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Effect of GA_3 on photosynthate allocation and invertase activity in radish plants grown on different potassium levels

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Abstract

The effect of GA_3 application to the swollen hypocotyl was studied in radish cultivars Saxa and Tetra Iłowiecka, supplied with various amount of K and grown in greenhouse in hydroponic culture. In low-K plants of both compared cultivars, strong depression of $^{14}CO_2$ assimilation preceded diminished export of current photosynthates. In plants with K^+-deficit, transfer for 3 days from low- to high-K solution stimulated photosynthesis without effect on ^{14}C-export. Three days after GA_3 treatment of the swollen hypocotyl $^{14}CO_2$ assimilation was stimulated while ^{14}C-retention in the blades was diminished, but only in low-K plants. In Tetra low-K plants with poorly developed storage organs, treatment with GA_3 caused their better supply with current photosynthates at the expense of the roots. In the Saxa cultivar, the pattern of photosynthate allocation was only slightly affected by GA_3 even in K-deficient plants; the swollen hypocotyl was already developed before K depletion from the nutrient solution. Nevertheless, in Saxa plants, GA_3 prolonged not only growth of the storage organ, but also enhanced acid invertase which at that time was greatly diminished in low- and high-K plants. In contrast, the relatively high activity of invertase in Tetra cv. was not affected by GA_3 treatment in low-K plants and was even depressed in high-K plants. This suggests that growth and accumulation of substances in the storage organ of radish plants and acid invertase activity greatly differ in their response to applied GA_3.

Key words: gibberellic acid, invertase, photosynthates distribution, potassium deficit, radish plant

INTRODUCTION

Storage organs like the swollen hypocotyl of radish plants comprise the following main activities: initiation of cambial activities, cell division and expansion, storage of carbohydrates (Hole et al. 1984). Thickening of the swollen hypocotyl is accompanied by both increase of cell number and size up to 35-40 days of plant age (Ting and Wren 1980, Joyce et al. 1983.). All the above mentioned processes are under hormonal control.

The response of radish plants to treatment with growth substances: IAA, GA_3 and zeatin, depends strongly on their stage of development (Starck and Stradowska 1977). In young radish plants with a high rate of leaf growth, treatment of swollen hypocotyls either with IAA, GA_3 or zeatin increased the $^{14}CO_2$ assimilation rate and ^{14}C-retention in the blades, causing competition for photosynthates between shoot and swoolen hypocotyl. This was in contrast to older plants with a high mobilizing power of the storage organ, promoted by exogenously introduced growth regulators (GR). This suggests the existence of a very different plant responsiveness, dependent on the stage of development, also postulated recently by Trewavas (1982) and many other authors. They suggest, that the growth-limiting factor is rather sensitive to growth substances than to their concentration.

In radish plants K deficit specifically depresses growth of the swollen hypocotyl (Starck et al. 1980), as a consequence of disturbances in translocation and accumulation of photosynthates, controlled among others by potassium. The well established effect of K on photosynthate translocation may be attributed to its role in phloem loading (Doman and Geiger 1979), as a determinant of membrane transport processes (Reinhold and Kaplan 1984), a stimulator of ATP-ase activity located in the phloem tissue and possibly involved in photosynthate unloading, owing to the arising of a hormone-controlled electrochemical gradient (Didehvar and Baker 1986). Potassium may also reflect membrane permeability to positive charge into the unloading cells, as postulated by Patric (1987).

In K-deficient radish plants, the restricted accumulation capacity of the swollen hypocotyl was improved by GA_3 and IAA, introduced locally into the storage organ (Starck et al. 1980), affecting source-sink relations, where current photosynthates become a factor limiting dry matter accumulation in the swollen hypocotyl in contrast to both the untreated, but low-K and high-K plants. Gibberellins may affect unloading of phloem in the sink (Patrick and Wereing 1980, Hayes and Patrick 1985) or both loading and unloading as Pereto and Beltram (1987) presented in pea plants. On the other hand, GA_3 probably also stimulates acid invertase synthesis and/or its activity (Jones and Kaufman 1971, Kaufman et al. 1973, Daie et al. 1986). This is a key enzyme contributing to the mechanism controlling the supply of sink organs with photosynthates (Eschrich 1980, Morris and Artur 1985, Claussen et al. 1986).

The aim of the present work was to compare the effect of GA_3 applied to the swollen hypocotyl of radish plants, which were supplied with different potassium doses, on photosynthate distribution and acid invertase activity in two differing radish cultivars.

MATERIALS AND METHODS

Radish plants of cultivars Tetra Iłowiecka and Saxa were grown in the spring in hydroponic culture, in a greenhouse on modified Hoagland solution with two levels of potassium, differing by 20-fold. The low-K (designated 0.1K) solution contained 23.5 μg cm^{-3}, the high-K solution – 470 μg cm^{-3} K (two times more than in standard Hoagland solution), designated as 2K.

The plants were grown in polyvinyl vessels containing about 10 dm^3 of solution with 30 plants in each. The nutrient solution was renewed once, 14 days after planting in the hydroponic culture brought to 0.1 K and 0.05 K for Tetra and Saxa plants, respectively. Water loss was made up daily with distilled water. There were no visible K-deficit symptoms in both cultivars up to the end of experiments.

Plants of both cultivars were collected for dry matter estimation and labelled with $^{14}CO_2$ two or three times (younger 23-29-day-old) and older (32-35-day-old) three days after GA_3 (Gibrescol) application to the surface of the upper part of the storage organ, in lanoline paste (30 mg GA_3, per 1 g of lanolin + 0.5 cm^3 of water). One series of each cultivar of older low-K plants was transferred for 3 days to 2K nutrient solution to diminish K-deficit. The K concentration was determined with an atomic absorption spectrometer in plants of all series, after ashing dry matter.

Plants were labelled with $^{14}CO_2$ in a plexiglass chamber during 30 min exposure, under natural irradiation. The distribution of ^{14}C-photosynthates was measured 2 h after the beginning of exposure. The radioactivity of individual organs was estimated by the use of a Tesla NZO_2605 scintillation counter equipped with NCZ 602 automatic sample exchanger. Most measurement were done in three or four replications (one plant per each). Statistical analyses were performed according to Student's t test. Conditions during $^{14}CO_2$ assimilation were as in Table 1.

Table 1

Conditions during $^{14}CO_2$ assimilation

Cultivar	Plant age (days)	Specific radioact., KBq mg^{-1} CO_2	CO_2 conc. % v/v
Tetra	28	92	0.09
	35	44	0.11
Saxa	29	82	0.04
	32	59	0.06

EXTRACTION AND ASSAY OF INVERTASE ACTIVITY (β-D-FRUCTOFURANOSIDE FRUCTOHYDROLASE EC 3.2.1 26)

Invertase extraction and activity were estimated according to Ricardo and Sovia (1974).

Storage organs from 5 plants (7-8 g of 0.1K and 30-40 g of 2K series) were homogenized at 4°C in the Na_2HPO_4-citric acid buffer, at pH = 7.5 and ionic strength 0.4. The unfractionated homogenate was dialyzed at 4°C for 24 h against 6 dm^3 of extracting buffer at 0.1 ionic strength and then was taken for assay of invertase activity. The reaction mixture (pH = 4.5) composed of 1 cm^3 of homogenate and 4 cm^3 of Na_2HPO_4-citric acid buffer (ionic strength 0.4) containing 50 mg sucrose was incubated at 30°C for 1 h. Reducing sugars were determined with 3-5-dinitrosalicylic acid, according to Bernfeld (1955). Linear regression analysis by the least squares method and standard deviations were calculated.

RESULTS

DYNAMICS OF PLANT GROWTH AT TWO POTASSIUM LEVELS

The plants grown in low-K solution (0.1 K series) exhibited drastically diminished potassium content in all the organs of both cultivars (Tables 2, 3): the lowest was in the roots and storage organ (cv. Tetra, Table 2) or in the storage organ (cv. Saxa, Table 3).

Table 2

Potassium content in plants (cv. Tetra)

Organs	Age (days)	0.1K			2K	
		n.t.	$+GA_3$	+K	n.t.	$+GA_3$
Total plant	28	284	260	–	925	1183
	35	315	235	700	1208	2083
Blades	35	213	243	350	1002	1131
Petioles + cotyledons	35	273	330	546	1535	1998
Swollen hypocotyl	35	749	524	804	1469	1569
Roots	35	423	483	596	633	782

n.t. – not treated, control plants.

Potassium content in the total plant – in μM in 28-and 35-day-old plants and in the individual organs – μM $(g\ d.m.)^{-1}$ of 35-day-old plants.

In the stage under investigaton, in Tetra plants from 2K nutrient solution (high-K plants), the highest growth rate was observed for the swollen hypocotyl and the lowest for the roots (Fig. 1). In contrast, in low-K plants the storage organ was poorly developed (Figs. 1A, 4).

Table 3

Potassium content in plants (cv. Saxa)

Organs	29-day-old		32-day-old				
			0.1 K			2 K	
	0.1K	2K	n.t.	$+GA_3$	+K	n.t.	$+GA_3$
Total plants	139	608	197	139	577	841	1123
Blades	305	1031	218	51	841	551	1062
Petioles + cotyledons	185	2031	108	45	374	1439	1763
Swollen hypocotyle	590	1210	585	462	885	636	1174
Roots	167	951	223	149	649	1044	890

Estimations – like in Table 3.

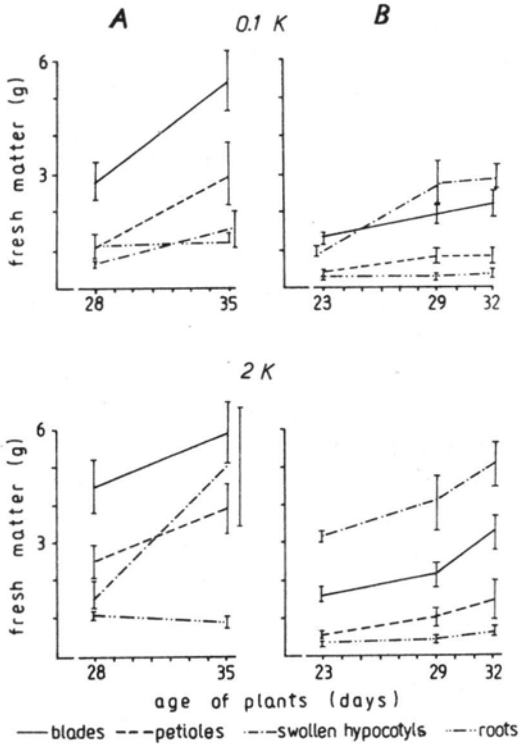

Fig. 1. Dynamics of growth of individual radish organs, expressed as their fresh matter. A – Tetra, B – Saxa. Bars indicate standard deviations

In the high-K plants of the Saxa cultivar the fresh matter of the swollen hypocotyl dominated all of the other plant organs, already in 23-day-old radish plants, although the rate of its increment was lower as compared with the analogous series of Tetra plants. Potassium deficit retarded less the storage organ growth of Saxa plants than of the Tetra cultivar, causing smaller reduction in the relatively high harvest index of Saxa plants, as illustrated below (Table 4).

Table 4

Harvest index of 35-day (Tetra) and 32-day (Saxa) old plants

Cultivar	0.1K	2K
Tetra	0.14	0.38
Saxa	0.39	0.47

The size and dynamics of Saxa storage organ dry matter increment of the 2K-series indicate a much earlier initiation of storage organ growth, before severe K-deficit in plants. This organ was stimulated by GA_3 treatment much more than the other ones (Fig. 2B). Transfer of low-K plants into full nutrient solution also stimulated growth of all plant organs, but especially of leaves (Fig. 2B). In contrast, Tetra plants responded much less to GA_3 and K treatment (Fig. 2A). The size of the root system exceeded significantly that of K-optimal plants, allowing for partial compensation of K absorption.

ASSIMILATION OF $^{14}CO_2$ AND PATTERN OF ^{14}C-PHOTOSYNTHATE ALLOCATION

In both cultivars, the K deficit had already diminished the CO_2 assimilation rate, calculated both per plant or blade fresh matter, in younger plants, when total ^{14}C-export from the blades was not yet affected (Tables 5, 6).

In the Tetra cultivar, in low-K plants the portion of ^{14}C exported from the blades was similar in younger and older plants, in contrast to its increase in K-optimal series, enhancing differences between low-K and high-K plants (Table 5).

In Saxa cv., export of current photosynthates decreased with age in both K-level plants, but more distinctly in low-K plants.

K-deficit affected ^{14}C-distribution much more in Tetra plants. In Tetra low-K younger plants, roots were the dominant ^{14}C-acceptor, as an organ which attained a relatively large size at the expense of the poorly developed storage organ. GA_3-treatment in both stages of development stimulated not only the $^{14}CO_2$ assimilation rate and enhanced ^{14}C-export, but also affected the ^{14}C-pattern of allocation, prefering ^{14}C-supply to the swollen hypocotyl at

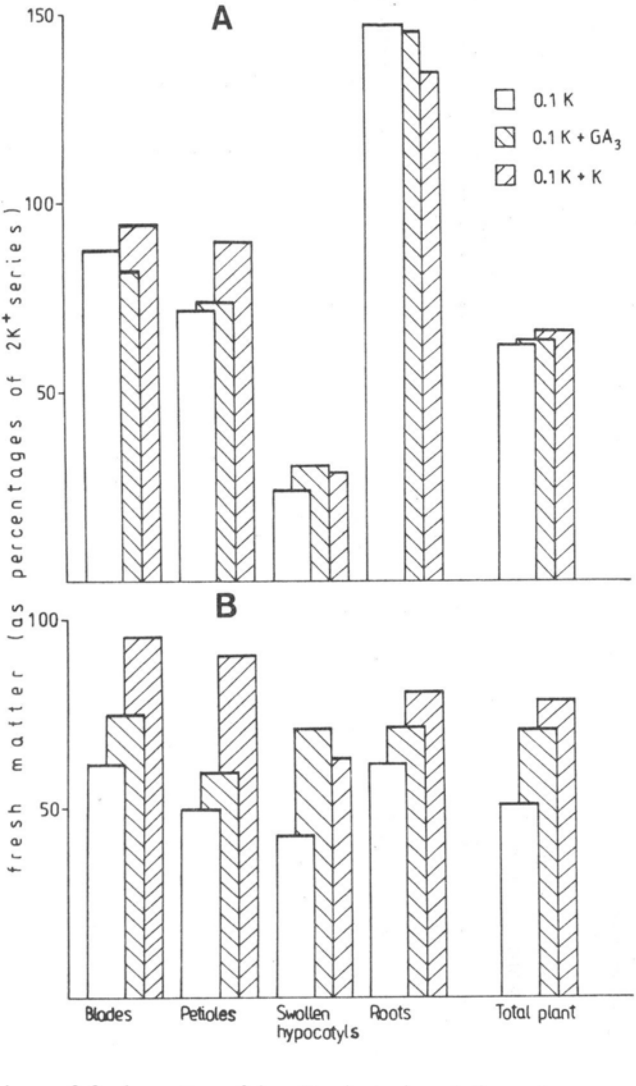

Fig. 2. Comparison of fresh matter of low-K plants in relative values – as percentage of corresponding organ of high-K plants

the cost of roots – in younger plants, or also petioles – in older ones (Table 5). Transfer of Tetra low-K plants to full nutrient solution slightly affected translocation of photosynthates, in contrast to high stimulation of the $^{14}CO_2$-assimilation rate. In the high-K series GA_3 did not significantly affect the above described processes.

In Saxa plants, K deficit strongly reduced the $^{14}CO_2$ assimilation rate, but affected much less ^{14}C-export and current photosynthate distribution in plants of both ages (Table 6). In all the cases the swollen hypocotyl attracted more

Table 5

Distribution of ^{14}C-photosynthates in plants (cv. Tetra) (total export assumed as 100 per cent)

Age of plants (days)	Series	Rad. of total plant, 10^6 cpm	$^{14}CO_2$ assimilation rate, 10^3 cpm g^{-1} fr.m.	^{14}C export (% of ^{14}C)	^{14}C-distribution		
					petioles	swollen hypocotyl	roots
28	0.1K n.t.	5.0	2.01	27.4	33.3	11.2	55.5
	+ GA$_3$	12.6	2.92	34.0	41.7	33.6	24.7
	2K n.t.	13.3	2.25	23.8	31.2	46.1	22.7
	+ GA$_3$	13.1	2.22	24.7	31.7	47.1	21.2
35	0.1K n.t.	2.1	0.36	27.9	59.3	28.2	12.5
	+ GA$_3$	2.7	0.59	38.9	35.8	55.6	8.6
	+ K	3.6	0.49	30.7	45.0	34.6	20.4
	2K n.t.	3.4	0.51	34.5	36.1	52.7	11.2
	+ GA$_3$	2.5	0.42	31.6	43.3	48.4	8.3

n.t. – not treated with growth substances, Rad. – radioactivity.

Table 6

Distribution of ^{14}C photosynthates in plants (cv. Saxa) (total export assumed as 100 per cent)

Age of plants (days)	Series	Rad. of total plant, 10^6 cpm	$^{14}CO_2$ assimilation rate, 10^3 cpm. g^{-1} fr.m.	^{14}C export (% of ^{14}C)	^{14}C-distribution		
					petioles	swollen hypocotyl	roots
28	0.1K n.t.	0.63	0.23	29.8	31.9	61.8	6.3
	2K n.t.	1.30	0.42	30.6	23.5	68.7	7.8
32	0.1K n.t.	0.66	0.23	15.6	34.9	54.7	10.4
	+ GA_3	0.71	0.24	25.6	29.9	60.4	9.7
	+ K	1.38	0.35	19.1	33.8	56.1	10.1
	2K n.t.	1.46	0.37	21.3	26.6	65.0	8.4
	+ GA_3	1.21	0.36	21.2	27.7	65.5	6.8

n.t. – not treated with growth substances, Rad. – radioactivity.

than half of the labelled compounds exported from the blades. Treatment with GA_3 increased ^{14}C-export with slight modification of ^{14}C-partitioning only in low-K series of older plants.

The ratio of ^{14}C-fixed per mg K, in plants of both cultivars, was higher in K-deficient plants than in those with optimal K supply (Table 7). In plants treated with GA_3, this ratio increased strongly, indicating a higher "nutrient efficiency" in the low-K series as a response to GA_3-supply. This seems to be a consequence of better root supply with assimilates owing to the higher rate of photosynthesis. In contrast, GA_3 application to high-K plants of both cultivars, diminished the "nutrient efficiency" ratio, especially in older Tetra plants.

Table 7

Nutrient efficiency ratio – $^{14}C/K$ plant

Cultivars	Age (days)	0.1K		2K	
		n.t.	$+GA_3$	n.t.	$+GA_3$
Tetra	28	17.6	48.6	14.4	11.1
	35	6.6	11.4	5.2	2.8
Saxa	29	4.5	–	2.1	–
	32	3.3	5.1	1.7	1.1

n.t. – control plants, not treated

In Tetra cultivars, the great variability of storage organ size in the particular plants was closely and positively correlated with their share in ^{14}C exported from the blades (Fig. 3) in younger plants. It may indicate that the mobilizing power of storage organs is proportional to their size expressed as fresh matter, but decreases with plant age.

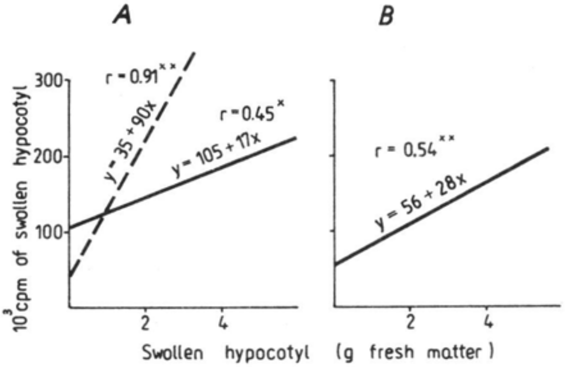

Fig. 3. Relationship between fresh matter of swollen hypocotyls and their radioactivity in Tetra (A) and Saxa (B) plants. A – Tetra, 28-day (— —) and 35-day (–) old plants, B – Saxa, 32-day old plants

This relationship is not very distinctly seen in older Saxa cv., where presumably factors other than size affected the activity of the swollen hypocotyl as a sink of photosynthates.

ACTIVITY OF ACID INVERTASE IN DEVELOPING STORAGE ORGANS

In Saxa cultivars, where the storage organ developed to full-size much faster than in Tetra plants, acid invertase activity declined rapidly both in high-K and low-K plants; GA_3 treatment strongly increased it in both K series in contrast to the 0.1K+K series (Fig. 4).

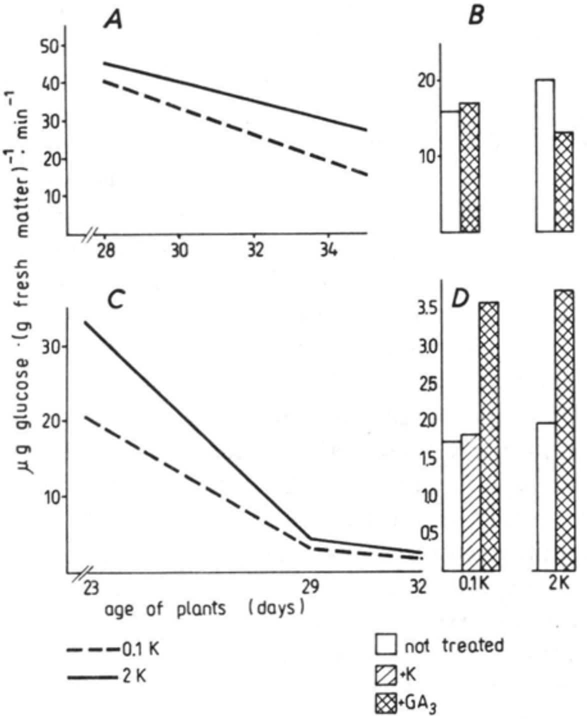

Fig. 4. Acid invertase activity of storage organ in Tetra (A and B) and Saxa (C and D) plants; age of plants: 38 days (B) and 32 days (D)

In Tetra plants with longer duration of growth of storage organ, acid invertase activity was much higher and diminished slightly with plant age. In all cases, K deficit reduced invertase activity. In the other experiment, done with 38-day-old plants, GA_3 diminished invertase activity in the 2K-series, but had no effect in low-K plants.

DISCUSSION

The compared cultivars, which have different rates and timing of storage organ formation, responded differently to K-deficit and GA_3 treatment. Plants of Saxa cv. developed a swollen hypocotyl much faster than Tetra, probably before the K-deficit became severe, therefore, at the time under investigation, the swollen hypocotyl was much less affected. In the control series (not treated with GA_3) their sink strength was probably determined more by storage of dry matter than by cell growth, which already declined. It correlated with diminished acid invertase activity in contrast to Tetra plants, confirming the observation of Jones and Kaufman (1971), Morris and Arthur (1984, 1986) on the close relationship between growth and acid invertase activity. Therefore, high activity of these enzyme in Tetra plants seems to be connected with protracted cell growth of the storage organ. Ricardo and Sovia (1974) also reported that in radish and turnip plants high activity of acid invertase was observed until plant maturity.

In spite of great differences in both cultivars, local application of GA_3 diminished the negative effects of K deficit, promoting transport of photosynthates to the storage organ of low-K plants owing to their sink strength stimulation, as reported by Ginzburg (1974) – in gladiolus, by Starck and Stradowska (1977) and Starck et al. (1983) – in radish, by Umoession and Fordward (1982) – in sunflower.

The apparent discrepancies between our results and those presented by Bender et al. (1986), McKee and Morris (1986) and by other authors quoted by them (indicating depression of carrot storage organ growth after spraying the shoot with GA_3), are perhaps caused by long term effects (a few weeks as compared with 3 days) and the different site of GA_3 application. Treatment of leaves with GA_3, instead of the storage organ, promoted growth of leaves as concomitant with reduction of storage organ size. Similar results were observed in our experiments, where the whole aerial part was treated with GA_3 (Starck and Stradowska, unpublished).

Exogenously applied GA_3 might affect the ratio of naturally occurring hormones favouring increase of auxin level, as reported by many authors (Jindal and Hemberg 1976, Law 1987), and stimulating ethylene production as early as after a few hours (Garcia et al. 1984), as has been observed in cowpea, but decreasing the cytokinin level, as Bender et al. (1986) observed in the root of carrot plants. On the other hand, K-deficit may also effect the hormone level. Anisimov and Bulatova (1982) in bean plants and sunflower, Michniewicz and Stopińska (1980) in pine described a decrease of auxin. Stopińska (1986) observed a diminished content of gibberellins in some bean plant leaves.

The increased mobilizing power of sinks in spite of possible changes in hormonal balance, seems to be causally connected with GA_3-stimulation of acid invertase activity, as also Morris and Arthur (1985) presented in bean plants. Explanation of our results presents difficulties since stimulation of invertase activity by GA_3 treatment was observed only in Saxa cultivars, both in high-K and low-K plants. Assuming that the hormonal level (or activity) and their balance differ in the compared cultivars, the suggestion may be advanced that growth as well as translocation of photosynthates – on the one hand, and invertase activity – on the other, differ in their response to endogenous GA level, perhaps because their optimal concentration is not the same. Therefore, the relatively high activity of invertase in Tetra cv. was not affected by GA_3 treatment in low-K plants and was even depressed – in high-K series presumably owing to the supraoptimal GA level. In contrast, Saxa plants with already decreased acid invertase activity in the storage organ, independent of K-supply responded positively to GA_3 application parallel to protraction of the storage organ cell-growth period.

The diminished negative effect of K-deficit caused by GA_3 in Chołuj's (1988) experiment, also done with radish plants of Saxa cv. was connected with its stimulating effect on K absorption. Nevertheless, in both cultivars of our experiments the total amount of K in GA_3-treated plants from the low-K series did not increase, but in the Saxa cultivar a strong remobilization from the leaves to the other organs was possible.

Similar K-remobilization was reported in low-K sunflower by Guardia and Benlloch (1980) and Benlloch et al. (1983). They suggested that GA_3 stimulated transport of photosynthates, owing to K-mobilization from older organs to growing ones. Nevertheless in the literature on this subject, some contradicting data is presented concerning the effect of GA_3 on absorption and distribution of K in plants. In wheat plants Dhakal and Erdei (1986) described GA_3 stimulation of K uptake in both low-K and high-K plants, without effect on their concentration. In the opinion of these authors, the K-level may modify the effect of many growth regulators (NAA, BA, ABA), but not in the case of GA_3. The concentration of K was influenced by auxin, cytokinin and ABA.

Radish plants grown at low-K level had a more efficient mechanism of K absorption, as postulated by Wild et al. (1979). In the experiments presented in Table 7, GA_3-treatment enhanced the $^{14}C/K$ ratio, suggesting higher K-efficiency in relation to photosynthetic production. Bender et al. (1986) presented similar results in P-deficient GA_3-treated carrot plants. Taking together the above results, their supposition, concerning the influence of the hormonal system on the "nutrient efficiency ratio" as a more general phenomenon, seems to be confirmed.

All of the results discussed above show a close relationship between potassium and GA_3 functioning as a part of the system regulating both allocation of photosynthates and their storage in the swollen hypocotyl.

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Wpływ GA_3 na rozmieszczenie produktów fofosyntezy i aktywność inwertazy w rzodkiewce o zróżnicowanym zaopatrzeniu w potas

Streszczenie

Badano wpływ traktowania zgrubienia hypokotylu rzodkiewki pastą lanolinową, zawierającą GA_3, na rozmieszczenie asymilatów w roślinach o zróżnicowanym zaopatrzeniu w potas. Rzodkiewki odmiany Saxa i Tetra Iłowiecka rosły w szklarni w kulturach hydroponicznych na zmodyfikowanej pożywce Hoaglanda, zawierającej 2-krotną zawartość K w stosunku do standardowej pożywki (symbol 2K) oraz 10-krotnie mniejszą (symbol 0,1K). U obu odmian deficyt ptasu powodował silne hamowanie wzrostu zgrubienia hypokotylu i intensywności asymilacji $^{14}CO_2$ wyprzedzających zahamowanie transportu asymilatów. Przeniesienie roślin z pożywki z deficytem K, na 3 dni, na pełną pożywkę stymulowało fotosyntezę bez wpływu na eksport ^{14}C-asymilatów. Traktowanie zgrubienia hypokotylu GA_3, badane po 3 dniach, u obu odmian powodowało wzrost intensywności asymilacji $^{14}CO_2$ i zmniejszało ^{14}C-retencję w blaszakach, ale tylko u roślin serii 0,1K.

U odmiany Tetra z deficytem potasu GA_3 stymulowała transport ^{14}C-asymilatów do organu spichrzowego, którego wzrost był bardzo silnie ograniczony. U odmiany Saxa GA_3 nieznacznie wpłynęła na dystrybucję ^{14}C asymilatów w serii 0,1K, podobnie jak w serii 2K; być może było to spowodowane rozwojem organu spichrzowego, jeszcze przed wyczerpaniem potasu w pożywce. Tym niemniej, GA_3 u odmiany Saxa przedłużyła nie tylko okres wzrostu organu spichrzowego, lecz również stymulowała aktywność kwaśnej inwertazy, która w badanym okresie w zgrubieniu hypokotylu miała już bardzą małą aktywność.

U odmiany Tetra w badanym okresie aktywność inwertazy była jeszcze wysoka i nie uległa zmianie po traktowaniu roślin GA_3, natomiast w roślinach z optymalnej pożywki uległa nawet zmniejszeniu. Wyciągnięto wniosek, że wzrost i akumulacja substancji pokarmowych w organie spichrzowym u obu odmian rzodkiewki oraz aktywność kwaśnej inwertazy wykazują inną reakcję na traktowanie roślin GA_3. Nasuwa to przypuszczenie, że optymalne stężenie gibereliny dla wzrostu i aktywności kwaśnej inwertazy nie jest jednakowe. Tym niemniej, uzyskane wyniki wskazują na zależność między zaopatrzeniem roślin w potas a funkcją GA_3 w regulacji dystrybucji asymilatów i ich akumulacji w organie spichrzowym rzodkiewki.