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SUGAR EFFECTS ON THE FORMATION OF BUCKWHEAT FLAVONOIDS: SOME NEW ASPECTS AND CONCLUDING REMARKS

Since our first report on the inhibitory effect of feeding sugars on the formation of anthocyanins in buckwheat seedling hypocotyls (Маргна, Оттер, 1968), continuing efforts have been made in our laboratory to open the nature of this unusual phenomenon. As a result it was found that the inhibition can be typically observed in intact plant material and is likewise manifested in derooted and decotyledonized seedlings, while in excised hypocotyls the sugar treatment either remains ineffective or even shows a tendency to be stimulatory for pigment formation (Margna et al., 1969, 1972a; Маргна, Оттер, 1971; see also Troyer, 1964; Scherf, Zenk, 1967). An evidence was obtained simultaneously that the inhibitory effect is somehow related to the protein biosynthesis and, most probably, is a function of primary changes taking place in this area of seedling metabolism (Margna, Otter, 1968).

The responses on the other hypocotyl flavonoids were found to be markedly different from those characteristic of anthocyanins. Concerning rutin, for example, a rather clear-cut stimulation of accumulation was observed in almost all cases of sugar feeding (Margna et al., 1972a). When isolated hypocotyls were employed, a marked increase occurred also in the accumulation of leucoanthocyanidins, yet the content of these compounds remained practically unchanged when intact seedlings were subjected to sugar treatment (Маргна, Оттер, 1971; Margna et al., 1972b).

As all flavonoids are closely related to each other biogenetically, it became evident that the problem cannot be solved on the basis of a particular group of flavonoids only, but needs complete analysis of changes within the whole set of flavonoid compounds present in the plant material. It seemed quite necessary therefore to follow sugar-induced changes also in buckwheat cotyledons which are characterized by a still more complex flavonoid composition than in hypocotyls (Margna et al., 1967).

Some preliminary results concerning flavonoid changes in the cotyledons of sugar-treated buckwheat seedlings were fragmentarily presented in an earlier paper (Маргна, 1970). In this communication complete data of these studies are described, except the results on leucoanthocyanidins which have been published elsewhere (Маргна, Оттер, 1971; Margna et al., 1972b). In addition we also included a number of new results about changes on the level of hypocotyls.

Experimental

Plant material and growth conditions. The experiments were carried out with young buckwheat (*Fagopyrum esculentum* Moench) seedlings raised under laboratory conditions on glass dishes, on two layers of filter paper moistened with an adequate amount of distilled water. Two growth regimes were generally used: A) the germinating seeds/developing seedlings were held in darkness for the first 56 h, then the seedlings received 16 h of light (illumination from white fluorescent tubes, light intensity $28,000 \text{ erg} \cdot \text{cm}^{-2} \cdot \text{sec}^{-1}$) and after that were returned to darkness for an additional 24 h (56D+16L+24D); B) the initial dark period of seedling development was prolonged to 72 h, after that the seedlings received 10 h of light and then, again, were transferred to a dark chamber for a 14 h final development in darkness (72D+10L+14D). In a series of experiments with seedlings of different age, additional variations of the duration of initial as well as of terminal dark periods of seedling development were involved. In experiments with isolated organs, the hypocotyls and cotyledons needed were excised from 80-h-old etiolated seedlings grown under standard conditions; the excised material was then placed on filter paper moistened with distilled water, and incubated for 16 h in light, followed by a 24 h incubation in darkness.

The temperature was held constant at $25 \pm 1^\circ \text{C}$ throughout all the stages of seedling development, except the experiments in which sugar treatment was combined with an additional treatment of seedlings with various temperatures. In that case, at the beginning, as usual, the seedlings were allowed to grow at 25° , but just after the end of the light period were transferred into temperature chambers to complete the final postillumination dark period of seedling development at either 15° , 25° , or 35° , respectively. The temperature conditions were held the same also in experiments with excised organs.

Treatments. Glucose was the main sugar used for experiments, but in some cases parallel series with fructose and sucrose were run additionally. In a standard procedure the seedlings were initially allowed to grow on water, and the sugars, in the form of water solutions, were added to growth medium of seedlings either before the onset or after the end of the light period. When intermittent light-dark regimes were used, the sugar solutions were introduced to seedlings before the onset of the illumination program. In some experimental series the seeds were sowed directly into corresponding sugar solutions. In experiments with isolated organs the material, immediately after the excision, was floated for 3–5 min in test-solutions, and then, as described, incubated on filter paper, moistened with the same solutions as those used for floating. If not otherwise stated, the concentration of sugars was equalled to 1 per cent both in growth medium of intact seedlings as well as in solutions used for floating. In combined feeding experiments with simultaneous introduction into growth medium glucose and phenylalanine the concentration of the amino acid was equalled to 10^{-2}M .

Flavonoid assay. Anthocyanins were determined photocolometrically by measuring the optical density of clear 1% HCl-ethanolic extracts from plant material in a photoelectric colorimeter, using a green filter of maximum transmission at 540 nm. Rutin in hypocotyls was measured by a procedure of repeated one-dimensional, rutin and glycoflavones in cotyledons — by two-dimensional ascending paper chromatography combined with a subsequent measurement of the optical density of the eluates of flavonoid spots spectrophotometrically at 360 nm (rutin), 350 nm (luteolinic glycoflavones — orientin and homoorientin), and 335 nm (apigeninic glycoflavones — vitexin and saponaretin), respectively (Margna, Margna, 1969). The content of all flavonoids was expressed in micrograms per seedling by using for calculations the following extinction coefficients: for anthocyanins — $2.7 \cdot 10^7$ (Scherf, Zenk, 1967), for rutin — $1.40 \cdot 10^7$, for vitexin and saponaretin — $1.94 \cdot 10^7$, and for orientin and homoorientin — $1.59 \cdot 10^7$ (Margna, Margna, 1969).

All experiments were run in 3 to 8 replications in space per treatment and were also replicated in time on at least 3 occasions. The results were subjected to evaluation by the statistical techniques of Student's significance test.

Results

Experiments with feeding sugars alone. As was shown by us previously, in hypocotyls the feeding of sugars is clearly inhibitory for anthocyanin accumulation when the seedlings, intact or decotyledonized, are continuously allowed to develop on sugar solutions or the sugars are fed to derooted seedlings through the cut ends of their hypocotyls prior to illumination. The inhibition was found less pronounced when the sugars were introduced, at the same point of seedling development, to intact or decotyledonized seedlings through their root system. With supplying glucose the inhibitory effect, however, was manifested rather steadily, though the absolute decreases were not so large, and cases of insignificant influence occurred occasionally (Margna et al., 1972a).

These observations met complete confirmation in our further experiments, yet some interesting facts were discovered additionally.

Using varying growth regimes we were able to demonstrate, first of all, that in hypocotyls the sugar influence is to some extent age-dependent. Though the effects were strictly significant in rare instances, multiple experiments unequivocally pointed to a certain regularity, indicating that an administration of glucose is inhibitory for anthocyanin accumulation preferentially in seedlings transferred into sugar medium at a comparatively early age, whereas in elder seedlings the treatment was either ineffective or even tended to be stimulatory (Tab. 1, A). This dependence

Table 1

The influence of glucose on the accumulation of anthocyanins in intact buckwheat seedlings grown under varying growth regimes ($\mu\text{g}/\text{seedling}$)

Regime	Glucose added to growth medium			
	prior to illumination		after illumination	
	Control	Glucose	Control	Glucose
A. Hypocotyls				
32D+16L+72D	0.51	0.40*	0.41	0.41
56D+16L+48D	1.94	1.76	1.66	1.78
80D+16L+24D	3.45	3.55	3.08	3.56*
32D+16L+24D	0.61	0.54	0.48	0.47
56D+16L+24D	1.79	1.67	1.70	1.75
80D+16L+24D	3.61	3.69	3.53	3.53
104D+16L+24D	4.63	4.56	4.44	5.00
32D+16L+3 cycles of (8D+16L)	4.20	3.87	—	—
56D+16L+2 cycles of (8D+16L)	4.08	4.49	—	—
80D+16L+8D+16L	5.26	5.27	—	—
B. Cotyledons				
32D+16L+72D	0.79	0.64*	0.74	0.68
56D+16L+48D	1.70	1.28*	1.35	1.18*
80D+16L+24D	2.61	1.72*	2.13	2.43
32D+16L+24D	0.88	0.57*	0.72	0.64
56D+16L+24D	2.02	1.38*	1.36	1.14
80D+16L+24D	2.74	1.93*	2.17	2.01
104D+16L+24D	2.85	2.42*	2.52	2.83
32D+16L+3 cycles of (8D+16L)	2.56	1.77*	—	—
56D+16L+2 cycles of (8D+16L)	2.88	2.20*	—	—
80D+16L+8D+16L	3.28	1.88*	—	—

* Here and in other tables and figures — significant effects at $P \leq 0.05$.

seemed to remain uninfluenced by varying durations of postillumination incubation of seedlings on sugar medium, but it showed a tendency to be modified by the illumination procedure: glucose added to growth medium prior to light exposure was inclined to act predominantly as an inhibitor of pigment formation, while being supplied to seedlings after illumination it tended to be active as a stimulator.

Another interesting aspect is a possible interaction between sugar and temperature treatments. As can be seen from Tab. 2, a suppression of pigment accumulation found in hypocotyls at lower temperatures was practically lost when the glucose-fed seedlings were held at 35° during the postillumination dark period. In seedlings fed with glucose at a later stage of development, a significant augmentation in the content of anthocyanins was actually evoked by the treatment at 35°.

Table 2

The accumulation of anthocyanins in intact glucose-fed buckwheat seedlings grown at different temperatures during a postillumination dark period, $\mu\text{g}/\text{seedling}$

Regime	Hypocotyls		Cotyledons	
	H ₂ O	Glucose	H ₂ O	Glucose
Glucose added to medium prior to illumination:				
56D+16L+24D				
15°	2.72	2.59	1.86	1.53*
25°	1.86	1.74	1.70	1.36*
35°	1.36	1.43	1.35	1.04*
72D+10L+14D				
15°	2.83	2.45*	2.27	1.73*
25°	2.60	2.53	2.19	1.48*
35°	1.88	2.20*	1.68	1.42*

Similar developmental and environmental interactions either could not be observed in cotyledons (Tab. 2) or were of rather limited importance (Tab. 1, B). Marked decrease up to 30–35 per cent as compared with anthocyanin level in control seedlings occurred in cotyledons in almost all cases of external sugar supply, the differences between the treated and untreated plants being smoothed out only in experiments with feeding glucose after illumination. Clear-cut inhibition of pigment formation in cotyledons was achieved regularly also with sucrose and fructose (Fig. 1),

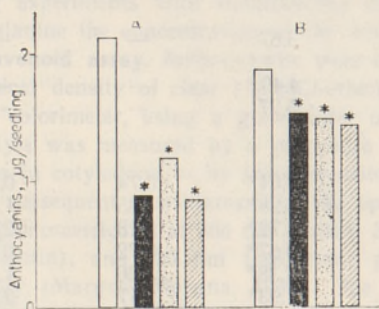


Fig. 1. Sugar-induced inhibition of anthocyanin formation in buckwheat cotyledons. A — seedlings grown on sugar solutions, B — sugars added to growth medium of intact seedlings prior to illumination; growth regime — 72D+10L+14D in both experiments. White bars — water controls, black bars — sucrose, dotted bars — fructose, shaded bars — glucose.

the two sugars which in hypocotyls were found effective only when used as permanent components of growth medium (Margna et al., 1969, 1972a). Thus, compared with hypocotyls, the sugar effects on anthocyanins were much more pronounced in cotyledons, emphasizing that sugar-dependent inhibition of anthocyanin accumulation in buckwheat seedlings

represents a response to external sugar supply, specifically typical of this kind of plant material.

The inhibition, however, is restricted to intact seedlings only. In excised cotyledons feeding sugars, as already reported (Маргна, 1970; Маргна, Ортеп, 1971), brings about an increase in pigment formation or at least shows a tendency to remain stimulatory but not inhibitory for this process (Tab. 3).

Favourable influence of sugars in isolated cotyledons was also spread to other flavonoid compounds, being sufficiently large to reach a level statistically significant for leucoanthocyanidins (Маргна, Ортеп, 1971; Margna et al., 1972b) and rutin (Tab. 3), but somewhat less for glycoflavones (Tab. 3). In intact seedlings supplied with sugars through the root system, the situation was more complicated. In general, the effect was inhibitory rather than stimulatory for both rutin and glycoflavone accumulation, being thus parallel to the effect on anthocyanins in these organs, but contrasting to the results obtained for rutin in hypocotyls (Margna et al., 1972a). When growing seedlings on a sugar solution, a marked decrease in the content of all five flavonoids, beyond doubt, almost always occurred (Tab. 4). Sugars introduced to seedlings prior to illu-

Table 3

Glucose effects on the accumulation of flavonoids in isolated buckwheat cotyledons		
	Content of flavonoids, $\mu\text{g}/\text{seedling}$	
	Control	Glucose
80D+16L+24D		
Anthocyanins	5.15	5.43
Rutin	48.6	56.7*
Vitexin	34.3	38.8*
Saponaretin	61.3	68.1*
Orientin	18.1	19.1
Homoorientin	36.7	38.3

Table 4

Sugar effects on the accumulation of rutin and glycoflavones in cotyledons of intact buckwheat seedlings

Regime	Content of flavonoids, $\mu\text{g}/\text{seedling}$				
	Rutin	Vitexin	Saponaretin	Orientin	Homoorientin
A. Seedlings grown on sugar solutions, 72D+10L+14D					
H ₂ O	42.7	28.9	51.4	16.6	29.3
Sucrose	31.0*	24.2*	46.7	14.2*	20.5*
B. Sugars supplied to seedlings prior to illumination, 72D+10L+14D					
H ₂ O	45.9	28.0	54.7	19.4	35.4
Sucrose	41.2	26.4	52.6	18.1	30.7
56D+16L+24D					
H ₂ O	25.0	31.3	53.9	11.4	21.7
Glucose	30.0	29.4	53.6	10.8	22.3

mination were, however, less effective and failed to produce stable results. Nevertheless it seemed that the tendency of inhibition was still predominant also under these experimental conditions.

Experiments with feeding sugars in combination with other nutritives. When buckwheat seedlings were supplied with sugars in combination with phenylalanine, characteristic interactions of the two nutritives were

Table 5

Modifying influence of glucose on phenylalanine-induced stimulation of anthocyanin accumulation in buckwheat seedlings

Regime	Content of anthocyanins, µg/seedling		
	Control	+Phenylalanine	+Phenylalanine +glucose
Cotyledons			
72D+10L+14D	2.50	1.91	1.61*
56D+16L+24D	1.94	1.70	1.23*
Hypocotyls			
72D+10L+14D			
intact seedlings	2.88	4.96	3.60*
derooted seedlings	2.09	2.78	2.00*
56D+16L+24D	2.51	4.73	3.22*

revealed in both seedling organs. Experimental data clearly showed that glucose (Tab. 5, Fig. 2) as well as fructose and sucrose (Маргна, 1970) are capable of cancelling the greater part of stimulation caused by phenylalanine in the accumulation of anthocyanins in hypocotyls, while in cotyledons an opposite effect of the amino acid on pigment formation is considerably intensified in the presence of glucose. The inhibitory influence was independent of whether the seedlings were initially grown on water or on a phenylalanine solution and, to a lesser extent, that influence was likewise revealed in seedlings grown on glucose or sodium acetate solutions (Fig. 2).

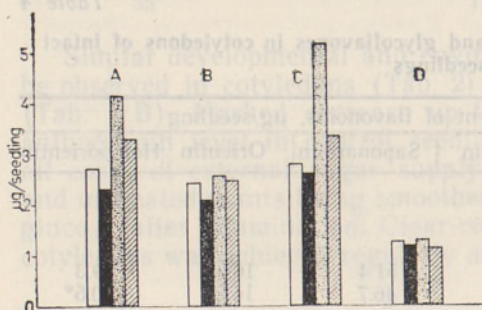


Fig. 2. Anthocyanin accumulation in hypocotyls of intact buckwheat seedlings supplied with various nutritives prior to illumination. White bars — water controls, black bars — glucose supplied, dotted bars — phenylalanine supplied, shaded bars — glucose and phenylalanine supplied in combination. Seedlings were grown on water (A), $5 \cdot 10^{-2}$ M glucose (B), 10^{-2} M phenylalanine (C) or $5 \cdot 10^{-2}$ M sodium acetate (D) solutions; growth regime — 72D+10L+14D.

In excised hypocotyls rather large phenylalanine-related stimulation of anthocyanin accumulation (ca +30%) showed no tendency to be suppressed (or enhanced) by the simultaneous presence of glucose in the incubation medium, which is in accordance with the overall small efficiency of sugar feeding in isolated buckwheat organs. By the analogy similar results could be expected also in isolated cotyledons but, instead, the following average results were obtained: cotyledons on water — 5.85, on 10^{-2} M phenylalanine — 10.02, and on a combined 10^{-2} M phenylalanine-1% glucose solution — 8.20 micrograms of anthocyanins per a pair of cotyledons, respectively.

Under similar feeding conditions the content of rutin and glycoflavones, analogous to isolated cotyledons fed with sugars alone (Tab. 3), showed a tendency to follow changes in an opposite direction, the average increase in flavonoids being equal to about 4–5 per cent as compared with

cotyledons supplied with phenylalanine. The relative increases thus remained here comparatively small, due to which they, as such, could hardly be considered significant. None the less, this tendency must be taken into account in comparing with other sugar effects. With an approximate absolute level of flavonoids of 220—240 micrograms of total rutin and glycoflavones per a pair of isolated cotyledons, a 5 per cent change in their content actually corresponds to about 11—12 micrograms of flavonoid substances. This amount is about twice as high as the maximal amounts of anthocyanins synthesized in isolated cotyledons on water and 6 times higher than the absolute reducing effect of glucose on phenylalanine-stimulated accumulation of anthocyanins in isolated cotyledons cited above. As precursor balance is likely existing between the biosynthetic routes of various flavonoid derivatives and, consequently, opposite changes in their accumulation may be interrelated, the observed inconsiderable per cent increase in rutin and glycoflavone accumulation seems large enough to be responsible for the marked opposite change simultaneously found in the formation of cotyledonary anthocyanins.

On the level of intact seedlings similar glucose-related modifications in the content of rutin and glycoflavones were not revealed in cotyledons. No increase or decrease of the effect of phenylalanine on rutin accumulation could be firmly established in hypocotyls either, although in some cases glucose seemed rather strongly to evoke extra stimulation above that caused by phenylalanine (Марина, 1970).

Discussion

As can be seen from the results of these and other sugar studies done in this laboratory with buckwheat seedlings, the dependence of flavonoid accumulation upon the sugar supply is of a rather complicated nature and may be largely modified by a number of external and endogenous factors. From those the following need to be especially emphasized:

a) Differences between intact seedlings and their excised organs — in isolated hypocotyls and cotyledons a general tendency of stimulation was typically characteristic for accumulation of all flavonoid derivatives in sugar media, while in intact seedlings feeding sugars either lacked clear-cut effects (leucoanthocyanidins) or resulted in a broader spectrum of responses (involving both stimulation and inhibition) depending on the type of flavonoids, organ specificity, etc. (for similar differences see Pogorzelska, 1965; Grill, 1967). This indicates that the regulatory mechanisms determining the accumulation of flavonoids must be much more complex in intact seedlings than in their isolated organs; in the latter the integrity of metabolic processes is partially destroyed and simpler regulatory principles (such as "more substrates — more products") obviously become predominating.

b) Endogenous differences in the metabolic pattern of hypocotyls and cotyledons — although the content of leucoanthocyanidins remained practically unchanged and, on the other hand, the accumulation of anthocyanins was generally reduced by external sugar supply in both organs of intact seedlings, this similarity of responses was not held with rutin formation: this process, contrary to anthocyanins, tended to be stimulated in hypocotyls, but inhibited in cotyledons. Under certain experimental conditions analogous reverse tendencies could also be revealed in the accumulation of anthocyanin pigments (in elder seedlings, at higher growth temperatures). As the absolute amount of rutin synthesized in hypocotyls is about 10 times higher than the amounts of anthocyanins, the

changes in its accumulation, even when relatively small, become determining, with the result that sugar effects, in terms of total flavonoids, are actually opposite in both organs: stimulatory in hypocotyls and inhibitory in cotyledons.

c) Age of seedlings — to judge by anthocyanin data on hypocotyls, a real possibility exists that with increasing age or, at least with increasing duration of the pretreatment dark incubation of seedlings, the internal conditions essential for flavonoid accumulation are somewhat altered. These alterations need not be as large as to cardinally modify the responses on the level of total flavonoids, but still sufficient enough to cause critical shifts in those related branches of flavonoid biosynthesis which are characterized by comparatively small gross yields of products and, therefore, are sensible already to relatively slight absolute changes in the pool size of common precursors (formation of anthocyanins).

d) Temperature-changes similar to those arising with ageing are also likely induced by alternating environmental temperatures, though under conditions of feeding sugars they, again, may remain comparatively small to interfere with the responses of flavonoids other than anthocyanins.

e) Feeding conditions — the inhibitory influence of external sugar supply on anthocyanin accumulation was much more pronounced on the background of high phenylalanine feeding than in the seedlings supplied with sugars alone. On the other hand, sugar introduced to seedlings together with 2,4-D — a phytotoxic compound partially blocking the processes of protein biosynthesis — failed to produce any decrease of anthocyanin accumulation in hypocotyls while occasionally the typical inhibitory effect was replaced by a slight stimulation (Margna, Otter, 1968). Similar modifications in responses may likewise arise with other combinations of nutritives.

f) Finally, sugar effects seem to follow certain variations also depending on whether the nutritives are fed to seedlings prior to or after the illumination program, although in the present experiments (Tab. 1) it remained unclear as to whether the differences observed were directly related to some light-dependent shifts in metabolism or were merely due to different durations of contact with sugars in light- and dark-fed seedlings.

At the present stage of knowledge it is not easy to interpret the primary mechanisms determining the particular modifications of sugar effects under each of the factors and experimental conditions listed, yet all this variability in responses unequivocally points out that balance shifts on the level of some substrate compound highly critical for flavonoid biosynthesis must be involved. Therefore a general conclusion can be drawn that feeding sugars, independent of which is the actual route of their utilization in seedling cells or which may be the processes initially covered, finally results in a change in the pool size of this critical precursor, which subsequently leads to an equivalent increase or decrease in flavonoid accumulation.

To judge by characteristic interactions of sugars and phenylalanine in combined feeding experiments, the absence of inhibitory influence of sugars on anthocyanin accumulation at suppressed protein synthesis (Margna, Otter, 1968), and correlative shifts within flavonoid and protein metabolism in seedlings fed with sugars (Оттер, Маргна, 1967; Маргна, Оттер, 1968), the most likely compound of such an importance seems to be phenylalanine — the key-metabolite in the biosynthetic pathway of flavonoids simultaneously being involved in the building of proteins.

Sugars introduced to seedlings may interfere with the balance of phenylalanine in two ways. First of all, they may cause an increase in the total amount of phenylalanine synthesized in seedling cells, the increase arising from the probable enhancement of carbon flow through the pentose phosphate pathway due to the availability of extra sugars. In that case the sugars act predominantly as substrate materials, and if there would occur no marked changes in the distribution of phenylalanine between flavonoid and nonflavonoid pathways, and the relevant enzymic capacities are sufficient, favourable conditions for an augmentation of total flavonoid accumulation must be created. Sugars fed to seedlings may, however, also act as energetic materials, and, through the action on that level, cause considerable shifts in the distribution ratio of phenylalanine between flavonoid biosynthesis and competitive processes. From those, the building of proteins represents one of the most important if not the sole competitor of flavonoid formation for that critical amino acid. As was shown in our earlier contributions (Оттер, Маргна, 1967; Margna, Otter, 1968), these processes are really stimulated in seedlings by sugar feeding, and therefore they have to utilize, under these conditions, larger portions of phenylalanine than in seedlings grown in water. With the same intensity of phenylalanine formation or with the synthesis of this common precursor increased only a little, the possibilities of channelling phenylalanine into the flavonoid pathway must be respectively reduced, thus providing a satisfactory explanation why under certain experimental conditions feeding sugars proves inhibitory to flavonoid accumulation.

It seems most likely that the postulated changes in the balance of phenylalanine in sugar-fed seedlings involve both an increase in the total amount of this compound synthesized in seedling cells as well as shifts of its distribution between competitive biosynthetic pathways. The final effect of sugar supply on the level of total flavonoids obviously depends upon which of the two tendencies becomes predominating. However, as opposite changes sometimes occur in the accumulation of individual flavonoids, the final sugar effect on the level of separate flavonoid derivatives apparently depends not only upon the amount of common substrate remaining free for being channelled into the general flavonoid pathway, but also upon some additional shifts in the distribution of the substrate between separate biosynthetic routes within the range of the flavonoid complex itself. Which are the primary endogenous mechanisms responsible for these secondary balance shifts, remains to be elucidated.

It must be noted that certain changes in the accumulation of flavonoids may also result from the direct or indirect influence of sugars on the activity of phenylalanine ammonia-lyase (PAL), the key-enzyme in the pathway from phenylalanine to flavonoids and other phenolics. Recent investigations of this laboratory have shown (Лаанест, Маргна, 1972) that marked sugar-induced shifts in the activity of PAL actually may occur in buckwheat hypocotyls and cotyledons, making functional dependence of flavonoid responses upon enzymic shifts quite possible. However, as the PAL-changes only partly correlated with the alterations simultaneously observed in the accumulation of flavonoids, and, besides, the level of PAL-activity in young buckwheat seedlings, by a number of other suggestions, hardly can be rate-limiting for flavonoid formation (Лаанест, Маргна, 1972, see also Swain, Williams, 1970), these enzymic changes seem to be of only secondary importance in determining the effect of sugars on flavonoid accumulation.

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SUHKRUTE MÕJU FLAVONOIDIDE MOODUSTUMISELE TATRAIDANDEIS: MÕNINGAID UUSI ASPEKTE JA LÕPPJÄRELDUSED

Resümee

Artiklis on esitatud koondandmed suhkrate mõju kohta antotsüaanide, rutiini ja glükoflavoonide moodustumisele tatraidandi idulehtedes olenevalt materjali vanusest ning kasvatamise ja mõjutamise tingimustest. Neid andmeid võrreldakse tulemustega, mis olid saadud hüpokotüülide uurimisel, ja analüüsitakse seejärel suhkrate toimemehhanismi ning põhjusi, millest võib tuleneda lõppefekti varieeruvus eri organites ja eri flavonoidide lõikes. Lõppkokkuvõttes tullakse järeldusele, et suhkrate sisestamisele järgnevad nihked flavonoidide moodustumises peavad olema seoses muutustega, mis esinevad selle protsessi varustatuses mingi fenüülpropanoidset struktuuri omava lähtesubstraadiga. Kõige tõenäolisemalt on niisuguseks lähtesubstraadiks fenüülalaniin.

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ВЛИЯНИЕ САХАРОВ НА НАКОПЛЕНИЕ ФЛАВОНОИДОВ В ПРОРОСТКАХ ГРЕЧИХИ: РЯД НОВЫХ АСПЕКТОВ И ЗАКЛЮЧИТЕЛЬНАЯ ОЦЕНКА

Резюме

Представлены сводные данные о влиянии сахаров на накопление антоцианов, рутина и гликофлавонов в семядольных листочках проростков гречихи в зависимости от возраста, условий выращивания и обработки материала. Сравнивая эти данные с результатами изучения того же вопроса в гипокотылях, авторы обсуждают механизмы действия сахаров и причины варьирования окончательного эффекта по отдельным группам флавоноидов, отдельным органам и при изменении условий эксперимента. Сделан вывод, что действие сахаров на формирование флавоноидов должно быть связано с внутриклеточными изменениями в обеспеченности этого процесса исходными субстратами, в частности предшественниками фенилпропаноидной природы (фенилalaniном).

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