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Transport of ^{14}C-IAA from leaves and shoots to different fruit parts

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Abstract

Transport of ^{14}C-IAA was studied in apple spurs of a 20-year-old McIntosh with one fruit and one shoot. Water solutions of IAA were applied to intact, pricked or scratched leaf blades, to decapitated shoots or to petioles (leaf-blade removed) at the end of June, July and August. ^{14}C-IAA (in an unknown form) was transported from intact leaves and shoots to pedicel, pericarp and seeds. Radioactivity of the pedicels increased every month while that of seeds reached maximum at the end of July and then markedly decreased in August. Total radioactivity of whole fruit doubled, at least, with every month due to enlargement of the pericarp. Pedicels deprived of fruits had their retention prolonged on spurs with leaves or shoots treated with 1 % IAA in lanoline. It is assumed that auxin delivered from shoots or still growing leaves at the time of its deficiency in seeds, restrains fruits from premature dropping. At the same time seeds seem to be protected by a regulatory system in pedicel against too massive flow of auxin from outside.

Introduction

Immature, growing apple seeds comprise a self-sufficient source of auxin and other hormones (Luckwill *et al.* 1969) which attract nutritional constituents necessary for growth and development of the whole fruit (Stösser and Naubeller 1972). There is no obstacle in pedicel to hormone transport from apple seeds (Grochowska 1974, Grochowska and Karaszewska 1978). Owing to its transport through pedicel, auxin secures fruit retention on the tree (Addicott *et al.* 1955).

The production of seed auxin in apple fruit temporarily ceases or markedly diminishes in mid-summer (Grochowska and Karaszewska 1976). At that time fruits might be supplied with hormones present in the transpiration stream (King 1976). When applied in lanoline to spurs and pedicels of apple fruits IAA, GA_3 and NAA prolonged fruit retention (Grochowska and Karaszewska 1978). However, direct auxin transport from vegetative organs to fruit parts is still controversial. It is of

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interest whether fruit pericarp and seeds are supplied with auxin derived directly from growing shoots and leaves.

Materials and methods

Ten apple spurs of 20-year-old tree (*Malus domestica* Borkh., cv. McIntosh) with one fruit and one growing leaf or shoot were treated using one of the following procedures:

A. Water solutions of 1-^{14}C-IAA (37 kBq, *Amersham*) and 2-^{14}C-IAA (73 kBq, *Amersham*) at concentrations of 8.5×10^{-5} M and 2.1×10^{-4} M, respectively, were applied to a growing shoot with a removed apex or to the intact leaf surface, or also to the petiole (leaf blade removed). 500 μl of radioactive solution was delivered to the shoot or petiole through a thin tube from a vial. Radioactive IAA in lanoline was also applied to a pricked surface or scratched nerve of the leaf blade. EDTA (20 mM Na-salt of ethylene-diaminotetraacetic acid) was applied to the top surface of pedicels to simulate active fruit absorbing system. After 3, 5, 21, 24 and 48 h exposure fruit parts studied were collected for analysis. Each treatment was applied in 7 or 10 replicates.

B. Water solutions (200 μl) of 1^{14}C-IAA (160 Bq μl^{-1}) at a concentration of 2.2×10^{-4} M was applied to the bottom surface of an intact leaf in ten replicates at the end of June, July, and August. To improve radioactive IAA translocation a cold GA_{4+7} at a concentration of 20×10^{-4} M was added to the half number of spurs in two terms (Grochowska and Karaszewska 1976, Maheshwari *et al.* 1980). Fruits were collected after 22-h exposure. Each fruit of both experiments was divided into pedicel, seeds and pericarp. They were weighed, ground with 80 % cold acetone and extracted for 48 h with one change after 24 h. Decanted extracts were freed of acetone and mixed with a scintillation fluid. The method efficiency in relation to standard radioactivity recovery was 87 %, on an average. Radioactivity of pedicel and seeds, as well as pericarp extracts was determined in a *Beckman* scintillation spectrometer *LS-40* (*Intertechnique*) using internal and external standards, respectively. Results after background and quenching corrections were evaluated statistically by Duncan's *t*-test.

C. "Cold" IAA (1 %) in lanoline paste was applied to the surface of spur or shoot leaf on spur with a single pedicel as fruit was removed. Control pedicels were treated with pure lanoline. Period of the pedicel retention on the spur was recorded in 20 replicates within 24 d.

Results and discussion

The first experiment (*A*) showed that radioactive IAA applied to leaves or shoots was transported, in an unknown form, to the pedicel, pericarp and seeds of the apple fruit growing on the same spur (Table 1). Within 3 h radioactivity reached the growing fruits when ^{14}C-IAA was applied to the decapitated shoots or petioles deprived of leaf blades. Radioactivity of all fruit parts increased with the time of translocation.

All wounds on the donor spur contributed to an increase of radioactivity of pedicels while seed and pericarp radioactivity was scarcely affected and remained at the level similar to radioactivity transported from the intact donor organs.

Table 1. Transport of ^{14}C-IAA from spur organs into different fruit parts.

IAA donor	Pretreatment	Application form	date	Transport [h]	Receptor pedicel	seed	pericarp	Ratio pedicel/ seed
					[Bq g^{-1}(f.m.)]			
Leaf	intact	solution	8 July	0	0	0	0	
				21	27.4	14.9	16.6	2
Shoot or petiole	Apex or blade removed	solution	8 July	3	196.5	0.8	1.0	245
				5	553.0	7.0	9.0	79
				21	1138.2	18.3	22.5	62
Leaf	pricked	lanoline	17 July	45	152.9	5.2	20.2	29
Leaf	veins scratched	lanoline	3 August	48	726.2*	5.7	24.7	127
				48	36.3**	0	0	

* 2-^{14}C-IAA; ** EDTA replaced removed fruit

If EDTA, which is able to sustain the permanent vascular transport, was applied to pedicels deprived of fruit, no increase in radioactivity accumulation in the pedicels was observed. It is assumed that pedicel itself is not able to accumulate radioactive IAA except in the presence of the fruit. Less labile IAA labelled with ^{14}C in the second carbon of the side chain, proved transport (in an unknown form) to distant fruits.

Study of ^{14}C-IAA absorption by the fruit parts at various periods of fruit growth (experiment *B*) showed an increasing absorption of ^{14}C-IAA by pedicels of fruits from the end of June to the end of August. An increase in radioactivity, progressive in time, was also found in fruit pericarps independently of the distance from the site of ^{14}C-IAA application (Table 2).

However, radioactivity accumulation by seeds was different from that of the pedicel and pericarp. Radioactivity of seeds markedly increased in July, then dropped to a very low level in August. The distance of labelled IAA application (spur or shoot leaf) had a little effect on the radioactivity accumulation by the seeds.

GA_{4+7} added to the radioactive IAA did not change the rate of radioactivity transport to the fruit parts in June; in July radioactivity absorption in the presence of GA_{4+7} was even reduced in all fruit parts.

Total absorbed radioactivity of the whole fruit doubled with every month mostly due to enlargement of the pericarp. No significant differences were observed in the total fruit radioactivity between different distances of auxin applications.

The translocation of IAA to the pedicels deprived of fruits was recorded by their prolonged retention on spurs whose leaves were treated with IAA in lanoline (experiment *C*), (Table 3). Treatments of spurs or shoot leaves with IAA caused an enlargement of retention by 40 to 30 % pedicels on spurs to 18 and 24 d, respectively, from the auxin application. A similar retention period showed pedicels treated with IAA. The control pedicels treated with lanoline alone dropped all after 15 d.

Table 2. Transport of ^{14}C-IAA to fruit from intact leaf at various stages of fruit growth.

Fruit part	^{14}C-IAA applied to spur leaf			long shoot leaf				
					+GA$_{4+7}$		+GA$_{4+7}$	
	June	July	August	June	June	July	July	August
Pedicel (*p*)	69.0*	219.3f	366.9g	30.4c	29.5c	87.2e	71.6d	400.2g
Seed (*s*)	13.1b	32.0c	4.1a	8.6ab	11.1ab	25.5c	8.5a	3.9a
Pericarp	10.8ab	9.3b	12.6b	6.7a	6.9a	8.1ab	2.8a	11.3b
Radioactivity ratio *p*/*s*	5	7	91	4	3	3	8	103
Whole fruit radioactivity	249.7*	685.9	1509.6	170.2	192.3	558.8	210.0	1411.8
Pericarp fresh mass	23.1*	73.8	119.8	25.4	27.9	69.0	72.4	125.0

* Mean of 10 replicates; means followed by the same letters are not significantly different (P=0.05).

Table 3. Effect of IAA application to spur and shoot leaves on the retention of pedicels (fruit removed).

IAA source	Retention of pedicel [%] Time from IAA application (July/August) [d] 7	10	12	15	18	21	24
Pedicel	100	80	80	55	45	25	25
Spur leaf	100	85	45	45	40	35	30
Shoot leaf	100	55	40	40	40	35	30
Control pedicel (IAA)	100	40	20	15	0	0	0

The retention enlargement of pedicels deprived of fruits after distant application of IAA entitled us to consider ^{14}C-IAA to be transported to fruit parts in its active from.

Distribution of radioactive IAA amongst particular parts of the fruit has proved dependent on pretreatment (cutting, pricking, scratching) which vegetative organs-donors received before the ^{14}C-IAA application. A huge increase in radioactivity in pedicels was observed when auxin was applied to decapitated shoots or petioles deprived of leaf blades. When intact leaves were treated with labelled IAA radioactivity of the fruit pedicels was relatively low.

However, radioactivity of seeds proved low and almost at the same level independently of the pretreatments given to the donor leaves or shoots. Ratios of pedicel to seed radioactivities, derived from ^{14}C-IAA applied to wounded donors, surpassed many times those from the intact donors (Tables 1 and 2, respectively). Those ratios may indicate a curious peculiarity of pedicel which seems to restrain radioactive IAA from its abundant and uncontrolled penetration into seeds. Therefore, we assume that pedicel may have some regulatory system that protects seeds against a massive flow *e.g.* of auxin which, in this particular case, seems to be transported through the xylem tissue open by the cuttings.

When applied together with ^{14}C-IAA, GA_{4+7} contributed to the decrease in radioactivity in individual parts of fruits probably due to the auxin enhanced basipetal transport (Grochowska and Karaszewska 1976a, Maheshwari *et al.* 1980, Rubery 1987).

The significant increase of radioactive auxin absorption by seeds at the end of July coincides with a drastic decrease in endogenous auxin production and exudation from these organs that was observed at the same time in four apple cultivars (Grochowska and Karaszewska 1976). Apple fruits ceased or markedly diminished their production of seed auxin in a more advanced stage of development (end of July, August). According to the auxin gradient theory of abscission regulation (Addicott *et al.* 1955) a steady flow of auxin through pedicel, independent of its direction (Grochowska and Karaszewska 1978) is considered an indispensable condition for fruit retention on the tree. This is also confirmed, in part, by the prolonged retention of pedicel alone (fruit removed) after applications of IAA to the distal donor leaves or shoots.

Therefore, acute deficiency of seed auxin and its diminished flow throught the pedicel, while not compensated by delivery from shoots (whose growth usually ceases at that time), may result in premature drop of fruits.

The fast growing pericarp is a sink of a great potency for the shoot auxin which, besides promotion of growth, directs the flow of nutrients necessary for further enlargement (Peel 1974, Bangerth and Ho 1984).

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