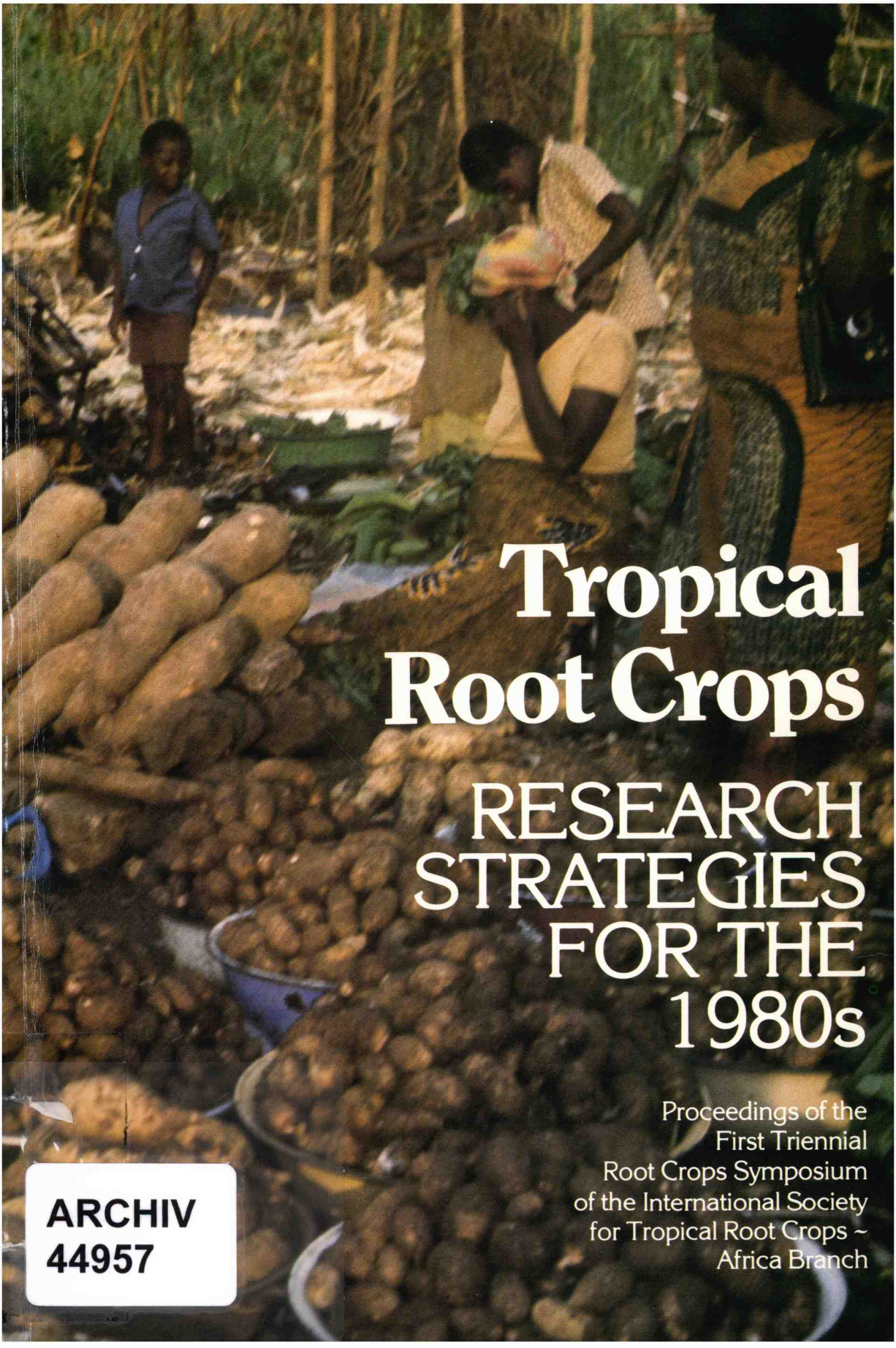

Tropical Root Crops

RESEARCH STRATEGIES FOR THE 1980s

Proceedings of the First Triennial Root Crops Symposium of the International Society for Tropical Root Crops ~ Africa Branch

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TROPICAL ROOT CROPS: RESEARCH STRATEGIES FOR THE 1980S

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CONTENTS

Yams

Cocoyams

METABOLISM, SYNTHETIC SITE, AND TRANSLOCATION OF CYANOGENIC GLYCOSIDES IN CASSAVA

M.K.B. BEDIAKO, B.A.TAPPER, AND G.G. PRITCHARD

DEPARTMENT OF BIOCHEMISTRY, UNIVERSITY OF SCIENCE AND TECHNOLOGY, KUMASI, GHANA; APPLIED BIOCHEMISTRY DIVISION, DSIR, PALMERSTON NORTH, NEW ZEALAND; AND DEPARTMENT OF CHEMISTRY, BIOCHEMISTRY AND BIOPHYSICS, MASSEY UNIVERSITY, PALMERSTON NORTH, NEW ZEALAND

We investigated the pathway of linamarin biosynthesis in cassava by vapour administration of ^{14}C-labeled precursors to cassava leaves. The incorporation of these precursors and of labeled valine administered by solution uptake was consistent with a pattern of linamarin biosynthesis established for other plants. It involves the reaction sequence through valine, isobutyraldoxime, isobutyronitrile, and 2-hydroxyisobutyronitrile. Administration of [^{14}C]valine to various organs of a cassava plant indicated that the leaf petioles, midribs, and shoot apex synthesize linamarin more efficiently than does the woody stem or the roots. No direct relationship was found between endogenous linamarin content and the organ's apparent ability to synthesize linamarin from exogenous valine. However, the low ability of leaf-blade tissues, root peels, and the edible flesh to incorporate valine into linamarin could be due to more active competing pathways removing the exogenously administered valine. We also investigated the translocation of linamarin in the cassava plant by following the path of leaf-synthesized linamarin translocated from the leaf to other parts of the plant. In both tuberous and nontuberous plants, a rapid loss of [^{14}C]linamarin has been shown to be due to translocation from the leaves. However, a residual component of [^{14}C]linamarin remained in the leaves. In senescing leaves, a continuous loss of both ^{14}C-labeled and endogenous linamarin occurred and left almost no residual component. This finding was attributed to both translocation and turnover. Translocated linamarin was distributed to all parts of the plant. An apical direction of linamarin distribution exists in the nontuberous plants, whereas root-directed linamarin translocation prevailed in the root plants. Leaf senescence apparently enhances linamarin translocation to the roots. We found there was little turnover of freshly synthesized [^{14}C]linamarin in detached leaves and root tissues. However low recoveries of [^{14}C]linamarin in the whole-plant translocation experiments suggest that active turnover is occurring during translocation or in certain tissues.

Essai sur la filière de la biosynthèse de la linamarine par la vaporisation de précurseurs appelés ^{14}C sur des feuilles de manioc. L'incorporation de ces précurseurs et de la valine administrés en solution correspond au modèle de biosynthèse de la linamarine établi chez d'autres plantes. Il comprend la suite des réactions à la valine, l'isobutyraldoxine, l'isobutyronitrile, et le 2-hydroxyisobutyronitrile. La vaporisation de valine sur les organes d'une plante de manioc a révélé que les pétioles, la nervure et l'apex des feuilles synthétisaient plus efficacement la linamarine que les tiges ligneuses ou les racines. On n'a trouvé aucune relation entre le contenu endogène de linamarine et la capacité apparente de l'organe à la synthétiser à partir de la valine. Cependant, le peu d'aptitude des tissus du limbe, des écorces des racines et de la chair comestible à incorporer la valine en linamarine pourrait provenir de l'existence de modes concurrentiels plus actifs qui neutraliseraient la valine administrée de l'extérieur. L'étude a aussi porté sur la translocation de la linamarine dans la plante en suivant la circulation de la feuille aux autres organes. Chez les plantes tubéreuses et non tubéreuses, cette translocation se traduit par une perte rapide de linamarine bien que les feuilles en retiennent une certaine quantité. Les feuilles âgées perdent continuellement la linamarine ^{14}C endogène presque sans conserver de résidu, phénomène attribué à la translocation et à la transubstantiation. Par la translocation, la linamarine a été distribuée dans tous les organes de la plante. Chez les plantes non tubéreuses, on a observé que la distribution de la linamarine suivait une direction apicale alors que chez les tubéreuses, la translocation était dirigée vers les tubercules. Il semble que la sénescence des feuilles favorise la translocation vers les racines. Les feuilles et les tissus des racines prélevés avaient peu transformé la linamarine qu'ils venaient de synthétiser. Cependant, la faible récupération de linamarine dans l'ensemble de la plante laisse envisager l'existence d'un phénomène actif de transubstantiation en cours de translocation ou dans les tissus mêmes.

Linamarin and lotaustralin, the cyanogenic glucosides of cassava, occur in all known cassava varieties and in all tissues of the plant. Possible pathways for cyanogenic glucoside biosynthesis

have been reported. Nartey (1968) reported a significant conversion of valine and isoleucine into linamarin and lotaustralin, respectively, by etiolated cassava seedlings. The actual biosynthetic pathways have not as yet been elucidated. The increasing role of cassava as feed and food intensifies the importance of an understanding of the metabolism of the cyanogenic glucosides contained in the plants. Participants at a conference on cassava toxicity in 1973 (Nestel and MacIntyre 1973) recommended such an investigation as useful to researchers screening and breeding for acyanogenic or low cyanogenic cassava. This paper reports on work done on linamarin biosynthesis in cassava, identifying the major sites of linamarin biosynthesis in the plant and investigating the possibility of translocation of linamarin from synthetic sites to other parts of the plant. The biosynthetic pathway was investigated by administration of some of the volatile precursors of linamarin, isobutyronitrile, isobutyraldoxime, and 2-hydroxyisobutyronitrile by a new technique in which the leaves were allowed to take up the precursor vapour in an enclosed glass chambre. Solution administration of L-[U-^{14}C]valine to various organs of the plant was used to investigate the biosynthetic sites. We labeled [^{14}C]linamarin in leaves with 2-hydroxy [I-^{14}C]isobutyronitrile vapour and followed the change in labeled linamarin content in the leaf and the distribution of linamarin to other parts of the plant.

EXPERIMENTAL PROCEDURE

SOURCE OF PLANT MATERIALS

Cassava seeds of unspecified varieties from Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia, were germinated in peat beds under glasshouse conditions (18–35°C and 75–90% relative humidity). Stakes of varieties Bega, Manioke, and Navolau obtained from the Ministry of Agriculture, Konorovia Research Station, Nansori, Fiji, were propagated in plastic troughs on peat beds. We obtained rooted sections of cassava either by using the shoot-apex method of Wholey and Cock (1975) or by suspending stakes in aerated water in free draining sand under mist. Rooted shoots or stakes were grown in solution culture or gravel culture nourished by the nutrient solution described by Forno et al. (1973).

SOURCE OF LABELED COMPONENTS

L-[U-^{14}C]valine was obtained from the Radiochemical Centre, Amersham, England. [I-^{14}C]isobutyronitrile (336 μCi/mmol) was prepared by a modification of the method by Smiley and Arnold (1960). The preparation and purification of the labeled compound are described elsewhere (Bediako 1977). 2-hydroxy[I-^{14}C]isobutyronitrile (262 μCi/mmol) was prepared by a modification of the method of Cox and Stormant with [^{14}C]NaCN and acetone. We purified the labeled cyanohydrin mixture by bubbling through it a gentle stream of nitrogen gas.

[U-^{14}C]isobutyraldoxime (0.848 μCi/mmol) was prepared by the action of hydroxylamine and isobutyraldehyde prepared from valine. The labeled oxime was purified on a gas–liquid chromatography (GLC) column at 110°C.

[I-^{14}C]linamarin was prepared by the administration of 2-hydroxy[I-^{14}C]isobutyronitrile to flax (*Linum usitatissimum*) seedlings. After standing overnight in illuminated chambres at 21°C, the seedlings were thrice extracted with 80% boiling ethanol, concentrated, and chromatographed on Whatman no. 3 mm paper with butanol saturated with water as solvent. The linamarin zone was eluted and frozen. Rechromatography of the eluate followed by elution and counting showed that the extract was radiochemically 80% pure. Linamarase was prepared by the method of Coop (1940).

ANALYTICAL METHODS

Plant materials were extracted in boiling 80% ethanol; insoluble residues were blended and reextracted in triplicate. Combined extracts were stored in a dark room at room temperature or reduced to dryness under vacuum at 50°C, the residues taken up in 20% propanol and stored at 0°C.

Paper chromatography and, thin layer chromatography (TLC)–electrophoresis were used to separate cyanogenic glucosides from other labeled compounds. Linamarin and lotaustralin were detected on chromatograms. [^{14}C]linamarin was estimated from eluates of chromatographic bands by enzymic hydrolysis followed by HCN trapping in alkaline solution and its assay by a colorimetric or potentiometric method. A gas chromatographic technique was also developed for linamarin assay. The method involves preparing TMS derivatives of linamarin and lotaustralin and assaying them on a Varian aerograph 1440 connected to an electron digital integrater and recorder.

We located ^{14}C-labeled compounds on chromatographic strips using a windowless radiochromatogram scanner. Radioactive compounds were detected after TLC–electrophoresis by radioautography with film exposure times up to 4 weeks. Radioactive spots or bands on chromato-

grams were eluted into scintillation vials. Scintillation mixture (1 : 2 Triton–Toluene solution containing 6 g Omniflour/litre) was added to sample eluates and ^{14}C activity determined with either a liquid scintillation spectrometer (Packard Tricarb 2002) with a wide and narrow window or a liquid scintillation system (Searle) with a teletype paper-punch connection.

ADMINISTRATION OF LABELED PRECURSORS

We detached leaf petioles under water and scalded the cut end briefly in hot water to arrest latex exudate. [^{14}C]valine was fed to the leaf by solution uptake through the cut end of the petiole. Then, the leaves were stood in beakers of water overnight at 21°C.

The volatile precursors [I-^{14}C]isobutyronitrile, 2-hydroxy[I-^{14}C]isobutyronitrile, and [U-^{14}C]isobutyraldoxime were administered to leaves by vapour uptake in a glass feeding chambre. The chambre consisting of a thick-walled circular glass dish (2 × 21 cm) with a ground rim was inverted over a leaf supported on a base glass plate. The leaf petiole passed through a side groove on the rim of the plate and a magnetic stirrer inserted in the chambre allowed vapours to be evenly circulated throughout the feeding period. The feeding chambre was made airtight with a layer of silicone gum laid between the dish and the base plate and tightly clamped down. Precursor solution was fed through an inlet septum on to the inner glass plate. The oxime and nitrile readily vapourized, but heat was required to vapourize the hydroxynitrile droplet. After various feeding times, residual vapours were trapped by water displacement into a 1 M NaOH solution. We recovered chambre washings to estimate precursor vapour uptake.

ADMINISTRATION OF [^{14}C]VALINE TO ROOT CORES AND PEELS

Root and peel tissues were fed with L-[U-^{14}C] valine by vacuum infiltration. The cores were punched from the edible portion and strips of peels were cut out after the outer corky layer was removed.

RESULTS AND DISCUSSION

PATHWAY OF LINAMARIN BIOSYNTHESIS

We administered ^{14}C-labeled linamarin precursors primarily to ascertain the suitability of the various precursors for subsequent studies on translocation and biosynthetic activity of different tissues. The results are of interest in connection with the pathway of linamarin biosynthesis (Table 1). The incorporation of the volatile precursors into linamarin in leaves from four different varieties was significant and was similar to that obtained for incorporation of valine. The results indicate that these volatile substances are efficient precursors of linamarin in cassava leaves. The data are consistent with the pathway of linamarin biosynthesis involving a reaction sequence from valine through isobutyraldoxime, isobutyronitrile, and 2-hydroxyisobutyronitrile to linamarin. This pathway has been demonstrated in *Linum* sp. by solution administration of labeled precursors. Enzymic investigation of a similar pathway has been reported in *Sorghum bicolor* by Conn and his co-workers. The involvement of analogous intermediates in this pathway suggests that the general pathway of cyanogenic glucoside biosynthesis is common in most cyanogenic species including cassava. It may be necessary in future investigations to examine the possible existence of an alternative pathway as well.

Such a study could involve the administration of ^{14}C-labeled precursors such as 2-hydroxyisobutyraldoxime in conjunction with the detection of relevant biosynthetic enzymes.

SITES OF LINAMARIN SYNTHESIS IN CASSAVA

The levels of cyanogenic glucosides in cassava tissues do not necessarily indicate which organs are responsible for the production of the cyanogenic glucoside. Table 2 presents data on incorporation of ^{14}C from valine into linamarin. Radiochromatogram scans of the ethanol extracts indicate that administered [^{14}C]valine was extensively metabolized in all tissues. The petiole tissues gave by far the highest percentage incorporation. The values for leaves, upper stem, and shoot apex were similar and were considerably higher than were those for the lower stem and underground tissues — the roots.

LINAMARIN BIOSYNTHESIS IN THE PETIOLATE LEAF SYSTEM

The experiments indicated that the leaves, petioles, and shoot apices are much more active in converting valine into linamarin than are mature stem and underground parts. Thus for follow-up investigations, we chose tissue systems showing large differences in percentage incorporation — the petiolate leaf and the root.

In our feeding experiments, labeled leaves were harvested at 0.5-, 4-, and 24-h intervals and dissected into petioles, midribs, and blade sections.

Table 1. Incorporation of precursors into linamarin in cassava leaves.

Cassava variety	Precursor	Treatment (μCi)	[^{14}C]linamarin μCi	[^{14}C]linamarin SA[b]	% ^{14}C incorporation
Manioke	Valine	0.954	0.164	5.2	17.2[a]
Navolou	Valine	0.700	0.070	2.0	12.5[a]
A	Valine	1.000	0.091	3.3	11.6[a]
Bega	2-OH-isobutyronitrile	3.820	0.790	13.6	20.6
Manioke	Isobutyronitrile	11.300	0.190	7.9	15.9
Manioke	Isobutyraldoxime	0.610	0.150	6.0	24.9

[a]Corrected for loss of carboxyl carbon.
[b]SA = specific activity (μCi/mmol).

Each tissue was then analyzed for [^{14}C]linamarin (Table 3). The time-course analyses showed that all the tissues of the leaf system incorporate [^{14}C]valine into [^{14}C]linamarin, although incorporation in leaf blade is very low. A high level of incorporation (35–57%) was attained in the leaf petioles. Such high incorporations are comparable only to the 48% incorporation of [^{14}C]valine into linamarin by *Linum usitatissimum*. In the midribs about 20% ^{14}C was incorporated into linamarin after 24 h — a lower rate than was found in the petioles but considerably higher than the 2% value attained in the leaf blades. The very low incorporation levels in the blade tissues could be due to a low biosynthetic capacity of the mesophyll tissue or to the transformation of much of the precursor into other substances before it reaches this tissue. However, similar low synthetic values were observed when the leaf blade was uniformly vapour-fed with 2-hydroxy[I-^{14}C]isobutyronitrile.

Endogenous linamarin in the blades was 11–17 mmol/g and that of the midribs was 31–33 mmol/g fresh weight. These values are higher than that of the petioles (6–8 mmol/g). Thus there seems to be no simple relationship between linamarin levels and biosynthetic activity. Physiologic factors within the leaf tissues may be a contributing factor. The ability of each tissue to store endogenously synthesized linamarin may be greater within the blade and midrib than in the petioles.

Biosynthesis by Root Tissues

The maximum values for incorporation of [^{14}C] valine into linamarin by both the root core and the root peels were low. The cores incorporated about 0.1%; the peels, about 1–2%. Despite these low levels of ^{14}C incorporation, the endogenous linamarin level in the peels was almost as high as in the leaves. The peel, like the leaf blade, may accumulate much of the linamarin it synthesizes. Nevertheless, much of the root linamarin may come from aerial organs of the plant as indicated by the translocation experiments.

Translocation of Linamarin in Cassava

The translocation of linamarin in cassava has scarcely been investigated. De Bruijn carried out

Table 2. Incorporation of valine into linamarin by cassava tissues.

Plant section	L–[U–^{14}C]valine μmol	L–[U–^{14}C]valine SA[b]	[^{14}C]linamarin μCi[a]	[^{14}C]linamarin SA[b]	% ^{14}C incorporation
Shoot apex	1.0	993	0.160	4.3	16.1
Upper leaves	2.0	496	0.088	2.5	8.9
Lower leaves	2.0	496	0.067	2.4	6.8
Upper leaf petioles	3.0	333	0.623	97.3	62.3
Lower leaf petioles	3.0	333	0.487	55.3	48.7
Upper stem	1.0	993	0.137	4.4	13.1
Lower stem	1.0	993	0.009	0.4	0.9
Primary roots	1.0	2000	0.040	71.4	2.4
Tuberous roots (plus peels)	3.0	333	0.063	1.1	6.3

[a]Corrected for an assumed loss of ^{14}COOH from L–[U–^{14}C]valine.
[b]SA = specific activity (μCi/mmol).

Table 3. Incorporation of [^{14}C]valine into linamarin by leaf tissues.

Leaf section	Metabolic time (h)	[^{14}C]linamarin		
		μmol/g	SA[a]	% ^{14}C in section
Basal petiole	0.5	8.65	3.1	4.4
Distal petiole	0.5	14.00	0.9	4.8
Midribs	0.5	33.00	0.2	2.0
Blade	0.5	15.20	0.2	0.8
Basal petiole	4.0	6.8	12.5	34.9
Distal petiole	4.0	6.9	19.7	57.1
Midribs	4.0	31.1	0.8	12.3
Blade	4.0	14.0	0.6	1.8
Basal petiole	24.0	7.6	16.6	41.6
Distal petiole	24.0	8.2	7.9	21.9
Midribs	24.0	32.8	1.2	20.2
Blade	24.0	17.0	0.7	2.1

[a]SA = specific activity (μCi/mmol).

stem ringing experiments on cassava and reported accumulation of cyanogenic glucosides above the point of incision. Therefore, we investigated the possibility that translocation of linamarin contributes to the endogenous linamarin in the root system. Specifically labeled linamarin was synthesized in situ in the leaf system. The ability of cassava leaves to synthesize linamarin from volatile precursors made it possible for us to administer 2-hydroxy[I-^{14}C]isobutyronitrile directly to an undamaged leaf still attached to the plant. Thus, we were able to follow the disappearance of the labeled linamarin from the fed leaf and its appearance in other tissues with minimum disturbance to the plant.

The time course of changes of [^{14}C]linamarin was followed in attached leaves of various plants by disc analysis, which provided a general indication of linamarin removal from leaves. Preliminary time-course analysis on detached and attached leaves indicated that linamarin breakdown alone did not account for the amount that it decreased in intact leaves.

The time-course patterns indicated a high rate of [^{14}C]linamarin removal from the leaf immediately after synthesis up to 69 h, after which the activity remained almost constant. This trend was found for upper and lower, fully expanded green leaves. Similar biophasic patterns of translocation have been reported for [^{14}C]photoassimilates in corn, sugar beets, and soybean.

The rates of [^{14}C]linamarin translocation from the leaves, however, differed between leaves of tuberous and nontuberous plants and also according to the age or position of the leaf on the plant. On nontuberous plants, the rate at which the lower leaves lost linamarin (as indicated by the time until

Table 4. Distribution (% of initial [^{14}C]linamarin synthesized in source leaf) of translocated linamarin in cassava plants.

Plant organ	Nontuberous plants		Tuberous plants	
	Upper leaf	Lower leaf	Fresh leaf	Senescing leaf
Tubers	–	–	2.4	6.0
Primary roots	0.1	0.2	0.7	0.4
Lower stem	0.2	0.3	2.2	5.3
Upper stem	0.3	0.2	0.7	0.5
Upper leaves	0.3	0.3	0.7	4.9
Lower leaves	ND[a]	ND[a]	0.7	0.5
Source leaf petioles	1.0	0.7	0.2	0.5
Source leaf	14.1	13.8	24.5	0.5
%[^{14}C]linamarin recovered	16.0	15.5	31.4	18.1

[a]ND = not detectable.

activity dropped to 50% of its initial level) was twice as great as the rate of an upper leaf.

The overall kinetic pattern suggests that some of the linamarin synthesized in the leaf is transferred into an immobile pool (after 96 h) from which it can be translocated only very slowly. This immobile pool could be in the cell vacuoles of the leaf-mesophyll tissue. Saunders et al. demonstrated that up to 90% of dhurrin synthesized in young *Sorghum bicolor* seedlings was located in the cell vacuoles. A similar accumulation in the cell vacuoles probably accounts for the slow phase, whereas the initial fast phase may be attributed to rapid loss from a more accessible pool in the plant cells.

An interesting finding of the time-course study was the apparently higher rate of [^{14}C]linamarin translocation from leaf blades of immature nontuberous plants than from the blades of tuberous plants. It appears that the presence of tuberous roots, which might be expected to constitute an effective "sink" does not increase the rate of linamarin translocated from individual leaves.

Translocation of freshly synthesized [^{14}C]linamarin proceeded in normal green leaves, whereas the endogenous linamarin levels remained virtually unchanged. This finding could be interpreted as indicating a steady condition between synthesis and translocation in the leaf tissues. In contrast to the situation in nonsenescing leaves, the senescing leaf blade showed a continuous loss of both endogenous and freshly synthesized [^{14}C]linamarin with the same initial rate. Similar losses of [^{14}C]photoassimilates have been reported on senescing leaves of *Beta vulgaris*.

The mature and immature cassava plants whose attached single leaves had been selectively labeled with [^{14}C]linamarin were harvested after 7 days, divided into various parts, extracted, and analyzed for [^{14}C]linamarin and endogenous linamarin. Because of turnover factors, [^{14}C]linamarin recoveries did not provide a quantitative assessment of the total linamarin translocated from the source leaf but were indicative of the general pattern of "source–sink" relationships between the leaves and other organs and tissues.

Mature green leaves retained about 80% of the total [^{14}C]linamarin recovered from the whole plant. There was not much difference in recoveries from upper and lower leaves or from tuberous and nontuberous plant leaves (Table 4). In marked contrast to this high retention, senescing source leaves retained only 0.5% of the initial [^{14}C]linamarin. By measuring total linamarin levels in attached and detached leaves undergoing senescence, we demonstrated that the loss of linamarin during senescence was attributable to both linamarin turnover and translocation.

In the young nontuberous plants, leaves above the source leaves contained a significant proportion (14–16%) of the translocated linamarin recovered. Thus, in young, nontuberous plants there is a predominantly upward translocation from older leaves to young leaves and shoot apices. The distribution of translocated linamarin in tuberous plants, however, appears to be directed toward the basal organs of the plant. After 7 days of translocation, the tuberous plants gave higher recoveries of [^{14}C]linamarin in the lower stem and roots than in other organs of the plant. Translocation from a senescing leaf to the root system was higher than it was from a nonsenescent leaf. Thus, although the presence of tuberous roots in cassava does not increase the rate of [^{14}C]linamarin translocation from an individual leaf, it does influence the general distribution of translocated [^{14}C]linamarin in the plants.

In translocation experiments using [^{14}C]CO_2 to label photoassimilates in tuberous cassava plants, Hume (1975) reported that 4.4% of the initial [^{14}C]photoassimilates were recovered from the roots after 7 days of translocation and 38% were recovered in the labeled leaves. Despite the varietal and cultural differences of the cassava plants used by Hume and in this experiment, his values are not very different from our observations. This fact suggests that linamarin and products of CO_2 assimilation in cassava are simultaneously translocated from leaves to the roots.