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STIMULATION OF SEABUCKTHORN (*Elaeagnus rhamnoides*) MICROBIAL SYMBIOSES

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Abstract

This paper reviews the present knowledge regarding the stimulation of the microbial symbioses of the sea buckthorn (Elaeagnus rhamnoides syn. Hippophae rhamnoides). Sea buckthorn is an actinorhizal plant, developing nitrogen-fixing symbioses with the actinobacteria from the Frankia genus. At the same time, sea buckthorn roots can form endomycorrhizal symbioses with various arbuscular mycorrhizal (AM) fungi. AM symbiosis increases nutrient uptake and nutrient use efficiency, especially on phosphorus and micro-elements. Due to these microbial symbioses, sea buckthorn is an efficient colonizer of marginal lands and a suitable crop for low-inputs organic/ecological farming. Helper bacterial strains were demonstrated to promote microbial symbiosis between Frankia actinobacteria or AM fungi with roots of other host plants. Only scarce and indirect information suggests the involvement of gram-positive, endospore-forming bacteria as a helper of microbial symbiosis for sea buckthorn. Also, there is no information regarding the role of rhizosphere signals in promoting the sea buckthorn microbial symbioses. The finding of this paper highlights the need for future works focused on the stimulation of sea buckthorn symbioses.

Key words*: sea buckthorn symbioses, Frankia actinobacteria, arbuscular mycorrhizal fungi, bacterial helper, rhizosphere signals.*

INTRODUCTION

Sea buckthorn, *Elaeagnus* (synonym *Hippophae*) *rhamnoides* (L.) A. Nelson cultivation is continuously expanding due to its high economic value and significant ecological benefits (Ciesarová et al., 2020). *E. rhamnoides* is a deciduous, thorny shrub native to different regions of Europe and Asia, with high resistance to cold and drought.

Eight subspecies of *E. rhamnoides* were described: *E. (H.) rhamnoides* spp. *fluviatilis* Soest, from Alpes, radiating also in Apennines and Pyrenees; *E. (H.) rhamnoides* spp. *rhamnoides*, from northwestern Europe; *E. (H.) rhamnoides* ssp. *carpatica* Roussi, Carpathian mountains, low Danube basin, northwestern shore of the Black sea; *E. (H.) rhamnoides* ssp. *caucasica* Rousi, between Black and Caspian sea; *E. (H.) rhamnoides* spp. *mongolica* Rousi, from the Altai Mountains, Lake Baikal basin, and Outer Mongolia; *E. (H.) rhamnoides* spp. *sinensis* Rousi, from western China and Inner Mongolia; *E. (H.) rhamnoides* spp. *turkestana*, from the northern part of Himalaya; *E. (H.) rhamnoides* spp. *yunnanensis*, from western China, Yunnan, western Sichuan (Swenson & Bartish, 2002).

In its wild state, the sea buckthorn has been recognized for millennia as a plant with health benefits in different parts of the world - in Europe, by the ancient Greeks, and in Asia, in early Chinese Pharmacopeia and ayurvedic medicine (Suryakumar & Gupta, 2011; Wani et al., 2016).

In the last decades, sea buckthorn started to be domesticated (Li & Schroeder, 1996). Various chemometric and molecular genetic techniques were developed to characterize the affiliation of different domesticated cultivars to different subspecies: *E. rhamnoides* subsp. *carpatica*, from Romania (Buzoianu & Socaciu, 2014); *E. rhamnoides* ssp. *sinensis*, *E. rhamnoides* ssp. *yunnanensis*, *E. rhamnoides* ssp. *turkestana* and *E. rhamnoides* ssp. *mongolica*, from China genetic pool (Liu et al., 2018), *E. rhamnoides* ssp. *mongolica* from Russia, China, and Mongolia (Ruan et al., 2004), *E. rhamnoides* ssp. *fluviatilis* from Latvia (Lacis & Kota-Dombrovska, 2014).

The economic and ecological benefits of sea buckthorn are directly related to its ability to form microbial symbioses, with nitrogen-fixing actinobacteria and with arbuscular mycorrhizal (AM) fungi. This paper aims to review the present knowledge related to the stimulation of the sea buckthorn symbioses and the importance of such technological intervention to enhance further the economic value and the ecological benefits of sea buckthorn cultivation.

Our goal is to highlight the existing gap in knowledge. The perspectives of the better exploitation of sea buckthorn symbioses by their stimulation through technological intervention are also considered and discussed.

BENEFITS OF SEA BUCKTHORN CULTIVATION

The high economic value of the sea buckthorn is determined by the beneficial effects on human health of the active ingredients from its fruits and leaves (Gatlan & Gutt, 2021).

Fruits are used to produce a nutritious, healthy beverage and seed oil (Beveridge et al., 1999). The pulp remaining from the mechanical extraction of juice and oil is further used for the production of food additives (X. Guo et al., 2019) and tocopherols (Kitrytė et al., 2017).

The healthy beverage produced by mechanical squeezing of the berry pulp retains most of the hydrophilic antioxidants (i.e., hydrophilic polyphenols/flavonoids and vitamin C/ascorbic acid) and the lipophilic bioactive ingredients, i.e., carotenoids, tocopherols, flavanols, and (mono)unsaturated fatty acids, including ω-7 palmitoleic acid (Bal et al., 2011; Ciesarová et al., 2020).

Due to this unique combination of active ingredients, sea buckthorn healthy beverage is highly efficient as a dietary supplement in various health conditions (Ursache et al., 2017). Sea buckthorn is efficient against metabolic disorders and associated cardiovascular diseases (Olas, 2016). Sea buckthorn has demonstrated antiproliferative effects on human liver and colon cancer cell lines (Grey et al., 2010) and on prostate, breast, and gastric adenocarcinoma (Boivin et al., 2007).

The antioxidant effect of sea buckthorn juice is involved in the prevention of both cancer and cardiovascular diseases (Olas & Skalski, 2022; Olas et al., 2018). Scavenging of the reactive oxygen species (ROS) and the resulting modulation effect on ROS level are also related to the immunomodulatory and anti-inflammatory effects (Ren et al., 2020).

E. rhamnoides is one of the few natural sources of the rare palmitoleic acid (16:1 n-7), a monounsaturated fatty acid (MUFA) with high physiological significance (Dąbrowski et al., 2022). Palmitoleic acid prevents and reverses the metabolic syndrome by increasing insulin sensitivity (Hu et al., 2019), mainly due to its lipokinine function, i.e., an endo-signal of adipose tissue (Frigolet & Gutiérrez-Aguilar, 2017). The carotenoids from sea buckthorn healthy beverage synergize the palmitoleic acid reversing effect on metabolic syndrome (Marcelino et al., 2020; Matsumoto et al., 2021). Carotenoids level is very high in sea buckthorn beverages, their specific color being related to this high carotenoids content (Pop et al., 2015).

The hydrophilic antioxidants from the sea buckthorn healthy beverage, ascorbic acid, and polyphenols also target metabolic syndrome and type II diabetes (Liu et al., 2019; Zheng et al., 2020). The flavonoids existing in the healthy beverages that are obtained from *E. rhamnoides* berry, ursolic acids (Grey et al., 2010), flavonoid aglycones, including quercetin, isorhamnetin, and kaempferol (Guo et al., 2017) and flavonol glycosides (Enkhtaivan et al., 2017), were proven to have pro-apoptotic and antiproliferative activity of the sea buckthorn extracts.

The oil obtained from sea buckthorn seeds is emollient and it is used in various cosmetic products (Beveridge et al., 1999). The dried sea buckthorn pomace has a high nutritional value due to its high content in lipids with essential fatty acids, proteins with high content of essential amino acids, and prebiotic fibers (Nour et al., 2021).

The leaves of sea buckthorn are used for the production of tea (Ma et al., 2019), and various types of extracts are used for cosmetic and dietary supplements (Asofiei et al., 2019; Criste et al., 2020).

The health effects of sea buckthorn are enhanced by organic farming. Organic farming has been proved to increase the polyphenols and flavonoids content on sea buckthorn leaves (Heinäaho et al., 2006) and fruits (Heinaaho et al., 2009). Sea buckthorn is an appropriate plant to be cultivated in organic farming because of its microbial symbioses with nitrogen-fixing actinobacteria and mycorrhizal (AM) fungi (Li et al., 1996; Tian et al., 2002). These symbioses significantly support fertilization and plant protection organic management.

The ecological benefits of sea buckthorn crops are water conservation and soil formation (La, 2020), marginal land colonization and reclamation of the degraded land (Enescu, 2014), and soil decontamination by immobilization of potentially toxic elements (Nowakowska et al., 2017). The ecological benefits of the sea buckthorn cultivation are also significantly promoted by its symbioses with nitrogen-fixing actinobacteria and AM fungi (Constandache et al., 2016; Zhao et al., 2013).

BENEFITS OF SEA BUCKTHORN SYMBIOSES

The symbioses between sea buckthorn and actinobacteria from *Frankia* genera generated nitrogen-fixing nodules. The difference between actinorhizal nodules and legume nodules is in hosting bacterial symbiont. In legume nodules, rhizobia differentiate in organelle-like structures, called symbiosomes, and in actinorhizal nodules, the bacteria remain not-differentiated (Holmer et al., 2017). The actinorhizal nodules are nitrogen-fixing nodules, the bacteria fixing atmospheric oxygen based on the carbohydrates supplied by the sea buckthorn (Nguyen & Pawlowski, 2017).

The sea buckthorn roots form endomycorrhizal symbioses with various arbuscular mycorrhizal (AM) fungi. AM fungi are essential for the mobilization of soil phosphorus and phosphorus acquisition by the plant (Smith et al., 2011). Besides the phosphorus, AM fungi also increase the bioavailability and uptake by the plant root of the microelements (Willis et al., 2013).

The benefits of the microbial symbioses are not related only to improved nutrient acquisition (Figure 1). Due to extended microbial symbioses, sea buckthorn is an excellent colonizer of marginal and/or degraded lands (Enescu, 2014). Both actinorhizal and AM symbioses immobilize potentially toxic elements (e.g., Cu ions), by different mechanisms - by detoxifycation by metallophore in the case of *Frankia* (Mohr et al., 2021) and by immobilization in the fungal mycelium by AM fungi (Cabral et al., 2015).

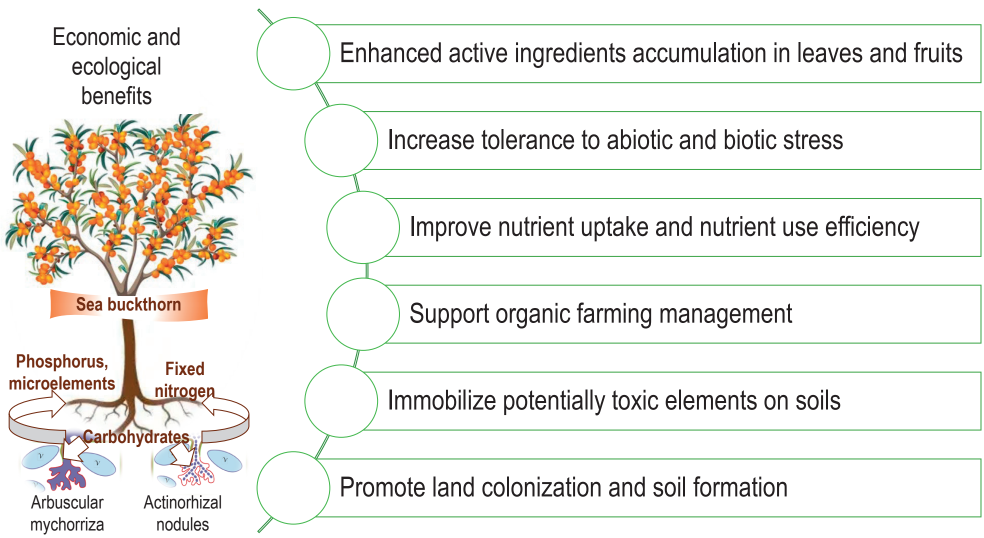

Figure 1. Illustration of the benefits of the microbial symbioses for the sea buckthorn

The benefits of microbial symbiosis for sea buckthorn are not limited to the support for the colonization of marginal and poor lands. The nitrogen fixation and improved phosphorus and microelement nutrition support organic farming management (Kalia et al., 2011). The AM symbiosis determines and improves nutrient uptake and nutrient use efficiency, leading to higher mineral content in sea buckthorn leaves (Jaroszewska et al., 2016). The actinorhizal symbiosis increase plant tolerance to abiotic stress (Diagne et al., 2013). Symbiosis with AM fungi also determines an increased tolerance to abiotic stress (Begum et al., 2019).
Several of the effects of microbial symbiosis on sea buckthorn performances are presented in Table 1. Actinorhizal and mycorrhizae symbioses enhance sea buckthorn performance, both in terms of economic added value and ecological services.

Table 1. Effects of the microbial symbioses on sea buckthorn performances

Symbiosis	Effect	Reference
Actinorhizal symbiosis	Ability to grow in soil with low available nitrogen	(Li et al., 2014)
Actinorhizal symbiosis	Detoxification of the potentially toxic element ions – e.g., Cu^{2+}	(Mohr et al., 2021)
Actinorhizal symbiosis	Enhancement of the content of the active ingredient	(Kanayama et al., 2008)
Mycorrhizae symbiosis	Enhanced growth in marginal land	(Zhang et al., 2020)
Mycorrhizae symbiosis	Increased level of mineral and bioactive ingredients in sea buckthorn leaves	(Jaroszewska & Biel, 2017; Jaroszewska et al., 2016)
Mycorrhizae symbiosis	Increased level of mineral and bioactive ingredients in sea buckthorn fruits	(Jaroszewska et al., 2018)

The microbial agents that form symbioses with the sea buckthorn have the characteristics of the microbial plant biostimulants. By definition, plant biostimulants enhance/benefit nutrient uptake, increase tolerance to abiotic stress and improve crop quality (du Jardin, 2015). AM fungi were included for almost a decade in the category of microbial plant biostimulant (Rouphael et al., 2015). Symbiotic nitrogen-fixing bacteria from *Frankia* genera were not yet considered plant biostimulants. However, the rhizobia that produce nitrogen-fixing nodules in legumes are already included in this category of microbial plant biostimulants (Hendriksen, 2022). These microbial plant biostimulants need better exploitation in the sea buckhorn farming system, especially in the organic farming system.

TECHNOLOGICAL INTERVENTION FOR STIMULATION OF SEA BUCKTHORN SYMBIOSES

Despite the importance of microbial symbioses for sea buckthorn cultivation, the technological interventions intended to stimulate/amplify the formation and development of such symbioses are insufficiently studied.
The microorganism from sea buckthorn symbioses interact in a synergic manner (Zhou et al., 2017), and dual inoculation stimulates plant growth and development and nitrogen fixation (Tian et al., 2002).
Actinobacteria from *Frankia* genera and AM fungi use common rhizosphere exo-signals to detect their host - e.g., flavonoids (Abdel-Lateif et al., 2012). The exchange of exo-signals between microbial symbionts and their host is promoted by the humic and fulvic acids (Capstaff et al., 2020; Gryndler et al., 2005).
Several rhizobacteria enhance the formation of symbiosis - helper bacteria for mycorrhizae and nitrogen-fixing bacteria (Frey-Klett et al., 2007; Ghodhbane-Gtari et al., 2021; Teng et al., 2015). These stimulation means could be included in technological interventions intended to enhance the formation of microbial symbioses (Table 2).

Table 2. Technological interventions that enhance microbial symbioses

Technological intervention	Target	Reference
Application of flavonoids to rhizosphere	Amplification of communication between microbial symbionts and their hosts	(Sugiyama, 2021)
Application of humic acid to the soil	To facilitate the exchange of exo-signals between microbial symbionts and their hosts	(Capstaff et al., 2020; Gryndler et al., 2005)
Application of polyamine rich material to the soil	Improvement of host reaction to symbiotic agents	(Atici et al., 2005; Cheng et al., 2012)
Inoculation with helper bacteria AM fungi	Support communication and interaction between hosts and AM fungi	(Frey-Klett et al., 2007)
Inoculation with helper bacteria for Frankia	Enhance tolerance to abiotic stress of the symbioses partners	(Ghodhbane-Gtari et al., 2021)

These stimulation means could be considered as a second plant biostimulant, intended to synergize the microbial sea buckthorn biostimulants - *Frankia* nitrogen-fixing bacteria and AM fungi. These could lead to the development of next-generation plant biostimulants with synergistic biostimulatory action (Rouphael & Colla, 2018). Figure 2 illustrates the concept of such synergist of microbial sea buckthorn plant biostimulant, leading to enhanced economic and ecological benefits from sea buckthorn cultivation.

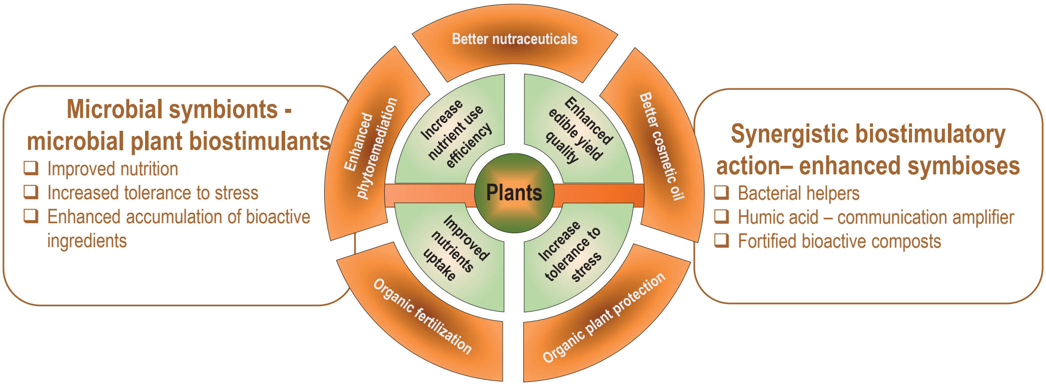

Figure 2. Illustration of the enhancers of the sea buckthorn symbiosis as next-generation plant biostimulants, with synergistic biostimulatory action

One integrated technological intervention is the application of bioactive composts fortified with AM fungi/*Frankia* bacteria helper. Bioactive composts include a large quantity of humic acids (Guo et al., 2019). Humic acid support communications between microbial symbiont and host plant roots (Shah et al., 2018).

The by-products from sea buckthorn berries harvesting, branches and leaves, are a good substrate for bioactive and biofortified compost production. The high flavonoid content of branches and leaves could further support the formation of sea buckthorn symbioses (Yang et al., 2009). Utilization of the by-products from sea buckthorn berries harvesting to produce a complex sea buckthorn biostimulant is an example of the circular bioeconomy, with direct economic benefits and ecological service (Xu & Geelen, 2018).

CONCLUSIONS

Sea buckthorn forms actinorhizal nitrogen-fixing symbioses with bacteria from *Frankia* genera and multifunctional symbioses with AM fungi. The sea buckthorn symbiotic microbes fulfill the characteristics of microbial plant biostimulants.

The stimulation means of sea buckthorn microbial symbionts represent next-generation plant biostimulants with synergistic biostimulatory action.

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