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Long Distance Translocation of Sucrose, Serine, Leucine, Lysine, and CO_2 Assimilates

II. OATS[1]

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ABSTRACT

To establish whether several amino acids were equally able to enter the phloem of oat (*Avena sativa* L.) plants and be transported, several ^{14}C-labeled amino acids were applied individually to an abraded spot on a fully expanded source leaf. The base of an immature sink leaf was monitored with a GM tube for time and rate of arrival of radioactivity. Transport of ^{14}C-sucrose and $^{14}CO_2$ assimilates was measured for a comparison. The applied L-serine, L-lysine, and L-leucine, as well as sucrose, entered the phloem and were transported to the sink leaf at rates between 1.16 and 1.83 cm/min. Transport velocity for CO_2 assimilates was 1.57 cm/min. A heat girdle near the top of the source leaf sheath blocked most transport, which indicated that transport was primarily through the phloem. Mass transfer rates for amino acids were only 3% as great as that for sucrose, suggesting different mechanisms of entry for sucrose than for amino acids into the phloem. The higher percentage of CO_2 assimilates mobilized to the sink leaf was attributed to the greater surface area of minor veins accessible to loading, as compared to those compounds supplied via an abraded spot. Serine was extensively metabolized in the source leaf, and radioactive products in the sink leaf mirrored those in the source leaf. Most radioactivity of lysine and leucine remained within these compounds in the source, path, and sink tissues. We concluded that there was no barrier to entry of amino acids into the phloem and transport therein. Data do not suggest a specific mechanism for entry of amino acids into the phloem.

Increasing the protein concentration of cereal grains is a goal of many plant scientists and nutritionists. We have been studying the physiological and biochemical factors regulating the protein concentration of oats (*Avena sativa* L.) or affecting the amino acid balance of the seed storage protein. Undoubtedly, the hydrolysis of leaf proteins which occurs during leaf senescence makes available a significant quantity of amino acid residues for remobilization to the developing grain. However, much of the requirement for seed protein must be met from current nitrogen assimilation and photosynthesis. Less than half of the seed protein at maturity in field-grown oats could be accounted for by remobilization of nitrogen assimilated before anthesis (17).

Previous experiments in our laboratory showed that when the flag leaf blade of a postanthesis oat plant was exposed to $^{14}CO_2$ for 2 hr, only five amino acids contained most of the radioactivity in the amino acid fraction of the flag leaf blade or its sheath (Cataldo, Schrader, and Peterson, unpublished data). The possible existence of some mechanism for limiting the entry of amino acids into the transport path was suggested by this observation.

There are few previous reports on amino acid transport in the phloem of gramineous species. Yamaguchi and Islam (22) applied several ^{14}C-labeled amino acids to the first leaf of barley (*Hordeum vulgare* L.) seedlings. Whole plant autoradiography after 24 hr revealed radioactivity in the expanding second leaf and the roots, which indicated probable phloem mobility. With the exception of applied valine, the translocated products were not identified. Amounts of radioactivity extracted from the bud varied among different applied amino acids, suggesting greater transport of some than of others.

The objective of our experiments was to determine if several amino acids were able to enter the phloem with equal facility, and be transported from a source to a sink tissue. We applied radioactive amino acid solutions to an abraded spot on a fully expanded source leaf, and monitored an expanding sink leaf with a GM tube for the arrival of radioactivity. We selected L-serine, an amino acid which was rapidly labeled during photosynthesis in $^{14}CO_2$, and L-leucine and L-lysine, amino acids in which label had not been detected (Cataldo *et al.*, unpublished data). The movement of sucrose, which is known to be actively loaded into the phloem and transported (19), and of $^{14}CO_2$ assimilates was also monitored for comparison with the movement of the amino acids.

MATERIALS AND METHODS

Plant Materials. Oat plants (*A. sativa* L. cv. Froker) were grown in environmental chambers in a 1:1 peat-vermiculite mixture, and irrigated with a complete nutrient solution (16). The illuminance was about 40,000 lux at the tops of the plants. The thermo- and photoperiods were 16 hr and the day/night temperatures were 23/18 C. The day before an experiment, a plant was selected whose sixth leaf was just emerging from within the sheath of the older leaves. The plant was trimmed to simplify the source-path-sink relationship as illustrated in Figure 1. The leaf blades and upper sheaths of the bottom three leaves were removed. The fifth and sixth leaves were then carefully worked out from within the sheath of the fourth leaf, and the fifth leaf was dissected away, which left the basal region of the immature sixth leaf exposed. A wooden applicator stick within the fourth leaf sheath served as a support. The plant was then placed in a fume hood illuminated with 45,000 lux of incandescent light, and programmed for the same photoperiod as the environmental chamber. The sixth (sink) leaf was shaded with aluminum foil.

Abraded Epidermis Feeding. An area 1/3 of the distance from the tip to the ligule of the fourth (source) leaf blade was abraded

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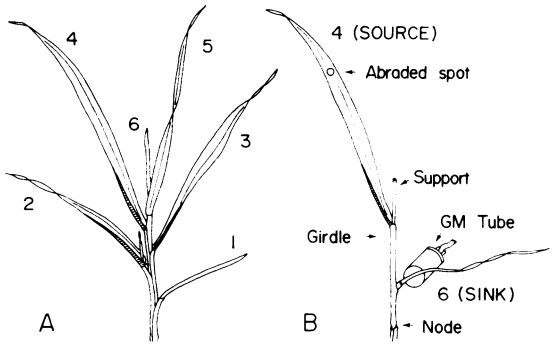

FIG. 1. A: Oat plant approximately 30 days after planting, and at the six-leaf stage used in these experiments; B: similar plant prepared for an experiment. The first through third leaves have been removed, the fifth and sixth leaves worked out from the enclosing sheath of the fourth leaf, and the fifth leaf removed to expose the base of the immature sixth leaf for monitoring with a GM tube. The support is a wooden applicator stick, inserted within the sheath of the fourth leaf.

as described by Housley *et al.* (10). Each treatment was repeated on three separate plants, once using 2 μCi of applied ^{14}C-labeled amino acid or sucrose, and twice using 10 μCi. A single heat-girdled plant (see below) was also used for each radioactive compound tested. The labeled compounds were supplied in 50 μl of 5 mM K-phosphate buffer (pH 6.5) to the abraded spot. The liquid was usually absorbed or evaporated in 30 to 40 min, and after absorption the spot was kept wet with buffer. Amino acids were applied at 10 mM concentration, and sucrose was applied at 100 mM. Specific activities of the applied compounds (μg C/μCi) were: sucrose, 71.8; leucine, 3.6; lysine, 3.6; serine, 1.8.

$^{14}CO_2$ Feeding. For $^{14}CO_2$ feeding, the distal 8 to 10 cm of the source leaf blade was enclosed in a Plexiglas chamber. An inlet and outlet port were connected with Tygon tubing through an electromagnetic piston pump to a vessel which held 100 μCi ^{14}C-sodium bicarbonate. $^{14}CO_2$ was generated by injecting lactic acid into the vessel through a serum stopper, and the mixture was heated. The pump was turned on, circulating the $^{14}CO_2$ through the leaf chamber for 5 min. Then the tubing was removed from the inlet port, venting the $^{14}CO_2$ out into the hood. The pump continued to circulate room air through the leaf chamber for a 115-min chase period. A single intact and a single heat-girdled plant were used for the $^{14}CO_2$ feeding experiments.

Heat Girdling. Plants were heat-girdled near the top of the source leaf sheath (Fig. 1) with a hot nichrome wire, as described by Housley *et al.* (10). The source leaf was monitored by β-gauging overnight (14) to determine if the relative water content had been altered by the heat girdle. Only plants whose source leaf maintained the same relative water content overnight were subsequently abraded and labeled.

Radioactive Monitoring. A thin end window GM detector tube (NC-108, Searle Analytic Inc.[3]) was positioned as near to the base of the sink leaf as possible (Fig. 1), and the leaf was taped to the end of the tube. The GM tube was connected to a rate meter whose output was recorded on a strip chart recorder.

Extraction of Tissue, Fractionation, and Radioactive Counting. At the conclusion of each experiment, 120 min after initial application of the isotope, the plant was excised at ground level, and the abraded spot rinsed with distilled H_2O. The plant was dissected into several parts, which were then sliced into small pieces with a razor blade and extracted twice with hot 80% (v/v) ethanol. The extracts were evaporated to dryness on a flash evaporator at 45 C, redissolved in 3 ml 80% ethanol, and an aliquot was counted in a mixture of 3.8 l dioxane-380 g napthalene-26.6 g PPO[4] in a Beckman liquid scintillation counter. Some of the extracts were fractionated into neutral, basic, and acidic fractions, by use of ion exchange columns (1). The basic fractions, which contained the amino acids, were chromatographed in two dimensions on thin layer plates of cellulose, with the solvents of Heathcote and Haworth (8). Radioactive spots were located by autoradiography with x-ray film, and identified spots were scraped from the plates into liquid scintillation vials and counted in toluene-PPO.

Table I. Transport Velocities and Mass Transfer Rates for Photosynthate and Applied Sucrose and Amino Acids

For sucrose and the amino acids, 10 μCi of the ^{14}C-labeled compound were applied to an abraded spot on the fully expanded fourth leaf. $^{14}CO_2$ was applied as a 5-min pulse, generated from 100 μCi ^{14}C-bicarbonate, to the distal 8 to 10 cm of the fourth leaf. The base of the immature sixth leaf was monitored with a GM tube for time and rate of arrival of radioactivity.

Radioactive compound fed	Velocity	Mass transfer rate
	cm/min	*ng C/min*
Sucrose	1.16	49.6
	1.37	63.9
Lysine	1.34	2.3
	1.83	1.6
Serine	1.72	0.4[1]
	1.55	2.1
Leucine	1.35	1.2
	1.43	1.4
CO_2	1.57	--

[1]This plant was abnormal, in that accumulation of radioactivity was much higher in the tip of the sink leaf, than in the base.

Calculation of Velocities and Mass Transfer Rates. Transport velocities were calculated by dividing the path length by the time required for detection of arrival of radioactivity at the monitored position of the sink leaf. To compute mass transfer rates from the arrival kinetics, the detection efficiency was estimated separately for each plant as follows. The GM tube diameter was 2.7 cm. Because radioactivity was extracted from the basal 10 cm of the sink leaf, this value was multiplied by 0.27 to estimate the amount of ^{14}C opposed to the GM tube. The GM tube was centered about 5 cm from the node. The cpm detected with the GM tube at the conclusion of the experiment divided by the above estimate equaled the detection efficiency. This method does not take into account any insoluble radioactivity, which was not determined, but is useful for comparative purposes. Rate of arrival of radioactivity (cpm/min) divided by detection efficiency (cpm/μCi) $\times$ specific activity of the applied compound (ng C/μCi) = mass transfer rate (ng C/min). Dilution of the applied compounds by endogenous pools was not accounted for.

RESULTS

Transport velocities, which ranged from 1.16 to 1.83 cm/min (Table I), are considered to be minimum velocities because detection efficiency with the GM tube is low, and radioactivity could have arrived in the sink before its detection (6). Differences in velocities among the amino acid and sucrose experiments were not significant. The transport velocity for CO_2 assimilates was within the range found for the applied compounds (Table I). Mass transfer rates for the various amino acids were of a similar magnitude, and were about 3% as great as the mass transfer rate for sucrose (Table I).

For applied sucrose and amino acids, most of the radioactivity remained in the fed spot, or moved into the leaf blade tip (Table

[3] Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the USDA and does not imply its approval to the exclusion of other products that may also be suitable.

[4] Abbreviation: PPO: 2,5-diphenyloxazole.

II). The immature sixth leaf was acting as a sink, in that a higher percentage of the radioactivity was accumulated there than in the adjacent internode or other path tissues (Table II). This was not the case for leucine, however, as more radioactivity was found in the internode below the fourth leaf node than in the sixth leaf. With one exception, radioactivity of the sink leaf decreased with distance from the node (data not presented). When sucrose was applied, more radioactivity was recovered in the sink and less remained in the source, than when amino acids were applied. Radioactivity from applied serine was more mobile than that from lysine and leucine. None of the compounds applied to the leaf via an abraded spot was transported to the sink leaf as completely as the CO_2 assimilates. Recovery of applied radioactivity was variable. Possible reasons for incomplete recovery of radioactivity include: transport to the roots, which were not extracted and analyzed; incorporation into ethanol-insoluble compounds; respiration; and the possibility that some applied radioactivity was not absorbed and was rinsed off before extraction of the tissue.

To establish whether transport was via the phloem, radioactive CO_2, amino acids, or sucrose was applied to the source leaf of plants that had been heat-girdled near the top of the source leaf sheath. In every case, when the source leaf sheath was heat-girdled, no radioactivity above background was detected by GM tube monitoring of the sink leaf. A small amount of radioactivity was extracted from tissues beyond the girdle (usually less than 0.1% per tissue) but the results clearly show that the girdle blocked transport of most of the radioactivity. Thus, the transport that we have observed by monitoring the arrival of radioactivity in the sink leaf with a GM tube represents movement through the phloem. The small amount of nonphloem transport was not detectable without extraction of the tissue.

Extracts of a representative part of several of the plant tissues were fractionated by ion exchange chromatography to yield a neutral (sugar), basic (amino acid), and two acidic fractions (organic acids and sugar phosphates) (1). Very little radioactivity was recovered in the sugar phosphate fraction, and data were combined for both acidic fractions. When $^{14}CO_2$ was fed, most of the radioactivity recovered was in the neutral fraction in all plant parts (Table III). In the fed blade, 11% of the radioactivity was found in amino acids and 6% in the acidic fractions. Along the transport path, from the source to the sink, the percentage of radioactivity in the basic fraction declined, and that in the neutral fraction increased. These results suggest either that among the photosynthetic products, sugar was available for transport before amino acids, or that differential unloading and metabolic conversion occurred along the path.

Table II. Percentage of Ethanol-Soluble Radioactivity Recovered from Various Plant Parts

The ^{14}C-labeled amino acids and sucrose were applied to an abraded spot on the fully expanded fourth leaf. Data are means of 3 plants. $^{14}CO_2$ was applied to a single plant as a 5-min pulse to the distal third of the fourth leaf. After 2 hours, the plants were excised at the base of the stem, dissected, and the various parts were extracted with hot 80% (v/v) ethanol and counted.

Plant Part	CO_2	Sucrose	Serine	Lysine	Leucine
	% of ethanol-soluble activity				
Blade tip	--	37.5 ± 3.1[1]	26.5 ± 2.0	43.1 ± 4.1	29.3 ± 0.9
Fed spot	35.5	24.1 ± 5.6	41.7 ± 2.2	30.6 ± 3.5	51.6 ± 6.0
Lower blade	5.6	15.8 ± 6.9	13.9 ± 0.6	17.6 ± 1.6	10.7 ± 2.7
Sheath	6.0	3.4 ± 1.3	3.8 ± 1.0	2.3 ± 0.1	2.4 ± 0.3
Internodes up	2.0	1.8 ± 0.7	1.1 ± 0.3	0.9 ± 0.2	0.6 ± 0.2
Sink leaf & apex	42.0	13.1 ± 5.2	9.0 ± 1.5	3.8 ± 0.9	2.0 ± 0.8
Internode down	8.9	4.3 ± 2.4	4.0 ± 1.4	1.7 ± 0.4	4.3 ± 2.5
Recovery, % of applied activity	4.1	54.4 ± 17.9	46.3 ± 10.9	53.4 ± 7.5	80.8 ± 14.1

[1] ± standard deviation of the mean.

Table III. Fractionation of 80%-Ethanol Extracts from Representative Plant Parts by Ion Exchange Chromatography

Extracts from various plant parts, previously treated with ^{14}C-labeled amino acids, sucrose, or CO_2 as described in the text, were fractionated on columns of AG 1-X8 and AG 50W-X4 to yield neutral (N), basic (B), and acidic (A) fractions. Data are averages of two plants.

Plant part	CO_2			Sucrose			Leucine			Lysine			Serine		
	N	B	A	N	B	A	N	B	A	N	B	A	N	B	A
	% of radioactivity														
Blade tip	--	--	--	95	3	5	1	96	3	3	86	11	68	24	8
Fed spot	83	11	6	96	1	3	2	97	2	4	87	9	61	26	13
Lower blade	88	8	4	86	8	6	4	87	10	8	85	8	67	22	11
Sheath	90	6	4	72	4	24	7	87	6	16	62	22	69	25	6
Sink leaf	93	1	6	89	5	6	7	86	7	8	69	22	76	17	8

When sucrose was applied to an abraded spot, most radioactivity remained in the neutral fraction, and there was little evidence of metabolism along the path or in the sink. With applied ^{14}C-leucine, almost all radioactivity remained in the amino acid fraction in all plant parts. When ^{14}C-lysine was fed, most of the label also stayed in the amino acid fraction, although some was converted to the acidic fraction in the sheath and sink leaf.

The results with ^{14}C-serine were markedly different from those with leucine and lysine (Table III). The amino acid fraction of the fed spot contained only 26% of the radioactivity; most was found in the sugar fraction. Similar distribution of radioactivity from serine was found for the other plant parts. These results indicate extensive conversion of ^{14}C-serine into sugar and, to a lesser extent, organic acids. Because the distribution of radioactivity among the three fractions was similar for all plant parts, the serine was probably metabolized in the fed spot, and radioactive serine and its metabolic products entered the transport stream with equal facility.

Analysis by TLC and autoradiography of the basic fraction of an extract from blade tip, fed spot, lower blade, sheath, and sink leaf tissues revealed the extent of amino acid interconversion. When ^{14}C-leucine was applied, greater than 90% of the radioactivity recovered was present in leucine or isoleucine for blade tip, sheath, and sink leaf. The corresponding values for lower blade and fed spot were 63 and 74%. The remainder of the radioactivity appeared in several other amino acids. Recovery of radioactivity in lysine, when ^{14}C-lysine was fed, ranged from 78 to 92% in the fed spot, path, and sink tissues. There was considerable metabolism in the blade tip, however, with only 49% of the ^{14}C remaining in lysine. Serine was also metabolized to a greater extent in the blade tip than in the fed spot or sink tissues. Only 54% of the basic fraction radioactivity recovered in the blade tip was in serine; alanine and glycine accounted for most of the remainder. In the fed spot and the sink, however, 79 and 84% of the basic fraction ^{14}C recovered remained in serine.

DISCUSSION

Results establish that these amino acids do enter the phloem, and are transported therein at velocities similar to that for sucrose. Our velocities fall within the range reported by Wardlaw (20) for wheat (*Triticum aestivum* L.) (0.65 to 1.80 cm/min). Chopowick and Forward (4) concluded that ^{14}C-alanine, applied to leaves of sunflowers (*Helianthus annuus* L.), was converted primarily to sucrose before transport by the phloem. We found that a large percentage of serine also was metabolized to sugar before transport. Evidence from our studies with lysine and leucine, which are not as active metabolically as serine or alanine, strongly suggests that these amino acids enter into the

phloem intact and are transported via the phloem to sink tissue.

These experiments do not establish a mechanism for the entry of amino acids into the phloem. According to Geiger (5), " 'phloem loading' is applied to the process by which the major translocated substances are selectively and actively delivered to the sieve tubes." A demonstration of active loading would require evidence for concentration of the applied substance in the minor veins and/or inhibition by metabolic inhibitors such as dinitrophenol (2, 3, 19). An enhancement of uptake by ATP has also been suggested as a criterion for active uptake (12, 19). We have not done these experiments. No selectivity was shown among these L isomers of amino acids, but D isomers might have been selectively excluded (11), had they been tried. Other workers have suggested that uptake of amino acids into the phloem is an active process (3, 12, 13).

If entry of amino acids into the phloem is facilitated by a carrier mechanism, one might expect that this mechanism would reach saturation as concentration of applied substances was increased. Shtarkshall and Reinhold (18) reported a multiphasic uptake curve for transport of α-amino isobutyric acid into barley leaf tissue. Birt and Hird (2) found normal Michaelis-Menten-type kinetics for uptake of several amino acids by carrot root tissue slices. The mechanism was saturated at about 50 mM. Both of these studies (2, 18), as well as studies on amino acid uptake by isolated chloroplasts (15), indicate uptake of amino acids by some carrier mechanism (9). Watson and Fowden (21) have reported an active and a nonmetabolic component to uptake of phenylalanine and tyrosine by seedling root tips.

In preliminary experiments, we measured the rate of arrival of leucine in the sink, at concentrations of applied leucine at the source from 2 to 60 mM (unpublished data). Rate of arrival appeared to reach saturation at 20 mM. Results were variable at higher concentrations, but tended to indicate lower rates than at 20 mM. We cannot explain these results.

Calculation of mass transfer rates involved some uncertainty because of the assumptions that were necessary. However, it is clear that rates for sucrose were much greater than those for amino acids. It was previously shown in sugar beet (*Beta vulgaris* L.) that translocation rates were similar for sucrose applied via an abraded spot or formed from photosynthesis (7). Since velocities for sucrose and amino acids in oats were similar, one must conclude that the rate-limiting step for the amino acids is entry into the phloem. This does not necessarily indicate that no mechanism other than diffusion is involved, but if there is a mechanism, it operates at a much lower rate.

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LITERATURE CITED

1. Atkins, C. A. and D. T. Canvin. 1971. Photosynthesis and CO_2 evolution by leaf discs: gas exchange, extraction, and ion-exchange fractionation of ^{14}C-labeled photosynthetic products. Can. J. Bot. 49: 1225-1235.
2. Birt, L. M. and F. J. R. Hird. 1958. Kinetic aspects of the uptake of amino acids by carrot tissue. Biochem. J. 70: 286-292.
3. Brovchenko, M. I. 1964. Amino acid uptake by conducting and assimilating tissues of leaves. Sov. Plant Physiol. 10: 349-355.
4. Chopowick, R. E. and D. F. Forward. 1974. Translocation of radioactive carbon after the application of ^{14}C-alanine and $^{14}CO_2$ to sunflower leaves. Plant Physiol. 53: 21-27.
5. Geiger, D. R. 1975. Phloem loading. *In:* M. H. Zimmerman and J. A. Milburn, eds., Transport in Plants. I. Phloem Transport. Springer-Verlag. New York. pp. 395-431.
6. Geiger, D. R., M. A. Saunders, and D. A. Cataldo. 1969. Translocation and accumulation of translocate in the sugar beet petiole. Plant Physiol. 44: 1657-1665.
7. Geiger, D. R., S. A. Sovonick, T. L. Shock, and R. J. Fellows. 1974. Role of free space in translocation in sugar beets. Plant Physiol. 54: 892-898.
8. Heathcote, J. G. and C. Haworth. 1969. An improved technique for the analysis of amino acids and related compounds on thin layers of cellulose. II. The quantitative determination of amino acids in protein hydrolysates. J. Chromatogr. 43: 84-92.
9. Higinbotham, N. 1973. The mineral absorption process in plants. Bot. Rev. 39: 15-69.
10. Housley, T. L., D. M. Peterson, and L. E. Schrader. 1977. Long distance translocation of sucrose, serine, leucine, lysine, and CO_2 assimilates. I. Soybean. Plant Physiol. 59: 000-000.
11. Joy, K. W. and A. J. Antcliff. 1966. Translocation of amino acids in sugar beet. Nature 211: 210-211.
12. Kursanov, A. L. and M. I. Brovchenko. 1961. Effect of ATP on the entry of assimilates into the conducting system of sugar beets. Sov. Plant Physiol. 8: 211-217.
13. Kursanov, A. L., M. I. Brovchenko, and A. N. Pariiskaya. 1960. Flow of assimilates to the conducting tissue in rhubarb (*Rheum rhaponticum* L.) leaves. Sov. Plant Physiol. 6: 544-552.
14. Mederski, H. J. 1961. Determination of internal water status of plants by beta ray gauging. Soil Sci. 92: 143-146.
15. Nobel, P. S. and Y-N. S. Cheung. 1972. Two amino-acid carriers in pea chloroplasts. Nature New Biol. 237: 207-208.
16. Peterson, D. M. and L. E. Schrader. 1974. Growth and nitrate assimilation in oats as influenced by temperature. Crop Sci. 14: 857-861.
17. Peterson, D. M., L. E. Schrader, D. A. Cataldo, V. L. Youngs, and D. Smith. 1975. Assimilation and remobilization of nitrogen and carbohydrates in oats, especially as related to groat protein concentration. Can. J. Plant Sci. 55: 19-28.
18. Shtarkshall, R. A. and L. Reinhold. 1974. Multiphasic amino acid transport in leaf cells. *In:* U. Zimmerman and J. Dainty, eds., Membrane Transport in Plants. Springer-Verlag, New York. pp. 338-342.
19. Sovonick, S. A., D. R. Geiger, and R. J. Fellows. 1974. Evidence for active phloem loading in the minor veins of sugar beet. Plant Physiol. 54: 886-891.
20. Wardlaw, I. F. 1965. The velocity and pattern of assimilate translocation in wheat plants during development. Aust. J. Biol. Sci. 18: 269-281.
21. Watson, R. and L. Fowden. 1975. The uptake of phenylalanine and tyrosine by seedling root tips. Phytochemistry 14: 1181-1186.
22. Yamaguchi, S. and A. S. Islam. 1967. Translocation of eight C^{14}-labeled amino acids and three herbicides in two varieties of barley. Hilgardia 38: 207-229.