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Carbon Transport and Root Respiration of Split Root Systems of *Phaseolus vulgaris* Subjected to Short Term Localized Anoxia[1]

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ABSTRACT

The influence of anoxia on carbon transport and root respiration was evaluated by applying [U-^{14}C]sucrose to the foliage. Translocation patterns to the root systems of two dry edible bean genotypes (*Phaseolus vulgaris* L.) were examined after a 3-day exposure to aerated and nonaerated environments. Localized anoxia of root systems was simulated by growing roots in split configurations and exposing half of the system to anoxic conditions. Anoxia of the root system for 72 hours reduced the movement of ^{14}C label into the roots with concurrent accumulations in the hypocotyl region. The translocation of ^{14}C label to anoxic roots was less than 50% of the aerated controls of both genotypes. Most of the ^{14}C label translocated to anoxic root systems was excluded from respiratory metabolism during the 3-hour pulse/chase period and was an order of magnitude less than the aerated controls. These observations suggest that the bulk of ^{14}C label which entered the root during the anoxic period was unavailable for metabolism by the enzymes of glycolysis and/or was diluted by a relatively large metabolite pool. A higher percentage of ^{14}C label was translocated to the aerated half of the localized anoxia treatment relative to the half of the aerated controls. The proportion of ^{14}C label translocated to the root system in the aerated control was 20 and 16% compared to 28 and 25% in the aerated localized anoxia treatment for the genotypes Seafarer and line 31908, respectively. Line 31908 partitioned a greater percentage of ^{14}C-labeled compounds to the actively growing fraction of the root system in the localized anoxia treatment than did Seafarer. This suggests a greater reliance on previously stored carbohydrate for immediate root growth in Seafarer than in line 31908.

Root systems growing in heterogeneous soil environments may be exposed to both aerobic and anaerobic conditions (3). Several studies have demonstrated compensatory growth in nonstressed areas of the root environment when portions of a root system were subjected to anoxic conditions (2, 23, 27). In a previous study, we reported phenotypic differences in the growth patterns of dry edible bean root systems subjected to localized anoxia (23). Root elongation during a 3-d treatment period occurred primarily in the existing roots of the MSU line 31908. In contrast, root elongation during the treatment period occurred mainly on newly initiated roots in other genotypes.

Since root growth rates are a function of the partitioning responses of plants during the treatment period and do not necessarily reflect translocation patterns occurring at the conclusion of the treatment period, short term ^{14}C labeling experiments were used to provide information on the pattern of carbon translocation within the plant at a particular point in time. Although a number of short term ^{14}C labeling studies have been conducted on flooded plants (10, 14–16, 26), there have been no reported measurements of the isotope losses to the root environment through exudation or respiration during the labeling period. Objectives of this study were: (a) to determine the translocation patterns for two dry edible bean genotypes whose root systems were subjected to short term (72 h) nonaerated, and localized anoxia treatments; and (b) to account for losses of ^{14}C label within the root environment during the labeling period.

MATERIALS AND METHODS

Plant Culture. Seeds of two *Phaseolus vulgaris* L. genotypes, Seafarer and MSU line 31908, were sterilized with 0.5% NaOCl solution for 3 min, then thoroughly rinsed with distilled H_2O and germinated in the dark on trays containing wet cheesecloth covered with moist paper towels. Temperatures within the incubator were maintained at 23 ± 0.5°C for germination and initial seedling growth. Primary root tips were removed 24 to 48 h after germination by cutting directly below the zone of basal root formation (30). This resulted in a split root system composed of basal roots which developed laterally from the main axis of the plant. Seedlings on the germination trays were given a 24-h exposure to light in a growth chamber (390 μmol m^{-2} s^{-1}) when the hypocotyls were >2 cm in length and transferred to cylindrical acrylic chambers designed to allow each half of the root system to be sealed in separate compartments. Two seedlings of the appropriate genotype were transplanted into each chamber. There were four replications of each treatment in a randomized complete block design.

Root system halves were grown in compartments containing approximately 1.1 liter of a modified half-strength Hoagland solution adjusted to a pH of 6. Nutrient solution O_2 partial pressures >0.19 atm O_2 were maintained by flowing filtered compressed air through fritted glass tubes at >150 cm^3 min^{-1}. The O_2 partial pressures used in the experiment are within the range of most arable soils (20). Light was excluded from the split root systems by placing the acrylic chambers into opaque polyvinyl chloride cylinders. Chambers were randomly positioned on the greenhouse bench. Supplemental cool white fluorescent light was used to provide a photoperiod of 16 h light and 8 h dark. PAR at midday ranged from 200 (cloudy) to 1,900 (clear) μmol m^{-2} s^{-1} at the primary leaf surface. Greenhouse air temperatures ranged from 21°C at night to an average of 25°C during the day with maximum temperatures as high as 35°C. RH ranged from 60 to 90% with values normally near 80%. The experiment was conducted in March and April.

Split Root Chambers. The split root chambers were constructed from clear acrylic cylinders 14 cm in diameter, 16 cm

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in height, and a wall thickness of 0.64 cm. The top, bottom, and center divider were constructed from black acrylic sheets, 0.64 cm thick. The bottom and center were sealed with methylene chloride cement which prevented the flow of air and liquid. The two plant ports consisted of 1.9 cm diameter black acrylic tubes located on both ends of the center black acrylic divider. The removable top was secured to the split root chamber by a silicone vacuum sealing compound. Plant stems were sealed with parawax, a 1:5 mixture of paraffin wax and vaseline. Entry and exit ports on both halves of the chamber provided for the entry and exit of filtered compressed air. Chambers were initially tested for leaks by pressurizing and checking for leaks with a manometer. Immediately before the 3 h pulse/chase period, the chambers were checked for gas leakage and made gas and liquid tight.

Aeration Treatments. Three aeration treatments were randomly allocated to the root systems of each cultivar after a period of 8 d of seedling growth in well-aerated environments. Aeration treatments consisted of two controls, both halves of the root system aerated (AC); both halves nonaerated (NC); and a localized anoxia treatment in which the gaseous treatments were split, with half of the root system aerated (ALA) and the other half nonaerated (NLA). O_2 partial pressures in the nonaerated treatments were maintained below 0.005 atm O_2 by equilibrating the nutrient solution with N_2 gas. A nontoxic neutral red staining technique (24) was used to indicate root growth during the treatment period by staining roots immediately before the aeration treatments.

[^{14}C]Sucrose Translocation. Carbon translocation was monitored by applying 15 μCi [U-^{14}C] sucrose (673 mCi/mmol; source, New England Nuclear; in 90% ethanol solution) to abraded areas of the middle leaflet of the oldest trifoliate. Carborundum paper was used to lightly abrade an area of approximately 1 cm^2. Phosphate buffer (5 mM adjusted to pH 6) was periodically added to the abraded area, to maintain a wet surface for 2 h after the [^{14}C]sucrose application. Source leaflets were removed from plants 2 h after labeling and rinsed with 5 ml of 80% ethanol to determine the amount of unabsorbed [^{14}C]-sucrose. Plants were dissected into various components after a 1 h chase period. Shoots were dissected into six components identified as the middle trifoliate source leaf, two trifoliate leaves adjacent to the source plus primary leaves, immature rapidly expanding trifoliates, stem above source petiole, stem below source petiole to cotyledonary node, and hypocotyl. White unstained root segments indicated growth which occurred during the treatment period. Root components included white segments of: (a) branched roots (basal and lateral roots bearing other lateral roots); (b) nonbranched lateral roots which emerged before staining; and (c) lateral roots which emerged after staining (23). Root systems which did not grow during the treatment period were not dissected but were otherwise treated similarly to the dissected roots. Photographs were taken of the root systems before dissecting. Component parts of roots and shoots were frozen on dry ice immediately following dissection and stored at −20°C.

Extraction of Ethanol-Soluble Compounds. ^{14}C-compounds were extracted from macerated plant tissue by hot (55°C) 80% ethanol for 1 h and filtered using preweighed dry filter paper. Residues were dried at 70°C and weighed. The filtrate was cooled to −120°C in Erlenmeyer (125 ml) flasks and flash evaporated in a VIRTIS Freezemobile II freeze dryer. The dried residues were resolubilized with 20 ml of hot 80% ethanol and subsequently divided into two equal aliquots, one being reserved for additional analyses. Aqueous counting scintillant (ACS, Amersham) (10 ml) was added to the samples for the determination of radioactivity. Each sample was counted twice on a LS-8100 Beckman Scintillation Counter. Plant components with counting efficiencies less than 30% or giving inconsistent duplicate readings were diluted to reduce color quenching and reanalyzed. Counting efficiencies for most components were generally in the range of 60 to 90%. Actual radioactivity (dpm) was determined by adjusting for background and quench. Control samples with no radioactivity were periodically subjected to the entire extraction procedure to determine background radiation and contamination.

Root Respiration. Root respiration of $^{14}CO_2$ was monitored by bubbling the exhaust gases from the gas-tight split root chambers into separate vials containing 20 ml of ethanolamine. Samples (1 ml) were withdrawn from the vials every 0.5 h. Methanol (2 ml) was added to each sample to increase ethanolamine solubility in the scintillation solution. Root exudation of ^{14}C-compounds was measured at harvest by acidifying a 10-ml sample of nutrient solution (pH 4.0–5.0) to remove HCO_3^- produced by root respiration, freeze drying, and determining radioactivity as stated previously. These values were adjusted for the total volume of nutrient solution in each split root compartment. Root respiration (CO_2 production) was evaluated 1 h before labeling the plants with [^{14}C]sucrose. Treatment gas flow rates were measured and gas samples were taken in triplicate using a 1-ml tuberculin syringe. Syringe needles were stoppered and the CO_2 concentrations determined by the modified Beckman model 865 IR CO_2 analyzer method of Schumacher and Smucker (22). This procedure was repeated for all treatments and background samples.

The experiment was designed and analyzed as a randomized complete block with four replications. Orthogonal comparisons were made between the aerated control and aerated portions of the localized anoxia treatments. Percentage and dpm data were analyzed as arcsine and natural logarithm transformations, respectively.

RESULTS

Shoot and Root Growth. Nonaeration of the complete root system significantly reduced the total growth of roots and increased shoot to root ratios in both genotypes. Shoot dry weights and leaf areas of the localized anoxia treatments were similar to the aerated control (Table I).

Roots in the aerated half of the localized anoxia treatments had similar total weights for both genotypes when compared to the aerated control. Localized anoxia resulted in an increased allocation of root dry weight to the aerated component of Seafarer but not in the 31908 line. The lower root dry weights of the nonaerated controls were similar to the nonaerated portions of the localized anoxia treatments (Table II).

Root Anoxia and ^{14}C Label Translocation. The reduced accumulation of dry matter in the nonaerated control is similar to previous observations of the effects of root system anoxia (3, 13). Absence of aeration to the entire root system reduced the trans-

Table I. *Modification of Shoot and Root Growth of Two Genotypes of Dry Bean by 72-Hour Aeration Treatments of the Root System*

Aeration treatments were aerated control (AC), nonaerated control (NC), and localized anoxia (LA) (n = 4).

Genotype	Aeration Treatments	Shoot Dry Wt	Root Dry Wt	Leaf Area	Shoot:Root Dry Wt
		mg plant^{-1}		*cm^2 plant^{-1}*	*ratio*
Seafarer	AC	495	166	93	3.0
	NC	448	83	86	5.4
	LA	509	134	95	3.8
31908	AC	948	270	210	3.5
	NC	782	111	162	7.0
	LA	856	209	193	4.1
	SE (±)	57	18	15	0.3

Table II. *Distribution of Dry Matter within Actively Growing (i.e. Unstained) Components of the Root Systems of Seafarer and 31908 Subjected to Three Aeration Treatments for 72 Hours*

Aeration treatments were aerated control (AC), nonaerated control (NC), aerated half of the localized anoxia treatment (ALA), and nonaerated half of the localized anoxia treatment (NLA). Values in each column followed by the same letter are not significantly different at the 5% level of probability using the LSD comparison.

Genotype	Aeration Treatment	Total Root Dry Wt	Root Growth during Treatment			
			Branch roots	Lateral roots previously emerged	New lateral roots	Total
			mg (1/2 plant)$^{-1}$			
Seafarer	AC	83 b	7 a	7 a	8 a	23 a
	NC	42 a				
	ALA	96 b	7 a	14 b	7 a	28 a
	NLA	39 a				
31908	AC	135 c	10 a	14 b	11 a	35 a
	NC	56 a				
	ALA	144 c	11 a	12 ab	13 a	36 a
	NLA	65 a				

location of ^{14}C-compounds to approximately 30 and 50% of the aerated controls for 31908 and Seafarer (Table III). The hypocotyl and stem tissue below the source leaf contained 54 to 61% of the ^{14}C label when plant root systems were devoid of O_2 (Table IV). The proportions of ^{14}C label translocated to the nonaerated half of the root systems of the localized anoxia treatments were similar to the nonaerated control (Table V). Up to 50% of the label translocated to the root system was respired and exuded by roots of the aerated treatments while less than 10% was lost by anoxic roots (Table VI). There was less activity in the ethanol-soluble extracts of the root systems of nonaerated treatments (Table VII).

Table III. *Activity of [^{14}C]Sucrose Recovered in the 80% Ethanol Wash from Source Leaf (Unabsorbed) and Extracted from the Shoots and Roots*

Translocated values represent recovered ^{14}C label minus ^{14}C label associated with the source leaf and unabsorbed ^{14}C sucrose. Aeration treatments are listed in Table I. Values in each column followed by the same letter are not significantly different at the 5% level of probability by the LSD comparison.

Genotype	Aeration Treatment	Unabsorbed	Retained by Source Leaf	Translocated
		dpm × 10^{-4} plant^{-1}		
Seafarer	AC	970 a	483 ab	232 a
	NC	910 a	1278 a	107 b
	LA	760 a	860 ab	202 ab
31908	AC	90 a	305 ab	137 ab
	NC	620 a	300 ab	37 c
	LA	800 a	225 b	112 ab

Although there were similar allocations of ^{14}C label between shoots and roots of the aerated control and localized anoxia treatments (Table VI), more ^{14}C label was transported to the aerated half of the root system relative to the aerated control when a portion of the root was subjected to anoxia (Table V). The orthogonal comparison between the aerated control and the aerated half of the localized anoxia treatment was significant for the percentage of label translocated to the root system when averaged across genotypes. The proportion of ^{14}C label translocated to the actively growing roots was increased by localized anoxia for the 31908 line but not for Seafarer (Table VIII). A comparison of the relative amounts of ^{14}C label translocated to the actively growing roots (Table VIII) and to the total root system (Table V) indicates that the majority of label was found in the nonexpanding portions of the root system in both genotypes.

Root Respiration. The quantity of CO_2 lost by a plant root system was greater for line 31908. However, respiration rates for the two genotypes were similar when adjusted for root system size. Root respiration rates of the aerated half of the localized anoxia treatments were 45% and 55% greater than the aerated

Table IV. *Distribution of ^{14}C Label among Various Shoot Components*

Percentages are based on total amount of ^{14}C label recovered as ethanol-soluble compounds plus root losses and excluding ^{14}C label retained within the source leaf. Aeration treatments are listed in Table I. Values in each column followed by the same letter are not significantly different at the 5% level of probability by the LSD comparison.

Genotype	Aeration Treatment	Primary Leaves and Oldest Trifoliates	Immature Trifoliates	Stem between Source and Hypocotyl	Stem above Source	Hypocotyl
				%		
Seafarer	AC	7 a	2 a	11 a	4 a	15 ab
	NC	14 a	11 a	23 bc	5 a	31 b
	LA	8 a	5 a	12 ab	10 a	18 ab
31908	AC	13 a	6 a	17 ab	6 a	14 ab
	NC	18 a	4 a	31 c	10 a	30 b
	LA	13 a	7 a	18 ab	7 a	11 a

Table V. *Proportion of ^{14}C Label Translocated from the Source Leaf to Half the Root System in Four Aeration Environments*

Percentages are based on total amount of ^{14}C label recovered as ethanol-soluble compounds and root-respired CO_2 excluding ^{14}C label retained within the source leaf. Aeration treatments are listed in Table II. Values in each column followed by the same letter are not significantly different at the 5% level of probability by the LSD comparison.

Genotype	Aeration Treatments	Root System	Soluble Exudates	CO_2 Respiration
			%	
Seafarer	AC	20.2 b	0.28 a	9.4 ab
	NC	7.6 a	0.02 a	0.1 c
	ALA	27.7 b	0.33 a	12.8 a
	NLA	4.6 a	0.02 a	0.4 c
31908	AC	15.6 b	0.14 a	5.5 b
	NC	3.0 a	0.15 a	0.2 c
	ALA	25.4 b	0.29 a	10.1 ab
	NLA	7.7 a	0.24 a	0.3 c

Table VI. *Distribution of the ^{14}C Label among the Shoot, Root, and Root Environment*

Root losses include both soluble exudation and gaseous respiration. Values for the root system include both halves of the root environments. Percentages are based on total amounts of ^{14}C label recovered as ethanol-soluble extracts of the shoots, excluding the source leaf, and roots plus root losses. Aeration treatments are lised in Table I. Values in each column followed by the same letter are not significantly different at the 5% level of probability by LSD comparison.

Genotype	Aeration Treatment	Shoot	Root System	Root Losses
			%	
Seafarer	AC	39 a	40 a	20 a
	NC	84 b	15 bc	1 b
	LA	53 a	33 a	14 a
31908	AC	56 a	32 ab	11 a
	NC	93 b	6 c	1 b
	LA	56 a	32 ab	11 a

Table VII. *^{14}Carbon Activity per Unit Root Dry Weight for the Root System and Respiratory Fractions of Four Root Environments*

Aeration treatments are listed in Table II. Values in each column followed by the same letter are not significantly different at the 5% level of probability by the LSD comparison.

Genotype	Aeration Treatment	Root System Activity	$^{14}CO_2$ Respiration
		dpm × 10^{-4} g^{-1} dry wt	
Seafarer	AC	430 ab	199 a
	NC	135 bc	1 de
	ALA	550 a	247 a
	NLA	238 abc	17 bc
31908	AC	145 ab	52 ab
	NC	14 d	1 e
	ALA	156 abc	55 ab
	NLA	108 c	5 cd

controls for Seafarer and 31908, respectively (Table IX). Less than 0.005% of the total carbon dioxide respired during the 3-h pulse/chase period was represented by $^{14}CO_2$.

Translocation of the ^{14}C label to sites of root respiration required at least 1 h (Fig. 1). Seafarer respired significantly more

Table VIII. *Distribution of ^{14}C Label within Actively Growing (i.e. Unstained) Root Components during the 3-Hour Treatment Period*

Values are for half the root system and are based on per cent translocation from the source leaflet. Values are given for aerated control (AC) and the aerated half of the localized anoxia treatment (ALA). Percentages are based on total amount of ^{14}C label recovered as ethanol-soluble compounds and root losses excluding ^{14}C label from the source leaf.

Genotypes	Aeration Treatment	Branched Roots	Lateral Roots Previously Emerged	New Lateral Roots	Total
			%		
Seafarer	AC	2	6	3	11
	ALA	2	4	3	9
31908	AC	1	3	2	6
	ALA	2	9	5	16[a]

[a] Represents significance at the 5% level of probability for comparisons between aeration treatments within cultivars. *F* tests based on the appropriate orthogonal comparison were used to determine probability of a difference.

$^{14}CO_2$ than did the 31908 genotype even though Seafarer root systems were smaller and respiration rates per dry weight were similar between genotypes (Table IX). Root respiration of $^{14}CO_2$ appeared to be linear for both genotypes 2 h after [U-^{14}C]sucrose was applied to the source leaf.

DISCUSSION

Shoot growth was influenced less than the roots by the aeration treatments of the roots. Root respiration rates (CO_2 respired per root dry weight) were similar and essentially no root growth occurred for both the nonaerated control and the nonaerated half of the localized anoxia treatments. However, the greater ^{14}C activity per unit root dry weight in the nonaerated half of the localized anoxia treatment compared to the nonaerated control indicates that the movement of ^{14}C-labeled compounds into anoxic roots is enhanced when a portion of the root system is aerated (Table VII) or may be due to isotopic dilution. Greater export of [^{14}C]sucrose from the source leaf in the localized anoxia treatments may have increased the ratio of ^{14}C-labeled sucrose and/or other ^{14}C-labeled metabolites in the total carbon pool of the phloem, resulting in greater ^{14}C activity per unit root dry weight in the nonaerated half of the localized anoxia treatment.

An examination of the translocated ^{14}C label, expressed as a percentage of the recovered ^{14}C label minus the ^{14}C label associated with the source leaf, indicates that there were no differences in the proportions of the ^{14}C-labeled materials which were translocated into the nonaerated root tissues (Table V).

Phloem transport of carbon into anoxic roots is indicated by the appearance of ^{14}C label in the roots and surrounding media of the nonaerated control and localized anoxia treatments. The proportion of translocated ^{14}C label within nonaerated root systems is reduced when compared to the aerated root system. These results agree with other short term ^{14}C-labeling studies of flooded plants (10, 14, 15, 26). However, when the time between labeling and harvest is lengthened to several hours or days, the amount of ethanol-soluble label found in the anoxic root system appears to be similar or even greater than that of the control (8, 29). This difference may be due to higher rates of metabolism, respiration, and re-translocation of ethanol-soluble compounds in the aerated controls compared to the long term anoxic root systems.

The proportion of ^{14}C label per unit dry weight of Seafarer roots, which was incorporated into CO_2 during the 3-h period,

Table IX. *CO_2 Production and Respiration by Half Root Systems of Seafarer and 31908*

Respiration rates are based on root dry weights. Percentages of ^{14}C in the total CO_2 respired during the last 30 min were determined by converting dpm to mol based on the specific activity of labeled sucrose and assuming universal labeling of carbon within the sucrose. Aeration treatments are listed in Table II. Values in each column followed by the same letter are not significantly different at the 5% level of probability by the LSD comparison.

Genotype	Aerated Treatments	Total CO_2 Production	Specific Respiration Rate	^{14}C Percentage of Total CO_2 Respired
		$\mu g\ (1/2\ plant)^{-1}\ h^{-1}$	$\mu g\ CO_2\ mg^{-1}\ h^{-1}$	$\% \times 10^3$
Seafarer	AC	1,515 bc	17.3 ab	4.6 a
	NC	568 cd	14.3 ab	0.1 a
	ALA	2,367 b	25.1 b	4.8 a
	NLA	483 c	12.5 a	0.4 a
31908	AC	2,320 b	17.9 ab	1.3 a
	NC	752 cd	13.3 a	0.1 a
	ALA	3,777 a	27.7 b	1.3 a
	NLA	948 cd	12.9 a	0.1 a

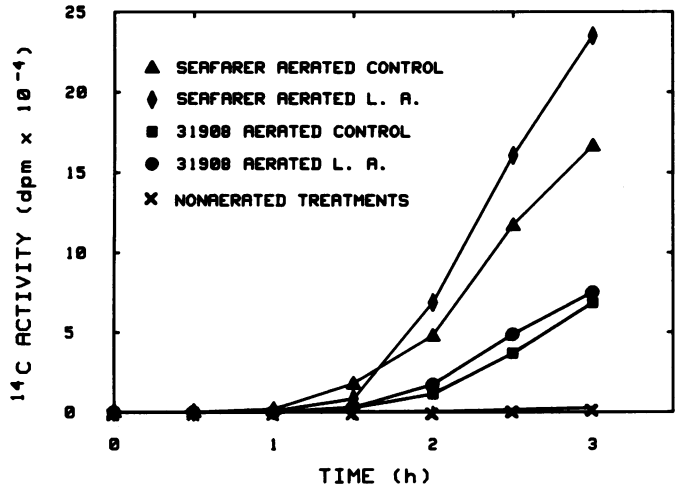

FIG. 1. Accumulation of $^{14}CO_2$ respired by the root system and collected in ethanolamine during the labeling period. The x axis refers to time in hours after labeling of the source leaf. F tests for comparisons between cultivars and between aeration treatments were significant at the 0.05 and 0.01 levels of probability, respectively. An orthogonal comparison of the aerated control and aerated portion of the localized anoxia treatments for both cultivars was nonsignificant.

was reduced from 32 and 31% for the aerated control and aerated half of the localized anoxia treatment to 0.7% and 6.6% for the nonaerated control and nonaerated half of the localized anoxia treatments, respectively. This occurred in spite of only slightly reduced rates of CO_2 production. The ratio of ^{14}C label recovered in the respiratory CO_2 to the ^{14}C label recovered in the ethanol-soluble fraction of the root system ranged from 0.47 to 0.35 for aerated root systems and from 0.01 to 0.09 for nonaerated root systems. These lower proportions of ^{14}C label in the respiratory fraction of nonaerated root systems indicate that the ^{14}C-labeled compounds translocated to the anoxic root system were less available for respiration than in aerated root systems.

There are several explanations which could account for a reduction in the proportion of ^{14}C label incorporated into the respiration CO_2 of the root system. Isotopic dilution of the ^{14}C label may have occurred within the nonaerated root systems. If metabolites such as sucrose were accumulated within the root system during the anoxia period, the ^{14}C label translocated to the nonaerated root systems could be diluted by the relatively larger metabolite pool in comparison to the aerated root system. An alternative explanation involves the restriction of metabolism of compounds represented by the ^{14}C label. This could occur if the ^{14}C-compounds within the nonaerated root system were either translocated as carbon compounds which are not readily metabolized or if the translocated compounds were converted into compounds not easily metabolized within the root system. A second type of restriction could occur if the translocated ^{14}C-labeled compounds were physically separated from the enzymes of the glycolytic pathway, for example if the ^{14}C-compounds were primarily located in the apoplast of the stele.

Phloem unloading in the roots initially occurs into the apoplast where sucrose is either taken up directly by cells within the stele (4) or hydrolyzed in the apoplast into fructose and glucose by an acid invertase (7). Entry into living cells either as sucrose or hexose requires active uptake (5, 9) which is greatly reduced under anoxic conditions. Movement of sugars out of the stele and into the cortex predominately occurs in the symplasm (6, 11). Soluble carbohydrates in the apoplast of the stele may also leak out at the point of secondary root emergence (19). The presence of ^{14}C label in the ethanol-soluble extracts of anoxic root systems with disproportionately lower levels of label in the respired CO_2 indicates that the majority of these photoassimilates may have been relatively unavailable for metabolism and/or that they were diluted by an excess of photoassimilates within the root.

The affect of anoxia on photoassimilate supplies within the root system is a subject of some controversy. Excised roots which are exposed to anaerobic conditions decrease in sugar content over time (20, 28). The addition of glucose to either excised or attached roots enhance root viability (28). Additionally, the capacity which some roots have for the enhanced catabolism of starch grains, during flooding, suggests there is a shortage of available sugar in O_2-stressed roots (18). However, several investigators have observed an increase in soluble carbohydrates in anoxic roots of intact plants suggesting sugar is not a limiting factor in flooded roots (1, 12, 17, 25). Papenhuijzen (17) suggested that compartmentalization of sugars occurs in roots exposed to anoxia and that root-associated microorganisms are unable to use these sugars during periods of nonaeration. The movement of sucrose into anoxic roots may result in the accumulation of apoplastic sugars in roots of flooded intact plants.

Localized anoxia tended to increase the movement of assimilates into the aerated half of the stressed root systems of both genotypes while having only a small effect on carbon movement

and use in the nonaerated half of the root systems. This supports our previous report in which localized anoxia stimulated root growth in the aerated half of the root system relative to the aerated control (23). The genotype 31908 appeared to allocate relatively more ^{14}C label to actively growing roots than Seafarer. In a previous study (23), we reported an increase in the growth of previously emerged roots during the localized anoxia treatment of line 31908 while localized anoxia stimulated the growth of those roots emerging during the treatment period for Seafarer. A pattern similar to that occurring for root growth was observed in the allocation of ^{14}C label for line 31908. Allocation of ^{14}C label for Seafarer in the localized anoxia treatment was essentially the same as that observed for the aerated control. These results indicate that Seafarer may have utilized stored carbohydrates for immediate root growth while 31908 utilized a greater quantity of current assimilates for growth.

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