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THE INFLUENCE OF TEMPERATURE ON THE ACCUMULATION OF FLAVONOIDS IN BUCKWHEAT AND SOME OTHER PLANT SEEDLINGS

Introduction

Living processes in plants are subject to permanent influence of alternating temperatures in surrounding medium, the range of temperature variations being rather large sometimes even at the period of active growth and development of plant organisms. It is likely, therefore, that a metabolic system exists in plants, which is capable to avoid possible unfavourable consequences of these fluctuations and to maintain a more or less normal level of processes critical for living activities. A part of this system may be the set of metabolic reactions leading, among others, to changes in the accumulation of anthocyanins and other flavonoid compounds in plant cells.

Up to now many visual observations on various objects have been made concerning the effect of temperature upon the development of anthocyanin pigmentation in plant tissues. In general it has been found that low temperatures have a favourable influence on this process whereas a rise in environmental temperature, as a rule, results in a decrease in visible pigment accumulation (Capite, 1955; Alston, 1958; Vega, Martin, 1963; Beguin, 1964; Creasy, 1966; Rossiter, Beck, 1966; Steponkus, Lanphear, 1969; for earlier observations see ref. Blank, 1958). In agreement with those observations are also the results of some experimental studies, in which the changes in anthocyanin content were measured quantitatively (Troyer, 1964; Paynot, Martin, 1968, 1969; Ulrychova, Sosnova, 1970; Sosnova, Ulrychova, 1972). However, in a variety of other laboratory investigations rather great variations in temperature were found to exert only a negligible influence on anthocyanin formation (Slabecka-Szweykowska, 1952; Станко, Закман, 1964; Creasy, 1966), while in some cases the most intense pigment accumulation took place at higher, but not at lower temperatures (Eberhardt, 1954; Siegelman, Hendricks, 1958; Troyer, 1964; Pogorzelska, 1965; Creasy, Maxie, Chichester, 1965).

Concerning other flavonoid compounds, only a few reports are known, in which the dependence of the accumulation of a separate flavonoid derivative upon changes in environmental temperature has been described. R. Bassler (1957) has shown experimentally that 9—35-day-development of buckwheat plants at a raised temperature (30 °C) brings about, in most cases, a considerable decrease in the content of rutin in the leaves as compared with the content of this flavonol in plants grown at 20°. M. Pay-

not and C. Martin (1968) have observed that an elevation of temperature from 17° to 30° results in, parallel to changes in anthocyanin accumulation, an almost complete disappearance of flavonols from the leaves of *Begonia gracilis*. An inhibitory effect of higher and a favourable influence of lower growth temperatures was also established in the case of isoflavone accumulation in subterranean clover (Rossiter, Beck, 1966; Rossiter, 1970). Information about the influence of temperature upon the formation of such widespread flavonoid compounds as flavones and leucoanthocyanidins is still completely lacking.

This brief survey shows that the problem is yet far from being adequately studied by quantitative methods, emphasizing that additional experimental researches would be highly desirable. The present investigation represents one of the possible approaches along these lines. It was undertaken, first of all, to shed new light into the problem of the influence of temperature on the accumulation of anthocyanins, but, in addition, an attempt was made to follow the temperature-induced changes on a broader scale, *viz.* on the level of all flavonoid derivatives simultaneously present in a plant object. The latter experiments were carried out with buckwheat seedlings which, on account of their specific flavonoid composition, made possible to involve into comparison, besides cyanidin-type anthocyanins, also leucoanthocyanidins, a flavonol-glycoside (rutin), and a four-membered group of glycoflavones consisting of vitexin, saponaretin, orientin, and homo-orientin (Margna et al., 1967).

Experimental

Plant material. The experiments were carried out with young buckwheat (*Fagopyrum esculentum* Moench), rye (*Secale cereale* L. var. *cereale*), red cabbage (*Brassica oleracea* L. var. *capitata* f. *rubra*), white mustard (*Sinapis alba* L.), radish (*Raphanus sativus* L. var. *sativus*), and turnip (*Brassica rapa* L.) seedlings. The seedlings were raised under laboratory conditions on glass dishes, on two layers of filter paper moistened with an adequate amount of distilled water. When intact material was employed, three 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 $erg \cdot cm^{-2} \cdot sec^{-1}$) and after that were returned to darkness for an additional 24 h; B) the same, except that the duration of the postillumination dark period was prolonged to 48 h; C) the germinating seeds were held in darkness for 48 h, then the seedlings were transferred into a light chamber for further development under intermittent light-dark conditions involving 3 cycles of 8 h light + 16 h darkness. In experiments with isolated organs, the hypocotyls and cotyledons (in trials with rye the coleoptiles and first primary leaves, respectively) were excised from 80 h-old etiolated seedlings grown under standard conditions; the isolated 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±1° throughout all the stages of seedling growth as well as of the incubation of excised organs, except the period during which the material was exposed to experimental treatment with various temperatures. Material was harvested and assayed immediately after the end of the final dark period.

Treatments. Three following temperature levels were used: 14—16°, 25° (control), and 35°. The plants were kept under varying temperature conditions either during illumination or during the postirradiation dark

period. When the seedlings were allowed to develop under intermittent light-dark conditions, the treatment of plants with various temperatures was repeated during each of the three successive dark periods. With isolated organs, postirradiation treatment of material was used, only.

In combined experiments with feeding various nutritive factors the test substances used, in the form of water solutions, were introduced to growth medium of seedlings before the onset of the illumination program. Isolated organs, immediately after excision, were floated for 3—5 min in test-solutions and then, as described, incubated on filter paper moistened with the same solutions used for floating. The concentrations of test-substances in growth medium of intact seedlings as well as in solutions used for floating of excised organs were chosen as follows: glucose — 1 per cent; phenylalanine — 10^{-2} M; NH_4NO_3 — 0.1 per cent.

Flavonoid assay. Anthocyanins were determined photocolorimetrically by measuring the optical density of clear 1 per cent HCl-ethanolic extracts from plant material in a photoelectric colorimeter using a green filter of maximum transmission at 540 nm (10 mm cuvettes). The quantitative determination of leucoanthocyanidins was performed by an analogous photocolorimetric procedure as described by V. S. Govindarajan and A. G. Mathew (1965). Rutin in buckwheat hypocotyls was measured by a procedure of repeated one-dimensional, rutin and glycoflavones in buckwheat 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 homo-orientin), and 335 nm (apigeninic glycoflavones — vitexin and saponaretin), respectively (Margna, Margna, 1969). The content of all flavonoid substances was expressed in micrograms per seedling by using for calculations the following extinction coefficients E: for anthocyanins and leucoanthocyanidins — $2.7 \cdot 10^7$ (Jurd, Asen, 1966), for rutin — $1.40 \cdot 10^7$, for vitexin and saponaretin — $1.94 \cdot 10^7$, and for orientin and homo-orientin — $1.59 \cdot 10^7$ cm^2/Mol (the three latter coefficients were adopted from Margna, Margna, 1969). As no more than about one third of the total leucoanthocyanidins present in a plant material can be transformed into anthocyanidins by the known quantitative methods for leucoanthocyanidins including that recommended by V. S. Govindarajan and A. G. Mathew (Swain, Hillis, 1959; Govindarajan, Mathew, 1965; Scherf, Zenk, 1967), a correction factor 3.0 was used to compute, from the values measured, the actual absolute amounts of leucoanthocyanidins in plant material.

All experiments were run in 3 to 5 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 and of analysis of variance.

Results

Experiments with buckwheat, radish, turnip, red cabbage, mustard and rye seedlings

Anthocyanins. When the seedlings were allowed to grow at various temperatures during a 24 h post-illumination dark period, a rather clear-cut favourable effect of lower and a restraining influence of higher temperatures on the development of anthocyanin pigmentation was generally observed (Tab. 1). This regularity was not held in red cabbage seedlings and mustard hypocotyls, only, in which an incubation at an intermediate temper-

Table 1

The accumulation of anthocyanins in various plant seedlings grown at different temperatures (°C) during a 24-h postillumination dark period, μg/seedling

Plant	Intact seedlings			Isolated organs		
	15°	25°	35°	15°	25°	35°
Buckwheat						
hypocotyls	2.72	1.80	1.43	4.22	3.67	3.10
cotyledons	1.70	1.60	1.28	5.25	4.90	4.37
Radish						
hypocotyls	1.17	1.02	0.52	—	—	—
cotyledons	—	—	—	—	—	—
Turnip						
hypocotyls	0.88	0.77	0.62	—	—	—
cotyledons	1.87	1.80	1.65	—	—	—
Red cabbage						
hypocotyls	3.97	4.82	2.78	2.20	2.30	1.98
cotyledons	8.77	10.27	6.77	12.28	14.67	10.30
Mustard						
hypocotyls	1.23	1.38	1.03	—	—	—
cotyledons	5.50	4.97	4.27	—	—	—
Rye						
coleoptiles	2.70	2.30	1.37	1.07	1.05	0.67
first primary leaves	3.34	3.40	2.47	2.35	2.78	2.08

Table 2

The accumulation of anthocyanins in intact buckwheat seedlings under prolonged postillumination treatment with various temperatures, μg/seedlings

Regime*	Temperature, °C		
	15°	25°	35°
56D+16L+48D at various t°:			
hypocotyls	3.13	2.05	1.37
cotyledons	1.60	1.55	1.12
48D+3 cycles of (8L+16D at various t°):			
hypocotyls	2.43	3.15	2.03
cotyledons	1.68	2.25	2.07

* Here and in Tab. 4—6:
D — darkness; L — light; numerals — duration in hours.

ature (25°) proved to be more favourable for pigment formation than a corresponding incubation at 15°. However, irrespective of whether the maximum anthocyanin accumulation occurred at 15° or 25°, in every case a rise in temperature to 35° brought about a considerable decrease in the pigment-synthesizing capacity of seedlings, resulting in an up to 2—2.3 times lower content of anthocyanins in both hypocotyls and cotyledons (in rye in coleoptiles and in the first primary leaves, respectively) as compared with the maximum level of pigments found in these organs. The same were the results also in isolated plant material, except that excised organs seemed to be less susceptible to changes in environmental temperature than were intact seedlings.

Feeding exogenous phenylalanine, glucose, and ammonium nitrate was not able to modify the temperature-dependence of pigment accumulation

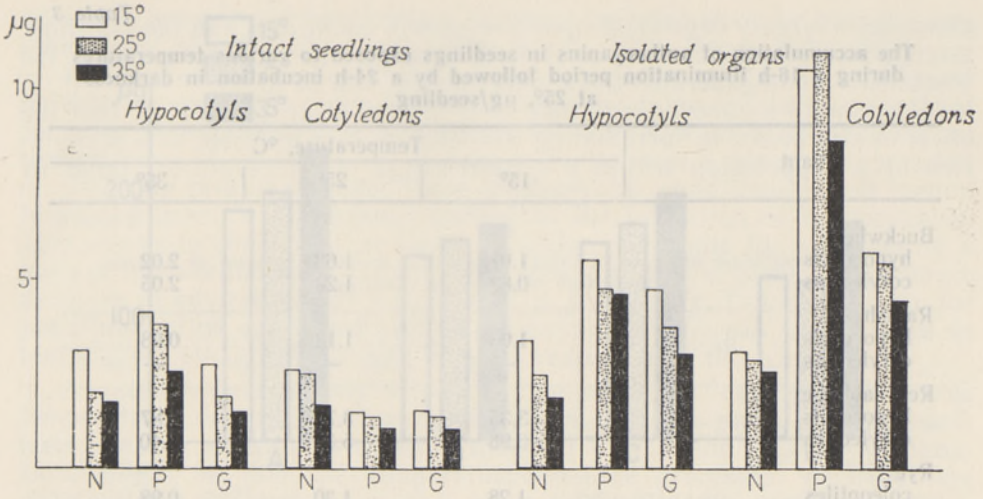

Fig. 1. The accumulation of anthocyanins in buckwheat seedlings fed with exogenous nutritive substances and exposed to different temperatures during a 24-h postillumination dark period (µg/seedling). N — 0.1 per cent NH_4NO_3; P — 10^{-2}M phenylalanine; G — 1 per cent glucose.

typical for buckwheat seedlings on water medium (Fig. 1). No modifications of the temperature effect occurred also in experiments in which the post-illumination development of buckwheat seedlings at various temperatures was prolonged to 48 h (Tab. 2). However, when the seedlings were allowed to develop under intermittent light-dark conditions with a repetition of the temperature treatment during each of the successive dark periods involved, a maximum pigment accumulation was observed at 25°, but not at 15°.

Unexpected were the results obtained with seedlings grown at various temperatures during a 16-h illumination period and then transferred into darkness for a 24 h incubation at 25° (Tab. 3). Under these conditions, both hypocotyls and cotyledons of buckwheat seedlings showed a response entirely opposite to that found in the seedlings exposed to various temperatures during a post-illumination dark period, the highest anthocyanin accumulation taking place now at 35°, and the lowest — at 15°, respectively. Analogous were also the results in red cabbage cotyledons, whereas radish seedlings showed a transition of a maximum anthocyanin accumulation from the seedlings incubated at 15° into the group of seedlings continuously grown at 25°. The response of rye seedlings remained similar to that found earlier.

Experiments with buckwheat seedlings

Leucoanthocyanidins. Contrary to anthocyanin accumulation rather susceptible to temperature changes in surrounding medium, the formation of leucoanthocyanidins showed but slight tendencies to be altered. Under post-illumination incubation of plants at various temperatures, certain regular changes in leucoanthocyanidins were observed, in fact, in hypocotyls, only, but even in these organs the differences remained comparatively small resulting in a statistically significant effect solely in the seedlings exposed to treatment during a prolonged dark period (Tab. 4). Nevertheless, this indicated that leucoanthocyanidin-forming processes are inclined to change in much the same direction as, under similar conditions,

Table 3

The accumulation of anthocyanins in seedlings exposed to various temperatures during a 16-h illumination period followed by a 24-h incubation in darkness at 25°, μg/seedling

Plant	Temperature, °C		
	15°	25°	35°
Buckwheat			
hypocotyls	1.07	1.63	2.02
cotyledons	0.82	1.23	2.05
Radish			
hypocotyls	1.03	1.18	0.68
cotyledons	—	—	—
Red cabbage			
hypocotyls	3.35	3.72	2.87
cotyledons	3.98	5.38	6.40
Rye			
coleoptiles	1.28	1.30	0.98
first primary leaves	3.57	3.62	3.20

Table 4

The accumulation of leucoanthocyanidins in buckwheat seedlings exposed to various temperatures, μg/seedling

Regime	Temperature, °C		
	15°	25°	35°
Intact seedlings			
56D+16L+24D at various t°:			
hypocotyls	104	91	104
cotyledons	192	187	195
56D+16L+48D at various t°:			
hypocotyls	**111**	**97**	**95**
cotyledons	205	198	208
48D+3 cycles of (8L+16D at various t°):			
hypocotyls	96	85	87
cotyledons	202	192	209
56D+16L at various t°+24D at 25°:			
hypocotyls	91	88	100
cotyledons	**168**	**181**	**234**
Excised organs			
80D+16L+24D at various t°:			
hypocotyls	124	131	129
cotyledons	226	236	230

the processes related to the formation of anthocyanins: i. e., they can be stimulated by lower and inhibited by higher temperatures.

In seedlings exposed to various temperatures during illumination the response, again, was of an opposite nature. Similarly to anthocyanins, the most intense formation of leucoanthocyanidins occurred here at 35° while at lower temperatures lesser amounts of these compounds accumulated. The favourable influence of higher illumination temperatures was especially pronounced in cotyledons (Tab. 4).

Rutin. Although higher temperatures occasionally tended to suppress (in hypocotyls) or enhance (in cotyledons) rutin accumulation, neither

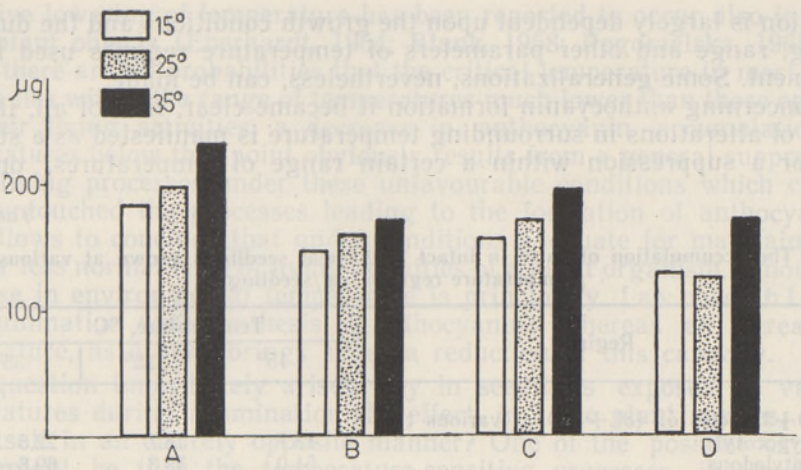

Fig. 2. The influence of temperature on the total amount of glycoflavones in buckwheat seedlings. A — 56D+16L+24D at various t°; B — 56D+16L+ +48D at various t°; C — 48D+3 cycles of (8L+16D at various t°); D — 56D+16L at various t°+24D at 25 C°.

stimulation nor inhibition of this process could be firmly established in seedlings when they were kept under various temperatures during a single 24-h or 48-h postillumination dark period. No reliable temperature-induced changes large enough to exceed significantly the level of spontaneous variability in the content of rutin within the seedling populations studied were revealed also in seedlings fed with phenylalanine, glucose, or ammonium nitrate. Rather great and stable shifts of rutin accumulation in both hypocotyls and cotyledons, however, took place when the seedlings were subjected to a repeated post-illumination treatment with various temperatures or were exposed to a range of different temperatures during illumination. As shown in Tab. 5, under these conditions an incubation of seedlings at 35° was much more favourable for rutin accumulation than a corresponding incubation at 25°, and, in cotyledons, still more effective in favouring this process as compared with seedlings grown at 15°.

Glycoflavones. Unlike other buckwheat flavonoids, glycoflavones showed no variations in their responses to different growth regimes, independent of whether the seedlings were grown at various temperatures either during illumination or during a single post-illumination dark period, or were allowed to develop under intermittent light-dark conditions with repeated post-illumination exposure of plants to different temperatures. In all cases the highest accumulation of each of the four glycoflavones occurred at 35° whereas a decrease in surrounding temperature progressively tended to reduce the amount of these compounds synthesized in cotyledons (Tab. 6, Fig. 2). The tendency was more or less firmly manifested over the whole group of glycoflavones, but the formation of vitexin and saponaretin, the apigenin-type tetrahydroxy-derivatives, was generally more affected by the changes in temperature regime than the processes leading to the formation of luteolinic pentahydroxy-glycoflavones orientin and homo-orientin.

Discussion

The results suggest that in young seedlings actively continuing their growth, development and differentiation during the period needed for the completion of experiments, the effect of temperature on flavonoid accu-

mulation is largely dependent upon the growth conditions and the duration, timing, range and other parameters of temperature regimes used for the treatment. Some generalizations, nevertheless, can be made.

Concerning anthocyanin formation it became clear, first of all, that the effect of alterations in surrounding temperature is manifested as a stimulation or a suppression within a certain range of temperatures, only. In

Table 5

The accumulation of rutin in intact buckwheat seedlings grown at various temperature regimes, μg/seedling

Regime	Temperature, °C		
	15°	25°	35°
48D+3 cycles of (8L+16D at various t°):			
hypocotyls	18.7	18.7	22.6
cotyledons	51.0	59.3	69.8
56D+16L at various t°+24D at 25°:			
hypocotyls	17.3	13.9	20.3
cotyledons	42.8	48.6	65.2

Table 6

Temperature-induced changes in the content of glycoflavones in cotyledons of intact buckwheat seedlings grown under various temperature (°C) regimes, μg/seedling

Regime	Orientin	Homo-orientin	Vitexin	Sapon-aretin
56D+16L+24D at various t°:				
15°	25.5	54.1	36.5	66.4
25°	25.7	58.5	39.3	75.2
35°	29.9	64.7	45.8	89.1
56D+16L+48D at various t°:				
15°	18.7	35.2	29.9	62.2
25°	20.1	37.1	34.1	66.8
35°	19.8	39.6	36.4	75.2
48D+3 cycles of (8L+16D at various t°):				
15°	23.4	45.5	26.0	60.1
25°	23.7	50.8	26.8	68.3
35°	24.1	53.3	32.8	84.1
56D+16L at various t°+24D at 25°:				
15°	20.2	34.3	24.5	51.1
25°	20.7	34.3	17.4	53.7
35°	21.6	36.6	35.3	77.7

other words, there presumably exists a critical temperature, a passage through which may result in a cardinal change of responses up to that point being characteristic of pigment accumulation under gradual decrease or increase of environmental temperature. To judge from experiments with plants exposed to various temperatures during a single postillumination dark period, in red cabbage seedlings the critical temperature must be located somewhere between 15° and 25° (see also Frey-Wyssling, Blank, 1943), whereas in other seedlings studied this point lies, most likely, in the region of 15° or below that. This is supported by the fact that a decrease in postillumination temperature from 15° to 5° ceased to induce any additional increase of pigment accumulation in buckwheat seedlings, but, instead, was rather unfavourable for this process. Similar unfavourable influence of

excessive lowering of temperature has been reported to occur also in some other plant objects (Eberhardt, 1954; Blank, 1958; Pogorzelska, 1965).

As there are all probabilities that the critical temperature in most plant objects lies within the range of temperatures much lower than those optimal for their living activities, a decrease in anthocyanin accumulation at temperatures below that point obviously results from a general suppression of all living processes under these unfavourable conditions which cannot leave untouched the processes leading to the formation of anthocyanins. This allows to conclude that under conditions adequate for maintaining a more or less normal level of living activities of a plant organism, a moderate decrease in environmental temperature is principally f a v o u r a b l e for postillumination dark synthesis of anthocyanins, whereas an increase in temperature, as a rule, brings about a reduction of this capacity.

A question immediately arises why in seedlings exposed to various temperatures during illumination the effect, in some plant species, manifests itself in an entirely opposite manner? One of the possible explanations might be that the temperature-sensitive processes involved are substantially different from each other in light and darkness, or are inversely susceptible and can be turned into opposite directions, depending on light conditions under which the temperature treatment is accomplished. It is not excluded, however, that the apparent light dependence of the effect of temperature is simply due to physiological differences between the seedling groups under investigation. If to take into consideration that high-temperature-grown seedlings in these experiments tended to be markedly superior in their development to seedlings grown at lower temperatures, a real possibility exists that the latter group of seedlings remains physiologically much less capable of synthesizing flavonoids than the seedlings exposed to light at higher temperatures. As a consequence, the effect of possible metabolic shifts generally responsible for temperature-induced changes in the accumulation of anthocyanins (and other flavonoids) may remain completely masked.

Additional complications seem to arise in attempting to interpret the effect of temperature on the accumulation of flavonoids other than anthocyanins. As became clear from the experiments with buckwheat seedlings, various flavonoid derivatives simultaneously present in a plant organism must not necessarily respond to a change in environmental temperature identically. Under experimental conditions most reliable for conclusions (postillumination treatment with various temperatures), the content of leucoanthocyanidins and rutin, for example, remained practically unaltered, thus indicating that the processes responsible for their formation must be much less susceptible to changes in the surrounding temperature than the processes leading to the formation of anthocyanins.

The relative stability of the leucoanthocyanidin- and rutin-forming processes found here largely resembles the relative inertness of these processes in respect to other external factors (light, feeding exogenous nutritive substances) observed by us earlier (Hallop, Margna, 1969; Халлоп, Маргна, 1970; Маргна, Оттер, 1971; Margna et al., 1972, 1973). This similarity allows to suggest that the differences between the three groups of flavonoids are not principal (in some specific manner distinguishing them from each other), but represent a phenomenon purely quantitative in its nature which is conditioned, as discussed elsewhere (Margna et al., 1972, 1973), by the differences in the complexity of their biosynthetic pathways and the resulting differences in the degree of relative saturation of these processes with common substrate materials due to which they are expected to show quantitatively different responses to possible shifts in cell metabolism. This

principle of regulation may be of universal importance in comparable situations, but this does not mean that in all cases it is necessarily realized in a way typical for buckwheat seedlings. In other leucoanthocyanidin or flavonol-containing plant objects more drastic responses to the alterations of temperature conditions are quite possible (cf., for example, Bassler, 1957).

Yet more intriguing is the clearly favourable influence of higher temperatures on the accumulation of glycoflavones, not only in the seedlings exposed to various temperatures during illumination (in which the flavonoid differences may be of a secondary nature), but, unexpectedly, also in those which underwent their temperature treatment during a postillumination dark period. An entirely opposite character of this response, as compared with anthocyanins, is obvious, indicating that a certain derivative-dependent specificity may still be involved. However, it would be rather imprudent to conclude, without having additional experimental evidence, that an enhancement of accumulation is generally typical of glycoflavones at higher temperatures and can be expected to occur regularly in all glycoflavone-synthesizing plant objects. None the less, the data clearly indicate that in some cases a decrease in the accumulation of a particular flavonoid at higher temperatures may be, at least partly, conditioned by a simultaneous increase in the accumulation of another related compound synthesized in the same tissue. This possibility can be easily understood when one considers that the flavonoids are all formed via a common biosynthetic pathway from a common key-metabolite (Neish, 1964), the pool of which may be limiting.

A brief word must be said regarding the metabolic mechanisms which may be responsible for the effect of temperature on flavonoid accumulation. A number of earlier authors, mainly because of the well-known activation of hydrolytic splitting of reserve polysaccharides by low temperatures, has attributed the low-temperature-dependent stimulation of anthocyanin accumulation to an enrichment of cells with soluble carbohydrates, thus suggesting a direct relationship between temperature-induced changes in both flavonoid and carbohydrate metabolism (Eberhardt, 1954; Blank, 1958; Kandeler, 1960; Pogorzelska, 1965). A surveying analysis of sugar and other related data has, however, shown that though positive correlations may sometimes occur (from more recent reports see Rossiter, 1970, 1972), a general increase in the content of soluble sugars by itself cannot play a determining role in securing an enhancement of flavonoid accumulation in plant tissues (Маргна, 1970). Therefore it seems that only those of the possible metabolic shifts may be critical, which, under varying temperatures, take place within the pentose phosphate cycle of carbon metabolism together with subsequent reactions related to building, transformation and utilization of phenylalanine, i. e. shifts within metabolic areas directly associated with the biosynthesis of flavonoid compounds.

This view is supported by a number of observations. It has been shown, for example, that the activity of glucose-6-phosphate dehydrogenase (EC 1.1.1.49) and 6-phosphogluconate dehydrogenase (EC 1.1.1.44), the two specific enzymes responsible for the functioning of the oxidative pentose phosphate cycle in plant cells, is considerably increased at lower temperatures whereas with a rise in temperature a marked decline in their activity takes place (Feierabend, 1970). Consequent on these enzymic changes, a general intensification of carbon flow through the pentose phosphate pathway must occur at lower temperatures resulting in that favourable conditions for an enhancement of cytoplasmatic biosyntheses, including formation of flavonoids, are presumably created in plant cells.

Increased levels of activity at lower temperatures are also characteristic of phenylalanine ammonia-lyase (EC 4.3.1.5) (Engelsma, 1970; Лаанест, Маргна, 1972). As this enzyme occupies a key-position in the biosynthetic pathway of flavonoids, a possible causal relationship between temperature-induced changes in its activity and flavonoid accumulation is rather clear-cut.

Finally, temperature-induced changes in flavonoid accumulation may also be a function of shifts at the level of protein synthesis. A marked suppression of amino acid incorporation into proteins at lower temperatures found by a number of authors (Тарлинская et al., 1969; Vallee, Perdrizet, 1971) makes quite possible that a stimulation of flavonoid accumulation under these conditions results from, at least partly, an increased availability of phenylalanine for this process.

The facts cited are still insufficient for final decisions, but anyway they are rather suggestive to allow a preliminary conclusion that the temperature-induced changes in flavonoid accumulation represent a secondary reflection of those metabolic shifts in plant cells which ultimately lead to perceptible changes in the supply of these processes with phenylpropane moieties.

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UDO MARGNA, LEMBE LAANEST, EVI MARGNA, MARGAREETE OTTER, TIIU VAINJÄRV

TEMPERATUURI MÕJU FLAVONOIDIDE MOODUSTUMISELE TATRA- JA MÕNEDE TEISTE TAIMELIIKIDE IDANDITES

Resümee

Tehti kindlaks, et temperatuuri mõju flavonoidide moodustumisele noortes arenevates idandites oleneb suurel määral mõjutusrežiimist ning avaldub eri klassidesse kuuluvate flavonoidide puhul erinevalt. Kui mõjutati valgustamisjärgsel pimeperioodil, siis stimuleerus antotsüaanide moodustumine temperatuuri alanedes üldiselt märgatavalt, temperatuuri tõustes aga pidurdus. Leukoantotsüaanide ja rutiinisisaldus muutus neis tingimustes suhteliselt vähe, glükoflavoonide puhul aga oli efekt selgelt vastupidine — madalamad temperatuurid (15 °C) inhibeerisid nende moodustumist, kõrgemad (35°) soodustasid. Temperatuuri varieerimine valgustamise ajal mõjus kõikidele flavonoididele ühteviisi: madalamate temperatuuride puhul oli nende sisaldus märksa madalam kui mõjutamisel kõrgemate temperatuuridega. Analüüsitakse põhjusi, millest võiksid oleneda need vastusreaktsioonide erinevused, ning arutatakse mehhanisme, mille kaudu temperatuur flavonoidide moodustamisele mõju avaldab.

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УДО МАРГНА, ЛЕМБЕ ЛААНЕСТ, ЭВИ МАРГНА, МАРГАРЕЕТЕ ОТТЕР, ТИЙУ ВАЙНЪЯРВ

ВЛИЯНИЕ ТЕМПЕРАТУРЫ НА НАКОПЛЕНИЕ ФЛАВОНОИДОВ В ПРОРОСТКАХ ГРЕЧИХИ И НЕКОТОРЫХ ДРУГИХ ВИДОВ РАСТЕНИЙ

Резюме

Установлено, что эффект температуры на формирование флавоноидов в молодых развивающихся проростках в значительной степени зависит от особенностей режимов воздействия, а также от класса флавоноидов, в который то или иное производное входит. При воздействии на проростки разными температурами после освещения накопление антоцианов при снижении температуры, как правило, заметно стимулируется, а при повышении, наоборот, ослабляется. Содержание лейкоантоцианов и рутина в этих условиях изменяется незначительно, накопление же гликофлавонов, противоположно антоцианам, при снижении температуры уменьшается, а при повышении — увеличивается. Варьирование температуры во время освещения приводит к одинаковым результатам во всех группах флавоноидов: их содержание при воздействии на проростки относительно низкими температурами (15 °C) всегда ниже, чем при воздействии более высокими (35°). В статье обсуждаются причины установленных различий в ответных реакциях проростков и механизмы, определяющие влияние температуры на формирование флавоноидов.

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