentration in leaves of mangosteen decreased with time after feeding, whereas ^{13}C concentration increased in the pericarp and aril of mangosteen fruit, demonstrating translocation of photosynthates into the fruits from leaves. At 96 h after $^{13}CO_2$ feeding, the highest distribution ratio of ^{13}C-photosynthates was observed in stems, followed in decreasing order by pericarp, leaf, aril, and receptacle and pedicel. Although the distribution ratio was low overall, the ratio in arils was highest in fruits from Sectors 1, 4, 2, 5, and 7; this finding was consistent with those of previous studies that found superior quality of fruit produced in these sectors. Further investigation is needed to clarify the relationship between fruit quality and partitioning of photosynthates in mangosteen, especially for difference of sugar accumulation in fruit among sectors.

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