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Distribution Pattern of Photosynthetic Assimilates as Affected by Phyllotaxis and Vascular System in Tomato Plants

Yoshihiro SHISHIDO
Morioka Branch, National Research Institute of Vegetables, Ornamental Plants and Tea
(Shimokuriyagawa, Morioka, Iwate, 020-01 Japan)

Abstract

Some studies were undertaken to identify the association of distribution pattern of photosynthetic assimilates with the phyllotaxis and vascular system in tomato plants. The vascular system of tomato consisted basically of four orthostichies with two vascular bundles from each leaf. It was clearly observed that the arrangement of the vascular system affected a distribution pattern of ^{14}C-assimilates. The source leaves exported only a smaller portion of their assimilates to young leaves located on the opposite orthostichy to them, as compared with those on the same as well as side orthostichies. Since tomato plants have a sympodial branching system, the leaf which was situated just above the inflorescence differentiated in advance to the inflorescence. The vascular bundles of the leaf in a sympodial branch near inflorescence developed in the location between the inflorescence and the leaf just above it. This vascular pattern cause a limited distribution of photosynthetic assimilates to the inflorescence from the leaf just above it.

Discipline: Horticulture
Additional key words: ^{14}C-assimilates, sink, source, sympodial branch, translocation

Introduction

The studies on translocation and distribution of photosynthetic assimilates in tomato plants, which were earlier undertaken by the author and his group, indicated that there existed a special inclination in the distribution pattern of assimilates between source leaves and sinks, and that the inclination was not disordered but primarily dependent upon their positional relationships on a stem[4,6].

In regard to the phyllotaxis of tomato plants, Lehmann[3] described that the leaves developed alternately with a 2/5 phyllotaxis. Usugami[7], however, demonstrated four orthostichies of phyllotaxis in tomato plants, which showed a combined divergence of 90° and 180°.

According to the study results obtained by the author[4], variations in the distribution pattern of photosynthetic assimilates showed a high correlation with the positions of leaves specified on the basis of four orthostichies. Therefore, the arrangement of vascular system corresponding to the relevant phyllotaxis might affect a pattern of distribution of photosynthetic assimilates.

To identify the phyllotaxis precisely, it is necessary to take some physiological index into account, in addition to the estimation based on external observations. In this context, there is a relevant issue to be revealed yet in tomato plants, which issue relates to the arrangement mechanism in a vascular system that links an inflorescence with the leaf just above it. It is observed that inflorescences develop with divergence of 180° on the opposite side of the respective leaves just above them, and that the distribution of photosynthetic assimilates from those leaves to the inflorescences just below them are lower in general than those from other leaves. Such a distribution pattern of assimilates has not well been explained by the present knowledge on arrangement mechanism in a vascular system.

The present paper accounts for the results of the studies pertaining to the above subjects.

Distribution of photosynthetic assimilates in each of the leaf positions on a stem

Table 1 indicates that in the upper two leaves, a higher percentage of distribution is observed in the uppermost leaf than in the next one, with one exception among the four orthostichies. This is the case in which the upper leaves were situated on the same or side orthostichy in terms of their relative positions to their relevant source leaf. However, when the leaves on the opposite side of orthostichy were included, the distribution to the leaves situated on the opposite side to the source leaf was lower, irrespective of uppermost leaf and next uppermost leaf.

Fig. 1 shows the distribution pattern at the growing stage of fruit thicking. The highest percentage of distribution took place in the first inflorescence, except the case in the 9th and 12th leaves (leaf just above the inflorescence). The 9th leaf of tomato plants under this experiment had a lateral shoot to be grown as the next main stem under a sympodial branching system. It was, in appearance, situated just above its relevant inflorescence. The distribution of assimilates from that 9th leaf to the second inflorescence was higher than that to the first

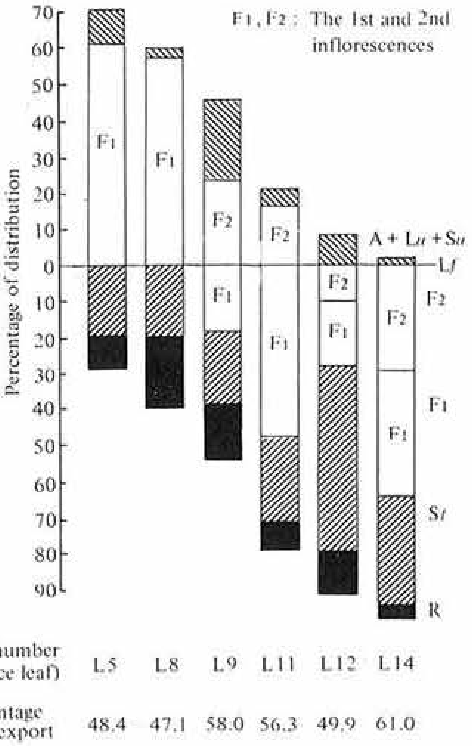

Fig. 1. Distribution pattern of the assimilates as affected by phyllotaxis
Ll: Basal leaf, A: Apex,
L*f*: Source leaf, L*u*: Leaves above or below L*f*, S*u*, S*l*: Stem above or below L*f*,
R: Roots.
Source: Shishido & Hori (1977)[4].

Table 1. Distribution of the assimilates to young leaves and apex in relation to phyllotaxis

Source leaf		Percent. distribution to uppermost leaf and next uppermost leaf					Percent. distribution to apex		
Leaf stage	Leaf number*	The same**	Side	Opposite	Side	The same**	The same***	Side	Opposite
6	2	10.3		3.1				14.0	
	3		3.2		9.6				10.8
	4		1.4		5.4		11.5		
7	2			4.1	20.7			10.8	
	3		9.1	2.2			17.5		
	4		4.6			12.2			5.1
8	2		22.3		10.0				6.7
	3			1.9		19.9		4.6	
	4	13.5		0.9				10.2	

* Leaf 1 is basal.

** Relative position to source leaf.

*** Relative position of outermost leaf to source leaf.

inflorescence. It was also observed in the 12th, which was situated on the same orthostichy with 9th leaf, that both of the first and second inflorescences did not function as a major sink.

Arrangement of a vascular system

A diagrammatic model of the arrangement of a vascular system in tomato plants is presented in Fig. 2. As indicated in Fig. 2, no direct connection is recognized between the two cotyledons, L1 and L2, and L3 and L4, respectively. In more general terms, there exists no direct route between $L2_{n-1}$ and L_{2n}. The direct route upward exists between L_{2n-1} and the right-hand side of L_{2n+1}, or the left-side of L_{2n+2}, and between L_{2n} and the left-hand side of L_{2n+1}, or the right-side of L_{2n+2}, providing that the plant has a clockwise phyllotaxis. The direct route downwards exist between L_{2n-1} and the right-hand side of L_{2n-2}, or the left-hand side of L_{2n-3}, and between L_{2n} and the left-hand side of L_{2n-2}, or the right-hand side of L_{2n-3}, respectively. This implies that the adjacent leaves, or L_{2n-1} and L_{2n}, have only an indirect route in the above-noted vascular system.

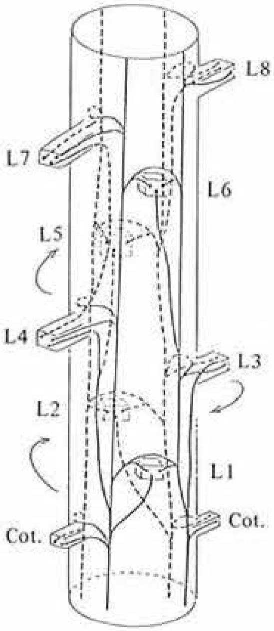

Fig. 2. Diagrammatic longisection of the stem showing course of vascular bundles and vascular supply to leaves in the plant with clockwise phyllotaxis
Cot.: Cotyledone, L: Leaves (L1 is basal),
— : Vascular bundle in the front of stem,
--- : Vascular bundle in the back of stem.

In reference to the arrangement of vascular system in connection with inflorescence and adjacent leaves, the system is shown in Fig. 3. The vascular bundles of the lateral shoot (Lat_b) of L_b just below the first inflorescence wedged themselves in the mid part between the main stem and the L_b bundles. This might have caused some impediment to the function of vascular bundles connecting the first inflorescence with L_b. It was however confirmed in the observation on stained vessels in the main stem that the L_b vascular bundles themselves run parallel to those bundles coupling with the first inflorescence, and that the staining solution readily moved through the former route[6].

The vascular bundles of the first inflorescence and those of leaf just above it were wedged by bundles of the lateral shoot of the leaf. (The lateral shoot, which is morphologically a sympodium, is called "a main stem" for its external appearance and cultural convenience.) As a consequence, a direct connection was not observed between the bundles of first inflorescence and those of leaf just above it. In the latter system, no exchange of the staining solution

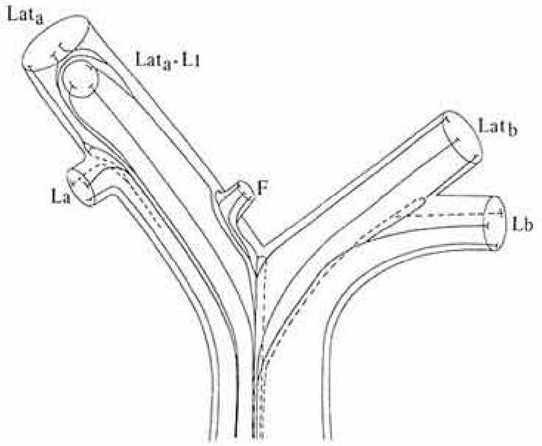

Fig. 3. Diagrammatic longisection of the stem showing vascular arrangement around the inflorescence
La: Leaf just above the inflorescence(F), Lat_a: Sympodium, Lat_a-L1: 1st leaf on the sympodium, Lb: Leaf just below F, Lat_b: Lateral shoot from Lb, —: Vascular bundle in the front of stem, ---: Vascular bundle in the back of stem.

took place. This proves that the vascular bundles of the first inflorescence run parallel to those of leaf just above it without any cohesion. Such an arrangement of vascular system held true irrespective of the number, i.e. even or odd of leaf just below the inflorescence.

Distribution pattern of the assimilates to inflorescence before anthesis from different leaf positions

Fig. 4 presents the leaf position to the inflorescence bearing different leaf number based on phyllotaxis of the four orthostichies. Tables 2 and 3 show the distribution of assimilates to the first inflorescence before anthesis from each leaf, as well as relative strength of each part as a sink (RSS). These tables indicate that the percentage of distribution and RSS are comparatively higher in the young leaves on the same orthostichy to their source leaves, followed by those on the side and opposite orthostichies in this order. The inflorescence before anthesis showed the same level of functions as a sink, which was equal to that of young leaf and much less than that observed during their fruit thicking growth. The percentage of distribution and RSS of the photosynthetic assimilates to the inflorescence from source leaves were therefore controlled by two factors: one was the relative position among those concerned leaves, and the other was the relative position of the inflorescence and their source leaves. The data obtained indicated that a close relationship

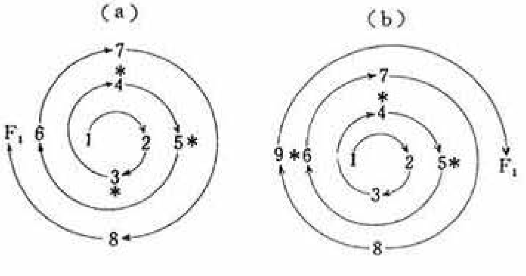

Fig. 4. Scheme of leaf arrangement and position of inflorescence on stem bearing 1st inflorescence after 8th leaf(a) and 9th leaf(b)

Table 2. Distribution of ^{14}C-assimilates and relative strength as a sink (RSS) in relation to source leaf position on the plant with the first inflorescence after initiation of 8th leaf*

Source leaf	Plant parts as sinks							
	7th leaf		8th leaf		1st inflorescence		Apex**	
	% distribution	RSS	% distribution	RSS	% distribution	RSS	% distribution	RSS
L3	1.31a***	15a	8.00a	308a	1.55a	310a	5.17	820
L4	4.98b	54b	0.34b	15b	3.94b	741b	1.66	265
L5	1.95a	24a	2.78b	126a	0.55c	89c	2.58	368

* The 8th leaf apparently situates above the 1st inflorescence.

** Apex is situated as relative position of outer most leaf to the source leaf.

*** Different alphabets imply significant differences at 5% level.

Table 3. Distribution of ^{14}C-assimilates and RSS in relation to source leaf position on the plant with the first inflorescence after initiation of 9th leaf*

Source leaf	Plant parts as sinks							
	8th leaf		9th leaf		1st inflorescence		Apex**	
	% distribution	RSS	% distribution	RSS	% distribution	RSS	% distribution	RSS
L4	1.24a***	16a	4.99a	131ab	1.16a	145a	4.58	188
L5	4.88b	72b	1.43a	50a	2.41a	271b	4.63	354
L6	2.13a	29a	6.95a	247a	0.59a	64b	12.63	509

* The 9th leaf apparently situates above the inflorescence.

, * The same as Table 2.

between the functions of four orthostichies and the distribution patterns of photosynthetic assimilates as source and sink existed among the same and side orthostichies, but not among the opposite orthostichies. This relationship proves that the position of the first inflorescence before elongation of its sympodium was born in accordance with the four-orthostichy system, even though that inflorescence was situated on the opposite side to L8 in appearance at the advanced stage of its growth.

Discussions

In tomato plants, the vascular bundles running toward a stem from the bilateral sides of petiol are connected with a semicircular-shaped vascular of the stem at the petiol, from which vascular two bundles are bilaterally developed upward and downward as well.

The same pattern as above is also maintained in the development of phyllotaxis in tomato which consists basically of four orthostichies. It is therefore concluded that the specific pattern of distribution of photosynthetic assimilates is determined with the following two factors: one is the arrangement of vascular bundles, and the other is the degree of connection between these bundles. No direct connection of vascular bundles exists between the leaves on the opposite orthostichies, and as a consequence, no exchange of the assimilates takes place. Connections are held through one and two vascular bundles between the leaves on the side and same orthostichies, respectively, and distributions of assimilates are affected by degrees of their connection.

Providing that the phyllotaxis and arrangement of vascular bundles in tomato plants are determined in accordance with four orthostichies, the position of leaf just above the first inflorescence should vary according to the number of its lower leaves, even or odd. If the inflorescence develops above the even number leaf, its position should be opposite to the leaf just above it with divergence of 180°. If the inflorescence develops above the odd number leaf, its position should be on the side orthostichy with divergence of 90°, whereas the apparent divergence is 180°. The distribution patterns of assimilates to the first inflorescence from leaves just below as well as above the first inflorescence were the same in those two cases, where the leaf number was even and odd at the fruit thicking stage. This feature is not conformable to the distribution patterns and RSSs obtained in relation to the inflorescence and its source leaves before anthesis.

It was observed in this experiment that the vascular bundles of new leaves wedged in between the inflorescence and the leaf just above it, thereby the direct connection of these two parts were hampered. In addition, the leaf just above the inflorescence might have supplied some nutrient to the lateral shoot from that leaf. These factors may justify the decreased trend of assimilates to the inflorescence from the leaf just above it.

Very few information is presently made available in regard to the developmental mechanism of secondary vascular bundles during the growth of sympodium in plants with a sympodial branching system. In case of tomato plants, however, it is concluded that their phyllotaxis consists of four orthostichies with divergence of 180° and 90°, and that the distribution of photosynthetic assimilates is closely associated with the arrangement of vascular system.

References

1) Gheorghiev, D. & Gheorghiev, H. (1963): Distribution of ^{14}C in blossom cluster, tip and leaves of tomato plants. *C. R. Acd. Bulg. Sci.*, **16**, 313–316.
2) Hori, Y. & Shishido, Y. (1977): Studies on translocation and distribution of photosynthetic assimilates in tomato plants. I. Effects of feeding time and night temperature on the translocation and distribution of ^{14}C-assimilates. *Tohoku J. Agr. Res.*, **28**, 26–40.
3) Lehmann, O. C. (1955): Das Morphologish System der Kulturetomaten. Speinger-Verlag, Berlin, 1–63.
4) Shishido, Y. & Hori, H. (1977): Studies on translocation and distribution of photosynthetic assimilates in tomato plants. II. Distribution pattern as affected by phyllotaxis. *Tohoku J. Agr. Res.*, **28**, 82–95.
5) Shishido, Y. & Hori, Y. (1991): The role of leaf as affected by phyllotaxis and leaf histology on the development of the fruit in tomato. *J. Jpn. Soc. Hort. Sci.*, **60**, 133–139 [In Japanese with English summary].
6) Shishido, Y., Seyama, N. & Hori, H. (1988): Studies on distribution pattern of ^{14}C-assimilates in relation to vascular pattern derived from phyllotaxis of tomato plants. *J. Jpn. Soc. Hort. Sci.*, **57**, 418–425 [In Japanese with English summary].
7) Usugami, H. (1964): Studies on the relation between bearing habit and phyllotaxis in tomato. *Agr. Hort.*, **58**, 559–562 [In Japanese].

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