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Root Growth and Partitioning of ^{13}C-labelled Photosynthate in the Seminal Root of Corn Seedlings as Affected by Light Intensity*

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Abstract : The effects of shading on growth and allocation pattern of photosynthate in the seminal root of corn seedlings were studied using ^{13}C as a tracer. Corn seedlings, preshaded for 2 days (light intensity was reduced to 57% or 25% of nonshaded plants), were fed with ^{13}C-labelled CO_2 for 2 h under given light conditions, then allowed to grow for the subsequent 3 days. The extension rate of the seminal axis was not affected by shading. The total number and length of laterals were reduced by shading, while a marked increase of number and length of laterals was observed in the specific region within 10 cm from the apex of shaded plants. The ^{13}C allocation to the laterals of the seminal root was reduced by shading ; in contrast, allocation was increased in the seminal axis. The decrease of ^{13}C allocation to the laterals was associated with the reduction of the development of laterals. The increase of ^{13}C allocation to the seminal axis was due to a marked accumulation of ^{13}C in the root tip and axis within 10 cm from the apex, and this accumulation was strongly associated with the enhancement of the growth of laterals and the extension of the axis that occurred in the same region.
Key words : $^{13}CO_2$ assimilation, Carbon partitioning, Light intensity, Root growth, Root system, *Zea mays* L.

トウモロコシ幼植物の種子根の生長と ^{13}C 標識光合成同化炭素の分配に及ぼす光強度の影響 : 巽　二郎・遠藤伸子・河野恭廣（名古屋大学農学部）

要　旨 : 光強度がトウモロコシ幼植物の種子根の生長と光合成同化炭素の分配に及ぼす影響を ^{13}C をトレーサーとして調べた．特に，根軸に沿った種子根の根軸と側根に着目した．2日間遮光処理したトウモロコシ（光強度を対照区の57%または25%に低下）に ^{13}C でラベルした CO_2 を2時間にわたって供与した．その後3日間にわたって種子根の生長と体内での ^{13}C の動きを追跡した．遮光処理は ^{13}C 同化時ならびにその後の実験期間中継続した．種子根の伸長速度は遮光の影響を受けなかったが，種子根軸上の総側根数・長は顕著に減少した．種子根軸に沿った，根端より10−30 cmの部位では第1次側根長（L型＋S型）の，同じく30-基部の部位では第2次側根の減少が生じた．これとは対照的に根端より10 cm以内では，S型側根数の著しい増加がみられた．同化後1日目における側根への ^{13}C の分配は，対照区と比較して低下したが，種子根軸では逆に増加した．側根への ^{13}C 分配の減少は側根の生長の減少と対応していた．根軸への ^{13}C の分配の増加は，特に根端および根端から10 cm以内の部位で顕著であり，この部位での側根の生長促進，根軸伸長の維持と対応していた．以上のように，種子根を構成する各部位の，遮光に対する生長反応とそこへの光合成同化産物の分配の様相が，平行的であることが示された．
キーワード : 光合成同化炭素，種子根，^{13}C の分配，トウモロコシ，光強度，根の生長．

The light environment for plants grown in the field varies continually. Light intensity changes in diurnal and seasonal time scales and fluctuates irregularly with weather conditions. Mutual shading of leaves progresses as plant canopies develop, particularly for densely-planted crops. These may lead to the change in rate of phloem loading of photosynthate in source leaves. Although fluctuation in transfer of the assimilate to export channels can be buffered by storage carbohydrates currently available for translocation, the rate of photosynthate supply to sink organs can be altered, particularly when low light irradiance is prolonged and reserve pools are exhausted[15]. Roots are a weak sink compared with aboveground parts[10,11,15], thus the growth and development of the root system is more susceptible to the alteration of light environment than the shoots.

A root system of graminaceous plants comprises seminal and nodal root systems. Single seminal or nodal root has a main axis (seminal

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or nodal axis) and branches which arise on main axis (first order laterals) and those which arise on laterals (higher order laterals)[10]. When rice plants are shaded or defoliated and photosynthate currently transferred to the root system is restricted, emergence and extension of main axes, particularly number and length of 1st and 2nd order laterals, and dimension of branching order are reduced[6]. Root diameter varies along root axes as well as among root members, and the transverse area of the phloem responsible for photosynthate transport in roots also varies considerably[12]. In the 1st and 2nd order laterals, where no further branches arise, the phloem often develops very poorly[7,12]. This suggests that the accessibility to photosynthate delivered via the phloem can be varied among root members constituting the root system, since there appeared to be an upper limit for specific transfer of assimilates in the phloem[15].

Many studies has been conducted on the growth of root systems in relation to photosynthate allocation in plants[10,15], however, most research has treated the root system as a mass. Very few reports are available which investigate the relationship between growth responses and photosynthate allocation in various parts of the root system.

The aim of the work described here is to explore the effects of low light intensity on the growth of seminal roots of corn seedlings in relation to the allocation pattern of photosynthate in the roots, using ^{13}C as a tracer. In particular we try to investigate the specific responses in growth and carbon partitioning in different regions of seminal roots.

Materials and Methods

Corn seeds (*Zea mays* L. cv. Golden Cross Bantam) were germinated on the stainless steel net floating on tap water. The 4 th day from germination, seedlings were selected and transplanted to three containers (16 l; 20 plants per container) filled with tap water containing 0.02 mM $CaSO_4$., then placed in an artificially-lit growth chamber (25°C; 14 h/10 h, light/dark; 880 μmol/m^2/s). Four days after transplanting, tap water was replaced with the nutrient solution containing; $(NH_4)_2SO_4$, 0.18 mM; K_2SO_4, 0.37 mM; $MgSO_4$, 0.18 mM; KNO_3, 0.55 mM; KH_2PO_4, 0.18 mM; $Ca(NO_3)_2$, 0.11 mM; Fe-EDTA, 0.04 mM. The solution was bubbled with air (10 l/min) continuously and renewed every 3 days. The pH of the solution was adjusted to 6.0 at renewals. On the 15 th day of germination seminal and nodal roots other than the primary seminal root were removed, thus leaving a single seminal root on the seedling. The seed remained was also removed from the seedling.

Shading: On the 16 th day, seedlings were separated into three groups; one group was left non-shaded (Control) and the other two groups were covered with black cheesecloth, which reduced the light intensity to 57% (S2 plot, 500 μmol/m^2/s) or 25% (S2 plot, 220 μmol/m^2/s) as compared with nonshaded plants (Control, 880 μmol/m^2/s at plant base level). Shading was continued subsequently for 5 days.

^{13}C feeding: Two days after the beginning of shading treatments, plants were placed in the assimilation chamber integrated to the feeding system (Fig. 1)[8], then allowed to assimilate ^{13}C-labelled CO_2 under given light regimes. The plants were exposed to labelled CO_2 (363 ± 5 μl/l, 32.5 atom% ^{13}C) under shaded (S1 and S2) or nonshaded (Control) conditions for 2 h.

Six plants of each plot were harvested just after termination of the assimilation (Day 0), then sampled on 24 h (Day 1) and 72 h after (Day 3). Harvested plants were immediately separated into mature leaves (1, 2, 3 and 4L), developing leaves (5 and 6L; if present), the stem, the seminal root, and the nodal roots (if present; nodal roots were removed prior to shading). For ^{13}C analysis, a half of the seminal roots were floated on iced water in a vat then axis tip (tip; 0.3 cm from apex) was separated. The rest of the seminal root was cut into segments along a seminal axis at 10 cm intervals from the root tip. The segment was further separated into lateral roots (laterals) and seminal axis (axis) except for the segments of tip-10 cm where very short laterals within 1 mm length emerged. These procedures were done within 20 min. The separated parts were frozen in liquid nitrogen then dried in an oven. The remainder of seminal roots were immersed in FAA solution.

^{13}C analysis: Triplicate samples of dried root parts were mixed together and ground with a porcelain mortar carefully so as to protect from possible contamination, since the amount

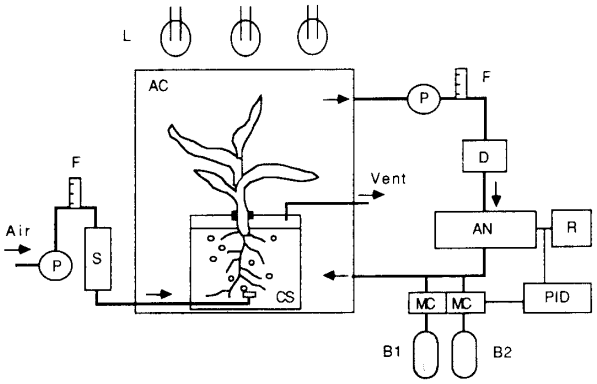

Fig. 1. Schematic representation of the system for $^{13}CO_2$ feeding to plants. AC, assimilation chamber; AN, $^{13}CO_2$ analyzer; B1, $^{12}CO_2$ cylinder; B2, $^{13}CO_2$ cylinder; CS, culture solution; D, dehumidifier; F, flow meter; L, BOC lamps; MC, mass flow controller; P, air pump; PID, PID controller; R, recorder and data processor.

of each root sample was very small (less than 15 mg DW). Dried samples of other plant parts were weighed and ground to a fine powder with a vibrating sample mill. The ^{13}C abundance in the sample was determined with a $^{13}CO_2$ analyzer (Model EX-130S, Japan Spectroscopic Co. Ltd., Tokyo Japan) after oxidizing a small amount of the samples (0.1—0.3 mg DW) at 900°C with oxygen gas flowing [9,14].

Amount of labelled carbon (A) in the plant samples was calculated from the following equation;

$$A=\frac{^{13}C \text{ atom } \% \text{ excess in the sample}}{^{13}C \text{ atom } \% \text{ excess in the air supplied}} \times \text{amount of carbon in the sample}$$

Amount of total carbon in the samples was estimated from sample dry weight assuming that the carbon/dry matter ratio was 0.45 and was constant over various parts of the plants.

Morphological measurements; The seminal roots stocked in FAA were rinsed by tap water then placed in a vat. After measuring the length of the seminal axis, the roots were cut into segments along the axis at 10 cm intervals from root tip in the same manner as described for sample preparation of ^{13}C analysis. The number and length of laterals (1 st and 2 nd order laterals) per segment and the length of every 1 st order lateral was measured. The 1 st order laterals which produced the 2 nd order laterals were denoted as the L-type laterals and those developing no higher order laterals as the S-type laterals. No lateral of the 3 rd order was observed.

Table 1. Effect of shading on length of seminal axis (mm) of corn seedlings[1]

Plot[2]	Days after shading 0	2	3	5
Cont.	544±19	644±41	605±30	636±39[3]
S1	—	613±36	663±14	667±41
S2	—	602±15	635±27[3]	640±23[3]

1) Data are expressed as the mean±standard error (n=3). Values in the same column are not significantly different at 5% level.
2) Light intensity was reduced to 57% (S1, 500 μmol/m^2/s) and 25% (S2, 220 μmol/m^2/s) of control (Cont., 880 μmol/m^2/s) plants.
3) n=2.

Results

Changes in dry weight of each plant part; Increment of dry weight of the shoots and seminal roots was reduced by shading treatments (Fig. 2). The magnitude of reduction of RGR was larger in the seminal roots than the shoots. The RGR of the laterals during the experiment period was 60% and 12% of Control for S1 and S2, respectively. On the contrary, the effect on the axis dry weight was not clear, since the increment of dry weight of the axis was very small in all treatments (RGR, 0—0.02) during the experimental period (data not shown).

Development of the seminal root; At the end of experiment, no significant difference in axis length was found among regimes (Table 1). In contrast, development of the laterals was greatly affected by shading treatments (Table 2). On Day 3 (five days after shading), total number of laterals (1 st order+2 nd order) was 73% and 35%, and total length of laterals was 74% and 42% of Control for S1 and S2, respectively.

Development of laterals along seminal axis; Figure 3 shows the distribution of laterals along the seminal axis on Day 3. In S2 plants, number of S-type laterals was reduced (67% of Control) in the regions of 10—20 and 20—30, while in the apical region of tip-10 S-type laterals were around 19 times densely developed, as

Table 2. Effect of shading on development of the laterals of seminal roots of corn seedings[1].

Plot[2]	Days after shading 0	2	3	5
		Total number of laterals per axis[3]		
Cont.	1290±136	2458±212	1824±458	3081±665
S1	−	ND[4]	ND	2253±526(73)
S2	−	1518±52(62)	1034±192(57)	1067± 27(35)
		Total length of laterals per axis(m)[3]		
Cont.	8.1±0.8	14.3±2.8	10.1±2.4	16.7±3.0
S1	−	ND	ND	12.3±2.5(74)
S2	−	8.7±0.3(61)	6.4±1.2(63)[5]	5.9±0.4(36)[5]

1) Data are expressed as the mean±standard error(n=3) ; values in parentheses are indicated as % of control.
2) See Table 1.
3) Total laterals=L-type+S-type+2nd.
4) Not detected.
5) n=2.

compared with Control. The number of L-type and 2 nd order laterals was smaller in S2 plants than Control, particularly in the regions of 10—20 and in 20—30, where no 2 nd order lateral was observed. In S1 plants distribution of the laterals of each category shows a transitional pattern between Control and S2.

The basic features of distribution pattern of length of laterals along the axis as affected by shading were similar to that described on number of laterals, therefore the data were not listed.

^{13}C incorporation in the plant ; Amounts of ^{13}C (labelled carbon) recovered in the whole plant are shown in Table 3. Just after the termination of $^{13}CO_2$ feeding (Day 0), amount of ^{13}C assimilated by plants for Control, S1 and S2 were 23.7, 14.3 (60% of Control) and 3.7 mg (16% of Control), respectively. By Day 3, substantial amount of ^{13}C incorporated initially by the plants was lost in each regimes, mainly due to respiratory loss during the period.

^{13}C allocation in the roots by Day 1 ; Figure 4 shows percent distribution of ^{13}C in the root system. Rapid increases of ^{13}C distribution in the root system (nodal+axis+laterals) by Day 1 was associated with the rapid decrease of ^{13}C share in the mature leaves occurred in the same period, which is similar to other results[4,14]. Percent distribution of ^{13}C in the

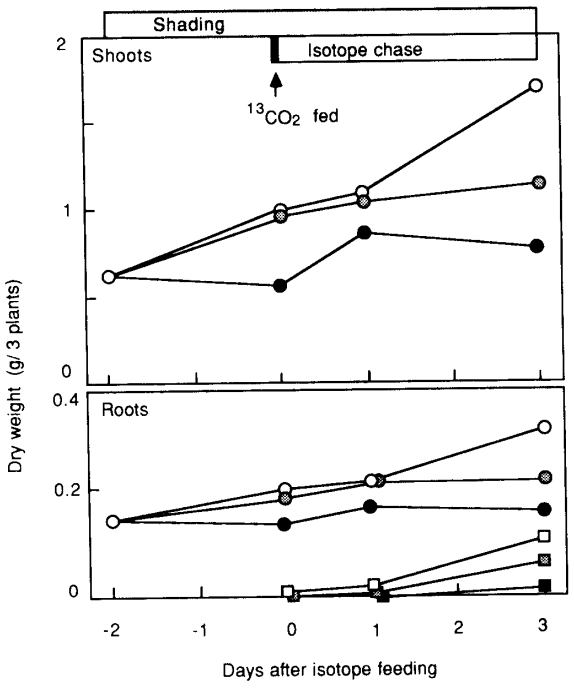

Fig. 2. Changes in dry weight of the shoots (upper, leaves+stem ; ○), the nodal roots (lower, □) and the seminal roots (lower, ○) during the experimental period. Control, S1 and S2 treatments (see Table 1) are expressed as the open, dotted, and filled symbols, respectively. Plants for S1 and S2 were shaded for 2 days prior to $^{13}CO_2$ feeding then grown under same condition for 3 consecutive days for isotope chase.

seminal root (axis+laterals) was reduced by shading, particularly in S2 plants. Amounts of ^{13}C translocated to the seminal roots by Day 1 were 1666 and 564 μg (77% and 26% of Control) in S1 and S2 plants, respectively.

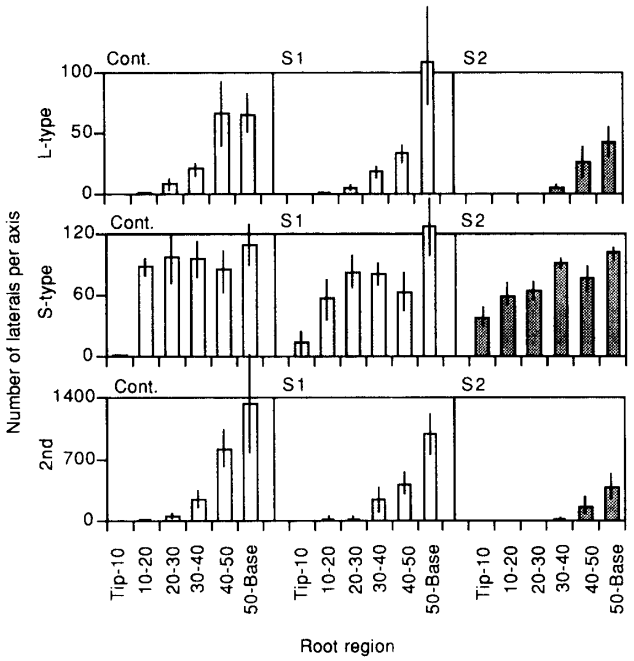

Fig. 3. Distribution of number of the laterals of L-type, S-type and 2 nd order along the seminal axis of corn seedlings (5 days after shading). Treatments for S1 and S2; see Table 1. Bars represent twice standard errors of the mean.

^{13}C allocation in the seminal root by Day 1; By shading ^{13}C share of the axis was increased from 4.3% (Cont.) to 5.3% (S2), although the amount of labelled carbon transferred to the seminal root was reduced considerably. As shown in Fig. 5 marked enhancements of ^{13}C accumulation in the tip and axis of tip-10 were found in the shaded plants. The ^{13}C shares of root tip and the axis of tip-10 were 1.8 and 1.9 times larger in S1, and 2.9 and 1.7 times larger in S2, as compared with the Control, respectively. The amounts of ^{13}C incorporated in the tip was 64, 85 and 65 μg for Control, S1 and S2, respectively.

By shading ^{13}C distribution in total laterals was decreased from 8.7% (Cont.) to 4.2%

Table 3. Recoveries of labelled carbon (^{13}C mg/3 plants) in the whole plants.

Plot[1)]	Days after $^{13}CO_2$ feeding 0	1	3
Cont.	23.69(100)	16.82(71)	22.06(93)
S1	14.30(60)	13.01(55)	7.79(33)
S2	3.74(16)	5.93(25)	3.31(14)

Values in the parentheses are expressed as % of control on Day 0.
1) See Table 1.

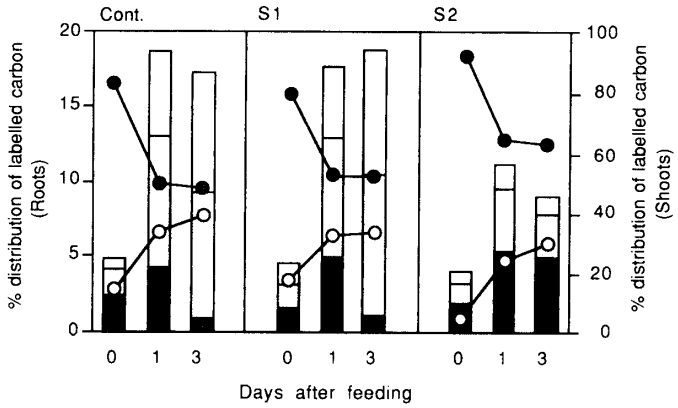

Fig. 4. Percent distribution of labelled carbon in the mature leaves (●), developing leaves+stem (○), nodal roots (□), seminal axis (■), and laterals (❑) of corn seedlings as affected by light intensity. Treatments for S1 and S2; see Table 1. Values are the average of 3 plants and expressed as the percentage of labelled carbon recovered in the plant on each sampling day.

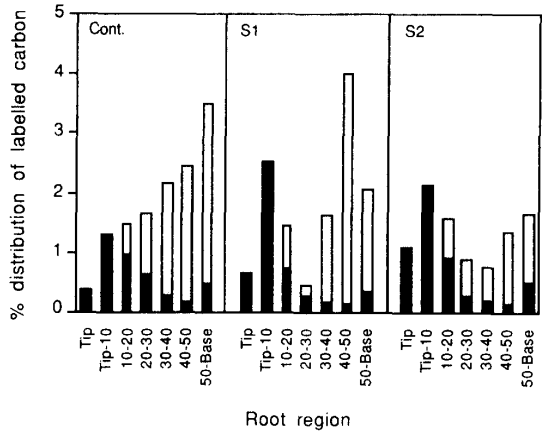

Fig. 5. Percent distribution of labelled carbon in the axis (■) and laterals (□) of different regions along the seminal axis of corn seedlings as affected by light intensity ; one day after $^{13}CO_2$ feeding. Treatments for S1 and S2 ; see Table 1. Values are the average of 3 plants and expressed as the percentage of labelled carbon recovered in the plant.

(S2). Except for the 40—50 region of S1 plants, ^{13}C share of the laterals was decreased by shading particularly in the basal regions (30—40, 40—50, 50-base), where most development of 2 nd order laterals took place (Fig. 3).

^{13}C allocation in the seminal root by Day 3; During the period from Day 1 to Day 3 a large percentage of the ^{13}C previously incorporated was lost from the axis of Control plants, especially in the tip and tip-10 around 94%—98% of the ^{13}C allocated by Day 1 was lost subsequent 3 days (data not shown). In contrast, for shaded plants, ^{13}C lost by Day 3 was smaller than Control in the tip and axis of tip -10 region, particularly in tip-10 region ^{13}C remained by Day 3 was larger as compared with Control. Amounts of ^{13}C found in the axis of tip-10 region were 7.1, 11.2 and 83.9 μg for Control, S1 and S2 regimes, respectively.

Discussion

Growth in dry weight of the seminal root was retarded as light intensity was lowered (Fig. 2). The amount and percentage of ^{13}C translocated to the seminal root was also decreased by shading treatments (Fig. 4). Although development of total laterals of the seminal roots was retarded (Table 2), extension rate of the seminal axis was not decreased significantly under low light intensities (Table 1). This indicates that proliferation and subsequent elongation of root cells responsible for axis extension takes place in shaded plants to a similar extent to the Control in the apical region of seminal axes. In corn roots, the most rapid cell division and cell enlargement occurred in the main axis within 2.5 mm and 10 mm from apex of root cap, respectively[3]. These zones correspond to the tip and an apical part of the tip-10 regions of the axis in the present experiment, respectively.

As shown in Fig. 4, allocation of ^{13}C-assimilates to the seminal axis was little affected or rather enhanced by shading, notwithstanding that ^{13}C allocation to the whole root system was reduced considerably. Patterns of ^{13}C distribution along seminal axis indicated that amount of ^{13}C incorporated to the apical region of axis (tip and tip-10) of shaded plants was not decreased significantly, but rather increased in percent distribution bases (Fig. 5). This suggests that, even under shaded conditions, the sufficient amount of photosynthate is unloaded in this apical region to meet demand for the carbon which is utilized for the extension of seminal axis. An intensive incorporation of ^{13}C to proteins and structuralcarbohydrates for construction of new tissues might take place in the tip and tip -10 of shaded plants, since a large proportion of ^{13}C translocated to these regions by Day 1 had remained by the end of chase period. Most of the labelled carbon remained by 3 days after isotope feeding was found in the structural materials in the roots[4].

Kawata and Matsui[5] cultured the rice seminal roots in vitro by means of the bi-media culture method, and changed the glucose content in the media which was supplied to the basal part of the roots on the course of root culture. They reported that when concentration of glucose was changed from 7% to 0.5%, development and extension of lateral roots in the axis zone which subsequently elongated after the treatment were greatly reduced, while the extension rate of the seminal axis was not reduced as compared with the Control during the subsequent 7 days of culture. Although they did not demonstrate localized accumulation of carbohydrates transferred from the media via the phloem, their result is consistent

with our result found in the present experiment in terms of axis elongation.

In the seminal root system transverse area of the phloem in vascular cylinder varies among root members, and in the root showing larger diameter have larger area of the phloem[7,12]. Supposing that conductivity of photoassimilates transported down in the root depends upon size of the phloem and the conductivity increases exponentially as the function of phloem size, photosynthate is more readily unloaded in the apical meristem of root members having larger root diameters than that with smaller diameters, and this trend can be amplified when carbon transfer from shoots becomes critical. According to this hypothesis, the present results can be interpreted that a larger channel for phloem transport in the seminal axis than laterals leads to an enhancement of preferential unloading of ^{13}C to the apical meristem of seminal axis as compared with laterals when current supply of ^{13}C from shoots is reduced. In fact, as ahown in Fig. 5, unloading of ^{13}C-assimilates to the laterals was reduced, particularly in the laterals developing 2 nd order laterals (Fig. 3) which have poor phloem sizes.

In the present experiment, however, development of 1 st order laterals was stimulated in the local region of axis within 10 cm from the apex of shaded plants (Fig. 3). This response is analogous to a vigorous extension of laterals which followed the removeal of the apex of main axes[1], suggesting possible shifts of hormonal balance occurred in the axis of present experiment.

It has been reported that when inorganic nutrients are supplied to a specific part of the seminal axis, the development of laterals in that part is enhanced[2]. In such cases for corn seminal roots, a specific incorporation of photosynthate to the zone of supply was demonstrated recently by Sattelmacher and Thoms[13]. Phytohormones are transported in the phloem down to the roots together with photoassimilates, particularly auxins transported from shoots to roots[10]. They suggested that enhancement of unloading of photosynthate might lead to endogenous shifts of hormonal balance responsible for the increased development of laterals in the zone of nutrient supply.

The result of Kawata and Matsui[5] for rice seminal roots indicated that lateral root developments were retarded along entire root axis including tip-10 cm region. This is not consistent with our results in terms of lateral roots development. The discrepancy may be partly due to the differences in carbohydrate levels supplied via the phloem to the roots, and partly due to the plant species used for experiments.

Many studies revealed that root development was severely depressed when plants were shaded for prolonged period[6,10]. The continuous extension of the axis and enhancement of development of laterals in the shaded plants found in the present experiment may be a temporal response of the roots. Further and more detailed experiments are needed.

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