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Variation in the export of ^{13}C and ^{15}N from soybean leaf: the effects of nitrogen application and sink removal

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Abstract

Translocation of carbon and nitrogen within a single source-sink unit, comprising a trifoliated leaf, the axillary pod and the subtending internode, and from this unit to the rest of the plant was examined in soybean (*Glycine max* L. cv. Akishirome) plant by feeding $^{13}CO_2$ and $^{15}NO_3$. The plants were grown at two levels of nitrogen in the basal medium, i.e. low-N (2 g N m^{-2}) and high-N (35 g N m^{-2}) and a treatment of depodding was imposed by removing all the pods from the plant, except the pod of the source sink unit, 13 days after flowering. The plants at high-N accumulated more biomass in its organs compared to low-N and pod removal increased the weight of the vegetative organs. When the terminal leaflet of the source-sink unit was fed with $^{13}CO_2$, almost all of the radioactive materials were retained inside the source-sink unit and translocation to rest of the plants was insignificant under any of the treatments imposed. Out of the^{13}C exported by the terminal leaflet, less than half went into the axillary pod, as the lateral leaflets claimed equal share and very little material was deposited in the petiole. Pod removal decreased ^{13}C export at high-N , but not at low-N. Similar to ^{13}C, the source-sink unit retained all the ^{15}N fed to the terminal leaflet at high-N. At low-N, the major part of ^{15}N partitioning occurred in favour of the rest of the plant outside the source-sink unit, but removal of the competitve sinks from the rest of the plants nullified any partitioning outside the unit. Unlike the situation in ^{13}C, no partitioning of ^{15}N occurred in favour of the lateral leaflets from the terminal leaflet inside the unit. It is concluded that sink demand influences partitioning of both C and N and the translocation of carbon is different from that of nitrogen within a source-sink unit. The translocation of the N is more adjustive to a demand from other sink units compared to the C.

Introduction

N and C metabolism are tightly linked in all biochemical pathways of the plant and demand for both the elements are are quite high. In the leaf oxidised forms of carbon and nitrogen are reductively assimilated into sucrose (Stitt and Quick, 1989) and amino acids (Miflin and Habash, 2002; Miflin and Lea, 1976) before they are translocated in the phloem to the sink for utilization (Lawlor, 2002). Sucrose is the major solute in the phloem translocate (Patrick, 1997) and the concentration of this material determines the turgor induced mass flow in the sieve tube. Thus, movement of nitrogenous materials depends on the flow of the sugars from the source to the sink and any manipulation of source or sink activity that influences carbon partitioning is expected to have similar influence on nitrogen movement. However, exceptions to this logic has been reported in the literature. Yoneyama et al. (1980) observed that the transfer ^{13}C from a matured leaf and its partitioning into various plant parts differed from that of ^{15}N, when both the elements were fed simultaneously to the leaf. Such aberrations can occur, because of the interaction of the end products of the assimilatory pathways with the enzymes regulating the processes of assimilation. In the leaf, both

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sucrose phosphate synthase and nitrate reductase compete for the carbon material and energy produced by photosynthesis (Foyer and Galtier, 1996) for activation of the C and N assimilatory pathways, respectively. However, some evidences indicate that C and N assimilatory pathways in leaf are not competitive for carbon and energy. There is continuous reciprocal co-regulation between the pathways (Champigny and Foyer, 1992; Huber et al., 1992). While sucrose can induce expression of NR gene (Botrel and Kaiser, 1997; Cheng et al., 1992; Klein et al., 2000; Vincentz et al., 1993) and increase nitrate assimilation (Stitt et al., 2002), its accumulation can result in a decline in carbon assimilation (Foyer and Galtier, 1996). Similarly, nitrate uptake is reduced by feedback inhibiton from its end products of nitrate assimilation (Gojon et al., 1998; Tischner, 2000), while it may be useful for promotion of activity of carbon fixing enzyme PEPcase (Foyer and Galtier, 1996). Thus, carbon metabolism is intricately related to that of nitrogen, and any effect impacting availability of one element in the environment of the plant is bound to have an influence on the other (Noctor and Foyer, 2000; Paul and Foyer 2001). While considerable information is available on interaction between the two assimilatory pathways (Lawlor, 2002) determining the acquisition of the elements into the plant (Vivin et al., 1996), less information is available on the nature of their partitioning to different sink organs by translocation. To resolve the confusion existing in the partitioning of C and N, an experiment has been designed to discriminate between the translocation of N and C from the leaf. The source and sink activities have been manipulated by varying the amount of nitrogen in growth medium and removal of pods from the plant, respectively.

Materials and methods

Plant material and growth conditions

Soybean (*Glycine max* L. cv. Akishirome) was grown in the experimental plots of Hiroshima University, Japan during the period from May to October, 1996. Commercial fertilisers containing N, P and K were applied in the basal medium at the ratio of 350:150:150 for high N treatment and 20:150:150 for the low N treatment. The soil of the experimental area was a granite regosol. Soil pH was adjusted to 6.0 before fertiliser application with dolomitic calcium carbonate (150 g m^{-2}). *Rhizobium japonicum* strain 10 was used for inoculation. The plants were spaced at a distance of 50 cm within a row and inter row spacing was 100 cm. Depodding treatment was imposed to both low and high nitrogen treatments by removing all visible pods from the plants at 13 days past flowering except the pod on the axil of the 4th trifoliate leaf from the shoot apex. The 4th trifoliate leaf, the pod in its axil and the subtending internode were considered a single source sink unit. The experimental design was a randomised block with three replicates.

$^{13}CO_2$ and $^{15}NO_3$ feeding

The plants reached the stage of flowering on day 58 after seeding. $^{13}CO_2$ was fed to the plants on day 14 after flowering by applying the stable isotopic carbon to the terminal leaflet of the 4th trifoliate leaf from the shoot apex. The leaflet was enclosed inside a transparent plastic bag (600 mL) containing a beaker with 1 g of $Ba^{13}CO_3$ (99 atom% ^{13}C). CO_2 was generated by introduction of 5 ml of 2 M $HClO_4$ into the beaker and the leaf was allowed to assimilate for one h under natural light. CO_2 concentration inside the bag increased to 650 μl L^{-1} in the first 10 min before declining to ambient level during next 20 min. Immediately after ^{13}C feeding, ^{15}N was fed to the same leaflet by dipping it into a beaker containing 100 mL of 100 mg kg^{-1} N as $K^{15}NO_3$(99.4 atom%) for 3 h. The leaflet was washed after N feeding with distilled water. During $^{13}CO_2$ and $^{15}NO_3$ feedings, the PAR (photosynthetic active radiation) ranged from 1707 to 1877 with average of 1760 μ mol. m^{-2} sec^{-1}.

Harvesting

Plants were harvested on d 2 and 6 after the assimilation. The ^{13}C fed leaf with its subtending stem internode and pod if any on the axil is considered a single source-sink unit (Tanaka and Fujita, 1974). At the time of harvest, this unit was separated from the rest of the plant parts. The source-sink unit was further separated into ^{13}C fed terminal leaflet, lateral leaflets of the same leaf, leaf petioles and the stem internode, pod shells and grain. The other parts of the plant were separated into leaves, grains, pod shells, stem internodes with leaf petioles and roots. The plant parts were dried in an open air oven at 80 °C for 72 h, weighed and ground to powder with a vibrating sample mill (Model TI-100, Heiko Co. Ltd. Iwaki, Japan).

^{13}C and ^{15}N analysis

^{13}C and ^{15}N abundance in plant material was determined with a mass spectrometer (ANCA-SL, Europa Scientific, Franklin, OH). The ^{13}C atom% excess in the plant sample was calculated as the difference in ^{13}C atom% between the sample and the standard pure chemical, glycine. The amount of labelled carbon (A) in the sample was calculated using the following equation

$$A = \frac{^{13}C \text{ or } ^{15}\text{Natom\% excess in the sample}}{^{13}C \text{ or } ^{15}\text{N atom\% excess in the control plant}} \times \text{amount of C or N in the sample}$$

The partitioning of the isotope was calculated as the percentage of the total label outside the fed leaflet. Export rate of the isotope was calculated by the equation mentioned below.

$$\text{Export rate of } ^{13}\text{C or } ^{15}\text{N} = \frac{^{13}\text{C or } ^{15}\text{ N in whole plant} - ^{13}\text{ C or } ^{15}\text{ N in fed leaflet}}{^{13}\text{C or } ^{15}\text{N in whole plant}} \times 100$$

Statistical analyses

All the experiments were analysed for the effect of treatments according to the expected mean sqauares given by McIntosh (1983). For mean separation, treatment sum of sqauares were partitioned by the method of orthogonal contrasts. The CVs of all response variables were below 10%.

Results

Plant biomass and grain yield

The plants had nearly reached the maturity stage of development and increase in biomass of the plants during the period of the treatments was marginal. The whole plant and pod weight were smaller at low-N than at high-N application (Figure 1). Pod removal increased the weight of the vegetative organs of the plant significantly at both nitrogen levels. The plants at high-N accumulated more nitrogen than that in low-N level and pod removal decreased the nitrogen contents (data not shown). Fifty one to 69% of the whole plant nitrogen was found in the grains of the control plants and only less than 2% of the element was available in the source-sink unit to which tracers were fed.

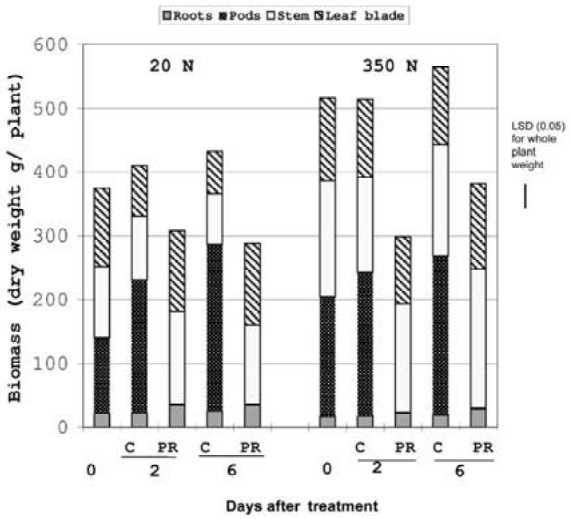

Figure 1. The effect of pod removal on biomass accumulation on plant parts of soybean plant at different N levels. C: Control; P: Pod removal.

Partitioning of ^{13}C

^{13}C atom % excess was high in the terminal leaflet to which $^{13}CO_2$ was fed (Table 1). The concentration of the isotopic carbon in the other two leaflets of the same leaf was almost similar to that of the terminal leaflet. The concentration of the material was very low in the petiole. Compared to the petiole, more ^{13}C moved into the seeds and pod shell on the axil of the leaf. The movement of the isotopic carbon was absolutely minimal to rest of the plant parts. Two days after feeding, ^{13}C atom % was higher at low-N than at high N within the organs of the source-sink unit, but at day 6, the difference between the two N-treatments decreased . Similarly, pod removal resulted in accumulation of high concentration of ^{13}C in the leaflets on day two after treatment at low-N compared to high-N, but on day 6, the effect of pod removal at low-N was not significant. Pod removal increased ^{13}C atom % of the seeds and pod shell significantly both at low and high N.

The export rate of ^{13}C from the terminal leaflet of the source-sink unit was nearly 80% at high level of N application and N deficiency did not decrease it significantly (Figure 2). Pod removal decreased the export rate significantly at both nitrogen levels on day 2, but the effect of pod removal was not significant at day 6. Most of the ^{13}C fed into the leaflet were retained inside the components of the source-sink unit and hardly any significant partitioning occurred into the other parts of

Table 1. The effect of pod removal and N level of growth medium on ^{13}C atom % excess in various parts of soybean plant

	Plant parts	2 d[1]					6 d[1]				
		20 N[2]		350 n[2]		LSD	20 N[2]		350 N[2]		LSD
		C[3]	P[3]	C[3]	P[3]	0.05	C[3]	P[3]	C[3]	P[3]	0.05
	Seeds	0. 557	0.303	0.543	0.505	NS	0.335	0.576	0.224	0.770	0.296
	Pod shell	0.220	0.102	0.139	0.227	0.11	0.117	0.394	0.084	0.418	0.217
Unit[4]	Terminal leaflet	2.297	2.840	1.176	1.948	0.799	1.499	1.002	1.344	2.036	0.88
	Lateral leaflets	2.073	2.486	1.674	1.285	0.766	1.323	1.412	1.531	1.785	NS
	Petioles	0.161	0.299	0.099	0.435	0.149	0.312	0.686	0.164	0.515	0.35
	Seeds	0.001		0.005		NS	0		0.002		NS
Others[4]	Pods	0		0		NS	0	0.005	0.002		NS
	Stem	0	0	0	0	NS	0	0	0	0	NS
	Roots	0	0	0	0	NS	0	0	0	0	NS
	Roots	0	0	0	0	NS	0	0	0	0	NS
	LSD (0.05)	1.362	1.301	0.833	0.842		0.874	0.561	0.832	0.854	

[1]2 d and 6 d: 2 and 6 days after treatment.
[2]20N: 2 gN m^{-2}; 350N: 35 gN m^{-2}.
[3]C: control; P: pod removal.
[4]Unit: a souce-sink unit; Others: other parts of the plant except the unit.

Table 2. The effect of pod removal and N level of growth medium on the percentage of ^{13}C partitioning into various parts of soybean plant

	Plant parts	2 d					6 d				
		20 N*		350 N*		LSD	20 N*		350 N*		LSD
		C	P	C	P	0.05	C	P	C	P	0.05
	Seeds	40.8	26.8	43.3	36.8	9.1	52.0	33.4	35.9	28.7	15.4
Unit	Pod shell	9.2	5.8	6.2	9.1	2.0	7.0	13.8	5.4	9.2	3.7
	Lateral leaflets	40.3	54.2	41.8	34.5	11.9	24.3	34.7	44.6	47.9	10.1
	Petioles	3.6	13.3	4.0	19.6	7.5	1.0	17.3	3.6	11.9	7.8
Others		6.4	0.0	4.8	0.0		19.0	0.8	10.5	2.4	

[1] 2 d and 6 d: 2 and 6 days after treatment.
[2] 20N: 2 gN m^{-2} ; 350N: 35 gN m^{-2}.
[3] C: control; P: pod removal.
[4] Unit: a souce-sink unit; Others: other parts of the plant except the unit.

the plant outside the unit (Table 2). Within the source sink unit, the percentage of ^{13} C distribution was high in the two lateral leaflets of the ^{13}C fed trifoliate leaf. The pod accumulated ^{13}C comparable to that of the two lateral leaflets within the unit, but movement of the material to the petiole was poor. At high-N level, less ^{13}C was found in the pods compared to the low-N on day 6, but the effect of nitrogen was just the opposite for the lateral leaflets . Pod removal decreased distribution of ^{13}C into the pod of the unit at low-N, but not at high-N. In contrast to this, partitioning was increased to lateral leaflets at low-N, but not at high-N by pod removal. Pod removal enhanced partitioning to petiole both at high and low-N.

Reduced nitrogen contents

The reduced nitrogen percentage was the highest in the grains and lowest in the petiole within the source-sink unit (Table 3). In the rest of the plant parts, the stem and roots possessed the lowest concentration of nitrogen. Nitrogen treatment did not exhibit consistent significant effect on the N content of the plant parts. In contrast to this, pod removal increased the concentration of N in all components of the source-sink unit

Table 3. The effect of pod removal and N level of growth medium on the reduced-N percentage in parts of soybean plant

	Parts	2 d				6 d				
		20 N		350 N		20 N		350 N		LSD
		C	P	C	P	C	P	C	P	0.05
Unit	Seeds	6.47	7.56	7.57	7.72	6.35	6.61	6.27	6.89	0.48
	Pod shell	1.92	2.30	1.86	2.61	1.31	1.92	1.92	5.52	0.57
	Lateral leaflet	3.42	4.34	3.34	3.26	2.51	2.72	2.52	3.47	0.55
	Lateral leaflets	3.29	3.69	3.47	3.35	2.57	3.13	2.73	3.19	0.45
	Petioles	1.20	2.72	0.86	1.96	0.85	1.89	0.74	1.45	0.49
Others	Seeds	6.50		6.57		6.10		6.46		NS
	Pod shell	1.88		2.01		1.47		1.80		0.36
	Leaves	3.40	4.33	3.36	3.43	2.69	2.92	2.99	3.47	0.35
	Stem	1.26	2.07	1.04	1.84	0.85	1.87	0.98	1.92	0.53
	Roots	1.43	1.57	0.91	1.01	0.76	1.34	0.94	1.23	0.29

[1] 2 d and 6 d: 2 and 6 days after treatment.
[2] 20N: 2 gN m^{-2} ; 350N: 35 gN m^{-2}.
[3] C: control; P: pod removal.
[4] Unit: a souce-sink unit; Others: other parts of the plant except the unit.

Table 4. The effect of pod removal and N level of growth medium on ^{15}N atom% excess in various parts of soybean plant

	Parts	2 d					6 d				
		20 N		350 N			20 N		350 N		
		C	P	C	P	LSD	C	P*C*P	LSD		
Unit	Seeds	606	2.1	12.0	5.2	6.39	4	7.9	3.3	3	3.99
	Pod shell	2.5	1.1	4.2	1.2	1.38	1	6.9	2.1	3.6	3.62
	Terminal leaflet	50.7	53.3	76.9	30.7	24.23	29.9	24.7	56.3	33.2	12.39
	Lateral leaflets	0.8	2.3	0.9	0.8	1.84	0.1	7.1	2.0	3	0.66
	Petioles	3.5	4.7	9.0	6.5	4.52	6.1	27.1	5.9	9.6	6.38
Others	Seeds	0.1		0			0.1	0			
	Pod shell	5.6			0		0		0		
	Leaves	0	2.1	0	0		0	0.7	0	0	
	Stem	0	2.4	0	0		0	2.3	0	0	
	Roots	0	0	0	0		0	0	0	0	

[1] 2 d and 6 d: 2 and 6 days after treatment.
[2] 20N: 2 gN m^{-2} ; 350N: 35 gN m^{-2}.
[3] C: control; P: pod removal.
[4] Unit: a souce-sink unit; Others: other parts of the plant except the unit.

at both low and high N levels. Similar to ^{13}C atom % excess, all the ^{15}N atom % excess were retained within the source-sink unit to which the tracer material was fed and very little of the material moved out to the rest of the plant parts (Table 4). Most of the isotopic material was found to be present in the terminal leaflet to which it was fed. But in contrast to ^{13}C, the ^{15}N atom % excess was very low in the two lateral leaflets of the trifoliate leaf to which the isotope was fed, and the pod growing on the axil of the leaf also did not receive enough of the ^{15}N . The ^{15}N atom % excess was higher at high-N level compared to low-N in most of

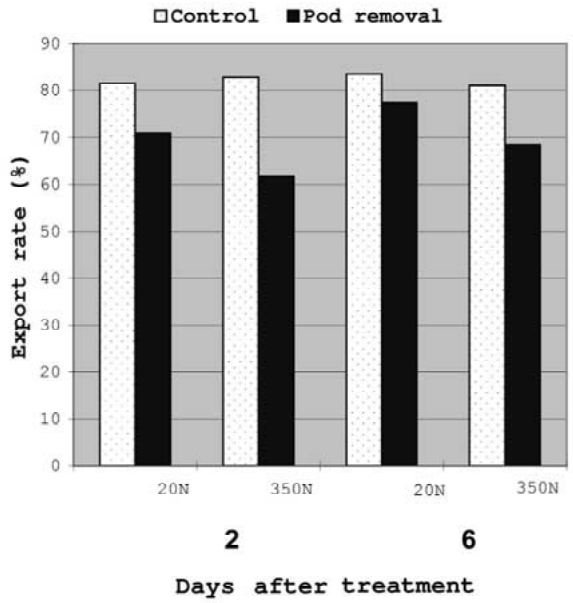

Figure 2. The effect of pod removal and N level of growth medium on export rate of ^{13}C from a terminal leaflet of a soybean trifoliate leaf.

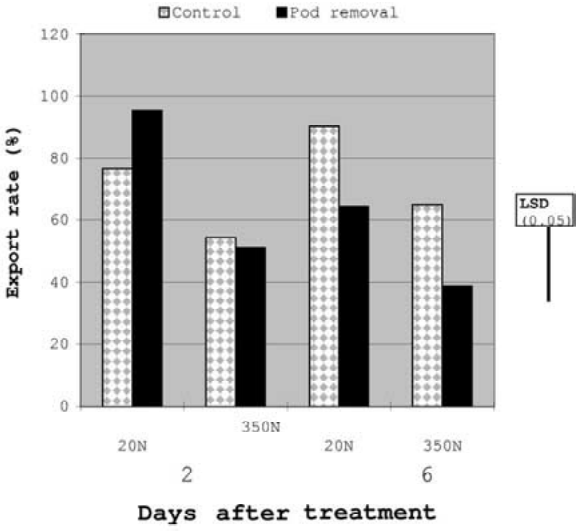

Figure 3. The effect of pod removal and N level of growth medium on export rate of ^{15}N fed from a terminal leaflet of a soybean trifoliate leaf. 20 N: 20 KgN/ha; 350 N: 350 KgN/ha.

the components of the source-sink unit. Pod removal decreased the ^{15}N atom % excess of terminal leaflet significantly at high N level, but at low N its effect was not significant.

Partitioning of ^{15}N

The export rate of ^{15}N from the terminal leaflet of the source-sink unit was low at high level of N application in comparison to that of low N (Figure 3). Pod removal did not influence the rate on day 2, but its effect at day 6 was significant. It decreased the export rate at both high and low N . The partitioning of ^{15}N was poor in the different plant parts of the source-sink unit at low N level, but it was very high at high N level (Table 5). Within plant parts of the unit, the grains received the maximum concentration of the material and concentration was very low in the lateral leaflets and petiole. At low level of N, distribution increased in favour of the rest of the plants, but this was not so at high-N. At high- N, pod removal decreased ^{15}N distribution in the grains of the axillary pod, but distribution increased in other organs like the lateral leaflets and petiole; the distribution to other vegetative parts within the rest of the plant parts was nil. At low-N, pod removal increased the distribution significantly in all components of the source-sink unit and a large amount of the isotope moved into the other plant parts outside the unit.

Discussion

Results obtained in the present experiment clearly revealed the difference between partitioning of carbon and nitrogenous compounds from the leaf. Partitioning of ^{13}C to the lateral leaflets from the terminal leaflet was very high (Tables 1 and 2), but it was not so for the ^{15}N (Tables 4 and 5). In contrast to ^{13}C, very little ^{15}N moved into the lateral leaflets after feeding. Since the lateral leaflets were active sink for the carbon, they could have also used the nitrogen assimilated by the terminal leaflet, but there was discrimination . The lack of co-ordination between the two types elements indicated that their translocation in the phloem was not similar. Generally, the proton coupled transporters located on cell membrane for sucrose and amino acids are symporters (Bush, 1993), and this similarity precludes any reason for variation in loading and unloading of the two types of materials in the cells of the terminal and lateral leaflets. Hence, it is believed that the difference in partitioning of the material occurred due to variation in mobility of the materials in the sieve tube. However, in phloem translocation most of the attention has been given to the role of major solute, i.e. sucrose and/or its derivative sugars (Patrick, 1997;

Table 5. The effect of pod removal and N level of growth medium on the percentage of ^{15}N partitioning into various parts of soybean plant

	Parts	2 d					6 d				
		20 N		350 N		LSD	20 N		350 N		LSD
		C	P	C	P	0.05	C	P	C	P	0.05
	Seeds	16.0	1.2	89.8	50.4	39.9	33.9	47.0	83.8	53.0	26.7
Unit	Pod shell	1.7	0.3	5.8	12.3	5.4	0.8	9.3	10.2	14.1	8.4
	Lateral leaflets	1.0	0.1	1.8	8.4	3.5	0	30.0	1.5	7.1	3.2
	Petioles	1.3	1.1	3.3	29.1	12.7	0.2	13.6	4.7	25.7	11.4
	Seeds+Pod shell	80.2		0			65.2		0		
Others	Leaves	0	41.8	0	0		0	0	0	0	
	Stem	0	55.7	0	0		0	0	0	0	
	Roots	0	0	0	0		0	0	0	0	

[1] 2 d and 6 d: 2 and 6 days after treatment.
[2] 20N: 2 gN m^{-2} ; 350N: 35 gN m^{-2}.
[3] C: control; P: pod removal.
[4] Unit: a souce-sink unit; Others: other parts of the plant except the unit.

Turgeon, 1995; Van Bel, 1993) and their role in signal transduction in the plant system has been highlighted (Koch, 1996). It is argued that principle and concepts of sugar unloading are applicable to the other phloem mobile solutes (Patrick, 1997) including nitrogenous materials. Therefore, our results emphasize the need for re-examination of the transport processes of sugars and nitrogenous solutes. Although it is agreed that the mass flow of solutes between the source and sink occurs due to pressure gradient in the sieve tube during translocation (Oparka and Cruz, 2000), the major solute can not always dictate the direction of flow of the minor solutes. It was reported that C/N ratio of different organs of sunflower plant were not identical (Yoneyama et al., 1980). Thus, the flux of C or N to a organ depends on their requirement in growth of the organ.

The analyses of export rates of the two elements have also confirmed the independence of C and N translocation in soybean plant. In the present study, the rate of export of ^{13}C from the leaf into the sink was approximately 40% at 6 d after $^{13}CO_2$ feeding (Table 2). This figure is comparable to those reported for ^{14}C assimilation in soybean, castor bean, *Nicotiana affinis* (Hofstra and Nelson, 1969), tomato (Tanaka and Fujita, 1974) , barley, oat, wheat, bean, pea and pepper (Grodzinski et al., 1998), but lower to some others, such as, sunflower, sorghum (Hofstra and Nelson 1969), corn (Tanaka and Yamaguchi, 1972), millet and sugarcane (Grodzinski et al.,1998). In our study, the export rate of ^{13}C from the terminal leaflet of the trifoliate leaf was 75–80%; but export rate from the whole leaf declined to approximately 40% as an identical amount of the ^{13}C were partitioned into the two lateral leaflets (Table 2). In contrast to this, export rate of ^{15}N from the trifoliate leaf was high, because no ^{15}N moved from the terminal leaflet to the lateral leaflets (Table 5). It may be possible that the demand for nitrogen in the fruits may be higher than that of carbon necessitating quick movement of the material after its feeding in the terminal leaflet. The demand for nitrogen in such organs decreased and export rate from the terminal leaflet decreased when the plants were grown at high level of N (Figure 3). Contrary to high N, export rate at low N increased from the terminal leaflet and ^{15}N were partitoned not only within the unit but also outside it and partitioning from the unit to rest of the plant parts discouraged temporally, when the pods were removed (Table 5). Thus, under nitrogen limiting conditions, export rate of N from the leaf is regulated not only by the fruit growing in its axil, but also by other sink organs existing on the other parts of the plant. Sink activity has been reported to regulate nitrate reduction in leaf of soybean (Nobuyasu et al., 1997). In contrast to this, carbon partitioning is rigid and less adjustible to a demand from other sinks.

Removal of pods decreased the export rate of ^{15}N from the terminal leaflet significantly with passage of

time (Figure 3), because the fruits were the major sink organs of the plant. Consequently, more nitrogen accumulated in the leaflets and petiole (Table 4). It is reported that pod removal in soybean affects nitrate reduction more than that of nitrate uptake or transport (Fujita et al., 1992), and such an effect in the present experiment might have led to the reduction of ^{15}N from the leaflet. Removal of pods did not have the effect of similar magnitude on ^{13}C accumulation (Table 1). Although export rate for ^{13}C declined by pod removal (Figure 2), it was much less compared to the large decrease in export rate of ^{15}N (Figure 3). Unlike the situation in ^{15}N partitioning, the unused isotopic carbons did not mobilise into the lateral leaflets of the source sink unit. These observations also suggest that translocation of C and N were not similar from the source to the sink.

During pod development fruits are the major sink for C and N assimilates from the source in legumes. The fruit needs both the elements as utilization of sugars in the sink is dependent on the provision of amino acids (Paul and Foyer, 2001). However, the requirement for nitrogen in a sink is higher than that of the carbon, because of its high protein contents (Pate, 1999).Therefore, discrimination in partitioning of the two elements, as observed in the present experiment, may be consequential to the difference in their translocation in the phloem in response to the quantum of demand induced by the sink. Besides, there are instances in lupin (Pate et al., 1979), pea (Pate and Armstrong, 1996) and apple (Malaguti et al., 2001), showing evidence of nitrogenous solutes moving in xylem towards the sink. During translocation, exchange of nitrogen solutes occurs between the xylem and phloem in legumes (Pate, 1999; Pate et al., 1979). Thus, nitrogen solutes enjoy additional advantage for faster translocation to sink than that of carbon (Pate and Arthur, 2000). In the present experiment, pod removal might have affected translocation of ^{15}N more than that of ^{13}C from the fed leaf by disrupting the communication occuring in both xylem and phloem. Tanaka and Fujita (1974) proposed that a tomato plant can be composed of several source-sink units. The photosynthates produced by a leaf preferentially go to the fruits within the unit; but when source activity exceeds sink demand within one unit, excess photosynthates from the unit move to another unit. A matured leaf usually transports to the nearest sink organ and togather they constitute one source-sink unit. Transport from one matured leaf to another is probably not possible as the phloem of the matured leaf is active in export but not in import (Yoneyama et al., 1980). In the present study, a similar phenomenon was observed not only for carbon compounds but also for nitrogenous compounds. The soybean plant is composed of source-sink units and each unit consists of a trifoliated leaf, subtending internode and truss (fruits on the axil of the leaf), which is similar to that of bean (*Phaseolus vulgaris* L.) (Tanaka and Fujita, 1979). In addition to this, it is also deduced that under low nitrogen, the plant mobilises more nitrogen export from the leaf compared to the carbon compounds.

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