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DOMINANT AMINO ACIDS, ORGANIC ACIDS AND SUGARS IN WATER-SOLUBLE ROOT EXUDATES OF C_4 PLANTS: A MINI-REVIEW

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Abstract

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The aim of this mini-review was to identify the dominant carbohydrates, organic acids and amino acids in water-soluble root exudates of plants which represent dominant compounds there. The study is focused on plants of C_4-type of metabolism taking into account available literature. From group of carbohydrates, those dominant are represented glucose, fructose, arabinose and sucrose. Between dominant amino acids occurring in root exudates of C_4-metabolism plants are alanine, serine, arginine, glutamine, glutamic and aspartic acid, glycine, proline, cystine, lysine and γ-aminobutyric acid. Citric, malic, tartaric, succinic, trans-aconitic represent the dominant organic acids. This knowledge may be useful for planning analyses of these compounds in root exudates of C_4 plants. Except for this preparation of synthetic root exudates to simulate rhizosphere of C_4 plants may be performed based on these results.

plant root exudates, organic acids, amino acids, sugars

Substances released by healthy and intact roots into the environment are in general, designated as root exudates. These substances affect composition of microbial community in immediate proximity of plant roots and processes taking place in the rhizosphere. Many compounds are released by plant roots, including inorganic ions and substances (O_2, H_2O, CO_2, H^+, HCO_3^-, OH^-, NO_3^-, K^+, HCN, NH_4^+, Na^+, Ca^{2+}, Mg^{2+}, SO_4^{2-}, Cl^-, PO_4^{3-}), amino acids, amides, sugars, aliphatic acids, aromatic acids, volatile aromatic compounds, gases such as ethylene, vitamins, peptides, proteins, enzymes, plant hormones, alcohols, ketones, olefins, urea, phytoalexins (Curl and Truelove, 1986; Vančura, 1988; Grayston *et al.*, 1996; Paynel *et al.*, 2001; Uren, 2007; Neumann and Römheld, 2007). Oxidative enzymes assessed in root exudates were e.g. haem-containing peroxidases, unspecific coper-containing oxidases, monooxygenases-hydroxylating and aromatic-ring cleavage dioxygenases (Gramss and Rudeschko, 1998). In total, 200 different carbon containing molecules are present in root exudates (Curl and Truelove, 1986), and up to 40% of the net carbon fixed during photosynthesis can be released into the rhizosphere (Whipps and Lynch, 1983, 1990). Root exudates can be sectioned according to their chemical character, properties and molecular weight (Rovira, 1956; 1969). Commonly, root exudates are divided into high molecular weight water-insoluble materials such as cell walls, sloughed-off material, other root debris and mucilage, and low molecular weight compounds denoted as water-soluble exudates such as sugars, amino acids, organic acids, hormones and vitamins (Rovira *et al.*, 1979; Cheng *et al.*, 1993; Traoré *et al.*, 2000). Of the low molecular weight root exudates, sugars, organic acids and amino acids form the dominant components (Aulakh *et al.*, 2001). Sugars, organic acids and amino acids efflux from roots is thought to occur by passive diffusion (Jones and Darrah, 1994; Shepher and Davies, 1994; Rroço *et al.*, 2002; Uren, 2007; Neumann and Römheld, 2007). With age of plants, the amount of organic acids in root exudates increased and the proportion of sugars and amino

acids decreased, expressed per weight unit of root dry weight (Smith, 1970; Aulakh *et al.*, 2001; Gransee and Wittenmayer, 2000; Uren, 2007). The intensity of exudation related to unit of root biomass was found to decrease with age of plants (Ferguson and Menge, 1982; Groleau-Renaud *et al.*, 1998), probably due to decreasing the metabolic activity of superficial root cells (Brimecombe *et al.*, 2007). At the same time, the release of higher amount of root exudates per plant was found in older plants due to increasing root biomass (Vančura *et al.*, 1977; Shepherd and Davies, 1994; Aulakh *et al.*, 2001).

The relative and absolute concentration of individual compounds in root exudates vary with the plant species, cultivars, plant's age, and environmental conditions including light intensity, temperature, nutritional status of plants, activity of retrieval mechanisms, various stress factors, herbicides, mechanical impedance, soil characteristics and activity of microorganisms in the rhizosphere (Bartels and Weier, 1965; Rovira, 1969; Hale *et al.*, 1971; Hale *et al.*, 1978; Rovira and Davey, 1974; Martin, 1977; Hale and Moore, 1979; Ferguson and Menge, 1982; Boeuf *et al.*, 1995; Paynel *et al.*, 2001; Neumann and Römheld, 2007).

In this work we have attempted to determine the occurrence of main individual compounds (amino acids, sugars and organic acids) in water-soluble root exudates of C_4 plants taking into account available literature.

DOMINANT COMPOUNDS IN WATER-SOLUBLE ROOT EXUDATES OF C_4 PLANT

Individual dominant sugars, amino acids and organic acids determined in root exudates of selected C_4 metabolism plants (*Zea mays*, *Sorghum vulgare*, *Sorghum bicolor*, *Panicum miliaceum*, *Bouteloua gracilis*, *Amaranthus retroflexus*, *Miscanthus sinensis*, *Miscanthus sacchariflorus*) are summarized in Table I. The concentrations of these compounds are not included in Table I. It is due to the use of different methods of root exudates collections and results expression including separation of net efflux of the organic compounds in some cases or expression of results in per cent of total (e.g. Gransee, 2001; Phillips *et al.*, 2004). The checklist may be useful to plan analyses of these compounds when other C_4 plants are studied, or when root exudates of C_4 plants need to be prepared synthetically to be applied to soil to create artificial rhizosphere and simulate degradation of organic pollutants by microorganisms as well as growth of degrading microorganisms and desorption of organic and inorganic pollutants (Hsu and Bartha, 1979; Haby and Crowley, 1996; Joner *et al.*, 2002; Ouvrard *et al.*, 2006). Synthetic root exudates can also be used to test their effect on development of microbial populations in soils polluted by heavy metals (Kozdrój and Dirk van Elsas, 2000).

I: *The most abundant* **c***ompounds found in water-soluble root exudates of C_4 plants (Gransee, 2001; Schwab et al., 1983; Vančura and Garcia, 1969; Klein et al., 1988; Hütsch et al., 2002; Lesuffleur et al., 2007; Phillips et al., 2004, 2006; Ayo Odunfa, 1979; Liu et al., 2004; Gaume et al., 2001; Nardi et al., 2002, 2005; Kayama, 2001).*

Class of components	Component
Sugars	Glucose, fructose, arabinose and sucrose
Amino acids	Alanine, serine, arginine, glutamine, glutamic and aspartic acid, glycine, proline, cystine, lysine and γ-aminobutyric acid
Aliphatic organic acids	Citric, malic, tartaric, succinic, *trans*-aconitic

SUMMARY

This mini-review is to identify organic compounds (amino acids, organic acids and sugars) which form a main part of water-soluble root exudates of C_4 plants. Appearance of individual representatives of these compounds differs according to plant species, cultivars, plant's age, and environmental conditions such as light intensity, temperature, and nutritional status of plants, activity of retrieval mechanisms, various stress factors, herbicides, mechanical impedance, soil characteristics and activity of microorganisms in the rhizosphere. When taken from different literature sources, five sugars, five organic acids and eleven amino acids were identified to be the dominant in water-soluble root exudates of C_4 plants. The checklist may be useful to plan analyses of organic compounds when other C_4 plants are studied. The obtained results may also be used as a directory for synthetic preparation of root exudates of C_4 plants to be used for different type of experiments.

SOUHRN

Dominantní aminokyseliny, organické kyseliny a cukry přítomné ve vodou rozpustných kořenových exsudátech rostlin C_4 – mini review

Cílem této práce je stanovení dominantních organických sloučenin přítomných v kořenových exsudátech rostlin s C_4 typem fotosyntézy, kterými jsou aminokyseliny, organické kyseliny a cukry. Podíl těchto látek i výskyt jejich zástupců je závislý na mnoha faktorech, např. rostlinný druh, kultivar,

věk rostliny, vlastnosti prostředí (světelná intenzita, teplota, živiny v půdě, příjem organických látek, různé stresové faktory, herbicidy, mechanický odpor prostředí, vlastnosti půdy a aktivita mikroorganismů v rhizosféře). Získané poznatky je možno využít při plánování analýz těchto exsudátů rostlin či při jejich laboratorní přípravě pro experimentální účely.

kořenové exsudáty rostlin, organické kyseliny, aminokyseliny, cukry

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