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Function of node unit in photosynthate distribution to root in higher plants

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Abstract

Leaf-root interaction is a critical factor for plant growth during maturation and activity of roots is maintained by a sufficient supply of photosynthates. To explain photosynthate distribution among organs in field crops, the node unit hypothesis is proposed. One node unit consists of a leaf and an upper adventitous root, as well as the axillary organs and the lower adventitious root, which is adjacent to one node. Using ^{14}C as tracer, the carbon distribution system has been clarified using spring wheat, soybean, tomato, and potato. The interrelationship among organs from the strongest to the weakest is in the following order: (*1*) within the node unit > (*2*) between the node unit in the same or adjacent phyllotaxy > (*3*) in the main root or apical organs, which are adjacent to the node unit. Within the node unit, ^{14}C assimilated in the leaf on the main stem tended to distribute to axillary organs in the same node unit. The ^{14}C assimilated in the leaf of axillary organs tended to distribute within the axillary organs, including adventitious roots in the axillary organ and then translocated to the leaf on the main leaf of the same node unit. In different organs of the node unit in the same or adjacent phyllotaxy, ^{14}C assimilated in the leaf on the main stem was also distributed to the organs (node unit) belonging to the same phyllotaxy in dicotyledons, while in monocotyledons, the effect of phyllotaxy on ^{14}C distribution was not clear. Among roots/apical organs and node unit, ^{14}C assimilated in the upper node unit was distributed to apical organs and ^{14}C assimilated in the lower node unit was distributed to roots. Thus the node unit hypothesis of photosynthate distribution among organs is very important for understanding the high productivity of field crops.

Additional key words: *Glycine*; *Helianthus*; *Lycopersicon*; node unit; photosynthate translocation; phytomer; phyllotaxy; phyton; source-sink relationship; *Triticum*.

Introduction

Osaki *et al.* (1996) pointed out that root activity during maturation is the most crucial factor for achieving high yield. To maintain high root activity, a sufficient amount of photosynthates must be supplied to roots. However, compared to the large amount of information available on the source-sink relationship, there have been very few studies on the system of photosynthate distribution from leaves to roots. Therefore we tried to establish a general model of photosynthate distribution for monocotyledon and dicotyledon plants. As Tanaka (1961) reported, the upper-positioned and lower-positioned leaves of rice plants are responsible for supplying photosynthates to apical organs and roots, respectively, and it is assumed that plant architecture, especially leaf position, is an important factor in photosynthate distribution. Accordingly, in this study we examined photosynthate distribution from the standpoint of plant architecture and leaf position.

Leaf primordia, axillary organs (tiller or branch), and adventitious roots are formed on each plant node. In monocotyledons, if the plant is separated into nodes, each internode includes primordia of a leaf, branch, and adventitious root, and thus from a single segment of internode the plant can potentially be re-grown. This minimum unit has been defined as a phyton or phytomer (Evans and Grover 1940, Kawata *et al.* 1963), with the plant being made up of a series of phytons. In the phytomer or phyton concept, a single internode includes upper-internode organs (leaf and upper adventitious roots) and lower-internode organs (*i.e.* axillary organs and lower adventitious roots) (Fig. 1). However, the upper and lower organs as defined by the phyton concept belong to a different phyllotaxy than the upper and lower organs as defined by the phytomer concept (Fig. 1). Nonetheless, the photosynthesised ^{14}C translocates predominantly to organs of the same phyllotaxy in sugar beet (Joy and Antcliff 1966), tobacco (Jones *et al.* 1959, Shiroya *et al.* 1961), willow (Shiroya *et al.* 1961, Ho and Peel 1969), soybean (Perkins *et al.* 1959, Lovell 1971), lupin (O'Neill

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1961), *Perilla frutescens* Britton var. *acuta* Kudo (Pate 1984), and potato (Osaki *et al.* 1991). Thus, the phyton concept does not adequately explain phyllotaxy based carbon translocation. In this paper, we therefore propose a new concept that combines the phyton and phyllotaxy concepts, which we refer to as the node unit concept. The node unit consists of organs across the node (Fig. 1).

Roots are classified into two types on the basis of origin: primary roots (tap roots or main roots) and adventitious roots (crown roots). Primary roots develop from the radicle root (seedling root), which originates from the apex of the embryo, and induce lateral roots. Adventitious roots develop from other parts of the plant body, such as the stem, petiole, or callus of cuttings (Fahn 1974). Adventitious roots of the stem generally develop from the upper and lower positions of the node, forming the upper adventitious and lower adventitious roots, respectively (Kawata *et al.* 1963). In dicotyledons and gymnosperms, primary roots show good development from lateral roots. In monocotyledons, the development of primary roots is weak, but the lower adventitious roots develop well and numerous branched adventitious roots form fibrous root systems. In the present terminology, the upper and lower adventitious roots in the node unit correspond to the lower and upper adventitious roots in the phyton unit, respectively (Fig. 1). In this paper we propose a system of photosynthate distribution to various organs of field crops, particularly roots, based on the node unit concept.

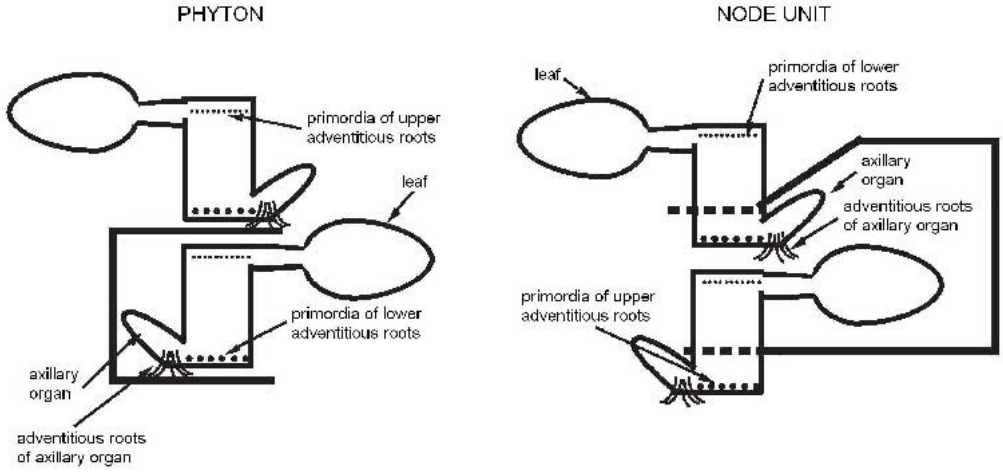

Fig. 1. Phyton and node unit models. In monocotyledons, upper and lower adventitious roots of the main stem are not formed after the panicle formation stage. In dicotyledons, since the stem generally grows above the ground, adventitious roots of the internode are not formed. However, if the node unit is formed underground, such as in the potato, adventitious roots are formed around the node unit, and the axillary organ is transformed to a stolon or tuber.

Materials and methods

Plants: Spring wheat (*Triticum aestivum* L. cv. M27), soybean (*Glycine max* (L.) Merr. cv. Tsurumusume), sunflower (*Helianthus annuus* L. cv. Hokuren), tomato (*Lycopersicon esculentum* Mill. cv. Kyoryokubeiju2), and potato (*Solanum tuberosum* L. cv. Dansyakuimo) were grown in pots. Tomato seedlings were transplanted. Mother tubers of potato plants were planted in vermiculite at a depth of 10 cm, and potato seedlings without a mother tuber were planted to a container (52×36×31 cm height). For fertiliser, 0.3 kg m^{-3} of N, P_2O_5, and K_2O each were applied to the soil in the form of ammonium sulphate, superphosphate, and potassium sulphate, respectively, to all plants except for sunflower. For sunflower, 0.4 kg m^{-3} of N, P_2O_5, and K_2O each were applied to the soil in the form of ammonium sulphate, superphosphate, and potassium sulphate, respectively. All pots were 500 cm^2 × 30 cm in size. All experiments and analyses were replicated three times.

Treatments: To form adventitious roots from internodes, the region from the 5th to the 9th node of the tomato stem was wrapped with wet cotton and covered with an aluminium foil sheet and the cotton was kept wet for 7 weeks. For dark treatment, spring wheat and soybean were placed under continuous darkness at their early maturation stages for 4 and 5 d, respectively.

$^{14}CO_2$ assimilation and ^{35}S-methionine absorption: 0.37 MBq $^{14}CO_2$ was assimilated by individual leaves, tillers, and branches during 1 h according to the method of Tanaka and Osaki (1983). Four days after $^{14}CO_2$ assimilation, plants were sampled, fixed to paper, and air-dried. For spring wheat, adventitious roots of each tiller and main stem were separated. 0.2 mM ^{35}S-methionine (0.37 kBq in 50 mm^3 of phosphate buffer, pH 7.5) was introduced to the leaf tip (cut in water using a razor blade) at the upper, medium, and lower positions of spring

wheat and soybean at the early maturation stage under natural light conditions. ^{35}S-methionine was introduced to the leaf tip for 1 h, separated at 4 d after absorption, then further separated into individual organs (the 2 mm tip of the absorbed leaf was cut to prevent surface contamination with ^{35}S-methionine).

Measurements of radioactivity of ^{14}C and ^{35}S: The amounts of ^{14}C and ^{35}S were determined as follows. Five to 15 mg of sample was added to a 20 cm^3 vial. Then 75 mm^3 water, 30 mm^3 acetic acid, and 0.5 cm^3 tissue solubiliser (*NCS-II*; *Amersham*, Ontario, Canada) were added. After 16-h incubation at 50 °C, 150 mm^3 of benzoyl peroxide solution (1 g per 5 cm^3 toluene) was added and then incubated at 50 °C for 30 min. After incubation, 1 cm^3 H_2O_2 was added and the sample was placed in darkness for 12 h. The mixture was then supplemented with 15 cm^3 toluene scintillator containing 60 mg DPO (2,5-diphenyloxazole), 3 mg POPOP {1,4-bis-[2-(5-phenyloxazolyl)] benzene}, 225 mg *Cab-O-Sil* (*Eastmann Kodak*, Rochester, NY, USA), 4.5 cm^3 *Nonion* (*NS-210*; *Nihonyushi Co.*, Tokyo, Japan), and 10.5 cm^3 toluene. The radioactivity was then measured with a liquid scintillation counter (model *LSC-502*; *Aloka Co.*, Tokyo, Japan).

Radioautographs of the dry samples were developed using X-ray film (*Fuji Photo Film Co.*, Tokyo, Japan) in a dark room for 1 week and the developed films were scanned with an *EPSON GT-8000* scanning machine (*Epson Corp.*, Nagano, Japan) to obtain semi-qualitative information on the radioactivity, because the density of the X-ray film corresponds to the count of radioactivity by *BAS-1000* (*Fuji Film*) which can count exact radioactivity, when several samples are estimated by both measuring methods. In this paper, we show only ^{14}C radioautograph data because most of the analyses were done by this method. All the experiments were performed in triplicate, but because the three ^{14}C distribution patterns were similar, only one set of results is presented.

Results

Node unit in dicotyledons: The phyllotaxy of soybean is 2/5 (McCauley and Evert 1988). When $^{14}CO_2$ was assimilated by the 2nd and 3rd leaves (66 d after sowing), assimilated ^{14}C remained mainly in the leaf fed with ^{14}C, but was also distributed to the 2nd and 3rd branches, respectively (Fig. 2*A,B*). These results indicated that the leaf and branch of each node on the main stem of soybean form a node unit. When $^{14}CO_2$ was assimilated by the 2nd branch, ^{14}C remained mostly in the ^{14}C-fed branch (Fig. 2*C*). Based on the above results, though the branch belongs to a node unit with the leaf on the main stem, the branch is a strong sink and thus photosynthates assimilated by the branch were mainly used for its own growth. ^{14}C assimilated by the 3rd leaf (n) was distributed to the 1st (n+2) and 5th (n+3) leaves, but was not distributed to the 2nd leaf (n+4) nor the 4th leaf (n+1). Therefore, a connection exists between the node units of the same or neighbouring phyllotaxy group (n node unit, n+2 node unit, and n+3 node unit) in soybean. On the other hand, ^{14}C assimilated by the 3rd leaf was distributed to various apical growing organs, such as developing leaves, regardless of phyllotaxy. ^{14}C assimilated by the 2nd leaf was also distributed to various organs. However, according to the phytomer model, the 2nd and 3rd leaves form a unit with the 1st and 2nd branches, respectively, while ^{14}C assimilated by the 2nd and 3rd leaves was not distributed to the 1st and 2nd branches, respectively, indicating that the phytomer is not a physiological unit. Since ^{14}C assimilated by the 2nd leaf was distributed more to the primary roots than by the 3rd leaf (Fig. 2*A,B*), it was assumed that ^{14}C in the main root was distributed from lower leaves.

Node unit in monocotyledons: When $^{14}CO_2$ was assimilated by the 1st leaf of spring wheat at the flowering stage (53 d after sowing), ^{14}C was distributed mainly to the ^{14}C fed-leaf and to the developing leaves and adventitious roots of the 1st tiller and, slightly, to the main stem (Fig. 3*B*). When $^{14}CO_2$ was assimilated by the whole 1st tiller, ^{14}C was distributed mainly to the 1st tiller and the 1st leaf (Fig. 3*D*). These results indicated that the 1st leaf and 1st tiller (including the adventitious roots of 1st tiller) formed the node unit (1st node unit). Since ^{14}C assimilated by the 1st leaf and the 1st tiller was distributed mainly to the adventitious roots of the main stem, the relationship between the 1st node unit and the adventitious roots of the main stem seemed to be strong.

When $^{14}CO_2$ was assimilated by the whole 2nd tiller, ^{14}C remained mainly in the 2nd tiller, with a high distribution to the adventitious roots (Fig. 3*C*). There was only a small amount of ^{14}C in the adventitious roots of the main stem and a negligible amount in the 2nd leaf. These results indicated that the 2nd tiller, including the adventitious roots, tended to be independent from the main stem with respect to ^{14}C distribution (Fig. 3*C*).

When $^{14}CO_2$ was assimilated by the flag leaf (Fig. 3*A*), ^{14}C was predominantly distributed to the strong sink (ear), while the distribution to the root was very small.

Phyllotaxy of ^{14}C distribution: In potatoes, when shoots sprout from the mother tuber, the node unit that exists underground consists of roots and stolon (or tuber) and retired leaf, and the node unit that exists above ground consists of leaf, branch, and retired roots. Thus, when potato plants were grown from a mother tuber, all potato roots were adventitious roots. When a potato stem was put in a 12 M HCl solution for 6 weeks, the vascular connections could be visualised and the phyllotaxy was

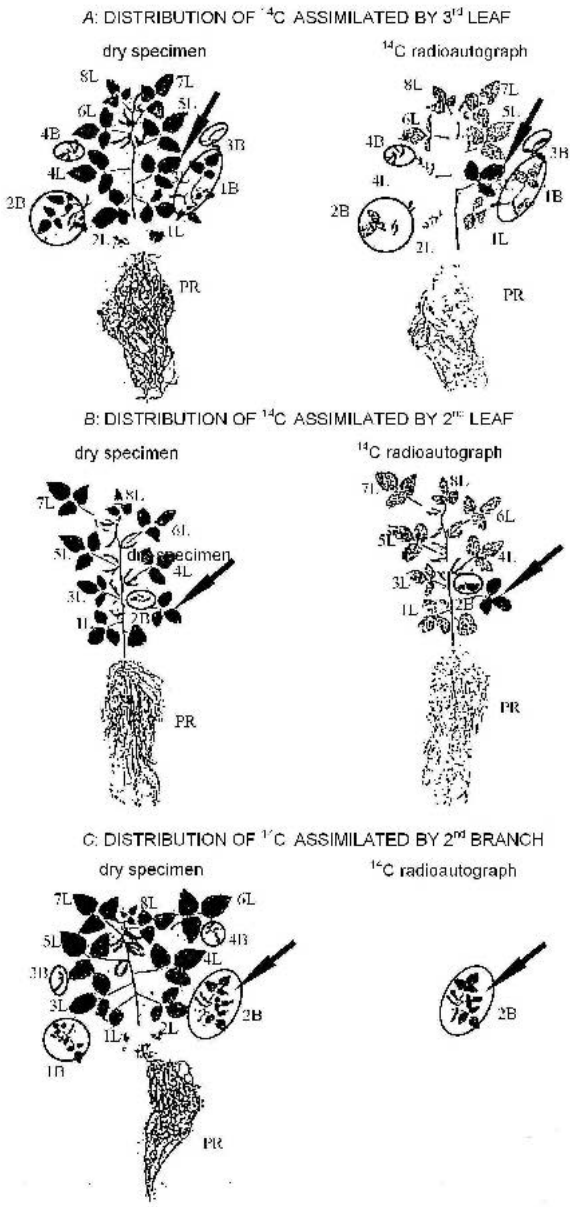

Fig. 2. Dried plant specimens and ^{14}C radioautographs of soybean at the early maturation stage at 4 d after feeding. *Arrows* indicate $^{14}CO_2$-fed leaf or whole branch. nL, n^{th} leaf; nB, n^{th} branch; PR, primary root. Numbers of leaves and branches are counted from the bottom.

Discussion

Applying the node unit concept to the ^{14}C distribution system of dicotyledons, the interrelationship among organs, from strongest to weakest, is in the following order: (*1*) within the node unit > (*2*) among the node unit in the same or adjacent phyllotaxy > (*3*) in the main root or apical organs, which are adjacent to node unit. Within a node unit, when $^{14}CO_2$ was assimilated by a leaf, ^{14}C was distributed to axillary organs, adjacent sink, and adventitious roots, if they existed. When $^{14}CO_2$ was assimilated by axillary organs, ^{14}C was distributed less to other organs.

Applying the node unit concept to the ^{14}C distribution system of monocotyledons, the strength of the interrelationship among organs is almost similar to dicotyledons. In monocotyledons before the primordia formation stage, the node unit contains the leaf, tiller, and adventitious roots of the tiller, and the tiller supplies the saccharides to its main and adventitious roots. However, those node units that emerge after the primordia formation stage do not contain the tiller and its adventitious

2/5 (Fig. 4*C*). According to Haywars (1938), McCauley and Evert (1988), and our present results, the bundle consists of 5 bundles: at the base of the semicircular petioles there are 3 large, neutrally located bundles and 2 smaller ones which are located at the outer edges. When $^{14}CO_2$ was assimilated by one of the compound leaves at the 4^{th} node unit (Fig. 4*A,B*), ^{14}C was distributed to L8, L9, the region above L9, R(1), R2, R4, and F1, indicating that ^{14}C was not only distributed to the same node unit, but also to the adjacent node unit *via* the vascular connection system (Fig. 4).

^{14}C-distribution to roots from individual leaves at various positions: In spring wheat, ^{14}C photosynthates of the 7^{th} leaf were translocated mainly to the upper organs, and less so to primary roots of lower organs; however, those of the 3^{rd} leaf were translocated mainly to the lower organs, especially the roots (Fig. 5). In soybean, ^{14}C photosynthate was translocated from the 2^{nd} (lower) and 4^{th} (medium) position to roots (Fig. 5). In sunflower and potato, ^{14}C photosynthate distribution was similar regardless of leaf position (Fig. 5).

^{35}S-methionine distribution to roots from leaf at various positions: When ^{35}S methionine was absorbed from the leaf tip at the early maturation stage of wheat and soybean, the lower leaf translocated ^{35}S to the roots (Fig. 6). Thus, not only photosynthates, but also nitrogen compounds were supplied to the roots from lower positioned leaves.

Effect of darkness on ^{14}C distribution: Under the control conditions, ^{14}C assimilated in wheat was distributed to other node units or other stems (especially when assimilated in lower leaves). When the plants were treated in darkness, however, ^{14}C distribution was restricted within node units (Fig. 7*A,B*). In soybean under the control conditions, the assimilated ^{14}C was distributed to other node units (especially when assimilated in lower leaves); however, when the plants were treated in darkness, ^{14}C distribution was restricted to within node units (Fig. 7*C,D*).

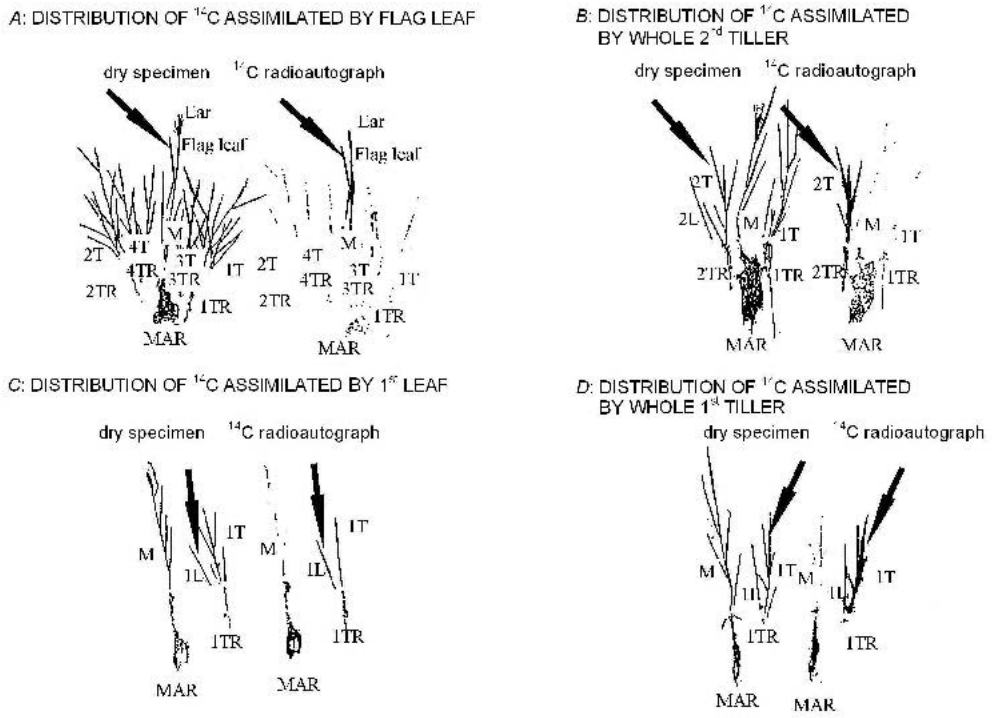

Fig. 3. Dried plant specimens and ^{14}C radioautographs of spring wheat at the heading stage at 4 d after feeding. *Arrows* indicate $^{14}CO_2$-fed leaf or whole tiller. M, main stem; L, leaf; T, tiller; MAR, adventitious root of main stem; TR, adventitious root of tiller. Numbers of leaves and tillers were counted from the bottom.

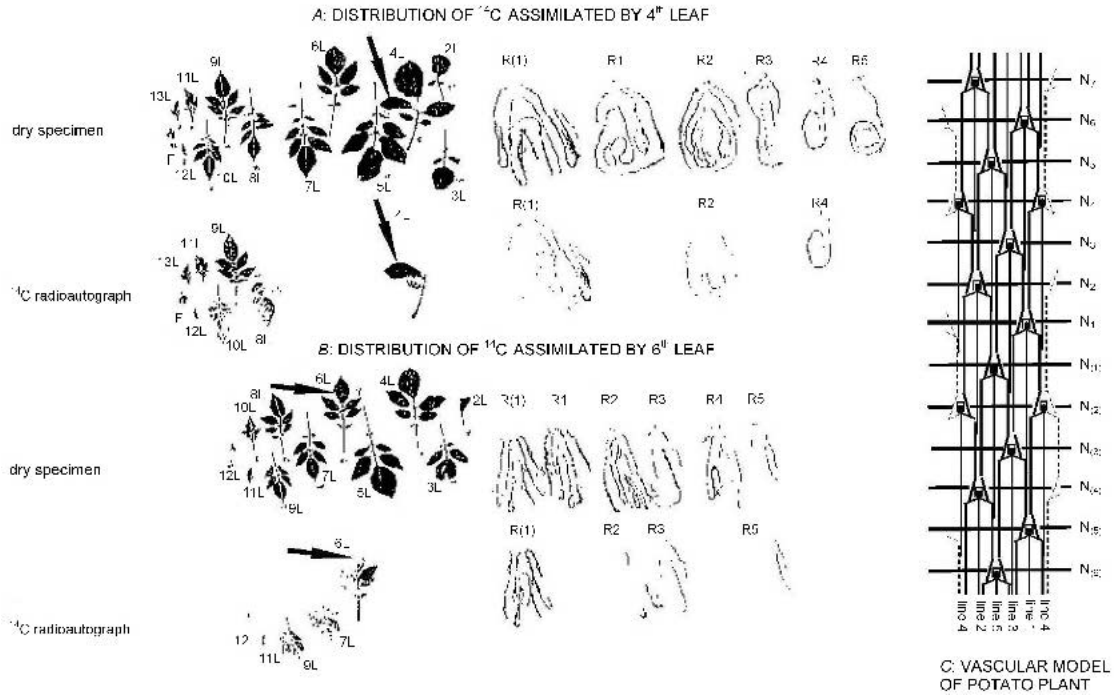

Fig. 4. *A*: Dried plant specimens and ^{14}C radioautographs of potato at the early maturation stage at 4 d after feeding to 4th leaf. *B*: Dried plant specimens and ^{14}C radioautographs of potato at the early maturation stage, 4 d after feeding to 6th leaf. *Arrows* indicate $^{14}CO_2$-fed leaf or whole branch. nL, nth leaf; nB, nth branch; PR, primary root. Numbers of leaves and branches are counted from bottom. *C*: Scheme of the bundle system of potato. The n in Nn indicates the node number counted from ground level. Nn and N(n) indicate the node numbers above ground and below ground, respectively.

roots. Thus in monocotyledons, the node unit at the lower position is more essential for saccharide distribution to roots. Adventitious roots of the main stem and ear of spring wheat do not belong to any node unit. Photosynthates are translocated to those organs from the nearest active unit. The interrelationship between the lower node unit and the adventitious roots of the main stem was also confirmed in wheat (current paper) and in rice (Tanaka 1961). Within a node unit, the relationship between the leaf on the main stem and the tiller is strong, and ^{14}C distribution from the leaf on the main stem to the tiller is dominant, while that from the tiller to leaf on the main stem is not always dominant.

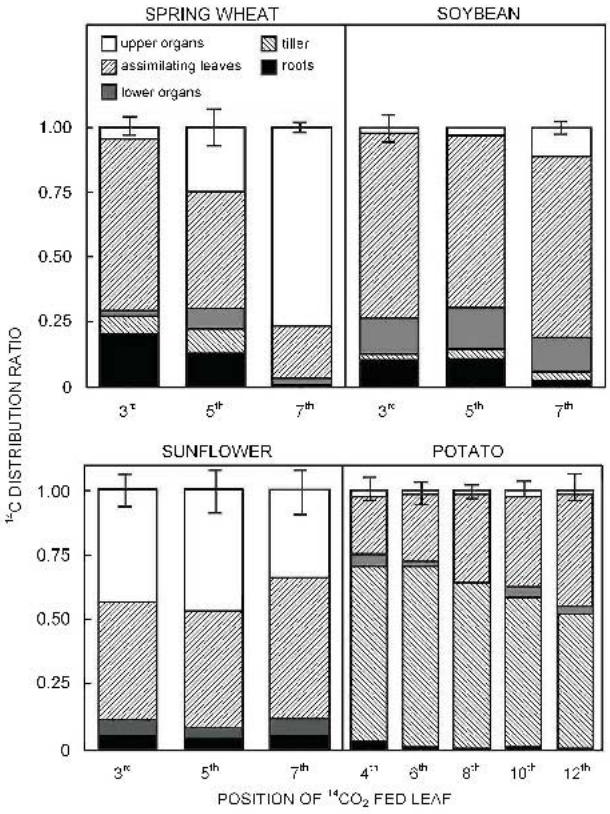

Fig. 5. Distribution of assimilated ^{14}C to other organs at 4 d after feeding to spring wheat and soybean. *Bars* in the figure indicate SE in whole plants.

^{14}C distribution based on the node unit concept – relationship of organs within the node unit: When $^{14}CO_2$ was assimilated by axillary organs, assimilated ^{14}C remained mainly in the axillary organs in wheat (Fig. 3*C,D*) and soybean (Fig. 2*C*), including the adventitious roots of the axillary organs in wheat (Figs. 3*C,D*). It was then distributed slightly to leaves in the same node unit in wheat (Fig. 3*D*). Thus, the ^{14}C assimilated in leaves on the main stem tended to distribute to axillary organs in the same node unit, while ^{14}C assimilated in leaves on the axillary organs tended to be distributed within axillary organs, then translocated to leaves on the main stem in the same node unit (Figs. 2 and 3). If the axillary organs grow actively, assimilated ^{14}C remains mostly in its own axillary organs, especially in dicotyledons. Accordingly, assimilated ^{14}C was distributed predominantly within the node unit.

Relationship among organs of the node units on the same or adjacent phyllotaxy: When $^{14}CO_2$ was assimilated by the leaf on the main stem, assimilated ^{14}C was also distributed to organs of the node unit in the same phyllotaxy in soybean (Fig. 2*A*). In potato, which has a 2/5 phyllotaxy, when $^{14}CO_2$ was assimilated by the leaf of the n^{th} vascular bundle, ^{14}C was distributed to organs of the

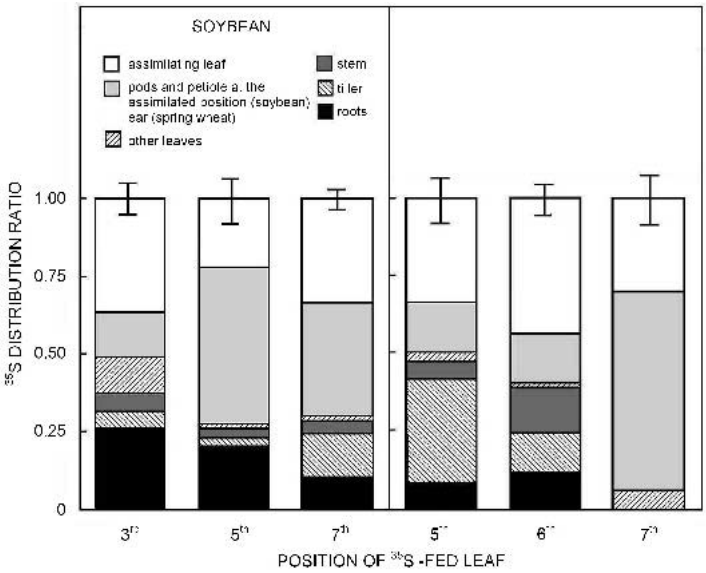

Fig. 6. Distribution of introduced ^{35}S to other organs at 4 days after feeding to spring wheat and soybean. *Bars* in the figure indicate SE in whole plants.

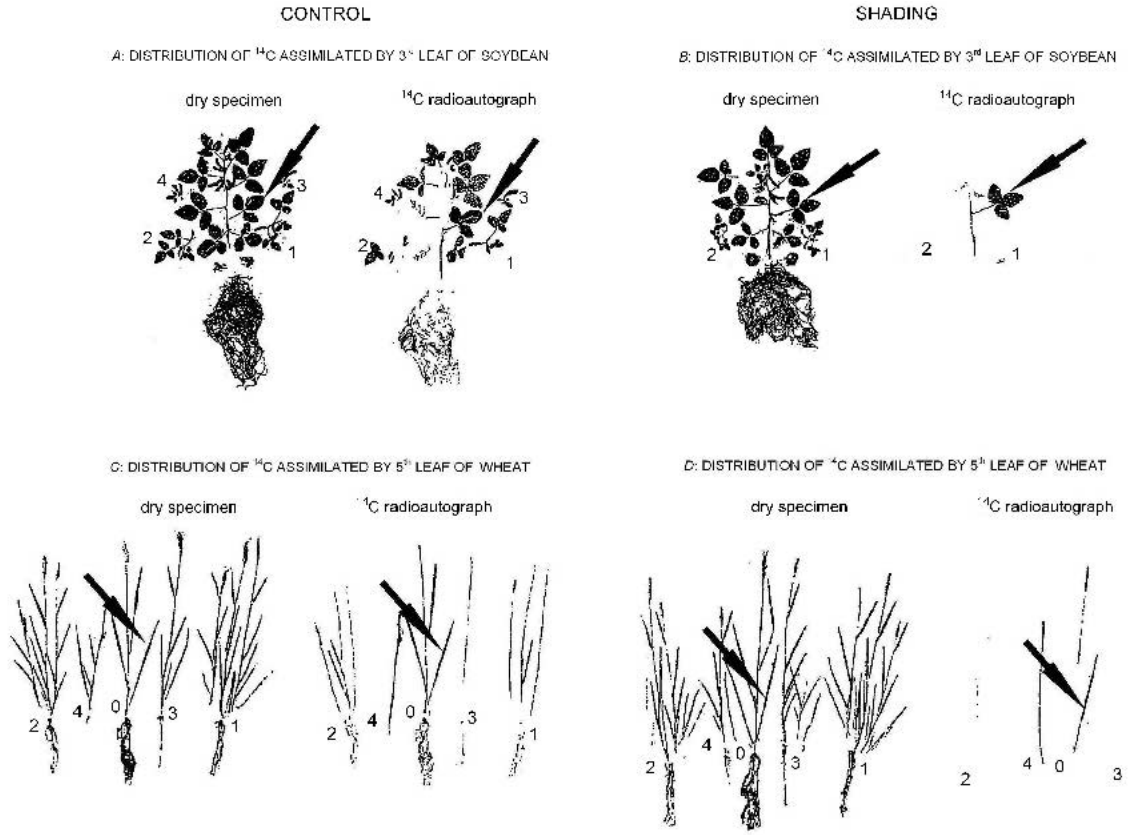

Fig. 7. Effect of shading on the translocation of ^{14}C in individual leaf of spring wheat and soybean at the early maturation stage.

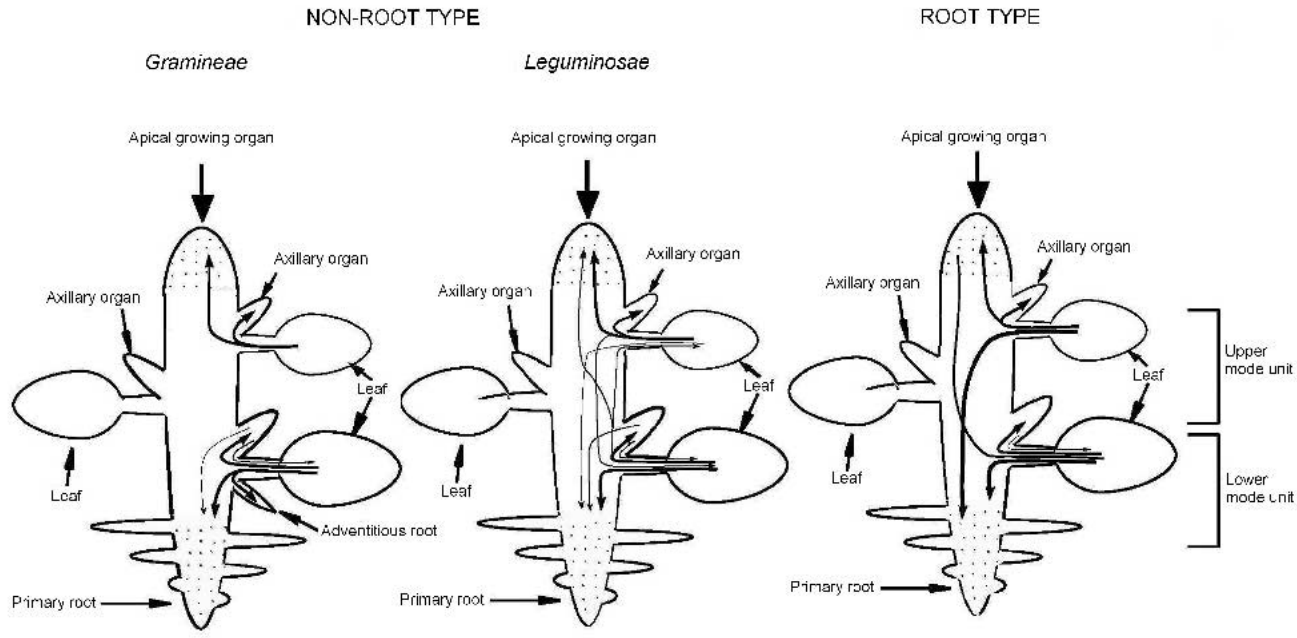

Fig. 8. A model of photosynthate distribution among organs based on the node unit hypothesis. *Long arrow*, large amount of photosynthate distribution; *medium arrow*, medium amount of photosynthates distribution; *short arrow*, small amount of photosynthate distribution. *Dotted area* indicates that photosynthates are distributed mainly by diffusion.

n^{th}, the $n+2^{nd}$, and the $n+3^{rd}$ vascular bundles (the $n+2^{nd}$ and $n+3^{rd}$ vascular bundles are adjacent to the n^{th} vascular bundle) (Fig. 4). Thus in dicotyledons, phyllotaxy is also an important factor for ^{14}C distribution, while in mono-

cotyledons, the effect of phyllotaxy on ^{14}C distribution is not clear.

Relationship between roots on the main stem (primary roots in dicotyledons and adventitious roots on the main stem in monocotyledons) and apical organs and node units: When $^{14}CO_2$ was assimilated by a leaf in the upper node unit (or in the lower node unit), assimilated ^{14}C was distributed to the apical organs (or to primary roots) in wheat (Figs. 3*A* and 5) and soybean (Figs. 2 and 5), respectively. However, the distribution of assimilated ^{14}C was not localised in apical organs and primary roots on the main stem, indicating that photosynthates were translocated to these organs by diffusion. Thus, apical organs and roots on the main stem do not connect directly to the node unit. Consequently, under resource limiting conditions, the growth of these organs is expected to be severely restricted because photosynthates are distributed by diffusion. In potato plants, ^{14}C assimilated by leaves was also distributed to the same or adjacent phyllotaxic adventitious roots, which developed from the node unit (Fig. 4). Thus, if roots develop from the node unit, ^{14}C assimilated by leaves is mainly distributed to the phyllotaxic adventitious roots in the same phyllotaxy or node unit.

Model of ^{14}C distribution to roots

Monocotyledons: In spring wheat, the 4th leaf expands before the primordia formation stage, and the 1st to 4th node unit on the main stem includes the leaf, tiller, and adventitious roots. At the vegetative stage, a large amount of ^{14}C was supplied to the roots from the leaves at the lower position (*i.e.* the 2nd to 4th leaves), because these node units have adventitious roots (Fig. 8). The 5th node unit, in the case of spring wheat, does not have roots. However, since this node unit is close to the main root, the 5th leaf supplies photosynthates to roots before maturation. While once the sink filling starts, the 6th leaf does not supply photosynthates to roots. Thus in monocotyledons, the position of node units is very important with regard to the supply of photosynthates to roots. Consequently, at vegetative stage, as node unit was condensed at the bottom, node units developed adventitious roots in soil. However, at reproductive stage, once shoot elongation started, node unit on elongated shoot had no roots because it was located above ground.

Dicotyledons (legumes): In soybean plants, the node unit does not normally include roots (Fig. 8). At all growth stages of soybean plants, the lower leaf supplies the photosynthates to roots.

Dicotyledon (root crops): In potato plants, the node unit below the ground includes adventitious roots. Thus the ^{14}C-saccharides in the roots were supplied from the upper node unit belonging to the same or adjacent phyllotaxic group (Fig. 4). Although sunflower is not a root crop, root growth and root activity remained until the late growth stage, based on the finding that the root to shoot ratio remained constant or decreased only slightly (Osaki *et al*. 1996). Therefore, it is assumed that the sunflower is a root crop-like crop. Thus, in root crops, the ^{14}C-photosynthate was generally and equally distributed to the roots, irrespective of the position of the leaf by which it was assimilated.

Function of lower leaf to roots – effect of dark treatment on ^{14}C distribution: For a canopy it is widely accepted that since leaves, stems, and roots at the lower position consume a large amount of photosynthates assimilated in the upper leaves, photosynthates will compete between the sink and lower organs (Tanaka 1961). However, Osaki *et al.* (1996) reported that when lower leaves (lower than the flag leaf) of rice plants were wrapped with an aluminium foil sheet, and $^{14}CO_2$ was assimilated by a flag leaf, translocation of ^{14}C to the lower organs, especially to roots, was restricted. To clarify the effect of shading on the distribution of photosynthates to roots, wheat and soybean were placed in darkness for 4 (wheat) and 5 (soybean) d, respectively. In the controls, ^{14}C was distributed to other node units, but under dark conditions ^{14}C distribution was strictly restricted to within node units both in wheat and soybean (Figs. 7 and 8). Thus, under mutual shading root activity decreased rapidly and lower leaves tended to be decomposed and translocated to fulfil the mineral requirements of sink organs.

Nutritient translocation to roots from a lower leaf: In wheat and soybean, a substantial amount of the ^{35}S-methionine absorbed by the leaf tip of lower leaves translocates to roots. In castor bean and tobacco, when $^{35}SO_4^{2-}$ was absorbed by leaf application, ^{35}S in phloem sap belong to 20 to 40 % of organic S-compounds: 70 and 67 % glutathione, 10 and 27-30 % methionine, and 10 and 2–8 % cysteine, respectively, among organic S-compounds, and in 60–80 % of inorganic S-compounds (Rennenberg *et al.* 1979, Bonas *et al.* 1982). Thus, sulphur in phloem translocates mainly in the organic form, however, organic sulphur compounds can be transported in the phloem. Since it is expected that methionine is less metabolised during translocation, methionine was used for the analogue of nitrogen compounds. When the 8th and 5th leaves at the 9-leaf stage of rice were soaked in 0.2 % ^{15}N urea solution over 7 d, the amount of ^{15}N translocated to roots was 1.7 times higher in the lower (5th) than in the higher (8th) leaf under no nitrogen treatment (Tatsumi and Kono 1981). Thus not only photosynthates, but also nitrogen compounds are supplied to roots from low positioned leaves.

Conclusion: To achieve a high yield, root activity during maturation is very important (*e.g.* Osaki *et al.* 1995).

Because root activity is maintained by a sufficient supply of an adequate amount of photosynthates, leaf-root interaction is a critical factor for plant growth during maturation. In monocotyledons, the lower leaves on the main stem and tiller supply the photosynthates to the main roots, and the tiller supplies photosynthates mainly to the tiller roots (Fig. 8). Therefore, lower leaves and tillers are important for supplying photosynthates to roots. In dicotyledons, lower leaves on the main stem supply the photosynthates to the main roots (Fig. 8). In this sense, plant type is very important for root activity (Osaki *et al*. 1996). Since sink organs of root crops are formed below ground, saccharides translocate mainly to below ground organs from all leaves (Fig. 8). Therefore, the roots of root crops have an advantage in saccharide supply over the roots of cereal or legume crops. This is the main reason why root crops have been shown to attain a high productivity in spite of their other inferior plant traits (Osaki *et al*. 1996). Thus, the node unit hypothesis of photosynthate distribution among organs is very important for understanding the high productivity of field crops.

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