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Review

Catecholamines are active compounds in plants

Anna Kulma *, Jan Szopa

Department of Genetic Biochemistry, Faculty of Biotechnology, University of Wroclaw, Przybyszewskiego Str. 63/77, 51-48 Wroclaw, Poland

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Abstract

Catecholamines are a group of amines with a 3,4-dihydroxy-substituted phenyl ring. In mammals they are known as neurotransmitters with glycogen mobilizing function. Catecholamines have also been found in many plants and their synthesis is regulated by stress conditions. Their role and actions are only partly understood. They are involved in many aspects of growth and development. They affect the actions of various plant hormones and regulate carbohydrate metabolism. They serve as the precursors of isochinolic alkaloids and melanin. Catecholamines protect plants against pathogens and are involved in nitrogen detoxification. In this review we present the state of current knowledge on plant catecholamines.

Keywords: Catecholamines; Dopamine; Norepinephrine; Plants

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1. Introduction

Catecholamines, notably dopamine, norepinephrine (noradrenaline) and epinephrine (adrenaline), are a group of biogenic amines possessing a 3,4-dihydroxy-substituted phenyl ring. They are widespread in animals and are well known as neurotransmitters in mammals. The best-understood example of the hormonal action of epinephrine and norepinephrine in mammals is their regulation of glycogen metabolism.

A long list of plant organisms and organs capable of catecholamine biosynthesis has been identified. As many as 44 plant species, 29 of which are present in the human diet [1], contain reasonable quantities of these compounds in each plant organ.

For example dopamine is found at high concentration in spathes of *Araceae* inflorescences [2], the pulp of yellow banana (*Musa acuminata*), red banana (*Musa sapientum* var. baracoa), plantain (*Plantago major*) and fuerte avocado (*Persea americana*). High levels of epinephrine and norepinephrine occur in peyote (*Lophophora williamsi*) [3] and Dona Ana cacti [4], lower in oranges (*Citrus sinensis*), apples (*Malus sylvestrus*), tomatoes (*Lycopersicon esculentum*), eggplants (*Solanum melongena*), spinach (*Spinaciaooleracea*), beans (*Phaseolus vulgaris*), and peas (*Pisum sativum*) [5]. In the last species concentration of adrenaline is less than 1 μg/g fresh weight and the level of noradrenaline is lower or near 3.5 μg/g fresh weight. In potato the highest catecholamine level is in mature leaves, and significantly lower levels in young and

* Corresponding author. Tel.: +48 71 37 56 326.
E-mail address: kulma@ibmb.uni.wroc.pl (A. Kulma).

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Table 1
Catecholamine content in selected plant species

Species	Catecholamine content (μg/g FW)		
	Dopamine	Epinephrine	Norepinephrine
1. Yellow banana (*Musa acuminata*), fruit pulp	42	NE	<3.5
2. Red banana (*Musa sapientum* var.baracoa), fruit pulp	55	NE	<3.5
3. Plantain (*Plantago major*), fruit pulp	5.5	NE	<3.5
4. Fuerte avocado (*Persea americana*), fruit pulp	4	NE	<3.5
5. Cavendish banana, fruit pulp	2.5–10	NE	<3.5
6. Cavendish banana, fruit peel	100	NE	<3,5
7. Cocoa (*Theobroma cacao*) been powder	1	NE	<3.5
8. Broccoli (*Brassica olereacea* var italica)	1	NE	<3.5
9. Brousel sprouts (*Brassica olereacea* var. gemmifera)	1	<1	<1
10. Oranges (*Citrus sinensis*)	<1	<1	<1
11. Tomatos (*Lycopersicon esculentum*)	<1	<1	<1
12. Aubergine (*Solanum melanogena*)	<1	<1	<1
13. Spinach (*Spinacia oleracea*)	<1	<1	<1
14. Beans (*Phaseolus vulgaris*)	<1	<1	<1
15. Peas (*Pisum sativum*)	<1	<1	<1
16. Potato (*Solanum tuberosum* var. Desiree-leaves	2–7	ND	1.9–6.9
17. Potato (*Solanum tuberosum* var. Desiree-tubers	<0.5	ND	<0.5

NE: not estimated; ND: not detected.

senescent leaves and in tubers [6]. The content of catecholamines in number of plants is presented in Table 1.

The abundance of aromatic amines in several plant organs argues for an active role in living processes.

2. Catecholamine metabolic pathway

The catetecholamine synthesis pathway (Fig. 1) in plants is similar to that in mammals and is initiated by two equally active routes [7,8]. In the first route tyrosine, the immediate precursor of catecholamines, is hydroxylated by tyrosine hydroxylase (TH) giving dihydroxyphenylalanine (L-dopa). The second route is started by substrate decarboxylation driven by tyrosine decarboxylase (TD) and results in tyramine production. Thus, dopamine is produced via hydroxylation of tyramine or decarboxylation of L-dopa [9].

Although both initiating steps are fully active, different plants favour different synthetic routes. For example in sweet banana (*M. sapientum*) dopamine originates from tyramine hydroxylation, but in Scotch broom (*Cytisus scoparius*) in peyote cactus (*L. williamsi*) and callus of *Portulacca* from dopa decarboxylation. Dopamine hydroxylation by dopamine hydroxylase leads to norepinephrine synthesis [3,10].

Catecholamines are metabolized by at least three pathways, including methylation, oxidation and conjugation with other phenolic compounds.

In mammalian cells the methylated derivatives of catecholamines and both 3-methoxy-4-hydroxy mandelic acid and homovanillic acid are the final products of their catabolism. Mandelic and homovanilc acids were not found in plants however methylated derivatives such as normethenephrine were found [6]. Thus, the catabolic pathway of catecholamines in plants differs from that in the animals. There is possibility that methylation can serve as a way for catecholamine deactivation. From study of animal cells it is know that methylation causes catecholamine inactivation [11]. Even though there were never extensive studies done, some data suggest that methylated compounds are no longer active in plants at least in some aspects of their activity [12].

Metylation of catecholamines can also be a part of synthesis of various derivatives. Extensive studies of the catecholamine metabolism in Dona Ana cactus (*Coryphantha macromeris*) reveal production and accumulation of various methylated catecholamine derivatives. Of these phenethylamines, normacromerine (*N*-methyl-3,4-dimethoxy-beta-hydroxyphenethylamine) is by far the most abundant [4].

Studies of plant tissue cultures grown in presence of labelled tyramine and dopamine showed that catecholamines are catabolised also via oxidation and oxidative polymerisation [13]. The plant amine oxidases [14] act indiscriminately on monoamines oxidising them to the corresponding aldehydes and thus participate in amine degradation. One of the more important chemical changes is dopamine oxidation by lipoxygenase leading to melanins [15].

Catecholamines and their derivatives can also form conjugates with phenolic acids. Some of them like par example *p*-coumaryladrenaline are implicated in plant defence [16].

Finally catecholamines serve as substrates for biosynthesis of other compounds active in plant cells. Dopamine in particular is an intermediate in alkaloid biosynthesis, most importantly of benzylisoquinolines like papaverine and morphine, of the hallucinogenic alkaloid mescaline, identified in many cactus species [3], and of tetrahydrobenzylisoquinoline alkaloids [17]. Schematic representation of metabolic routes of catecholamines in plants with comparison to animals is presented in Fig. 2.

3. Involvement of catecholamine in diverse cellular processes

Since the early days of catecholamine discovery in plant, researchers have been intrigued by the question of the physiological significance of these compounds. Although the physiological meaning is still not completely understood a number of functions for catecholamines can be proposed.

First, dopamine was identified as a strong water-soluble antioxidant. For suppressing the oxygen uptake of linoleic acid in an emulsion and scavenging a diphenylpicrylhydrazyl radical, dopamine had greater antioxidative potency than glutathione, food additives such as butylated hydroxyanisole and hydroxytoluene, the flavone luteolin, the flavonol quercetin, and catechin, and similar potency to the strongest antioxidants gallocatechin gallate and ascorbic acid.

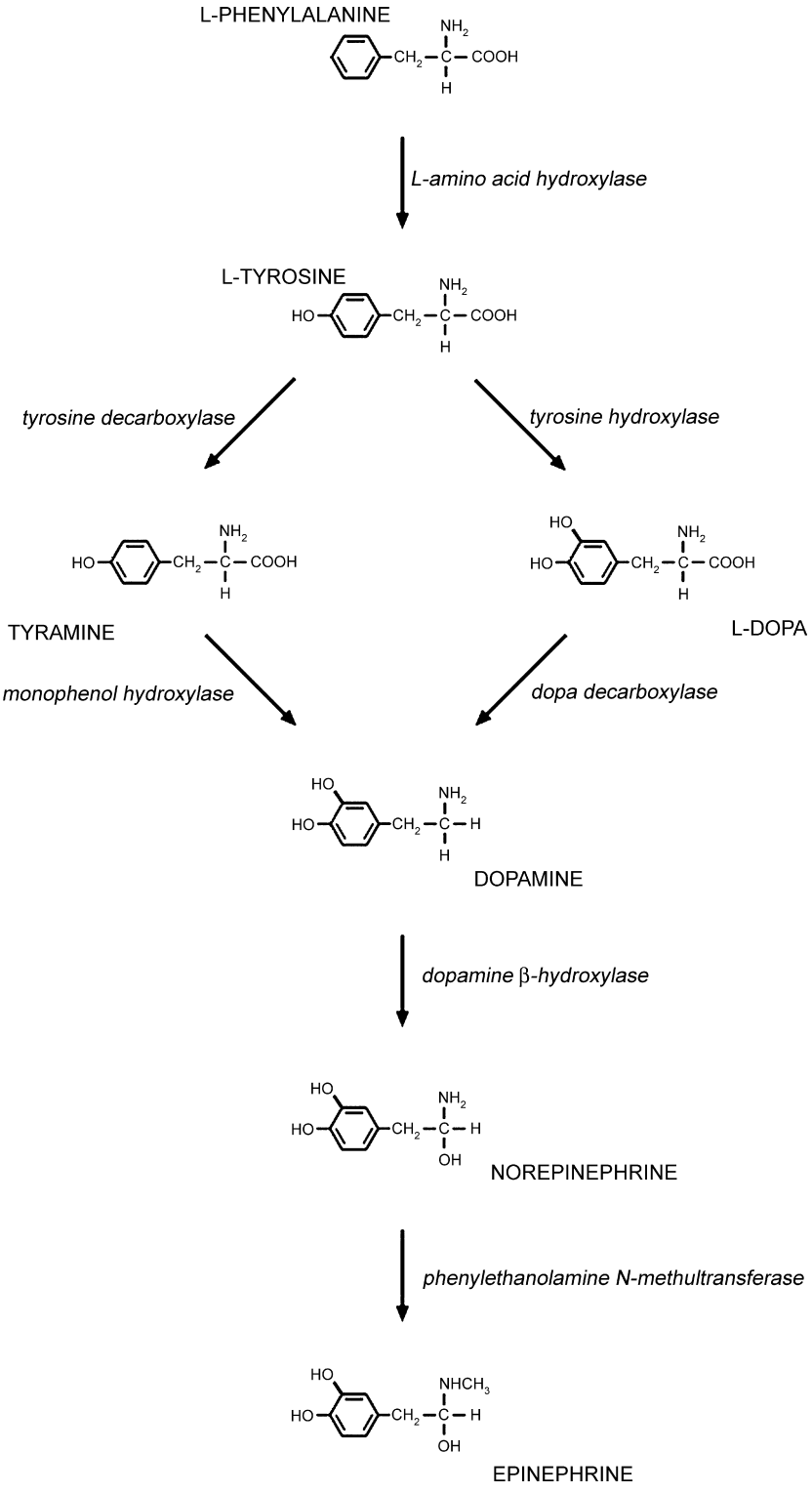

Fig. 1. Plant catecholamine synthesis pathway.

Although there is no strong evidence at present that catecholamines by themselves can act as antioxidants *in vivo*, their function in mediating photosynthetic reduction of oxygen is remarkable [18]. The superoxide anion radical is known to be the first product of photosynthetic reduction of oxygen mediated by a variety of electron carriers. The effectiveness of many electron carriers, and the toxicity of the superoxide they produce, rule out oxygen reduction as a physiological component of normal photosynthesis. The results with isolated spinach chloroplasts demonstrate that adrenaline and dopamine can mediate photosynthetic reduction of oxygen. These compounds might function as chemical analogues of a proposed natural mediator, or oxygen-reducing factor, that allows oxygen reduction to participate in energy transduction in

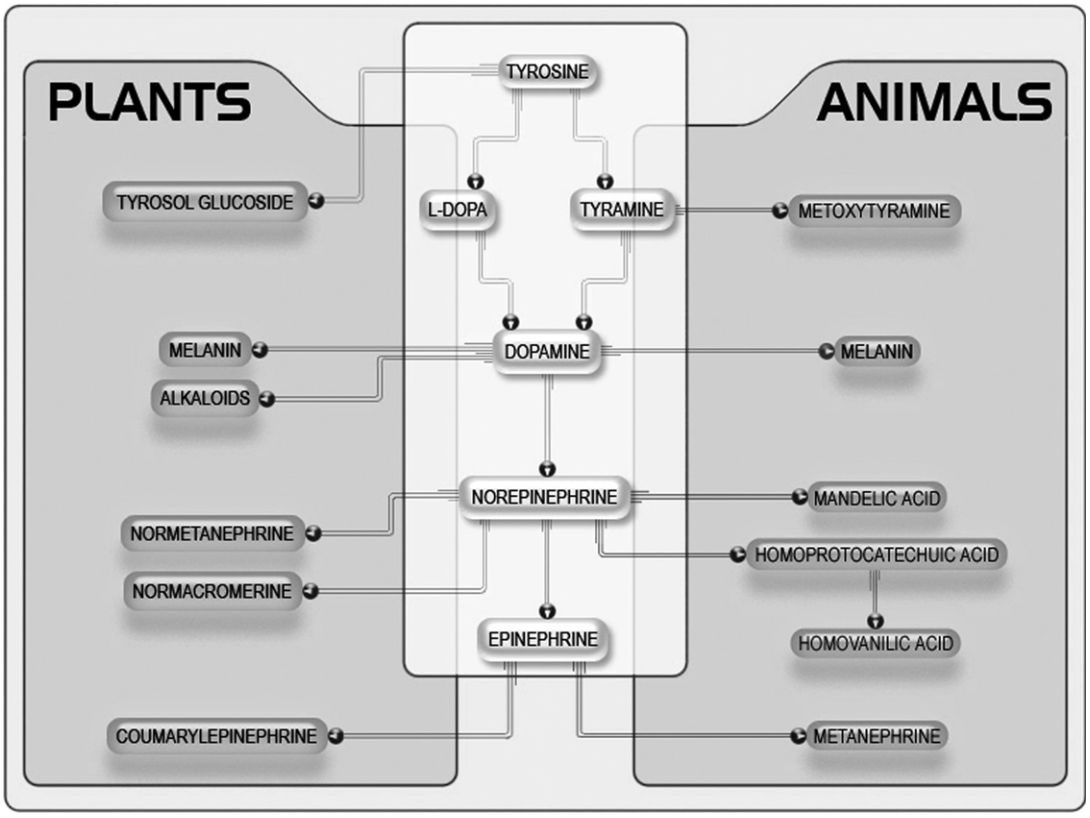

Fig. 2. Derivatives of catecholamines in plants with comparison to animals.

photosynthesis. The fully oxidised form of adrenaline, adrenochrome, also acts as a mediator in photosynthetic oxygen uptake, but only by reducing oxygen to superoxide [19]. However if really some derivative of catecholamines can serve in this way *in vivo* remain to be investigated.

Second, the catecholamine gives organisms the possibility to fine-tune the response to stress conditions. The effect is probably partly due to antioxidative properties of the compounds and their derivatives (oxidation of dopamine leads to production of melanin, potent free radical scavenger) and cell wall deposition of derivatives. For example catecholamine synthesis is much higher in darkness in *Portulacca* callus [20]. In contrast in the subantarctic crucifer *Pringlea antiscorbutica* levels of dopamine (together with some other amines) decreased during heat stress [21].

Wounding of the cactus *Carnegiea gigantea* causes leaking of latex-milk and increase of the dopamine level in callus tissue [22]. The levels of dopamine, epinephrine and normetanephrine increase in potato leaves 5 min after wounding. The highest rise was observed in case of norepinephrine [6]. Other stress conditions such as drought, ABA treatment and UV increased significantly dopamine level in potato plants [23]. In those same plants norepinephrine increase was noted after ABA, drought and NaCl treatment. In contrast catecholamine levels were lowered in red light, cold and darkness.

Conjugates of hydroxycinnamic acid with tyramine and dopamine, methoxytyramine and octopamine are found in a wide range of plants. Synthesis of these amides is activated by fungal elicitors, attempted infection by fungi, viruses, and bacteria and in some cases by wounding. These amides have been proposed to form a physical barrier against pathogens because they are usually found as integral cell wall components [24].

The hydroxycinnamoyl-tyramine conjugates were found in onion root cell walls and were able to inhibit growth of fungi [25]. The enzyme catalysing hydroxycinnamoyl synthesis (tyramine transferase, THT) is engaged in resistance to pathogen infection as was shown in the case of *Phytophtora infestans* [26]. Elevated levels of mRNA encoding THT and other enzymes involved in hydroxycinnamic acid biosynthesis were observed after pathogen attack [16]. An accumulation of the phenolic conjugates feruloyltyramine (FT) and *p*-coumaroyltyramine (CT) was observed in pepper (*Capsicum annuum*) after infection, with strains of *Xanthomonas campestris* [24]. Recently *p*-coumaryloctopamine [27] and *p*-coumaryladrenaline were identified as new products associated with pathogen resistance [16].

The analysis of transgenic plants strongly supports the view of catecholamines as active compounds in plant response to infection. Expression of TD in canola (*Brassica napus*) leads to decreased cell wall digestibility as evidenced by protoplast release efficiency. Plants with a three- to four-fold increase in TD activity showed a 30% decrease in cellular tyrosine pools and a two-fold increase in cell wall-bound tyramine compared with wild-type plants [28].

Overexpression of parsley tyrosine decarboxylase resulted in increased levels of tyramine in potato tubers [29] and were found to show increased resistance to *Erwinia carotovora* and

potato virus Y infection [23]. Importance of catecholamine metabolic pathways for plants pathogen resistance is in light of recent discoveries indisputable. However if it is only due to cell wall derivatives or if catecholamines may stimulate some other defence responses in more direct way remains to be seen.

Third, catecholamines affect plant growth and development by their interaction with phytohormones. Over two decades ago dopamine was identified as a factor necessary for hypocotyl growth in lettuce seedlings [12]. Later a substantial stimulation of growth in cultures of tobacco (*Nicotiana tabacum*) thin cell layers and *Acmella oppositifolia* "hairy root" cultures was achieved by micromolar concentrations of biogenic amines acting in concert with auxin [30]. Epinephrine at 10–100 μM stimulated somatic embryogenesis from orchardgrass (*Dactylis glomerata* L.) leaves cultured on Schenk and Hildebbrandt (SH) medium supplemented with 30 μM of indole-3-acetic acid (IAA) [31].

The overall regulatory effect of catecholamines on growth is probably mediated via auxin oxidation status. It was shown that dopamine can inhibit IAA oxidation *in vitro* as well as *in vivo* via inhibition of IAA oxidase and the reaction is highly specific [31]. The thesis that catecholamines may act in concert with auxins is supported by data from studies on *A. oppositifolia* hairy root culture, which can grow without addition of plant hormones. Dopamine promoted cell expansion on medium supplemented with IAA and kinetin but there was no effect on cells incubated in basal medium. Kinetin alone was unable to promote growth [30].

Exogenous dopamine and norepinephrine in 50 μM concentration and epinephrine in 100 μM concentration stimulate ethylene synthesis in leaves of sugarbeet [32]. The same effect was detected in potato suspension cell culture [33] and in orchardgrass culture at epinephrine concentrations of 10 μM [31]. In orchardgrass ethylene production caused by epinephrine at 500 μM concentration inhibited somatic embryogenesis. Addition of 8 μM cobaltous chloride, an ethylene biosynthesis inhibitor, to the medium restored ethylene emanation to the level observed in cultures grown on medium without supplements but did not alleviate the decreased embryogenic response [31].

Even though there is a lot of evidence suggesting catecholamine interactions with plant hormones at this point it is necessary to mention that all data concerning catecholamine–hormone interaction is over decade old and it will be important to see some more confirmation using more advanced methods developed recently.

Fourth, catecholamines influence plant flowering. In gibbous duckweed *Lemna gibba* flowering was stimulated by epinephrine at 100 nM concentration and at two orders less by norepinephrine. The noradrenaline and adrenaline at 1 μM concentration added to liquid culture medium of short-day duckweed (*Lemna paucicostata*) promoted its multiplication rate and flowering. At concentration 10 μM fronds were greener and healthier than when grown on control medium. Further increase in catecholamine level (200 μM) resulted in inhibitory effects on multiplication rate and size of fronds without influence on flowering [34]. Further work shows that in *Lemna paucicostata* catecholamines act in concert with alpha-keto-linolenic acid [35]. It was established that the chemical structures essential to influence flowering are catechol and ethylamine groups (dopamine) [36]. Catecholamines are able to relieve inhibition of flowering caused by other agents like sugar in *Lemna gibba* [37] or sucrose and ammonium ions in *Lemna pussicostata6746* [38]. The mechanism of catechoalmine influence on plant flowering remains unsolved.

Fifth, catecholamine influence on plant sugar metabolism was established. Dopamine, norepinephrine and epinephrine levels are severely decreased in tubers stored at 4 °C [6]. It is commonly known that soluble sugar levels and respiration increase during storage, at the same time as starch levels decrease [39].

One of major drawbacks in plant catecholamine studies is their low level. Even though development of a very sensitive identification method (by GC–MS) enabled identification of catecholamines in different potato tissue [6], more information about their effect on plant carbohydrate metabolism can be derived from studies of transgenic plants with increased catecholamine levels. Increased levels of catecholamines can be achieved via different approaches. Overexpression of tyrosine decarboxylase, one of key enzymes of catecholamine synthesis pathway [29], human dopamine receptor [40] and 14-3-3 protein [41] lead to increased levels of catecholamines in potato plants. Reduced catecholamine levels were achieved in potato by repression of all 14-3-3 isoforms [42]. It is known that 14-3-3 proteins regulate activity of many cellular proteins by protein–protein interaction—the tyrosine hydroxylase was identified as one of first 14-3-3's binding partners [43], and recently plant tyrosine decarboxylase interaction with 14-3-3 protein was identified (Kulma et al., unpublished data).

In all transgenic plants changes in carbohydrates levels were observed suggesting catecholamine involvement in sugar metabolism, possibly in a manner similar to that observed in mammalian cells [42]. In mammalian cells epinephrine and norepinephrine activation leads to glycogen breakdown via inactivation of glycogen synthase and activation of phosphorylase. The data obtained from study of transgenic plants with changed catecholamine levels support the view of the functioning of a similar system in plants, possibly via the same stages. Positive correlation of catecholamine level and sucrose, glucose and fructose content was observed in plants overexpressing tyrosine decarboxylase (TD) and dopamine receptor (HD1). At the same time negative correlation with starch level was detected. However, these identical data resulted from modification of different carbohydrate metabolism routes. In HD1 plants, starch synthesis was inhibited as a result of decrease in the activity of sucrose synthase (SuSy), phosphoglucomutase (PGM) and ADP-glucose pyrophosphorylase (AGPase). In TD plants, however, increased starch mobilisation (starch phosphorylase activation) and sucrose re-synthesis (SPS activation) were noted [40].

4. Catecholamine putative receptor

Up to now the catecholamine receptor has not been identified in plants. However several experiments indirectly support the view that receptors for adrenaline or noradrenaline

are present in plants. First, over decade ago the catecholamines were found to bind to membranes with constants similar to those of adrenoreceptors in mammals [44]. Second, propranolol, an antagonist of beta-adrenergic receptors in animals, has been shown to suppress partially flowering of duckweed and this effect was relieved by the addition of adrenaline [34]. Potato plants grown on alprenolol, a catecholamine agonist, were characterized by a bushy phenotype and yellowish leaves [41]. Third, the human dopamine receptor D1 expressed in potato plants resulted in remarkable increases in catecholamine levels and changes in sugar metabolism [40].

Fourth, newly identified DoH-CB proteins could mediate catecholamine action in plants. This class of proteins contains both dopamine-beta-hydroxylase activity and a cyt b561 electron-transport domain (CB) and thus combines in one protein properties of two enzymes necessary for adrenaline production. *In silico* analysis of DoH-CB proteins from *Arabidopsis thaliana* shows that structural features of both CB and DoH domains are well conserved. It is interesting that some of DoH-CB proteins were found to be auxin inducible. The DoH domain was also identified in another auxin-inducible protein AIR 12. These proteins are very good candidates for mediators of catecholamine function in plants and can provide a link between auxin and catecholamine action since some of the proteins containing the dopamine binding domain are induced in response to auxin [45].

5. The enzymes of catecholamine biosynthesis

Although catecholamines affect several cellular processes, their biosynthesis is also regulated. The activity of enzymes involved in catecholamine synthesis (tyrosine decarboxylase TD, tyrosine hydroxylase TH, and L-dopa decarboxylase DD) was increased in potato leaves treated with abscisic acid. In high salt conditions only TD activity was increased and in drought both TH and DD were activated. UV light activated predominantly DD activity. Leaves of plants grown in the dark and under red light conditions were characterised by significantly decreased activities of all the three enzymes whereas plants grown in cold conditions had decreased activity only of DD. In all stress conditions the normetanephrine level and thus SAM-dependent methylase activity was significantly decreased [23]. Interestingly tyrosine decarboxylase and dopa decarboxylase are differentially regulated by environmental signals.

The promoter of tyrosine decarboxylase was shown (in GUS studies) to be activated in response to wounding and pathogen

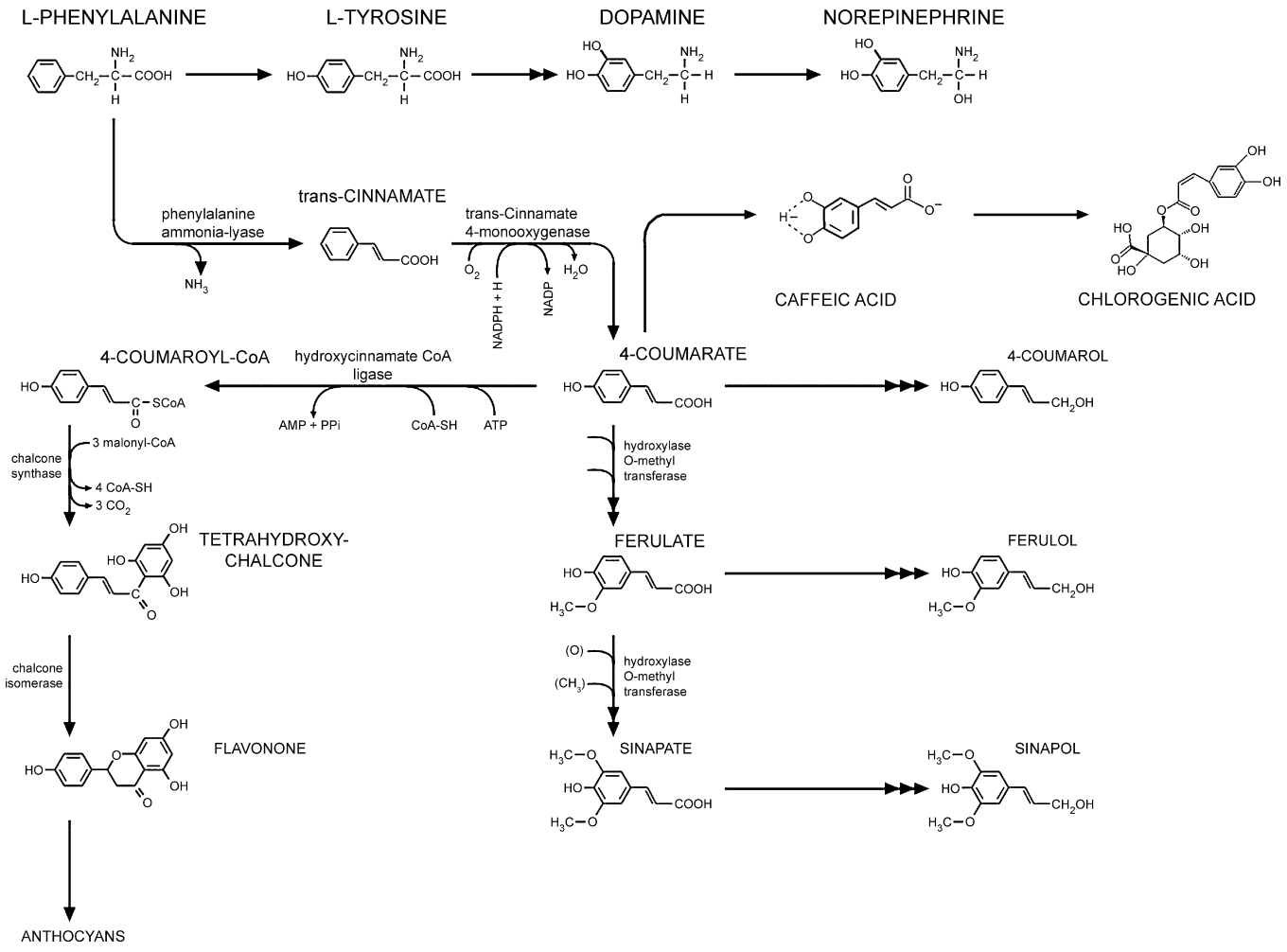

Fig. 3. Simplified phenylopropanoid pathway.

attack [46]. In opium poppy expression of tyrosine decarboxylase is tissue- and developmentally regulated [47] and conserved in transgenic tobacco [48]. It was reported that TD gene expression level increased as a result of pathogen attack [49]. Thus the overall suggestion is that catecholamine biosynthesis is primarily regulated by environmental signals.

6. Concluding remarks

Initially after the discovery of neurotransmitter substances in plants it was proposed that they might function as a deterrent to insect predators and foraging animals [10]. There is new data suggesting that dopamine hydrochloride can be used as an antiherbivore defence compound by the green alga *Ulvaria obscura* [50]. It was also suggested that catecholamines might simply be products of synthesis and degradation pathways of other metabolites [51].

Recent evidence suggests that the catecholamine function is more complex. They influence many aspects of plant physiology. Involvement in oxidative status, action in concert with phytohormones in regulation of plant growth, stress responses and regulation of sugar metabolism suggests that they have important regulatory functions. They display a rapid transient increase in plant leaves submitted to wounding, water stress and ABA treatment. Catecholamines are required in very small quantities and they are readily modified (methylated) during course of action. The metabolic effect produced by plant catecholamine is specific, in regulating starch breakdown. Also characteristic is that they are produced mainly in leaves but affect specific physiological responses in another part (tubers) of the organism. Thus taken together the entire data presented make it conceivable that catecholamines might play a general role in plant physiology. The molecular mechanism of their action is however as yet very poorly understood and further investigation will be helpful in final elucidation of their function in plants.

7. Perspectives

The phenylpropanoid biosynthetic pathway is one of the most extensively studied tightly orchestrated metabolic networks in plants (Fig. 3) The pathway branches as flavonoids, lignins, chlorogenic acid and salicylic acid provide the compounds with antioxidant and anticancer activity, protect against infection and involved in pathogen signal transduction. Since phenylopropanoids are defined as plant compounds derived form phenylalanine, the catecholamines should be included into them. The investigation of catecholamine branch of phenylpropanoid pathway is however at the initial stage when compared to other branches. Recently developed transgenic technology is a new tool for studying physiological relevance of this compound for plant physiology. A metabolic engineering approach has now provided direct evidence for the role of catecholamine in carbohydrate metabolism and plant response to stresses. It is however not known in details the compound catabolism and the perspective of the use of plant overproduced catecholamine for oral treatment of patients with Parkinson disease. Also the intriguing question is how catecholamines are assembled with other component of phenylpropanoid pathway. The possible concert action of catecholamine and monolignols was pointed out. Since catecholamine biosynthesis is affected by stresses the potential coordination of their synthesis with other compounds of pathway might occur. Nothing is as yet known on catecholamine signal transduction in plant. It is our hope that using genetic engineering approach the respective receptor and mediating signal transduction compounds can be finally identified.

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References

[1] M. Kimura, Fluorescence histochemical study on serotonin and catecholamine in some plants, Jpn. J. Pharmacol. 18 (1968) 162–168.
[2] M. Ponchet, J. Martin-Tanguy, A. Marais, C. Martin, Hydroxycinnamoyl acid amides and aromatic amines in the inflorescences of some *Araceae* species, Phytochemistry 21 (1982) 2865–2869.
[3] J. Lundstrom, Biosynthesis of mescaline and tetrahydroisoquinoline alkaloids in *Lophophora williamsii* (Lem.) Coult. Occurrence and biosynthesis of catecholamine and other intermediates, Acta Chem. Scand. 25 (1971) 3489–3499.
[4] W. Keller, R. Yeary, Catecholamine metabolism in a psychoactive cactus, Clin. Toxicol. 16 (1980) 233–243.
[5] J. Feldman, E. Lee, C. Castleberry, Catecholamine and serotonin content of foods: effect on urinary excretion of homovanillic and 5-hydroxyindoleacetic acid, J. Am. Diet Assoc. 87 (1987) 1031–1035.
[6] J. Szopa, G. Wilczynski, O. Fiehn, A. Wenczel, L. Willmitzer, Identification and quantification of catecholamines in potato plants (*Solanum tuberosum*) by GC–MS, Phytochemistry 58 (2001) 315–320.
[7] K.H. Kong, L.J. Lee, H.J. Park, S.H. Cho, Purification and characterization of the tyrosinase isozymes of pine needles, Biochem. Mol. Biol. Int. 45 (4) (1998) 717–724.
[8] U. Steiner, W. Schliemann, D. Strack, Assay for tyrosine hydroxylation activity of tyrosinase from betalain-forming plants and cell cultures, Anal. Biochem. 238 (1996) 72–75.
[9] I. Nagatsu, Y. Sudo, T. Nagatsu, Tyrosine hydroxylation in the banana plant, Enzymologia 43 (1972) 25–31.
[10] T. Smith, Secondary plant products, in: E.A. Bell, B.V. Charlwood (Eds.), Encyclopedia of Plant Physiology New Series, vol. 8, Springer-Verlag, Berlin, 1980, pp. 433–440.
[11] Y. Li, X. Yang, R.B. van Breemen, J.L. Bolton, Characterization of two new variants of human catechol-*O*-methyltransferase in vitro, Cancer Lett. 230 (2005) 81–89.
[12] S. Kamisaka, Catecholamine stymulation of gibberylin action that induces letucce hipocotyl elongation, Plant Cell Physiol. 20 (1979) 1199–1207.
[13] E. Meyer, W. Barz, Degradation of phenylethylamines in plant suspension cultures, Planta Med. 33 (1978) 336–344.
[14] R. Medda, A. Padiglia, G. Floris, Plant copper-amine oxidases, Phytochemistry 39 (1995) 1–9.
[15] M.A. Rosei, C. Blarzino, C. Foppoli, L. Mosca, R. Coccia, Lipoxygenase-catalyzed oxidation of catecholamines, Biochem. Biophys. Res. Commun. 200 (1994) 344–350.
[16] E. Roepenack-Lahaye, M.-A. Newman, S. Schornack, K.E. Hammond-Kosack, T. Lahaye, J.D.G. Jones, M.J. Daniels, J.M. Dow, *p*-Coumar-

oylnoradrenaline, a novel plant metabolite implicated in tomato defence against pathogens, J. Biol. Chem. 278 (2003) 43373–43383.
[17] H. Guinaudeau, J. Bruneton, Isiquinoline alkaloids, in: Waterman P.G (Ed.), Alkaloids and Sulphur Compounds, Academic Press, London, 1993, pp. 373–419.
[18] K. Kanazawa, H. Sakakibara, High content of dopamine, a strong antioxidant, in Cavendish banana, J. Agric. Food Chem. 48 (2000) 844–848.
[19] J. Allen, Superoxide as an obligatory, catalytic intermediate in photosynthetic reduction of oxygen by adrenaline and dopamine, Antioxid. Redox. Signal. 5 (2003) 7–14.
[20] R. Endress, A. Jager, W. Kreis, Catecholamine biosynthesis dependent on the dark in betacyanin-forming *Portulaca* callus, J. Plant Physiol. 115 (1984) 291–295.
[21] F. Hennion, J. Martin-Tanguy, Amines of the subantarctic crucifer *Pringlea antiscorbutica* are responsive to temperature conditions, Physiol. Plant. 109 (2000) 232–243.
[24] M. Newman, E. von Roepenack-Lahaye, A. Parr, M.J. Daniels, J.M. Dow, Induction of hydroxycinnamoyl-tyramine conjugates in pepper by *Xanthomonas campestris*, a plant defense response activated by hrp gene-dependent and hrp gene-independent mechanisms, Mol. Plant Microbe Interact. 14 (2001) 785–792.
[25] J. Grandmaison, G.M. Olah, M.R. Van Calsteren, V. Furlan, Characterisation and localisation of plant phenolics likely involved in the pathogen resistance expressed by endomycorrizal roots, Mycorhizza 3 (1993) 155–164.
[22] J. Bruhn, J. Lundstrom, Alkaloids of *Carnegiea gigantean*. Arizonine, a new tetrahydroisoquinoline alkaloid, Lloydia 39 (1976) 197–203.
[23] A. Swiedrych, K. Lorenc-Kukula, A. Skirycz, J. Szopa, The catecholamin biosynthesis route in potato is affected by stress, Plant Physiol. Biochem. 42 (2004) 593–600.
[26] H. Holfeld, W. Schurmann, D. Scheel, D. Strack, Partial purification and characterisation of hydroxycinnamoylcoenzyme. A. tyraminehydroxycinnamoylotransferase from cell suspension culture of *Solanum tuberosum*, Plant Physiol. 107 (1995) 545–552.
[27] F. Matsuda, H. Miyagawa, T. Ueno, Beta-1,3-glucooligosaccharide induced activation of four enzymes responsible for *N-p*-coumaroyloctopamine biosynthesis in potato (*Solanum tuberosum* cv.) tuber tissue, Z. Naturforsch. 55 (2000) 373–382.
[28] P.J. Facchini, M. Yu, C. Penzes-Yost, Decreased cell wall digestibility in canola transformed with chimeric tyrosine decarboxylase genes from opium, Plant Physiol. 120 (1999) 653–664.
[29] A. Swiedrych, J. Stachowiak, J. Szopa, The catecholamine potentiates starch mobilization in transgenic potato tubers, Plant Physiol. Biochem. 42 (2004) 103–109.
[30] C.M. Protacio, Y. Dai, E.F. Lewis, H.E. Flores, Growth stimulation by catecholamines in plant tissue/organ culture, Plant Physiol. 98 (1992) 89–96.
[31] A. Kuklin, B. Conger, Enhancement of somatic embryogenesis in orchard grass leaf cultures by epinephrine, Plant Cell Rep. 14 (1995) 641–644.
[32] E.F. Elstner, J.R. Konze, B.R. Selman, C. Stoffer, Ethylene formation in sugar beet leaves, Plant Physiol. 58 (1976) 163–168.
[33] Y. Dai, P. Michaels, H. Flores, Stimulation of ethylene production by catecholamines and phenylethylamine in potato cell suspension cultures, Plant Growth Regul. 12 (1993) 219–222.
[34] J.P. Khurana, B.K. Tamot, N. Maheshwari, S.C. Maheshwari, Role of catecholaminesin promotion of flowering in a short-day duckweed, *Lemna paucicostata* 6746, Plant Physiol. 85 (1987) 10–12.
[35] M. Yokoyama, S. Yamaguchi, S. Inomata, K. Komatsu, S. Yoshida, T. Iida, Y. Yokokawa, M. Yamaguchi, S. Kaihara, A. Takimoto, Stress-induced factor involved in flower formation of Lemna is an alpha-ketol derivative of linolenic acid, Plant Cell Physiol. 41 (2000) 110–113.
[36] S. Yamaguchi, et al., Identification of a component that induces flowering of Lemna among the reaction products of alpha-ketol linolenic acid (FIF) and norepinephrine, Plant Cell Physiol. 42 (2001) 1201–1209.
[37] Y. Oota, Removal of sugar inhibition of flowering in *Lemna gibba* G3 by catecholamines, Plant Cell Physiol. 15 (1974) 63–68.
[38] M.J. Ives, H.B. Posner, Epinephrine, propanolol and the sucrose-ammonium inhibition of flowering in *Lemnaa pausicostata* 6746, Plant Physiol. 70 (1982) 311–312.
[39] L.M. Hill, R. Reimholz, R. Schroder, T.H. Nielsen, M. Stitt, The onset of sucrose accumulation in cold-stored potato tubers is caused by an increased rate of sucrose syntthesis and coincides with low levels of hexose-phosphates, an activation of sucrose phosphate synthase and the appearance of a new form of amylase, Plant Cell Environ. 19 (1996) 1223–1237.
[40] A. Skirycz, A. Swiedrych, J. Szopa, Expression of human dopamine receptor in potato (*Solanum tuberosum*) results in altered tuber carbon metabolism, BMC Plant Biol. 5 (2005).
[41] G. Wilczyński, A. Kulma, I. Feiga, A. Wenczel, J. Szopa, Manipulating of 14-3-3 protein expression results in the changes of catecholamine content in potato plant, Cell. Mol. Biol. Lett. 3 (1998) 75–91.
[42] A. Swiedrych, M. Zuk, J. Szopa, Fizjologiczne i metaboliczne konsekwencje manipulacji biosynteza katecholamin w ziemniakach (physiological and metabolic consequences of catecholamine biosynthesis in potato-review in polish), in: Z.Z.P. Krajewski, P. Kachlicki (Eds.), Genetyka w ulepszaniu roslin uzytkowych-Rozprawy i monografie IGR PAN, Agenacja Rekalamowa PRODRUK, Poznan, 2004, pp. 147–161.
[43] M. Roberts, J. Salinas, D. Collinge, 14-3-3 Proteins and the response to abiotic and biotic stress, Plant Mol. Biol. 50 (2002) 1031–1039.
[44] V.V. Roshina, Biomediators in chloroplast of higher plants. 4. Reception by photosynthetic membranes, Photosynthetica 24 (1990) 539–549.
[45] W. Verelst, H. Asard, Analysis of an *Arabidopsis thaliana* protein family, structurally related to cytochromes b561 and potentially involved in catecholamine biochemistry in plants, J. Plant Physiol. 161 (2004) 175–181.
[46] S. Park, A.G. Johnson, C. Penzes-Yost, P.J. Facchini, Analysis of promoters from tyrosine/dihydroxyphenylalanine decarboxylase and berberine bridge enzyme genes involved in benzylisoquinoline alkaloid biosynthesis in opium poppy, Plant Mol. Biol. 40 (1999) 121–131.
[47] P. Facchini, V. deLuca, Phloem-specific expression of tyrosine/dopa decarboxylase genes and the biosynthesis of isoquinoline alkaloids in opium poppy, Plant Cell. 7 (1995) 1811–1821.
[48] P. Facchini, C. Penzes-Yost, N. Samanani, B. Kowalchuk, Expression patterns conferred by tyrosine/dihydroxyphenylalanine decarboxylase promoters from opium poppy are conserved in transgenic tobacco, Plant Physiol. 118 (1998) 69–81.
[49] P. Facchini, A.G. Johnson, J. Poupart, V. de Luca, Uncoupled defense gene expression and antimicrobial alkaloid accumulation in elicited opium poppy cell cultures, Plant Physiol. 111 (1996) 687–697.
[50] K.A. Van Alstyne, A.V. Nelson, J.R. Vyvyan, D.A. Cancilla, Dopamine functions as an antiherbivore defense in the temperate green alga *Ulvaria obscura*, Oecologia 148 (2006) 304–311.
[51] P.B. Applewhite, Serotonin and norepinephrine in plant tissues, Phytochemistry 12 (1973) 191–192.