



A Review on Castor Root Exudates

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Abstract: Castor (*Ricinus communis*) is an important oilseed crop in India's arid and semi-arid regions. Its seeds yield 50% oil, rich in ricinoleic acid (80–85%), used in numerous industrial products. Castor roots play a vital role in plant growth and resilience, particularly under stress conditions like drought, salinity, low temperature, and heavy metal toxicity. Castor root architecture varies between tall and dwarf types and are influenced by seed quality, temperature, and oxygen availability. Root exudates, including sugars, amino acids, proteins, organic acids, lipids, and phenolics, facilitate nutrient uptake, microbial interactions, and stress mitigation. These exudates also contribute to metal detoxification, salt stress, low moisture or fertility levels to survive plants in adverse conditions. Phenolic root exudates offer disease resistance, while lipids and fatty acids aid in signalling for microbial communication. Fertilization and growth regulators influence root architecture and biomass too. Understanding castor root physiology and exudate composition is crucial for improving crop productivity, stress tolerance, and soil microbial ecology under changing environmental conditions.

Keywords: Castor, *Ricinus communis*, root exudates, rhizosphere, oilseeds, heavy metal.

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1. Introduction

Castor (*Ricinus communis*) is a well-known commercial oilseeds crop of arid and semi-arid regions of India. Castor seed oil is a valuable raw material and intermediary for many paints, varnishes, dye, emulsifiers, cosmetics, lubricants, insulators, nylon-11, plasticizers etc. Owing to its wide

industrial applications, castor oil is in high demand globally. India is the leading country in castor production and export. Commercial cultivation of castor has been increased year after year especially in the Indian states of Gujarat, Rajasthan, Telangana, Andhra Pradesh, Tamil Nadu. Castor seeds typically contain about 50% oil, which is rich in a unique fatty acid—ricinoleic acid, comprising 80–85% of the oil content. Additionally, castor cake (deoiled cake or DOC), a by-product of oil extraction, can be used for soil amendment especially in salt affected soil; and to improve the soil organic matter content (Shah *et al.*, 2022). Castor crops also demonstrate remarkable tolerance to harsh conditions such as drought and heavy metal stress (Gersony and Holbrook, 2022). Therefore, understanding the castor root exudates is of considerable interest.

2. Castor Root Characteristics

Castor plants are broadly classified into tall and dwarf types based on their root structure. The tall type of castor plants has a long, well-developed taproot system extended up-to few metre length and sufficient laterals and secondary roots. In contrast, dwarf types display variable root architecture depending on the variety and agronomic practices, often with a less prominent taproot.

In arid regions, root growth in castor often outpaces shoot development, unlike under irrigated conditions (Weiss, 1983). This extensive root system enables efficient moisture uptake during droughts. The root system is closely associated with seed yield, as it enhances nutrient and water absorption, contributing to overall biomass production. Castor roots are influenced by various factors discussed below:

2.1. Seed weight and harvest order

Seed weight and seed coat strength & integrity directly impact germination potential. Seeds with insufficient accumulated reserves, seed coat colour, or weight germinated poorly and malformed embryos were also the cause for poor germination of castor seed (Carvalho *et al.*, 2010). The seed from different order of spikes (primary, secondary, and tertiary) do not show any difference in the germination; however, castor seeds reportedly not losing the germination potential if stored in optimum conditions upto 12

months. However, the germination is affected in stored under moist and damp conditions (Machado *et al.*, 2010). It was also reported that removal of the caruncle had no effect on the germination of castor seed (Severino *et al.*, 2012b).

2.2. Effect of temperature

Low soil temperature slows down the castor seed germination. The suitable temperature for castor seeds to germinate ranges between 25- 31°C, with a minimum of 14°C and a maximum of 36 °C (Moshkin, 1986). The duration between sowing to emergence (germination) varies from 10 days at 19°C and upto 23 days at 10°C (Weiss, 2000). The hard and thick seed coat is perhaps the reason for the slow germination of castor seed. Scarified castor seeds were able to germinate faster than regular seeds under low temperature. Slow germination at lower soil temperature is perhaps related to the fatty acid composition and the metabolic breakdown of the fatty acids after absorption of water. When the castor root system undergoes low soil temperature, many physiological processes also happen in the shoot such as leaf growth, water flow, and carbohydrates relations were negatively correlated even when the canopy is under optimal air temperature. At field conditions, roots are frequently exposed to temperatures out of the optimal range (Poire *et al.*, 2010).

2.3. Oxygen sensitivity

Castor roots are highly sensitive to the soil condition of hypoxia. Flooding for 2–6 hours significantly reduces root conductance and abscisic acid production in roots and also the CO₂ uptake, stomatal conductance, leaf elongation, transpiration. The high requirement in soil aeration is consistent with the high sensitiveness of castor root to hypoxia caused by flooding or soil compaction (Else *et al.*, 2001). Prolonged flooding for 3-4 days can cause permanent damage to castor roots and the chances for crop failure after four days of continuous flooding (Severino *et al.*, 2012).

2.4. Aluminium toxicity

Castor crop is normally grown in a wide variety of soil pH conditions. At lower soil pH due to the presence of high exchangeable aluminium in soil

colloids the castor cultivation is compromised. Aluminium toxicity occurs when the soil pH is lower than 5.5, leading to low levels of exchangeable bases and organic matter. In acidic soil conditions, higher availability of aluminium in the soil solution, negatively impacting castor root growth and functionality could be observed (Severino *et.al.*, 2012).

2.5. Salt tolerance

The tolerance to salinity varies among different castor genotypes (Silva *et al.*, 2008). Castor has good salt tolerance, but “early seedling” is the most sensitive for soil salinity. The salinity threshold for castor seed germination was found to be 7.1 dS m⁻¹ (caused by NaCl) because the germination was reduced to 75% and the seedling survival was less than 70% with a salinity higher than that (Zhou *et al.*, 2010). Reduced and slower germination of castor seed due to salinity is commonly observed (Nobre *et al.*, 2012, Severino *et al.*, 2012b). After germination, the cotyledons of castor were able to accumulate high amounts of Na⁺, therefore the plant can counter the salt stress. Under normal soil conditions, the main role of castor cotyledons is providing resources to support root development. Under salt stress the root/cotyledon ratio decreased from 0.52 to 0.27 due to the reason that cotyledon got more carbon than the root to maintain the development of the unique photosynthetic organ during the early seedling stage. At higher salt levels, chlorophyll synthesis and electron transfer are enhanced to maintain a high photosynthesis rate. Roots also develop an increased level of unsaturated fatty acids to improve cell wall fluidity and to protect cells from salt toxicity; the root also accumulates Na⁺ to maintain a high K⁺/Na⁺ ratio in the cotyledon and preserve metabolic activity (Wang *et al.*, 2019). It is presumed that the presence of differentially expressed genes (DEGs) for differential salt tolerance in wild and cultivated castor plants also several phytohormones and transcription factors are responsible for salt-tolerance. Under salt stress, 2C protein phosphatases (PP2C) homologs are upregulated. Six and four IAA homologs were prominently upregulated in the commercially cultivated and wild castors genotypes, respectively. Moreover, major jasmonate response genes are significantly upregulated under salt stress. Seedlings exposed to NaCl showed lower enrichment of DELLAs, which are growth inhibitors and regulating plant

growth and development through the binding to gibberellins' receptors (Lei *et al.*, 2021).

2.6. Effect of fertilization or manuring

Castor crop is responsive to the fertilizer application. Castor shoot and root dry mass increased due to application of higher doses of compost or FYM and fertilization; also, the shoot/root increased in response to increasing doses of manure (Lima *et al.*, 2009). Increased level of nitrogen application, the shoot/root ratio was not influenced in the normal soil nitrogen availability, but it increased under nitrogen deficiency and reduced under excess nitrogen supply (Lima *et al.*, 2011). The inadequate supply of phosphorus leads to more reduction in shoot growth than in the root growth, which may be due to less biomass allocation to roots in phosphorus deficient conditions (Jeschke *et al.*, 1996). The salinity also affects the root biomass at different proportions depending on the nitrogen availability; however, the influence of salinity on the shoot biomass was independent of nitrogen (Nobre *et al.*, 2012).

2.7. Effect of growth retardants

Soil moisture and salinity redefine the root architecture in castor. The growing part of the castor root cannot regenerate and any damage to this portion of the root has a significant loss in the root system formation (Severino *et al.*, 2012b). The treatment of castor seeds with mepiquat chloride (the plant growth regulator which inhibits gibberellin synthesis) resulted in plants with reduced height and leaf area, but the root growth was not affected (Rigon *et al.*, 2011).

3. Castor root exudates

Chemically root exudates are grouped as low-molecular-weight organic compounds, which are diffuse passively from the root surface and upon which plants has very little or no control at all. The rate of root exudate diffusion is higher in the root tip portion than in the mature root regions. Root exudates, which can account for up to 40% of the carbons ingested during photosynthesis, are discharged into the soil. They also serve as food for microorganisms present in the close vicinity of roots and

hence has capacity to change the chemical and physical characteristics of the soil. Root exudates (e.g. organic acids, sugars, amino acids, etc.) play as signaling molecules, changing the interactions between microorganisms and plants, among microbes-microbes and plants-plants. Nearly seventeen different compounds were identified in the root exudate of *R. communis*, mainly ester (37.8%), alcohol (23.8%), ethers (18.8%), and other amides (13.3%), acid (3.27%), phenol (2.48%), and paraffin (0.57%). The three compounds with the highest content were 1,2-benzenedicarboxylic acid-bis(2-methylpropyl) ester (28.6%), (2S,3S)-(+)-2,3-butanediol (18.6%), and 1-(2-butoxyethoxy) ethanol (9.78%) (Li *et al*, 2024).

3.1. Carbohydrates

The carbohydrates compounds found in root exudates are mostly arabinose, glucose, galactose, fructose, sucrose, pentose, rhamnose, raffinose, ribose, xylose and mannitol. Sugars like glucose dominate root exudates. Glucose, fructose, and sucrose are essential for both the plant and microbes in the rhizosphere as readily available energy sources for soil microbes, which in turn break down organic matter and mineralize nutrients. Also, simple sugars like glucose and sucrose help release nutrients from the soil and make them available to the plant. These sugars can bind with metal ions and organic molecules, facilitating the uptake of nutrients like nitrogen, phosphorus, and potassium. Besides, simple sugars also promote the growth of beneficial soil microorganisms, including those involved in nitrogen fixation and mycorrhizal fungi. These positive and negative interactions are essential for nutrient uptake and stress tolerance. Oligosaccharides like raffinose and stachyose act as signaling molecules for soil microbes, encouraging symbiotic relationships, particularly with nitrogen-fixing bacteria and mycorrhizal fungi. While some oligosaccharides like raffinose also help the plant cope with abiotic stresses such as drought, salinity, and high temperatures by stabilizing proteins and cellular structures. The exudation of oligosaccharides may enhance nutrient cycling in the rhizosphere, leading to improved nutrient uptake by the plant. Polysaccharides like cellulose and pectin help form soil aggregates by binding soil particles together. This improves soil porosity, water retention, and aeration, which are essential for root growth. They also facilitate the movement of nutrients

and water through the soil, making nutrients more accessible to plant roots. Polysaccharides are used by rhizosphere microorganisms as carbon sources.

3.2. Amino Acids

Amino acids (Glutamic acid, Aspartic acid, Glycine, etc.) play a significant role in synthesis and regulation of the activity of the auxin phytohormones (Staswick, 2009), which function in many physiological processes including root development and architecture (Woodward and Bartel, 2005). Soil-borne microbes attract toward amino acids positively than other root exudate chemical components, promoting the richness of the microbial community at the plant root–soil interface. Amino acids are key intermediary in the soil nitrogen cycle and generation of ammonium from amino acids in soil is carried out by extracellular amino acid oxidases (Moe, 2013) Castor plants exude a variety of amino acids, which serve as signalling molecules, nutrient sources, and microbial attractants. The amino acids, especially histidine and cystine, played an important role in chelating metal, improving root uptake and root–to–shoot translocation of metal in the plant (Table 1). The most commonly exuded amino acids in castor include:

Table 1: Concentrations of different amino acids in the castor root exudates

Amino acids	Concentration ($\mu\text{mol/g}$ dry plant) at 40 days growth	Role of castor root exudates in plants
Glycine	0.089	Involved in stress responses and metal detoxification
Alanine	0.226	Plays a role in energy metabolism during oxygen-limited conditions
Cystine	0.211	Important in sulfur metabolism and defense responses
Methionine	0.063	Important in sulfur metabolism and defense responses
Tyrosine	0.014	Tyrosine is also a precursor for tocopherols, plastoquinone, and ubiquinone, essential compounds for plant survival.
Lysine	0.050	Building block for proteins and a precursor for glutamate, a signaling amino acid involved in plant growth and stress responses
Histidine	0.274	Involved in metal chelation and detoxification of heavy metals like zinc and copper

3.3. Proteins in Root Exudates

Enzymatic and non-enzymatic proteins that play a role in soil nutrient cycling and plant defense for castor (Table 3). The exudates of castor have

a variety of proteases, including cysteine proteases. These proteases play a role in nutrient acquisition, defense against stressors, and interactions with the rhizosphere microbiome.

Table 2: Enzymatic and non-enzymatic proteins found in the castor root exudates

Enzymatic and non-enzymatic proteins	Role in castor plants
Proteases	Break down organic nitrogen compounds into simpler amino acids for plant uptake.
Peroxidases & Chitinases	Play a role in pathogen defense by degrading fungal cell walls.
Phytochelatin & Metallothioneins	Involved in detoxifying heavy metals in contaminated soils
Lectins	Help in microbial recognition and symbiotic interactions
Expansins	Assist in cell wall modifications, influencing root elongation and exudation patterns

There is an increase in total protein content in the root exudates of castor roots exposed to elevated levels of heavy metal nickel. These were due to the inducement of some protein (cysteine) under Ni stress involved in metallothionein (metal ion homeostasis). However, decrease in protein content (33.79%) in castor leaves due to Ni toxicity (150 mg/ kg soil) compared to control after 60 days of sowing which was attributed to the low level of protein synthesis and protein degradation (Baudh *et al.*, 2015). Additionally, under cadmium exposure to castor roots, castor leaves had decreased protein content by half when compared to the control. In another study, the protein content decreased by 80% due to increasing concentration of lead toxicity at a concentration of 200 and 400 μ M Pb.

3.4. Phenolic Compounds

Castor crop is affected by several biotic and abiotic stresses. The wilt disease is caused by a soil borne pathogen *Fusarium oxysporum* f. sp. *Ricini*, is a major disease of castor. Under this disease. The castor roots may be infected through the root tips, wounds in the roots, or at the formation point of lateral roots. A key plant defense mechanism against such infections is the activation of the phenylpropanoid pathway. Phenylpropanoid metabolism triggers a cascade of biochemical reactions to produce important phenolic

compounds involved in defense responses of a host plant. Higher phenolic acids such as caffeic and ferulic acid have been observed in wilt resistant castor genotypes, proving the establishing plants naturally resistant to pathogens may have inherently higher phenolic contents. Lignin precursors (phenolic acids) may exert a toxic effect on pathogens or, by binding to fungal cell walls, make them more rigid and impermeable, thus hindering further growth or uptake of water and nutrients. Wound-induced chlorogenic acid, ferulate alkyl esters and cell wall-bound phenolic esters may act directly as defense compounds or may serve as precursors for the synthesis of lignin, suberin and other wound-induced polyphenolic barriers. Salicylic acid, found in infected resistant genotypes, may also contribute to systemic acquired resistance.

3.5. Lipids and fatty acids

Lipids play diverse roles in regulating plasma membrane processes and mediating cellular signaling. Plasma membrane lipids are crucial for the plant's interaction with the surrounding microbiome, influencing various symbiotic relationships. Lipids affect the entire microbial colonization process, thereby shaping the rhizosphere microbiome. As chemical signals, lipids facilitate interactions between plant roots and microbes (both beneficial and pathogenic), and among microbes themselves. These interactions modulate plant defense responses upon contact or recognition. The primary lipid classes in the plasma membrane include glycerophospholipids (GP), glycerolipids (GL), sphingolipids (SP), and sterol lipids (ST). These lipids participate in essential regulatory processes, including cell signaling and intracellular transport.

3.6. Organic acids

The exudation of organic acids such as citric acid, malic acid, oxalic acid, and tartaric acid plays a vital role in metal storage, tolerance, and detoxification. To counteract metal toxicity in the soil, castor plant roots secrete low-molecular-weight organic acids. These compounds form stable metal-ligand complexes, reducing metal bioavailability and mobility, thus preventing metal uptake or minimizing accumulation in sensitive root tissues. Organic acids can also chelate metal ions that enter the cytosol,

converting them into non-toxic or less toxic forms. Castor plants produce various ligands capable of chelating toxic metals such as Cd, Cu, Ni, and Zn. Citric, malic, and tartaric acids are particularly effective at binding these metals, enhancing plant tolerance in contaminated soils. Citric acid, in particular, exhibits high affinity for Fe, Cd, Cu, and Ni.

The acidification of the rhizosphere via organic acids can increase the bioavailability of certain nutrients and metal ions. Organic acids in root exudates act as chelating agents, and citric acid has been found to enhance the storage of Fe and Al in tissues near the vascular bundles of rhizomes. Additionally, both EDTA and citric acid significantly increased the accumulation of Mn, Zn, Cu, Pb, and Cd (Huang *et al.*, 2016). Concentrations of succinic, tartaric, and malic acids were found to increase gradually with higher Cu levels in the solution (Table 4).

Table 3: Concentrations of different low molecular weight organic acids in the castor root exudates

<i>Low molecular weight organic acids</i>	<i>Concentration ($\mu\text{mol/g dry plant}$) at 40 days growth</i>
Oxalic	3.20
Succinic	0.66
Tartaric	16.44
Citric	10.04
Malic	31.94

4. Factors affecting the release of root exudates in the rhizosphere of castor

Root exudation is a dynamic process influenced by various biotic and abiotic factors. The quantity and composition of exudates released by castor roots depend on environmental conditions, plant physiological status, soil properties, and microbial interactions. Understanding these factors is crucial for optimizing plant growth, improving soil fertility, and enhancing beneficial microbial activity in the rhizosphere.

4.1. Effect of drought on castor root exudates

Moisture availability and salinity are other environmental factors influencing castor germination. No castor seed was able to germinate

in a soil with moisture equivalent to 22% of the field capacity, but the germination was around 40% with 29% of soil moisture (Severino *et al.*, 2012b). As the severity of the drought increases, the total volume of root exudates is likely to decline while the allocation of the ratio of carbon to root exudates rises (Preece and Penuelas, 2016). Drought increased the amount of carbon allocated to soil organic carbon and root sucrose. The rate of soil respiration was greater in soil that had more root exudates from plants that had experienced drought compared to soil that had exudates from drought-unaaffected plants supports this theory (De Vries *et al.*, 2018).

4.2. Effect on soil pH on castor root exudates

Root exudates reduced pH by 0.2–0.5 units in the rhizosphere compared to the bulk soil. The pH of root exudate solution was strictly dependent on the type and quantity of low molecular weight organic acids secreted by the root of castor (Huang *et al.*, 2016). There were significant negative linear correlations between the pH of the root exudate and the concentrations of succinic ($R = -0.96$), tartaric ($R = -0.98$), and citric ($R = -0.90$). Although the pH of the root exudate and the concentration of oxalic presented positive linear correlation ($R = 0.86$).

5. Conclusion

Root exudates of *Ricinus communis* (castor) play a significant role in plant growth, its adaptation in adverse soil and environmental conditions. These exudates comprise a variety of compounds, including organic acids, amino acids, phenols, and other secondary metabolites, which are released into the rhizosphere through the roots they interact with soil particles; also attract microbial flora and nurture a rich biodiversity in the castor rhizosphere. Castor can tolerate heavy metals due to its specific root exudates. The composition of root exudates changes in response to heavy metal stress, in a dynamic mechanism. The root exudates of castor are multifaceted, influencing nutrient uptake, plant stress responses, and interactions with neighbouring plant species, thereby playing a crucial role in its ecological adaptability.

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