

Catecholamines in Plants

A. I. Kuklin and B. V. Conger*

Department of Plant and Soil Science, University of Tennessee, Knoxville, Tennessee 37901-1071, USA

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Abstract. Catecholamines (CAs) are neurotransmitters in mammals. They have been found in 44 plant families, but no essential metabolic function has been established for them. They are precursors of benzo[c]phenanthridine alkaloids, which are the active principal ingredients of many medicinal plant extracts. CAs have been implicated to have a possible protective role against insect predators, injuries, and nitrogen detoxification. They have been shown to promote plant tissue growth, somatic embryogenesis from in vitro cultures, and flowering. CAs inhibit indole-3-acetic acid oxidation and enhance ethylene biosynthesis. They have also been shown to enhance synergistically various effects of gibberellins.

Chemical substances that play important role(s) in animal neural transduction have also been found in plants. For example, acetylcholine is a synaptic mediator in the cholinergic system which transmits information between the pre- and postsynaptic membranes in mammals. In plants, acetylcholine has been shown to influence leaf movement, seed germination, plant growth, and membrane permeability to ions (Tretyn and Kendrick 1991).

Other neurotransmitters, also found in plants, include a group of aromatic amines that possess a 3,4-dihydroxyphenyl nucleus and are known as catecholamines (CAs) (Fig. 1). Their physiologic role in animal cells is well studied (Darnell et al. 1990). Epinephrine (adrenalin) is a hormone involved in

rapid responses to stress. Dopamine and its cell receptors have been researched extensively because of their implication in schizophrenia and Parkinson's disease (Taubes 1994).

The objective of this review is to summarize the occurrence of CAs in plants and their effects on plant growth and development and to discuss possible mechanisms of their action.

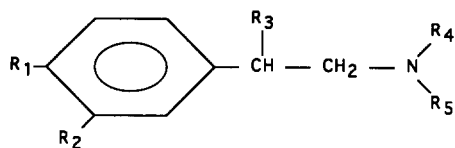
Occurrence and Biosynthesis of CAs in Plants

Dopamine, norepinephrine, epinephrine, and their precursors phenylethylamine and tyramine, as well as other derivatives, have been detected in 44 plant families, including at least 29 species grown for human consumption (Smith 1977, 1980). Feldman et al. (1987) measured the CA content in a number of fruits and vegetables by radioenzymatic assay. The concentration of dopamine in the pulp of yellow banana (*Musa acuminata*), red banana (*Musa sapientum* var. baracoa), plantain (*Plantago major*), and fuerte avocado (*Persea americana*) was 42, 54, 5.5, and 4 $\mu\text{g/g}$ FW, respectively. Cocoa (*Theobroma cacao*) bean powder, broccoli (*Brassica oleracea* var. italica), and Brussels sprouts (*B. oleracea* var. gemmifera) contained 1 $\mu\text{g/g}$ FW, of dopamine. A low dopamine concentration (<1 $\mu\text{g/g}$ FW) was detected in oranges (*Citrus sinensis*), apples (*Malus sylvestris*), tomatoes (*Lycopersicon esculentum*), eggplants (*Solanum melongena*), spinach (*spinacia oleracea*), beans (*Phaseolus vulgaris*), and peas (*Pisum sativum*). Epinephrine was measured to be <1 $\mu\text{g/g}$ FW, and norepinephrine was ≤ 3.5 $\mu\text{g/g}$ FW in these plants.

Some pheochromocytomas and carcinoid tumors in man synthesize and secrete CAs. Diagnoses of such tumors may be carried out by measurement of CAs or their metabolites in plasma or urine (Feldman et al. 1987). Therefore, the importance of knowledge about the CA presence in plants is ac-

Abbreviations: CA(s), catecholamine(s); FW, fresh weight; dopa, 3,4-dihydroxyphenylalanine; DW, dry weight; TCL, thin cell layer; dicamba, 3,6-dichloro-2-methoxybenzoic acid; GA, gibberellic acid; IAA, indoleacetic acid; cAMP, adenosine, 3',5'-cyclic monophosphate; ACC, 1-aminocyclopropane-1-carboxylic acid.

* Author for correspondence.



Compound:	R ₁ :	R ₂ :	R ₃ :	R ₄ :	R ₅ :
Phenylethylamine	H	H	H	H	H
Tyramine	OH	H	H	H	H
Dopamine	OH	OH	H	H	H
Norepinephrine	OH	OH	OH	H	H
Epinephrine	OH	OH	OH	H	CH ₃

Fig. 1. Chemical structures of some catecholamines (tabular form arranged as in Protacio et al. 1992).

centuated by dietary considerations. Patients who are diagnosed for excretion of 5-hydroxyindoleacetic acid in their urine are advised to have a diet with foods lacking these compounds (Feldman et al. 1987).

Applewhite (1973) reported that organs of movement, the pulvini and tendrils of *Albizia julibrissin*, *P. sativum*, *Mimosa pudica*, and *Passiflora quadrangularis*, showed the highest concentration of serotonin and norepinephrine compared with other vegetative parts. Tyramine and dopamine were present in a large number of Araceae inflorescences studied by Ponchet et al. (1982). They accumulated in amounts of 0.5–4.0 mg g⁻¹ FW only in tropical species of the Philodendroideae and Monsteroideae. These plants are tropical creepers, and they contain CAs, not only in their inflorescences but also in their leaves, stems, and adventitious roots (see Concluding Remarks section).

The formation of betalains in stems and flowers is one of the characteristics of the Portulacaceae. In addition, dopamine and norepinephrine have been detected in high concentrations in *Portulaca oleracea*. In a study on the CA concentration in callus of *Portulaca grandiflora*, Endress et al. (1984) showed that epinephrine and norepinephrine are accumulated only during culture in the dark. Dopamine synthesis was also enhanced by dark cultivation.

Wichers et al. (1993) reported the occurrence of L-dopa in the roots, stems, and leaves of *Mucuna pruriens*. The L-dopa content in the leaves and roots decreased within 4 weeks after germination. Dopamine was detected only in the leaves, and its content increased within 2–3 weeks. The authors also showed a fivefold increase in dopamine content in cell suspension cultures of *M. Pruriens* upon addition of the growth regulator 2,4-dichlorophenoxyacetic acid.

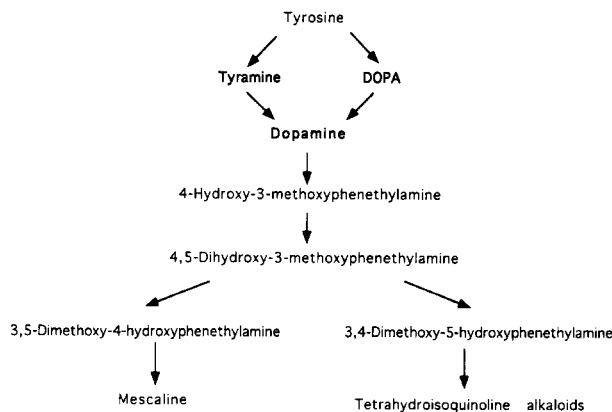


Fig. 2. Biosynthetic pathway of L-dopa and dopamine leading to the synthesis of mescaline in the cactus *L. williamsii* (redrawn from Smith 1980).

CAs are the precursors of a series of tetrahydrobenzylisoquinoline alkaloids. In the peyote cactus, *Lophophora williamsii*, phenylalanine is hydroxylated to tyrosine, which is hydroxylated further to L-dopa or decarboxylated to tyramine, leading to the synthesis of mescaline as shown in Figure 2 (Paul 1973, Smith 1980). The hallucinogen mescaline comprises 1% of the cactus, DW. The consumption of dried peyote buttons or flowers causes mental exhilaration. Their use in intoxicating enema rituals has been discussed by deSmet (1983) and is the major reason for this plant being under strict federal control in the United States (Nobel 1994). In banana fruit, tyramine is hydroxylated to dopamine, which is hydroxylated further to norepinephrine (Smith 1980).

The pathway from tyrosine to dopamine and 4-hydroxyphenylacetaldehyde, which gives rise to (*S*)-norcoclaurine, has been described as a complex ‘‘metabolic grid’’ (see Kutchan 1994). (*S*)-Norcoclaurine is the first alkaloidal intermediate in the pathway leading to (*S*)-reticuline, which occupies an important step in the biosynthesis of benzo[c]phenanthridine alkaloids.

Accumulation of CA in Cells

In mammals CAs are stored in the adrenal medulla in neurotransmitter storage vesicles or chromatin granules. The uptake of dopamine by the storage vesicles is dependent on ATP, Mg²⁺, and temperature (Scherman et al. 1983). Accumulation is linear only during the first 4 min of exposure. In contrast, Homeyer and Roberts (1984) found that dopamine accumulation by *Papaver somniferum* organelles

from latex that sedimented at 1,000 ×g remained linear over the first 60 min at 25°C. Accumulation was found to be affected by the pH of the medium in which this organelle fraction was incubated. The addition of ATP and Mg²⁺ had an insignificant effect. It has not been possible to distinguish the sequestering organelle(s). However, the authors showed that the uptake mechanisms for alkaloids and CAs are distinctly different.

Role of CAs in Plants and Interaction with Hormones

Protective Role

No essential metabolic function for CAs in plants has been established. Smith (1977) suggested that CAs and their derivatives may benefit the plant by acting as deterrents to insect predators and foraging animals and for this reason may be of agricultural significance. The resistance of sugarbeet (*Beta vulgaris*) to the fungus *Cercospora beticola* may be related to the presence of dopamine.

Homeyer and Roberts (1984) supported the idea that dopamine may have a role in protection against penetration of the plant outer surface. Physical damage causes some *Papaver* species to bleed latex, which, when exposed to air, forms a brown melanin-like substance that seals the wound. The release of dopamine and polyphenolase suggests a role of CAs in plant protection; however, this possibility needs further study.

Wound tissue formation in the saguaro cactus *Carnegiea gigantea* was accompanied by an increase in dopamine concentration (Steelink et al. 1967). The presence of previous wound tissue appeared to stimulate dopamine production in the surrounding healthy tissue.

Amides of hydroxycinnamic acid with tyramine have been found in onion (*Allium cepa*) root cell walls and may directly inhibit hyphal growth of fungal pathogens (Grandmaison et al. 1993). The enzyme catalyzing the synthesis of these amides, tyramine hydroxycinnamoyl transferase, is probably involved in the resistance reactions of potato (*Solanum tuberosum*) to *Phytophthora infestans* and was characterized recently (Hohlfeld et al. 1995).

Applewhite (1973) suggested that CAs might be intermediate products of synthetic or degradation pathways. It has been supposed that they may play an important role in the detoxification of ammonium- and nitrogen-containing compounds since they are formed during dissimilation of amino acids (see Grosse 1982, Roshchina and Roshchina 1993).

Morphogenetic Processes

Epinephrine and norepinephrine included in liquid medium for culture of the short-day duckweed (*Lemna paucicostata*) substantially promoted its multiplication rate and flowering (Khurana et al. 1987). Epinephrine increased the root length and protein content in 5-day-old seedlings of *Vigna unguiculata* (Kaur and Thurkral 1990).

Protacio et al. (1992) showed that CAs at micromolar concentrations caused a dramatic stimulation of growth in tobacco (*Nicotiana tabacum*) TCLs and *Acmella oppositifolia* "hairy root" cultures. Epinephrine (10–100 μM) stimulated somatic embryogenesis from orchardgrass (*Dactylis glomerata*) leaves cultured on SH medium (Schenk and Hildebrandt 1972) containing 30 μM IAA (Kuklin and Conger 1995). Epinephrine at 10 μM also enhanced somatic embryogenesis from leaves cultured on medium containing the synthetic auxin dicamba.

Results from different in vitro plant systems (Christou and Barton 1989, Kuklin and Conger 1995, Protacio et al. 1992) showed that CAs in millimolar concentrations are inhibitory to the growth of plant cultures. Leaves from orchardgrass cultured on SH with 30 μM dicamba and 1 mM epinephrine turned dark brown (Kuklin et al. 1994). However, some somatic embryos were obtained which were germinated into viable plants.

In experiments with tobacco calli, Christou and Barton (1989) found that adding a hydroxyl group to the aromatic ring enhanced toxicity; that is, dopamine was more toxic than octopamine. Epinephrine, with two hydroxyl groups on the benzene ring and a methyl group on the amine, was lethal to all tested calli that were initiated from hypocotyls, stems, and leaves of tobacco (*N. tabacum*), cotton (*Gossypium hirsutum*), soybean (*Glycine max*), and corn (*Zea mays*).

Gibberellins

An attempt to clarify the physiologic role of CAs was made by studying factors affecting the elongation of lettuce (*Lactuca sativa*) hypocotyls. Katsumi et al. (1965) suggested that the action of gibberellic acid (GA) in promoting shoot growth in intact cucumber seedlings was mediated by a factor(s) supplied by the cotyledons. Kamisaka (1973) showed in lettuce seedlings that this "cotyledon factor" was stable against heating at 100°C for 15 min, permeated the dialysis membrane, and was extractable with ethyl acetate. Its biologic activity was not re-

placed by IAA, kinetin, cAMP, vitamins, sucrose, or inorganic nutrients. This factor was identified as dihydroconiferyl alcohol (Shibata et al. 1974). Its structural similarity to CAs prompted Kamisaka (1979) to study the role of CAs in lettuce hypocotyl elongation. He demonstrated that epinephrine was active in synergistically enhancing the GA effect on this response. The hydroxyl group in the *meta* position was shown to be important for the biologic activity of CAs. *trans*-Cinnamic acid completely inhibited the action of CAs as in the case of dihydroconiferyl alcohol. *trans*-Cinnamic acid has an antiauxin activity. The author negated the possibility that CAs are kinds of auxin since IAA did not enhance the effect of GA on hypocotyl elongation.

Ethylene

Exogenous dopamine (5–100 μM) stimulated ethylene biosynthesis in illuminated chloroplast lamellae from sugarbeet leaves (Elstner et al. 1976). Isolated chloroplasts showed an enhanced production of superoxide free radical ions upon addition of dopamine in a reaction that is cyanide sensitive. This suggested that a phenoloxidase, together with dopamine, was responsible for the activation of oxygen, and this oxygen appeared to be one of the prerequisites for ethylene formation. The proposed mechanism for the involvement of dopamine in the light-dependent production of superoxide free radicals by chloroplast lamellae and its involvement in ethylene biosynthesis is shown in Figure 3.

Protacio et al. (1992) reported a threefold increase in the rate of ethylene evolution from tobacco TCLs after inclusion of CAs in the medium. Dai et al. (1993) found that dopamine and norepinephrine at 50 μM and epinephrine at 100 μM stimulated ethylene production in potato suspension cultures. The endogenous ACC levels were increased in parallel with the release of ethylene. These results suggested that the increase in ethylene promoted by monoamines is mediated via the well known ACC biosynthesis pathway (Adams and Yang 1979). Thus the synthesis of ACC may be the key point of the monoamine-ethylene link in the potato cell suspension system.

Stimulation of ethylene emanation by epinephrine at >10 μM was also reported for orchardgrass leaves cultured on SH medium with 30 μM IAA (Kuklin and Conger 1995). Epinephrine and norepinephrine (10–100 μM) did not affect ethylene emanation when added to SH medium supplemented with 30 μM dicamba (Kuklin and Conger 1994, 1995). Higher concentrations, however, caused a significant increase in ethylene emanation.

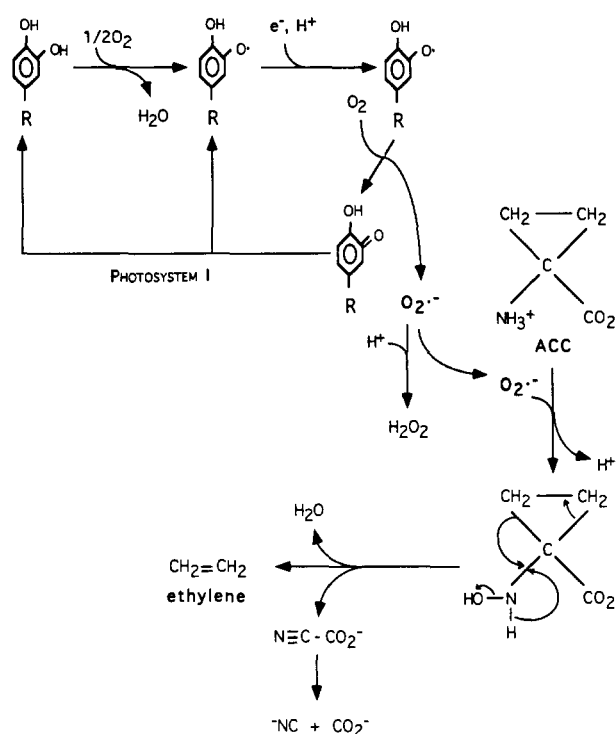


Fig. 3. Mechanism for the involvement of dopamine in the light-dependent production of a superoxide-free radical and ethylene synthesis (after Adams and Yang 1979 and Elstner et al. 1976).

Ethylene affects plant tissue cultures in various ways depending on the species studied and concentration levels (Biddington 1992). Increased ethylene emanation from tobacco TCLs (Protacio et al. 1992) and orchardgrass leaf cultures (Kuklin and Conger 1995) by CAs did not seem to be involved directly in the morphologic processes studied as shown by ethylene biosynthesis inhibitors.

IAA

Protacio et al. (1992) reported that the addition of dopamine to TCL cultures resulted in a fourfold reduction of [1-¹⁴C]IAA (included in the medium) decarboxylation. The authors presented experimental evidence in support of CA inhibition of oxidase activity in tobacco TCLs which prevented IAA degradation. In a similar experiment Kuklin and Conger (1995) showed a threefold decrease in the decarboxylation of IAA by orchardgrass leaf cultures when 10 μM epinephrine was included in the medium. Inhibition of IAA oxidation by CAs might explain their stimulatory effect on morphogenetic processes in tissue culture.

More than 30 years ago Lee and Skoog (1965) observed that catechol and hydroquinone at ≤ 128

μM promoted the growth of tobacco callus. Lee et al. (1982) studied the effects of substituted phenols on IAA oxidation and showed that 11 of 13 substituted *o*-diphenols tested were inhibitors of IAA oxidation. Whether CAs play a role in IAA catabolism in tissue culture and in plants is not known. Protacio et al. (1992) proposed that CAs may regulate auxin catabolism *in vivo*. New ideas concerning IAA catabolism (for discussion see Normanly et al. 1995) raise questions and point out directions for further research. A time course study of changes in endogenous CA content related to IAA concentration might provide information on possible relationships between these compounds.

Cytokinins

The transfer of a part, called T-DNA, of the *Agrobacterium* tumor-inducing (Ti) plasmid into the plant nucleus provides for hormone biosynthesis. Genes have been found in the T-DNA which encode enzymes for both auxin and cytokinin biosynthesis. Christou and Barton (1989) reported that crown gall cultures, obtained by transformation of tobacco with various *Agrobacterium* strains, did not become necrotic when CAs in millimolar concentrations were added to the culture medium. The toxicity was overcome either by endogenous generation of cytokinins in the calli due to the T-DNA-encoded isopentenyl transferase, an enzyme engaged in cytokinin biosynthesis, or by exogenous kinetin. Apparently, prior exposure of cells to cytokinins, whether as exogenously supplied kinetin or endogenously generated due to the T-DNA-encoded enzymes, activated a resistance mechanism to the high CA concentrations applied. The authors showed that CA uptake was not affected and concluded that other possible reasons need to be investigated.

CAs as Possible Biomediators in Plants

Khurana et al. (1987) reported that propranolol, a β -adrenergic blocking agent, partially suppressed flowering of duckweed at 10^{-4} M. Inhibition of flowering by propranolol was relieved by the addition of epinephrine. Flowering was induced even under noninductive photoperiods by the inclusion of cAMP in the culture medium (Khurana et al. 1988). These experiments indicated a possible existence of CA receptors and involvement of a cAMP messenger system.

Dopamine, norepinephrine, and epinephrine were shown to participate in the intercellular regu-

lation of ion permeability and photophosphorylation of chloroplasts (Roshchina 1989, 1990a). Pharmacologic studies on the stimulation of photophosphorylation induced by CAs demonstrated that their membrane-binding constants were similar to known adrenoreceptors in mammals (Roshchina 1990b). The author speculated about the existence of plant adrenoreceptors and proposed a model for CA involvement in a signal transduction pathway in chloroplasts. These findings need experimental confirmation.

Biotechnology Applications

Parkinson's disease is characterized by a marked decrease in the concentration of dopamine in the human brain. There has been much interest in the use of L-dopa for the treatment of parkinsonian patients (Hornykiewicz 1973). Unlike D/L-dopa, which is effective with a 2–3-month delay and has many side effects, L-dopa gives better results and remains an effective parkinsonian drug (Huber and Cummings 1992, Pearce 1992).

Chatopadhyaya et al. (1994) reported a two-stage culture method for the production of L-dopa by cell suspensions of *M. pruriens*. Bioreactor production of the compound and optimization of the process will be needed for its commercialization.

CAs are used in the first steps of benzo[c]phenanthridine alkaloid biosynthesis. These alkaloids are the active principals of extracts from many medicinal plants used all over the world (Kutchan 1994). Understanding the mechanisms of control of CA biosynthesis may lead to new ways of modifying medicinal plants.

Concluding Remarks

The abundance of CAs in spathes of Araceae inflorescences (Ponchet et al. 1982) raises the question of whether these compounds might have a role in reproductive organogenesis. The spathe is a "floral leaf" developing before the sex organs and thus is of importance for reproduction in monocotyledonous plants. High concentrations of CAs in organs of movement such as pulvini and tendrils (Applewhite 1973, Ponchet et al. 1982) suggest a possible role in the adaptation of some plants to a changing environment. Whether CAs may be linked to morphogenetic or adaptational processes is not clear at present.

New insights into the biochemistry of amide formation between hydroxycinnamic acid and CAs might throw light on the role of CAs in protection

against pathogen attacks (Hohlfeld et al. 1995 and references therein). Understanding the basis of CA interaction with plant hormones may lead to improved techniques for plant regeneration.

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