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REVIEW

ANIMAL NEUROTRANSMITTER SUBSTANCES IN PLANTS

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Summary. Chemical substances that play essential role in neurotransmission in animals, such as acetylcholine and biogenic monoamines (e.g. dopamine, noradrenaline, adrenaline, serotonin) have also been demonstrated in plants. Acetylcholine and catecholamines are believed to act as deterrents to insect predators and foraging animals but data about their possible role as biomediators in plants are accumulating. Acetylcholine is probably involved in regulation of physiological processes in plants as germination, flowering, morphogenesis and especially in phytochrome-controlled plant growth and development. Biogenic monoamines have been shown to modulate morphogenesis and reproductive organogenesis, to play a role in adaptation of some plants to a changing environment. Dopamine, noradrenaline and adrenaline were shown to participate in intercellular regulation of ion permeability and photophosphorylation of chloroplasts. Hydrophylic animal neurotransmitter substances are suitable candidates for signalling molecules in plants but their acceptance as biomediators in plants needs much more experimental information.

Key words: plants, acetylcholine, dopamine, noradrenaline, adrenaline, serotonin

The transfer of information from cell to cell in the nervous system takes place at specialized sites of contact called synapses by means of neurotransmitters. At such sites the pre- and postsynaptic cells assemble a complex apparatus for rapid and efficient synaptic transmission. Presynaptic specializations include active zones of clusters of vesicles containing different neurotransmitters along with exocytotic machinery for

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release of neurotransmitters into the synaptic cleft which separates the nerve terminal from its target. The postsynaptic apparatus includes aggregates of receptors for the neurotransmitters anchored in the postsynaptic membrane.

Chemical substances that play essential role in peripheral and central neurotransmission of animals, such as acetylcholine and biogenic monoamines (e.g. dopamine, noradrenaline, adrenaline, serotonin) have also been demonstrated in the plant kingdom (Tretyn and Kendrick, 1991; Kuklin and Conger, 1995). Although their function in plants is not clear, data about a possible participation in the regulation of physiological processes in plants are accumulating. The purpose of this article was to review briefly the evidence for the occurrence and possible role as biomediators in plants of chemical substances acting as neurotransmitters in animals.

Acetylcholine

Acetylcholine was discovered in nonanimal cells in the beginning of the century and afterwards its presence has been revealed in many species of lower and higher plants as well as in bacteria and fungi (Tretyn and Kendrick, 1991). Acetylcholine has been detected in the tissue of more than 50 plant species belonging to all major systematic groups as Amaranthaceae, Aquifoliaceae, Betulaceae, Compositae, Cucurbitaceae, Graminae, Leguminosae, Pinaceae, Plantaginaceae, Rosaceae, Solanaceae, Umbeliferae, Urticaceae. Acetylcholine concentrations in plants vary from nanograms to micrograms per gram fresh weight of tissue. The highest concentrations of acetylcholine have been found in the nettle species *Urtica dioica* L. and *Urtica ureus* L.. Many medicinal plants, such as *Viscum album* L., *Digitalis purpurea* L., *Digitalis lanata* L. also contain large amounts of acetylcholine. Acetylcholine isolated from plant material shows identical properties to that occurring in the nerve cells. The acetylcholine level has been shown to vary depending on the developmental phase of the plant and on environmental conditions. As a rule the highest acetylcholine concentrations are found in young growing parts of plants (Tretyn and Kendrick, 1991). Young leaves are believed to be the predominant site of acetylcholine synthesis in plants. Both the acethylcholine synthesizing enzyme, choline acetyltransferase, and the acetylcholine degrading enzyme, cholinestrase, have been assessed in plants. The enzymes show similar properties to the respective enzymes in animals, suggesting that acetylcholine undergoes similar metabolism in plants as it does in animals (Fig. 1). Choline acetyltransferase, which participates in acetylcholine synthesis from its precursors, choline and acetyl-CoA, has been demonstrated in the plant species *Urtica dioica* L., *Pisum sativum* L., *Spinacia oleracea* L., *Heliantus annuus* L. Acetylcholinesterase has been found in tissues of more than 100 plant species but the absence of acetylcholine hydrolysis has been reported in 65 plant species (Hartmann and Gupta, 1989). The presence of acetylcholine receptors in plants has been suggested

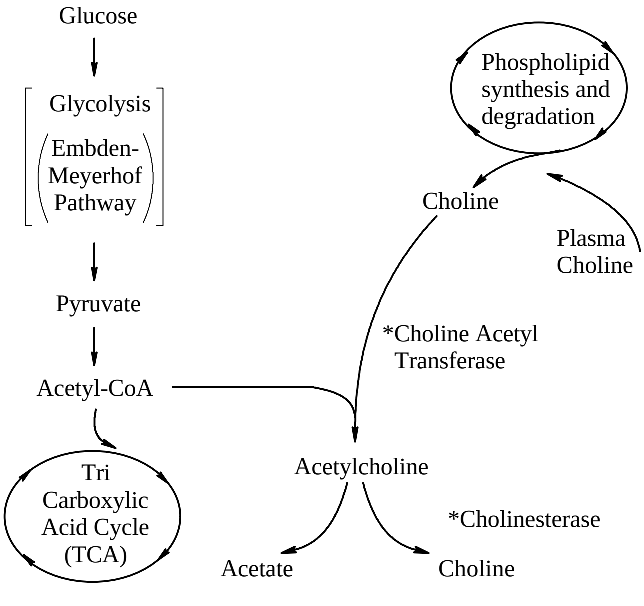

Fig. 1. Acetylcholine metabolism

as well. Thus, binding sites for acetylcholine have been demonstrated in extracts from roots and in cell wall fraction from *Phaseolus vulgaris* (Hartmann and Gupta, 1989). It has been further proposed that the acetylcholine receptors may regulate membrane permeability, or they may be linked with enzymes controlling specific metabolic pathways (Fluck and Jaffe, 1976). The use of specific agonists (muscarine, nicotine) and antagonists (atropine, D-tubocurarine) of acetylcholine receptors in animals provide indirect evidence for the existence of acetylcholine receptors in plants. However, more data are needed to accept the occurrence of acetylcholine receptors in plants.

Several early investigations prompted a participation of acetylcholine in regulation of physiological processes in plants and especially in phytochrome-controlled plant growth and development. The fact that endogenous acetylcholine has been found in the seeds of a number of plant species *Phaseoulus aureus* Roxb., *Pisum sativum* L., *Artocarpus champeden* Merr., *A. integra* Merr., *Carum copticum* Benth.) indicates that acetylcholine could be a factor involved in the regulation of germination. In the cotyledons of germinating bean seeds the total acetylcholinesterase activity increased between the second and third day of germination, remained constant till the sixth day and then decreased with cotyledon aging (Lees et al., 1978). The acetylcholine level was very low in the first two days of germination, increased rapidly with a maximum on the fourth day followed by a rapid decline to nearly undetectable levels. In the presence but not in the absence of light germination of photoblastic (light sensitive) seeds is also modulated by acetylcholine (Tretyn and Kendrick, 1991). In respect to modulation of plant growth acetylcholine mimics the effect of red light in inhibiting the development of secondary roots in bean seedlings (Fluck and Jaffe, 1976) but other experiments have demonstrated that acetylcholine can stimulate growth (Tretyn and Kendrick, 1991). In the latter cases the effect of acetylcholine has been accounted for its interaction with different growth regulators, such as auxin, gibberellins or ethylene. Acetylcholine has been shown to affect flowering in duckweeds, i.e. under continuous irradiation acetylcholine inhibited flowering in *Lemna gibba* G1 but stimulated it in *Lemna perpusilla* Torr. Moreover, an implication of acetylcholine in processes associated with membrane permeability as stimulation of adhesion of root tips to a glass surface and influence on leaf movement has been suggested. It has been further proposed that the primary mechanism of action of acetylcholine in plant cells is via the regulation of membrane permeability to H^+, K^+, Na^+ and Ca^{2+} ions (Hartmann and Gupta, 1989). In conclusion, a number of experiments have demonstrated that acetylcholine can mimic the action of red light in the regulation of some aspects of photomorphogenesis in plants (Fluck and Jaffe, 1976). However, data have also been published which demonstrate the lack of correlation between acetylcholine and phytochrome action (Hartmann and Gupta, 1989). Recent studies on protoplasts isolated from etiolated wheat leaves have again focused attention on the role of acetylcholine in plants. In the presence of Ca^{2+} ions acetylcholine like red light stimulates swelling of protoplasts which is known to be under phytochrome control (Tretyn and Kendrick, 1991). It has also been suggested that acetylcholine receptors similar to those in animal cells may be present in the protoplasts isolated from etiolated wheat leaves. Based on experiments with specific agonists and antagonists of animal acetylcholine receptors Tretyn and Kendrick (1991) proposed the existence of two main types of acetylcholine receptors muscarinic and nicotinic in protoplasts from wheat leaves.

Biogenic monoamines

Catecholamines dopamine, noradrenaline, adrenaline 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, 1980). High concentrations of dopamine have been measured in the pulp of yellow banana (*Musa acuminata*), red banana (*Musa sapientum* var. baracoa), plantain (*Plantago major*) and fuerte avocado (*Persea americana*) but low in oranges (*Citrus sinensis*), apples (*Malus sylvestrus*), tomatoes (*Lycopersicon esculentum*), eggplants (*Solanum melongena*), spinach (*Spinacia aleracea*), beans (*Phaseolus vulgaris*), and peas (*Pisum sativum*) (Feldman et al., 1987). In these plants the concentration of adrenaline was less than 1 µg/g fresh weight and the concentration of noradrenaline was lower or near 3.5 µg/g fresh weight. The fruits and leaves but not the tubers of the potato (*Solanum tuberosum*) contain detectable amounts of another aromatic monoam-

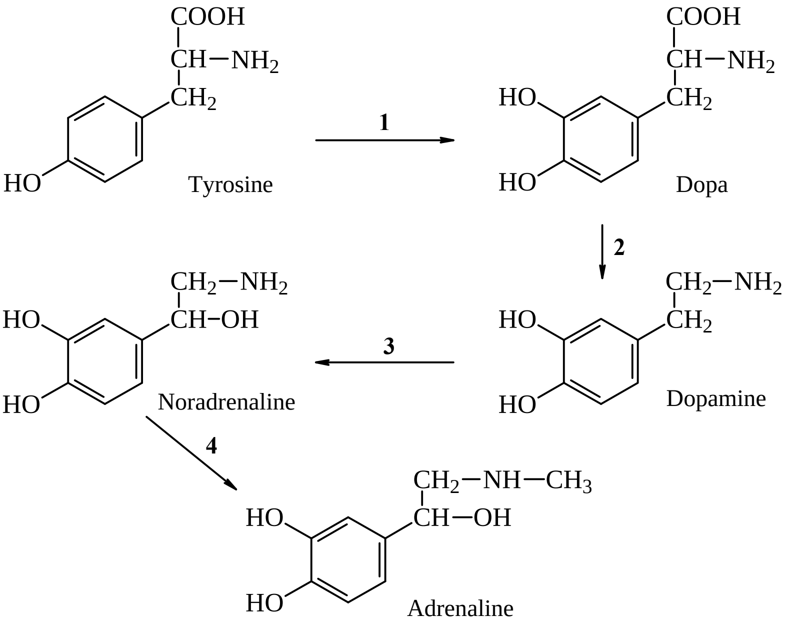

Fig. 2. Main synthetic pathway of catecholamines. **1** – tyrosine hydroxylase; **2** – dopa-decarboxylase; **3** – dopamine-β-hydrolase; **4** – phenylethanolamine-*N*-methyl-transferase

ine serotonin (in order of µg/g fresh weight) (Engstrom et al., 1992). Serotonin also occurs in fruits (e.g. pineapple, bananas, tomatoes) and seeds (walnuts).

Synthetic pathways characteristic for the synthesis of cathecholamines in animals have also been described in plants (Fig. 2). In banana fruit, tyramine is hydroxylated to dopamine, which is further hydroxylated to noradrenaline (Smith, 1980). Accumulation of dopamine, noradrenaline and adrenaline in *Portulaca grandiflora* has been observed only in the dark (Endress et al., 1984). The occurrence of catecholamine synthesizing enzymes DOPA-decarboxylase and L-tyrosine carboxylase has been shown in *Cytisus scoparius* and in barley roots respectively (Tocher and Tocher, 1972; Hosoi, 1974). Aromatic amino acid decarboxylase in company with hydroxylase, necessary for the formation of serotonin (Fig. 3), are synthesized *de novo* at the onset of serotonin synthesis (Grose, 1984). The existence of amine oxidases, enzymes which catalyze the oxidation of amines, has been described in plants (Medda et al., 1995). Plant amine oxidases, which could be Cu-containing and flavin-containing, oxidize particularly diamines and polyamines to the corresponding aldehyds. These enzymes indiscriminately act on monoamines and could thus participate in the degradation of biogenic monoamines. The enzyme found in *Thea sinensis* has a narrow substrate specificity and acts only on monoamines.

Up to now no essential metabolic function of catecholamines in plants has been unequivocally established (Kuklin and Conger, 1995). It has been proposed that

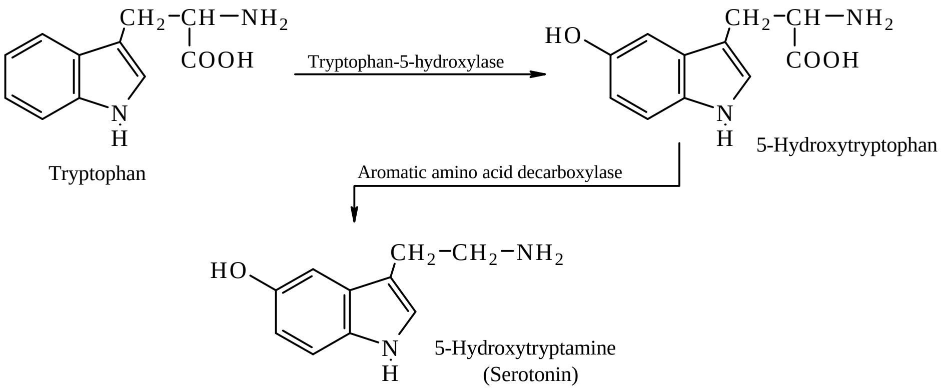

Fig. 3. Synthesis of serotonin

catecholamines and their derivatives might act as deterrents to insect predators and foraging animals (Smith, 1980). The resistance of sugarbeet (*Beta vulgaris*) to the fungus *Cercospora beticola* has been suggested to be due to the presence of dopamine. Catecholamines and especially dopamine might be involved in the protection against penetration of the outer plant surface. Thus, wounds in some *Papaver* species are sealed by a brown melanin-like substance accompanied by release of dopamine and polyphenolase (Homeyer and Roberts, 1984). Wound tissue formation in the saguaro cactus *Carnegiea gigantea* is accompanied by increase in dopamine concentration (Kuklin and Conger, 1995). A protective role for serotonin has also been suggested (Grose, 1982). Serotonin has been reported to be one of the physiologically active compounds accumulated in the stinging nettle of *U. dioica* and in trichomes in the pods of *Mucuna pruriens*. It has also been suggested that catecholamines might be intermediate products of synthetic or degradation pathways (Applewhite, 1973). Consistently, catecholamines have been shown to be precursors of a series of tetrahydrobenzylisoquinoline alkaloids. The peyote cactus (*Lophophora williams*) contains high concentrations of the hallucinogen mescaline which is synthesized after hydroxylation of tyrosine to L-dopa or by decarboxylation to tyramine (Smith, 1980). A role of serotonin as a secondary plant product involved in ammonia detoxification in seeds of walnuts (*Juglans regra*) is also proposed (Grose, 1982).

The abundance of aromatic amines and especially of dopamine and tyramine in spathes of Araceae inflorescences (Ponchet et al., 1982) prompts for a role in reproductive organogenesis. The spathe is a “floral leaf” developing before the sex organs and is thus important for reproduction of monocotyledonous plants. Tropical species of the families Philodendroideae and Monsteroideae contain high concentrations of catecholamines in the leaves, stems, adventious roots (as a rule these plants are tropical creepers) but highest concentrations were estimated in their inflorescences (Kuklin and Trentyn, 1995). The high concentrations of noradrenaline and serotonin found in organs of movements, the pulvini and tendrils of *Albizzia julibrissin*, *P. sativum*, *Mimosa pudica*, and *Passiflora quadrangularis* compared with other vegetative parts suggest a possible role in the adaptation of some plants to a changing environment. Biogenic monoamines might also be involved in modulation of morphogenic processes. Thus, noradrenaline and adrenaline added to liquid culture medium of short-day duckweed (*Lemna paucicostata*) promoted its multiplication rate and flowering (Khurana et al., 1987). A substantial stimulation of growth in cultures of tobacco (*Nicotiana tabacum*) thin cell layers and *Acmella oppositifolia* “hairy root” was achieved by micromolar concentrations of biogenic amines (Protacio et al., 1992). Adrenaline stimulated somatic embryogenesis from orchardgrass (*Dactylis glomerata*) (Kuklin and Conger, 1995). However, higher (milimolar) concentrations of catecholamines are inhibitory to the growth of plant cultures.

In the attempt to clarify the physiological role of catecholamines in plants, studies on their interaction with plant hormones were performed. Thus, adrenaline was

Table 1. Processes and functions in plants modulated by acetylcholine and biogenic monoamines

Substance	Process (function)
Acetylcholine	Germination Flowering Leaf movement Photomorphogenesis Protoplast swelling Ion permeability
Dopamine	Protective role Reproductive organogenesis Ion permeability
Noradrenaline	Adaptation to environmental changes Flowering Morphogenesis Ion permeability
Adrenaline	Protective role Somatic embryogenesis Reproductive organogenesis Flowering Ion permeability
Serotonin	Protective role Adaptation to environmental changes Flowering Morphogenesis Ion permeability

shown to act synergistically enhancing the effect of gibberillic acid on lettuce (*Latuca sativa*) hypocotyl elongation (Kuklin and Conger, 1995). Exogenous dopamine in concentrations of 5–100 μM stimulated ethylene biosynthesis in illuminated chloroplast lamellae from sugarbeet leaves (Elstner et al., 1976). A threefold increase in the rate of ethylene production from tobacco thin cell layers was observed after inclusion of catecholamines in the medium (Protacio et al., 1992). Dopamine, noradrenaline and adrenaline stimulated ethylene production in potato suspension cultures (Dai et al., 1993). Catecholamines have been suggested to play a role in the catabolism of indoleacetic acid. 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 (Khurana et al., 1987). These experiments are indirect support for the existence of specific receptors for adrenaline or noradrenaline. Dopamine, noradrenaline and adrenaline were shown to participate in intercellular regulation of ion permeability and photophosphorylation of chloroplasts (Kuklin and Konger, 1995 and references therein).

To summarize generally, data are presented for a role of animal neurotransmitter substances in the modulation of some physiological processes in plants (Table 1). Plants are unique in their cell–cell communication since typical plant cells are encased in a cell wall, constantly exposed to an extracellular matrix. Adjacent plant cells almost always have cytoplasmic connections through plasmodesmata which join the endoplasmatic reticulata of neighbouring cells. Hydrophilic animal neurotransmitter substances are suitable candidates for signalling molecules in plants but their acceptance as biomediators in plants which fulfill criteria resembling the criteria for neurotransmitters in animals, need much more experimental information.

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References

Applewhite, P. B., 1973. Serotonin and norepinephrine in plant tissues. Phytochemistry, 12, 191–192.

Dai, Y., P. J. Michaelis, H. E. Flores, 1993. Stimulation of ethylene production by catecholamines and phenylethylamine in potato cell suspension cultures. Plant Growth Regul., 12, 219–222.

Elstner, E. F., J. R. Konze, B. R. Selman, C. Stoffer, 1976. Ethylene formation in sugar beet leaves. Plant Physiol., 58, 163–168.

Endress, R., A. Jager, W. Kreis, 1984. Catecholamine biosynthesis dependent on the dark in betacyanin-forming *Portulaca callus*. J. Plant Physiol., 115, 291–295.

Engstrom, K., L. Lundgren, G. Samuelsson, 1992. Bioassay-guided isolation of serotonin from fruits of *Solanum tuberosum* L. Acta Pharm. Nord., 4, 91–92.

Feldman, J. M., E. M. Lee, C. A. Castleberry, 1987. Catecholamine and serotonin content of foods: effect on urinary excretion of homovanillic and 5-hydroxyindoleacetic acid. J. Am. Diet. Assoc., 87, 1031–1035.

Fluck, R. A., M. J. Jaffe, 1976. The acetylcholine system in plants. In: Commentaries in Plant Science, Ed. H. Smith, Pergamon Press, Oxford, pp. 119–136.

Grose, W., 1982. Function of serotonin of walnuts. Phytochemistry, 21, 819–822.

Hartmann, E., R. Gupta, 1989. Acetylcholine as a signalling system in plants. In: Second Messengers in Plant Growth and Development, Eds. W. E. Boss and J. D. Morre. A. R. Liss, New York, pp. 257–287.

Homeyer, B. C., M. F. Roberts, 1984. Dopamine accumulation in *Papaver somniferum* latex. Z. Naturforsch., 39c, 1034–1037.

Hosoi, K., 1974. Purification and some properties of L-tyrosine carboxylase from barley roots. Plant Cell Physiol., 15, 429–440.

Khurana, J. P., B. K. Tamot, N. Maheshwari, S. C. Maheshwari, 1987. Role of catecholamines in promotion of flowering in a short-day duckweed, *Lemna paucicostata* 6746. Plant Physiol., 85, 10–12.

Kuklin, A. I., B. V. Conger, 1995. Catecholamines in plants. J. Plant Growth Regul., 14, 91–97.

Lees, G. L., R. Lahue, J. E. Thompson, 1978. Changes in the acetylcholine titre of senescing cotyledons. J. Exp. Bot., 29, 1117–1124.

Medda, R., A. Padiglia, G. Floris, 1995. Plant copper-amine oxidases. Phytochemistry, 39, 1–9.

Ponchet, M., J. Martin-Tanguy, A. Marais, C. Martin, 1982. Hydroxycinnamoyl acid amides and aromatic amines in the inflorescences of some Araceae species. Phytochemistry, 21, 2865–2869.

Protacio, C. M., Y. Dai, E. F. Lewis, H. E. Flores, 1992. Growth stimulation by catecholamines in plant tissue/organ culture. Plant Physiol., 98, 89–96.

Smith, T. A., 1980. Plant amines. In: Secondary Plant Products, Encyclopedia of Plant Physiology, New Series. Eds. I. A. Bell and B. V. Charlwood, Springer Verlag, Berlin, vol. 8, pp. 433–460.

Tocher, R. D., C. S. Tocher, 1972. DOPA decarboxylase in *Cytisus scoparius.* Phytochem., 11, 1661–1667.

Tretyn, A., R. E. Kendrick, 1991. Acetylcholine in plants: presence, metabolism and mechanism of action. Bot. Rev., 57, 33–73.