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HYDROXYLAMINE-INDUCED SHIFTS IN THE UTILIZATION OF EXOGENOUS SUBSTRATES FOR C-GLYCOSYLFLAVONE BIOSYNTHESIS IN BARLEY SEEDLINGS

Recent investigations at our laboratory on the hydroxylamine-induced inhibition of flavonoid biosynthesis in buckwheat seedlings revealed marked differences in the responses of various derivatives. The relative suppression proved to be clearly dependent upon the complexity of individual flavonoids: it was comparatively small in case of leucoanthocyanidins, somewhat more pronounced within the group of C-glycosylflavones, and the highest in case of the most complex derivatives present, rutin and anthocyanins. In similar experiments with primary leaves of barley, hydroxylamine revealed a strong inhibitory effect on flavonoid accumulation as well, yet no clear-cut differences between individual compounds were found. It was probably due to the rather close chemical structure of the three C-glycosylflavones of barley seedlings. In spite of the absence of apparent quantitative differences in the responses of individual flavonoids, some internal shifts in the distribution of precursors between them still might have occurred in barley under hydroxylamine treatment. An indirect evidence for the occurrence of such shifts can be derived from the fact that hydroxylamine at concentrations which did not suppress flavonoid accumulation withdrew stimulatory effect of L-phenylalanine in buckwheat seedlings (Марпна et al., 1978).

In the present article an attempt was made to investigate possible hydroxylamine-induced metabolic shifts in barley seedlings by means of tracer technique. For that purpose the effect of hydroxylamine on the incorporation of exogenous L-phenylalanine and L-tyrosine into C-glycosylflavones of barley was studied and the distribution of exogenous substrates between individual compounds of different structure was compared at various levels of hydroxylamine treatment.

Material and methods

The experiments were carried out with isolated primary leaves of barley excised from 90 h old etiolated seedlings raised under laboratory conditions in tap water. The excised material was incubated for 16 h in light on filter paper moistened with distilled water (control I), with solutions of L-phenylalanine and L-tyrosine (control II) or with a mixture of hydroxylamine and amino acid (illumination from white fluorescent tubes, light intensity 29,000 erg·cm^{-2}·sec^{-1}; temperature +25 °C). The concentration of hydroxylamine in acting solutions was 10^{-3}, $5 \cdot 10^{-3}$ and 10^{-2} M, that of L-phenylalanine — $2 \cdot 10^{-3}$ and 10^{-2} M and of L-tyrosine — $2 \cdot 10^{-3}$ M. The label was introduced into the acting solution by

complementing it with a radioactive preparation of the corresponding [1-^{14}C]-D,L-amino acid. Specific activity of the acting solutions was 5 μCi/ml.

After incubation the plant material was thoroughly washed with water in order to remove external label and was then assayed. Content of C-glycosylflavones was determined spectrophotometrically after their separation by two-dimensional paper chromatography in a mixture of isoamyl alcohol-petrol ether-acetic acid-water, 3:1:3:3, organic phase (I) and 3 per cent acetic acid (II) (Laanest, 1978). Content of individual derivatives was expressed in nmols per seedling.

Radioactivity of individual flavonoids was assayed directly on the chromatographic spots of corresponding C-glycosylflavones using a special device adapted for direct paper radiometry. Radioactivity of the dried plant material was measured in a Vacutronic VA-Z-310 Geiger counter.

The experiments were run in 3—4 independent series. Measurements included 3—5 parallels.

Results

Preliminary investigations showed that etiolated barley seedlings contain only traces of saponarin and lutonarin 3′-methyl ether which cannot be assayed spectrophotometrically. Lutonarin was not detected in etiolated seedlings at all. One can assume therefore that the amount of C-glycosylflavones found in tissues after light treatment was entirely formed during light exposure. A possibility that the final amount of flavonoids could reflect a state of dynamic equilibrium between their formation and decomposition was excluded due to the metabolic stability of barley C-glycosylflavones (Лаанест, Вайнъярв, 1980).

Seedlings incubated in solutions of radioactive phenylalanine or tyrosine or in a mixture of both of them imbibed up to 44 nmols of exogenous material per seedling (Лаанест, 1981). Moderate concentrations of hydroxylamine somewhat decreased the uptake of amino acids, whereas at the highest concentration of hydroxylamine (10^{-2} M) the uptake of phenylalanine and tyrosine from incubation solutions was reduced more than twice, on the average. From the total amount of amino acids taken up, only a comparatively small portion was incorporated into flavonoids. Even in control seedlings not treated with hydroxylamine that portion did not exceed 3—4 per cent. Hydroxylamine markedly decreased biosynthetic utilization of exogenous precursors for building flavonoids. At the highest dose of the inhibitor it was about 25—30 times lower than in untreated seedlings.

The inhibitory effect of hydroxylamine on C-glycosylflavone accumulation depended on its doses and was strongest at the concentration of 10^{-2} M. 10^{-3} M hydroxylamine used together with phenylalanine generally did not inhibit flavonoid formation as compared with the water control but it completely nullified the stimulatory effect of 10^{-2} M phenylalanine (Table 1). Simultaneously with dose-dependent inhibition at the level of total flavonoids, characteristic shifts in the biosynthesis of individual compounds were observed. In all cases the accumulation of luteolinic derivatives, lutonarin and its 3′-methyl ether was relatively much more suppressed than the accumulation of saponarin, the apigeninic analogue of lutonarin. This tendency is well illustrated by the changes in the quantitative ratios of saponarin (S) and of the sum of luteolinic compounds (L+M) as presented in Table 1. In phenylalanine-fed

Table 1

Formation of C-glycosylflavones from exogenous L-phenylalanine in hydroxylamine-treated barley leaves

Background	Hydroxylamine, M	Saponarin (S)			Lutonarin (L)			Lutonarin 3′-methyl ether (M)			Sum of flavonoids			Ratio S : (L+M)	
		Total, nmol/ seedling	Formed from exogenous phenylalanine		Total, nmol/ seedling	Formed from exogenous phenylalanine		Total, nmol/ seedling	Formed from exogenous phenylalanine		Total, nmol/ seedling	Formed from exogenous phenylalanine		Total	Formed from exogenous phenylalanine
			Absolute amount, nmol/ seedling	% from total amount		Absolute amount, nmol/ seedling	% from total amount		Absolute amount, nmol/ seedling	% from total amount		Absolute amount, nmol/ seedling	% from total amount		
Water	—	38.5			10.1			11.6			60.2			1.8	
L-phenylalanine, $2 \cdot 10^{-3}$ M	—	37.4	5.41	14.5	12.4	2.89	23.3	12.0	2.50	20.9	61.8	10.8	17.5	1.5	1.0
	10^{-3}	38.7	1.92	5.0	11.8	0.70	5.9	9.05	0.49	5.4	59.6	3.11	5.2	1.9	1.6
	$5 \cdot 10^{-3}$	17.9	0.46	2.5	3.09	0.14	4.7	3.77	0.09	2.3	24.8	0.69	2.8	2.6	2.0
	10^{-2}	7.04	0.12	1.7	1.13	0.03	2.9	1.11	0.02	2.0	9.28	0.17	1.8	3.1	2.4
L-phenylalanine, 10^{-2} M	—	42.9	11.9	27.8	14.8	5.29	35.8	13.9	5.16	37.0	71.6	22.4	31.3	1.5	1.1
	10^{-3}	40.0	4.91	12.3	11.6	2.23	19.2	9.39	1.35	14.4	61.0	8.49	13.9	1.9	1.4
	$5 \cdot 10^{-3}$	18.9	1.64	8.7	3.84	0.61	15.9	3.38	0.30	8.9	26.1	2.55	9.8	2.6	1.8
	10^{-2}	7.06	0.41	5.8	1.01	0.12	12.1	1.39	0.08	5.6	9.46	0.61	6.4	2.9	2.1

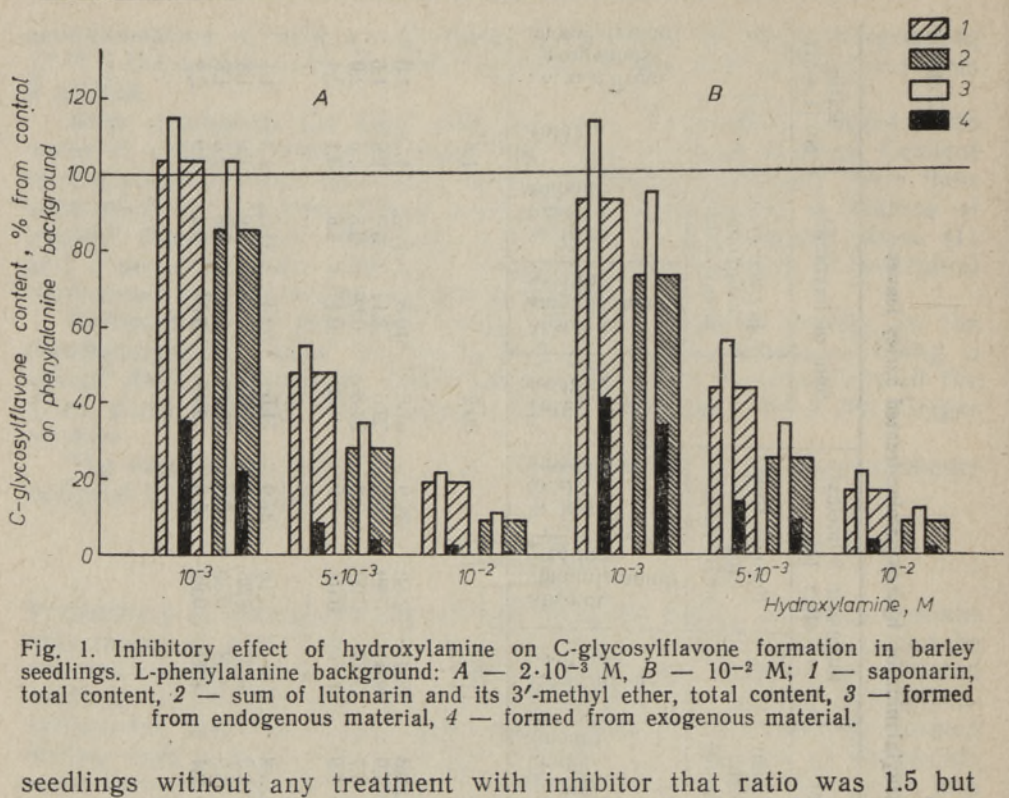

Fig. 1. Inhibitory effect of hydroxylamine on C-glycosylflavone formation in barley seedlings. L-phenylalanine background: *A* — $2 \cdot 10^{-3}$ M, *B* — 10^{-2} M; *1* — saponarin, total content, *2* — sum of lutonarin and its 3′-methyl ether, total content, *3* — formed from endogenous material, *4* — formed from exogenous material.

seedlings without any treatment with inhibitor that ratio was 1.5 but an application of rising concentrations of hydroxylamine led to a gradual increase of the ratio, clearly indicating that the formation of luteolinic derivatives was much more inhibited. In case of the highest level of hydroxylamine (10^{-2} M) the corresponding ratio was, in fact, twice as high as in the phenylalanine control.

The tracer technique enabled us to differentiate between the flavonoid fractions formed from endogenous and exogenous substrates. It is evident that hydroxylamine blocked, in the first place, incorporation of exogenous substrates into C-glycosylflavones: the higher the concentration of hydroxylamine in the medium, the less became the relative portion of individual flavonoids formed from exogenous material (Table 1). Even in case of 10^{-3} M hydroxylamine which revealed only a slight, if any, effect on the total content of C-glycosylflavones, the fraction formed from exogenous phenylalanine decreased approximately three times.

From the total content of C-glycosylflavones estimated spectrophotometrically and its fraction formed from labelled exogenous material one can calculate the portion synthesized from endogenous precursors. Figure 1 represents relative changes in the amount of saponarin and the sum of two luteolinic derivatives as compared with the content of the corresponding fractions in control seedlings fed with exogenous phenylalanine without any hydroxylamine treatment. The figure once again demonstrates that the biosynthesis from exogenous material was relatively much more sensitive to inhibition than the biosynthesis from endogenous precursors.

Figure 1 and the ratios S : (L+M) calculated for the fractions of corresponding compounds formed from exogenous precursors (Table 1) show that here again the formation of saponarin was less sensitive to the inhibitor.

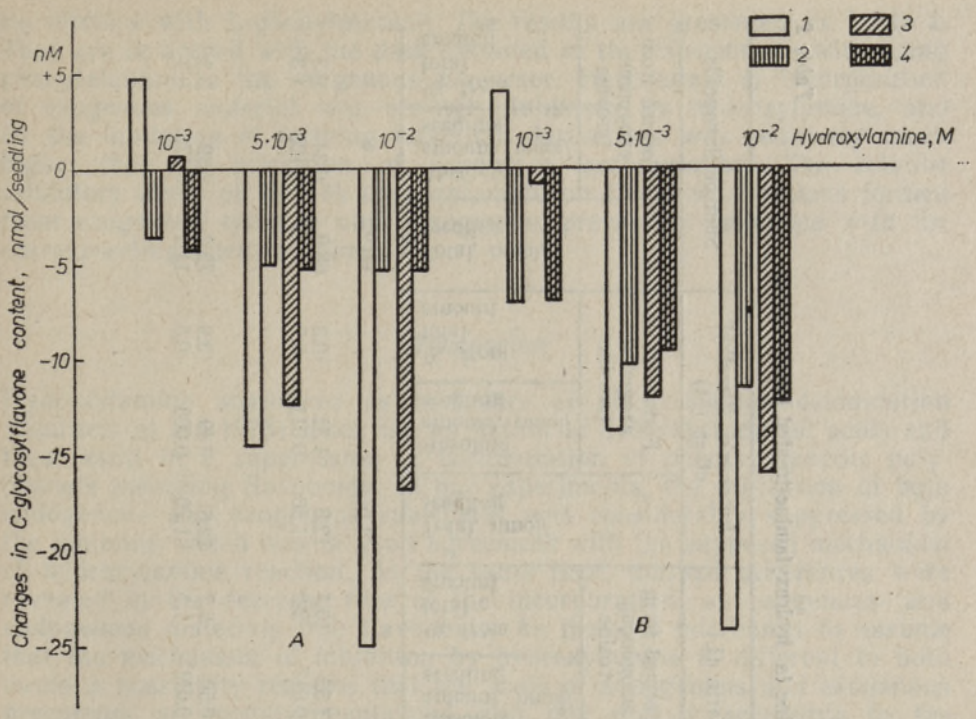

Fig. 2. Absolute changes in the incorporation of endogenous and exogenous substrates into barley C-glycosylflavones in hydroxylamine-treated seedlings. L-phenylalanine background: *A* — $2 \cdot 10^{-3}$ M, *B* — 10^{-2} M; saponarin formed from endogenous (*1*) or exogenous (*2*) material; sum of lutonarin and its 3′-methyl ether formed from endogenous (*3*) or exogenous (*4*) material.

It is of interest to note that although the relative inhibitory effect of hydroxylamine on flavonoid formation from exogenous substrate was different in case of saponarin and luteolinic derivatives, the absolute hydroxylamine-caused decreases in the incorporation of exogenous phenylalanine were rather similar (Figure 2). However, that is not surprising: in phenylalanine control both saponarin and luteolinic derivatives incorporated practically an equal amount of exogenous material (S : (L+M) = 1, Table 1). This level was different for $2 \cdot 10^{-3}$ and 10^{-2} M phenylalanine (approximately 5.4 and 12 nmols per seedling, respectively), and the absolute decreases in the incorporation of exogenous phenylalanine in both variants showed a corresponding difference. On the contrary, the S : (L+M) ratio of incorporation of endogenous material before inhibitor treatment was 1.7 for both phenylalanine concentrations (31—32 nmols into saponarin and 18—19 nmols into luteolinic compounds), and the absolute decreases in the incorporation of endogenous precursors were equal for both backgrounds, being determined by the structure of the corresponding flavonoid and the concentration of the inhibitor.

The effectiveness of exogenous L-tyrosine as a precursor for C-glycosylflavone formation is not as high as that of exogenous L-phenylalanine (Лаанест, 1981). Therefore it seemed not necessary to undertake detailed comparative inhibition studies on tyrosine background. Still, in order to detect possible differences in hydroxylamine action on tyrosine incorporation, 10^{-2} M hydroxylamine was applied together with L-tyrosine and

Table 2

Formation of C-glycosylflavones from exogenous L-tyrosine in hydroxylamine-treated barley leaves

Background	Hydroxylamine, M	Saponarin (S)			Lutonarin (L)			Lutonarin 3′-methyl ether (M)			Sum of flavonoids		
		Total, nmol/ seedling	Formed from exogenous tyrosine		Total, nmol/ seedling	Formed from exogenous tyrosine		Total, nmol/ seedling	Formed from exogenous tyrosine		Total, nmol/ seedling	Formed from exogenous tyrosine	
			Absolute amount, nmol/ seedling	% from total amount		Absolute amount, nmol/ seedling	% from total amount		Absolute amount, nmol/ seedling	% from total amount		Absolute amount, nmol/ seedling	% from total amount
Water	—	38.5			10.1			11.6			60.2		
L-tyrosine (labelled), $2 \cdot 10^{-3}$ M	—	42.9	3.70	8.6	12.3	1.32	10.7	12.8	1.32	10.3	68.0	6.34	9.3
	10^{-2}	7.51	0.10	1.3	0.76	0.017	2.2	1.50	0.011	0.7	9.77	0.128	1.3
L-tyrosine (labelled), $2 \cdot 10^{-3}$ M+ L-phenylalanine (unlabelled), 10^{-2} M	—	46.2	1.40	3.0	13.4	0.50	3.7	12.6	0.49	3.9	72.2	2.39	3.3
	10^{-2}	8.40	0.056	0.7	1.01	0.011	1.1	1.70	0.008	0.5	11.1	0.075	0.7

its mixture with L-phenylalanine. The results are presented in Table 2. They are in accord with the data obtained in the experiments with using phenylalanine as the exogenous precursor. Here again i) incorporation of exogenous material was strongly inhibited by hydroxylamine, and ii) the inhibition of forming luteolinic derivatives was relatively much higher than the inhibition of saponarin accumulation. The relative inhibitory effect of 10^{-2} M hydroxylamine on flavonoid fractions formed from exogenous tyrosine and endogenous precursors coincided with the corresponding phenylalanine data.

Discussion

Hydroxylamine analogues as inhibitors of phenylalanine deamination (Amrhein et al., 1976) block the formation of hydroxycinnamic acids and thus result in a suppression of accumulation of phenylpropanoic polyphenols including flavonoids. In our experiments, the utilization of both endogenous and exogenous substrates was considerably suppressed by the inhibitor, which was in good agreement with the supposed mechanism of hydroxylamine reaction. At the same time, marked differences were revealed in the decrease rate of the incorporation of exogenous and endogenous materials into flavonoids. As there is no reason to assume that the mechanism of inhibition by hydroxylamine is different in both cases, a possibility remains that the pools of endogenous and exogenous precursors are compartmentalized and not equally accessible to the action of the inhibitor. It has been demonstrated that the intermediates of phenylpropanoid metabolism produced endogenously are not in equilibrium with the compounds added exogenously (Löffelhardt, Kindl, 1975; Czichi, Kindl, 1975a, b, 1977; Steiner, 1975, 1977; Margna, Margna, 1978a, b; Amrhein, 1979; Holländer et al., 1979). The results presented here support this assumption.

In our previous experiments (Маргна et al., 1978) where no exogenous amino acid was added to the inhibitor and incorporation changes of only endogenous precursors could be followed, hydroxylamine decreased the final amount of barley flavonoids by a factor of 1.5 ($5 \cdot 10^{-3}$ M) or 3 (10^{-2} M hydroxylamine). When calculating analogous ratios from the data presented in Table 1, a 2- or 6-fold decrease in the incorporation of endogenous precursors into the sum of flavonoids was detected, respectively. The somewhat more significant effect of hydroxylamine observed here might have been due to a partial suppression of endogenous amino acid formation caused by the presence of excess free phenylalanine and tyrosine supplied exogenously. These amino acids were shown to affect the activity of shikimate pathway in numerous plants (Cotton, Gibson, 1968; Chu, Widholm, 1972; Gilchrist et al., 1972; Gilchrist, Kosuge, 1974; Bickel, Schultz, 1979 and others) and, consequently, an end-product feedback control over the rates of endogenous biosynthesis of phenylalanine and tyrosine could have possibly occurred in the treated plants. An indirect evidence of such a possibility was obtained in our previous experiments with barley seedlings where feeding exogenous phenylalanine and tyrosine brought about a considerable decrease in the utilization of endogenous substrates for flavonoid synthesis (Лаанест, 1981).

We have reported recently that individual C-glycosylflavones of barley seedlings reveal considerable differences in the rate of their biosynthesis from exogenous and endogenous precursors: exogenous substrates showed

much higher relative rates of incorporation into more complex, *resp.* less accumulating luteolinic derivatives as compared with the relative rates of their formation from endogenous precursors (Лаанест, 1981). The present study has revealed analogous differences between different pathways: formation of more complex luteolinic derivatives proved to be relatively more sensitive to external influences. Calculations (by the data of Table 1) showed that addition of hydroxylamine resulted in a 1.8-fold ($5 \cdot 10^{-3}$ M) or 5-fold (10^{-2} M hydroxylamine) reduction in the amount of saponarin formed from endogenous precursors, yet the decrease in the corresponding values was practically twice as great when biosynthesis of lutonarin and its methyl ether was concerned. In respect to the exogenous substrates, quite similar differences were observed. A treatment with $5 \cdot 10^{-3}$ M hydroxylamine reduced the absolute amount of saponarin formed from exogenous material 7 to 12-fold while in case of 10^{-2} M inhibitor the suppression was 25 to 45-fold. At the same time the decrease in the incorporation of exogenous substrates into luteolinic derivatives was 12 to 24- and 50 to 95-fold, respectively. As resulting from these differences, an increase in the share of saponarin in the total amount of barley C-glycosylflavones occurred in the treated plants.

It is generally established that sequentially acting enzymes in phenylpropanoid metabolism are bound to particulate cell fractions and act as multienzyme complexes. It is supposed that the conversion of phenylalanine to phenolic substances, including flavonoids, branches out early at the level of the amino acid, and, as soon as L-phenylalanine has entered such a complex, the sequence of conversions should already be determined (for references see Czichi, Kindl, 1977). It seems that these different enzymic complexes are not in an equal position as regards their capacity of consuming common precursors in buckwheat seedlings (Margna, 1977a; Margna, Margna, 1978a, b). The complexes involved in the biosynthesis of simpler flavonoids evidently consist of fewer links and are usually better supplied with precursors, while there seems to be much lower relative saturation with substrates in the sites of forming more complex derivatives (for detailed discussion see Margna, Margna, 1978b). If this is also the case in barley seedlings, one has to expect that under conditions of diminished substrate supply resulting from hydroxylamine treatment the substrates would be channelled preferably into the shorter pathways, *resp.* for the biosynthesis of simpler compounds. The results of the present study are in agreement with that assumption and thus support the idea of the regulation of flavonoid formation on substrate level suggested by U. Margna (1977b).

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HÜDROKSÜÜLAMIINI PÕHJUSTATUD NIHKED EKSOGEENSE SUBSTRAADI KASUTAMISES C-GLÜKOSÜÜLFLAVOONIDE SÜNTEESIKS ODRAIDANDITES

Artiklis kirjeldatud katsetes töödeldi odraidandite esimesi pärislehti hüdroksüülamiiniga radioaktiivse L-fenüülalaniini või L-türosiini foonil. Hüdroksüülamiin pidurdas märgatavalt flavonoidide sünteesi, eriti eksogeensest substraadist, ja põhjustas spetsiifilisi nihkeid endogeense ja eksogeense materjali jaotumises eri derivaatide vahel. Eksogeensete aminohapete lülitumine flavonoididesse pidurdus tugevasti isegi tingimustes, mis oluliselt ei mõjustanud sünteesitud flavonoidide üldhulka. Odraidandite kolmest C-glükosüülflavoonist osutusid luteoliini derivaadid lutonariin ja selle 3′-metüülester tundlikumaks inhibiitori toime suhtes kui apigeniini derivaat saponariin. Tulemused on kooskõlas flavonoidide akumulatsiooni substraatse regulatsiooni ideega ja kinnitavad oletust, et fenüülpropanoidide ainevahetuse vaheühendid rakus on kompartmentaliseeritud.

Лембе ЛААНЕСТ

ВЛИЯНИЕ ГИДРОКСИЛАМИНА НА ИСПОЛЬЗОВАНИЕ ЭКЗОГЕННЫХ СУБСТРАТОВ ДЛЯ СИНТЕЗА *C*-ГЛИКОЗИЛФЛАВОНОВ В ПРОРОСТКАХ ЯЧМЕНЯ

Изолированные первичные листья ячменя обрабатывали разными дозами гидроксиламина на фоне меченых *L*-фенилаланина или *L*-тирозина. Гидроксиламин значительно подавлял образование флавоноидов, особенно из экзогенного субстрата, и вызывал специфические сдвиги в распределении эндогенных и экзогенных субстратов между отдельными производными. Включение экзогенных аминокислот сильно подавлялось даже в условиях, в которых общее количество синтезированных флавоноидов практически оставалось неизменным. Из трех *C*-гликозилфлавонов проростков ячменя лютеолиновые производные — лютонарин и его 3′-метиловый эфир — оказались относительно более чувствительными к действию гидроксиламина, чем их апигениновый аналог сапонарин. Эти результаты согласуются с идеей о субстратной регуляции накопления флавоноидов и указывают на вероятную компартментализацию промежуточных соединений фенилпропаноидного обмена.