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REVIEW

Seaweed extracts' multifactorial action: influence on physiological and biochemical status of Solanaceae plants

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Abstract

Seaweeds are one of the important marine bioresources which are nowadays termed as eco-friendly stimulators of crop growth, stress tolerance, and yielding. In this review, we give an update of the current state of our understanding of the seaweed extracts (SWE) effects on the physiological alterations they induce in Solanaceae vegetables. SWE may provide a powerful and environmentally friendly approach to nutrient management. A pool of common bioactive molecules of SWE provides enhancement of the antioxidant machinery of treated plants providing balanced development, earlier flowering, and enhanced fruiting. The basic mechanisms of SWE action seem to be unspecific for tomato, pepper, and eggplant. They include accelerating growth, nutrient uptake, and photosynthesis performance, which can induce plant tolerance to adverse environmental conditions, improve flowering, fruit setting, and yield, and enhance nutritional quality of the crops. The mechanism of SWE action is complex because of multielement composition and cross-action between constituents.

Keywords

algae biostimulants; tomato; eggplant; pepper

Introduction

Solanaceous crops have been subjected to intensive human selection, allowing their use as models to study the interface between plants and agricultural techniques. Tomato (*Lycopersicon esculentum* Mill.), pepper (*Capsicum annuum* L.), and eggplant (*Solanum melongena* L.) are one of the most important vegetable crops around the world in terms of human consumption and other industrial values. Tomato is rich in phenolic compounds, phytoalexins, protease inhibitors, glycoalkaloids, and carotenoids, but especially in lycopene and ß-carotene, vitamins C, E, and A [1]. The main polyphenols found in eggplant are phenolic acids (chlorogenic, caffeic, and *p*-coumaric acid), and it is also rich in anthocyanins like nasunin and delphinidin conjugates [2]. Pepper fruits contain vitamins, mainly A and C, flavones (luteolin), flavonols (myricetin, quercetin), and capsaicinoids [2]. Tomato has been widely used also as a model fruit-bearing crop. Knowledge obtained from the studies conducted on tomato can be easily applied to pepper, eggplant, and other Solanaceae vegetables [3]. Tomato, pepper, and eggplant are native to subtropical climate zone, but the cultivation takes place also in temperate regions, in field and under covers to support fruits for all-year-round fresh market and processing. All mentioned vegetables are fast growing and high yielding, consequently they have high demands regarding microclimatic and soil conditions, including balanced fertilization [4]. Because of their considerable economic importance as food, these species have been bred to improve productivity, fruit quality, and tolerance to biotic and abiotic stresses. The correct balance between the root system, assimilation surface, and the number of generative organs in these crops is a necessary requirement of high yield potential. This is the reason of labour-consuming growing practices enhancing proper vegetative–generative parts balance, flowering and fruit setting, for example grafting, pruning, flower hormonization, etc. [5,6]. Application of proecological technologies for Solanaceae fruit crops is highly recommended in modern horticulture. Biostimulants, especially seaweed extracts, are one of the most suitable approach in this matter.

Biostimulants are defined as organic materials and/or microorganisms that are applied to the plant to enhance nutrient uptake, stimulate growth, and enhance stress tolerance or crop quality [7]. Among biostimulants, the main categories being intensively investigated and described in comprehensive reviews are fungi and their derivatives [8,9], rhizobacteria [10], seaweed extracts [11], silicon [12], chitosan [13], humic and fulvic acids [14], and the phosphite [15]. Seaweed extracts have complex chemical composition including polysaccharide, fatty acids, vitamins, phytohormones, and mineral nutrients [16]. Additionally, seaweed extracts (SWE) constituents show synergistic/antagonistic activity, so the effects of their application are difficult to predict, especially in crops cultivated under dynamic environmental conditions [16].

Finally, we attempted to assess response of Solanaceae family vegetables, grown for edible berries, to biostimulant action on overall plant status as well as fruit yield and quality. We gave special attention to the use of various SWE in tomato, pepper, and eggplant production, the crop response, and the possible modes of action.

Seaweeds extracts as biostimulants

The term "seaweeds" is referred to macroalgae, comprising nearly 10,000 species native to inshore marine ecosystems. Some of them have been used as animal and human food and also as manure since prehistoric times [17]. Brown seaweeds, *Alaria esculenta*, *Ascophyllum nodosum*, *Durvillea potatorum*, *Ecklonia maxima*, *Ectocarpus siliculosus*, *Fucus serratus*, *F. spiralis*, *F. vesiculosus*, *Macrocystis pyrifera*, have been reported to possess plant-growth promoting activity and thus their extracts have been most frequently applied in modern horticulture [16,18]. SWE can induce plant tolerance to adverse environmental conditions, accelerate growth, improve flowering, fruit setting and yield, and enhance nutritional quality of crops [16,18]. Increased interest in SWE application results from their proecological character. SWE mechanism of action on plants is intricate and still not clear because of the complex composition and cross-action between constituents. Polysaccharides, i.a., alginates, fucoidans, laminarans, lichenan-like glucans and fucose containing glucans, comprise up to 30–40% of SWE dry weight. Their physiological action is multidirectional; for example alginates promote plant growth, while laminarins are elicitors of plant defense responses to stress [19,20]. Alginic acids showed soil-conditioning properties through chelating of metal ions and improving their availability for plants [21]. The physiological effect of SWE is elicited by growth promoting compounds of SWE: auxins, cytokinins, gibberellins, abscisic acid, ethylene, brassinosteroids, jasmonates, salicylic acid, and strigolactones [22,23]. SWE contain osmolytes, like mannitol or betaine, and their analogues. Glycine betaine, γ-aminobutyric acid betaine, δ-aminovaleric acid betaine, and laminine were reported in *A. nodosum* extracts. As osmoprotectants, they accelerate stress tolerance of plants [24,25]. Brown seaweeds extracts are rich in total phenolics. Phenolic compounds possess high antioxidant activity, and they can also chelate metal ions [26,27]. SWE contain elements (N, P, K, Ca, Fe, Mg, Zn, Na, S) which directly improve the nutritional status of plants [28].

SWE can be applied directly to the soil, mixed with irrigation water and applied as drip irrigation, but the most common way of application is foliar spraying. Plants in a stage of vegetative development and just prior to flowering are the most relevant for SWE application in order to stimulate fruit setting and maturation. SWE enhance certain growth parameters during early stages of plant development and ensure proper translocation of assimilates during the generative stage [29]. Morning hours, when the leaf stomata are open, are most suitable for effective foliar application of SWE [17].

Effect of SWE on tomato, eggplant, and pepper growth, nutritional status, photosynthesis, and stress tolerance

The protective effects of SWE against environmental stresses concerning adverse abiotic conditions (drought, salinization, chilling or hot stress, deficiency of macro- and microelements), unfavorable weather conditions, biotic factors action are referred [17]. Soil applied SWE are a direct source of nutrients; they also increase efficient nutrient uptake by the root system and improve soil properties, stimulating root system growth and its functional properties (Fig. 1). Biostimulated eggplant roots could effectively penetrate deeper soil horizons and were able to absorb more nutrients even from distant places and deeper soil levels. *Ecklonia maxima* stimulated the growth of in vitro-cultured tomato roots [30]. Crouch and van Staden [31] determined that *E. maxima* extract improved root development in tomato, increased both the root:shoot ratio and accumulation of plant biomass. The authors suggested stimulation of root growth through endogenous auxins and related compounds of SWE. Kumari et al. [32] reported an increase in root length, shoot length, and fresh weight in tomato treated with *Sargassum johnstonii* extracts. Zodape at al. [33] received similar results also as an effect of *S. johnstonii* application, and Stępowska [34] by *Ascopyllum nodosum* application. A larger root system was more effective in water and nutrient utilization leading to enhanced root and shoot growth and improved plant physiological status [29,31–33,35]. The references regarding positive effects of SWE are not always unambiguous. For example, an experiment performed by Koyama et al. [36] showed that *A. nodosum* extract increased the tomato yield without altering the characteristics of fruits and vegetative growth, while tomato plants treated with SWE showed more numerous and bigger cells of vascular bundles, with thicker and stronger lignified xylem and phloem secondary walls than untreated control plants. It could have contributed to more efficient transport of water with mineral substances in the tomato plant and increased the fruit weight [37]. Similar observations were reported for bell pepper [38]. Hernández-Herrera et al. [39] stated that root growth-promoting activity of polysaccharide-enriched SWE resulted from the signaling role of oligosaccharides. These compounds were found to induce changes in endogenous phytohormone metabolism of tomato plants by selective regulation of phytohormone metabolic genes. SWE enhanced also eggplant growth parameters, i.e., plant height and leaf area, as well as N, P, K, crude protein, carbohydrates, and chlorophyll in leaves as a result of the presence of elements, growth regulators, amino acids, and vitamins that could control cell division, maintain photosynthetic rates, improve plant resistance, and delay plant senescence [40]. The increase in chlorophyll content was a result of reduction in chlorophyll degradation caused by betaines provided by SWE [40]. Dobromilska and Gubarewicz [41] determined similar reaction of cherry tomato to SWE treatments. Sprayed plants had greater transpiration and assimilation intensity, chlorophyll, carotenoids, as well as N, P, K, Ca, Zn, Fe, and nitrate contents in leaves. Carrasco-Gil et al. [42] investigated the effect of SWE on tomato plants with

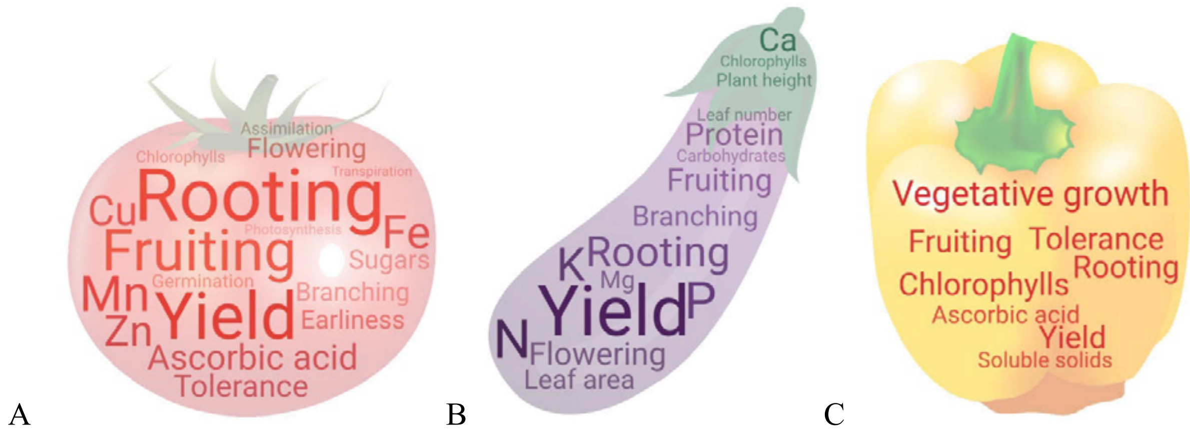

Fig. 1 Tag clouds including the parameters increased by SWE application in tomato (**A**), eggplant (**B**), and pepper (**C**). Sources provided in "References".

nutrient imbalances. Mn, Zn, and Cu concentrations in roots and shoots were significantly increased with *A. nodosum* extract application. The contribution of mentioned elements to the nutrient solution from all SWE products was 7–17%. These values do not justify the variation observed in the mineral concentration in the plant. Stępowska [34] showed the increased weight of pepper leaves and shoots, main stem diameter, leaf area, and chlorophyll content in leaves as effect of SWE treatment. Manna et al. [43] linked the increased growth of pepper to the presence of cytokinin and auxin precursors in *A. nodosum* extract, which increase the cell division as well as optimal partitioning and utilization of metabolics.

SWE have been reported to increase abiotic stress tolerance of many crops. In tomato, three commercial products based on *A. nodosum* extracts had a differentiated role in drought protection through changes of chlorophyll and osmolyte levels, MDA production, dehydrin isoform pattern, and dehydrin gene expression [44]. The application of commercial SWE on Fe-deficient tomato plants activated the antioxidant system increasing SOD and CAT activity [42]. SWE mitigated salt stress in pepper plants through increase of proline, SOD, POD, and CAT activities [45]. The observed biological effects result from the action of both small organic molecules and from polymers contained in the SWE products which can regulate gene action to provide systemic resistance systems in plants.

Effect on plant defense system against biotic factors

Several reports have shown that SWE induce protection against fungal, bacterial, and viral pathogens in plants. Defense response occurs after perception of signal molecules, called elicitors, derived from pathogens or from the host plant [35]. SWE polysaccharides can act as elicitors of plant defense responses and enhance resistance against pathogens. Early study of Featonby-Smith and van Staden [46] showed that SWE reduced root damage from nematode *Meloidogyne incognita* predation in tomatoes whether applied to the foliage or as a soil drench. SWE did not reduce the abundance of nematodes in the soil but lowered their number inside the roots. According to Radwan et al. [47], SWE in the soil reduced the number of galls and juveniles of *M. incognita* and decreased the infestation of tomato plants by root-knot nematodes. Application of *Spatoglossum variabile*, *Melanothamnus afaqhusainii*, and *Halimeda tuna* extracts can suppress rotting fungi *Rhizoctonia solani* and *Fusarium solani* on tomato roots as well as nematode's galls on roots and nematode's penetration in roots [48]. SWE of different brown algae species reduced necrotic lesions induced by *A. solani*. *Ulva lactuca* extracts induced the expression of systemic wound response genes. *Caulerpa sertularioides*, *Padina gymnospora*, and *Sargassum liebmannii* extracts were involved in the other, unidentified mechanisms [35]. *Ascophyllum nodosum* enhanced foliar resistance to *Phytophthora capsici* in pepper [49]. SWE, applied as a soil drench to pepper plants, reduced *Verticillium* wilt of pepper through improving plant fitness and increasing resistance to pathogens [50]. *Spatoglossum variabile*, *Stokeyia indica*, and *Melanothamnus afaqhusainii* extracts showed significant suppressive effect on root rotting fungi *Fusarium solani* and root knot nematode *Meloidogyne incognita* in eggplant [51]. Due to their effects as plant protectants, algal extracts represent an alternative tool for disease and pest control in Solanaceae crops.

Effect on flowering biology, yield potential, and fruit quality

Flowering intensity as well as pollination effectiveness are directly correlated with tomato, pepper, and eggplant yield. The early flowering and fruiting in the treated plants might be due to the fact that such plants were able to build suitable carbohydrate reserves early. Fruit set acts as a strong sink for metabolites with the earlier fruits taking the bulk of the energy. Commonly, abundant fruit set results in the decrease of fruit size [52]. This phenomenon is technically controlled by shoots, leaves, flowers, and/or fruit sets pruning. There is evidence that SWE can act as regulators causing balanced flowering and fruit setting. Increased yield may be due to uniform fruit set and latter fruit weight through better canopy establishment, better inception of light, and through significant reduction in interplant competition for solar energy and nutrients [5,53]. Abd El-Gawad and Osman [40] demonstrated the positive effect of SWE foliar application on the number, size, and yield of eggplant fruits. SWE had a significant effect on the earliness of flowering, number of flowers, and fruit set percentage in eggplant. Abundant flowering could be the effect of increased vigor of plants [40,54]. SWE foliar spraying increased fruit number and weight of bell pepper [34,52]. Similar results were reported earlier by Eris et al. [55]; *A. nodosum* extract spraying significantly increased pepper fruit size, yield, and biochemical parameters, i.a., chlorophylls and soluble solids content, but not titratable acidity and pH. Similar results were reported for eggplant after *A. nodosum* extract application regarding fruit yield, number of fruits per plant, number of branches per plant, fruit length and width in pepper [56], as well as antioxidant activity and selected mineral contents [57].

SWE applied in the form of foliar spraying during vegetative development and just prior to flowering stimulated tomato fruit development. SWE-treated plants showed higher levels of cytokinins in the roots, increased translocation of these hormones to shoots and fruits, and their enhanced production within the fruit itself [31]. Ofosu-Anim et al. [58] and Reeta et al. [59] found an increased number of flowers and fruits in tomato with application of SWE. Plants sprayed with SWE formed a greater percentage of set fruits in relation to nonsprayed control. The favorable influences of biostimulants on the chemical characteristics of tomato fruit may be ascribed to its stimulative effect on photosynthesis process and concentration of some promoter hormones such as cytokinins which are closely involved in cell division, protein, carbohydrates, and chlorophyll formation [60]. SWE positively affected dry matter content, ascorbic acid, and a suitable ratio of sugars to acids in greenhouse tomato [37,61,62], while field tomato cultivation did not prove SWE potential in climatic conditions of Poland. Biostimulant application increased lycopene content and incidence of physiological disorders but decreased the level of dry weight, ß-carotene, vitamin C, soluble sugar contents, and total antioxidant activity of fruits [63]. In the conditions of South Italy, the marketable yield of pepper and numbers of fruit were significantly greater under the conventional system than the organic one, with no effects of the biostimulants. However, some fruit quality attributes, like soluble solid contents, were increased by biostimulant application [56]. Reeta et al. [59] observed a significant increase in ascorbic acid content in tomato and chilli pepper due to application of seaweed liquid fertilizers. SWE can be considered positive for some qualitative characteristics of the tomato, eggplant and pepper fruit. The analysis of reference sources showed that designs of experiments focused on seaweed application to Solanaceae crops are highly diversified (Tab. 1). Biological material, growing conditions, methods of cultivation, and most importantly, SWE doses, ways and times of application are highly heterogeneous. This could explain incompatible results, but would also allow for better targeting of future research focusing on SWE as forward-looking biostimulants.

Conclusions

Seaweed extracts are characterized by nonspecific action in tomato, eggplant, and pepper cultivation. They accelerate physiological processes in plants like macro- and micronutrient uptake, photosynthesis, and biomass production. Moreover, exogenous SWE application promotes balanced vegetative and generative development, crucial for proper fruiting in mentioned vegetables. The observed biological effects are elevated metabolite reserves enabling early flowering as well as more effective and uniform fruit setting and better plant productivity. Seaweed extracts could be used as eco-friendly plant stimulants. They can also play a pivotal role in organic tomato, eggplant, and pepper farming practices toward sustainable agriculture.

Tab. 1 The diversification of designs of experiments focused on seaweed application to Solanaceae crops.

Seaweed species / preparation	Crop/cultivar	Cultivation technique	Application and doses	References
Ascophyllum nodosum / Biozyme and Goëmar BM 86	Tomato 'Esmeralda' F_1 'Dual Plus' F_1	Field, Poland	Foliar spraying (extract 0.5 dm^3 ha^{-1}), first application 2 weeks after transplanting, followed by two applications in 14-day intervals.	[63]
A. nodosum / Goëmar Goteo	Tomato Azarro F_1, Lemance F_1, Admiro F_1, Ladiva F_1	Greenhouse, Poland	Extract 0.1% applied with drip drop irrigation system, directly after planting and next applications in high temperatures conditions.	[37]
A. nodosum / Goëmar Goteo	Tomato 'Alboney' F_1	Greenhouse, Poland	Watering (0.1% and 0.2%), four times in two combinations. 1, 7, 14, 21 (×4) and 1, 7 days after planting tomato plants to destination place, plus two times in July during full fruiting.	[37]
A. nodosum / Bioalgeen S90	Tomato 'Alboney' F_1	Greenhouse, Poland	Watering (extract 0.2%), in 30-day intervals during growing season.	[37]
A. nodosum	Tomato 'Master'	Field, Egypt	Foliar spraying (extract 500 mg L^{-1}), 35 and 50 days after transplanting.	[60]
A. nodosum	Tomato 'Piccolo' F_1	Greenhouse and field, Brasil	Foliar spraying (extract 0.3%), in 21-day intervals.	[36]
A. nodosum	Tomato 'Moneymaker'	Growing chamber, Ireland	Foliar spraying (extract 0.33%), application program before and after drought stress (first on 35-day-old plants).	[44]
A. nodosum and *Durvillea potatorum*	Tomato 'Moneymaker'	Growing chambers, Spain	Foliar spraying (extract 1.1 mL L^{-1}), first application during the growth and second – at the beginning of Fe deficiency.	[42]
Ascophyllum nodosum / Goemar BM86	Eggplant 'Epic' F_1 'Flavine' F_1 'Gascona' F_1 'WA 6020' F_1	Field, Poland	Foliar spraying (extract, 1.5 dm^3 ha^{-1}), first application 2 weeks after transplanting, followed by two applications in 14-day intervals.	[57]
A. nodosum	Eggplant	Field, Iran	Foliar spraying (extract 2 g L^{-1}), first application 20 days after transplanting and second – at blooming period.	[64]
A. nodosum / Biozyme	Chilli pepper 'Jalwa'	Field, India	Seedling spraying (extract, 10 mL L^{-1}) + soil application at vegetative stage (granules, 20 kg ha^{-1}) + foliar spraying (extract, 500 mL ha^{-1}) at flowering stage.	[43]
A. nodosum / Bio-algeen S90, Goëmar Goteo	Pepper 'Lustro' F_1	Foil tunnel, Poland	Fertigation (0.2% of Bio-algeen S90 and 0.1% of Goëmar Goteo), first 2 days after pricking and the last 7 days before planting.	[34]
A. nodosum / Lysodon Alga-Fert	Pepper 'Akron'	Pot experiment, Italy	Foliar spraying (250 g hL^{-1}), seven applications.	[56]
Bio-algeen S-90	Tomato 'Conchita' F_1	Unheated foil tunnel, Poland	Foliar spraying (extract 0.3%), first application at the 2–3 true leaf stage, then before planting, at the beginning of flowering, and at the beginning of yielding.	[61]
Ecklonia maxima / Kelpak	Tomato 'Rana'	Field, South Africa	Soil drench (0.4% and 1.0%) during seedling production, foliar spray (extract 0.4%) every 7 days.	[31]
Ecklonia maxima / Kelpak	Pepper 'Orobelle' F_1, 'Indra' F_1, 'King Arthur' F_1	Greenhouse, South Africa	Foliar spraying (extract 4%) 2 h prior to transplanting followed by three foliar applications in 21-day intervals.	[52]
Ecklonia maxima / Kelpak	Pepper 'Soroksari'	Pot experiment, Serbia	Substrate application 200 mL per pot (extract 0.5% and 0.1%) to 5-week-old plants.	[50]

Tab. 1 Continued

Seaweed species / preparation	Crop/cultivar	Cultivation technique	Application and doses	References
Ulva lactuca, *Caulerpa sertularioides*, *Padina gymnospora*, and *Sargassum liebmannii*	Tomato 'Rio Fuego'	Laboratory, greenhouse, Mexico	Extract (0.2%, 0.4%, and 1.0%) application as soil drench or foliar spraying in 7-day intervals.	[65]
Spatoglossum variabile, *Stokeyia indica*, or *Melanothamnus afaqhusainii*	Eggplant	Field, Pakistan	Thirty-five g of dry powder per 1 m^2 of soil, powder mixed with the soil before transplanting.	[53]
Stoechospermum marginatum	Eggplant 'CO-2', 'EG 203'	Pot experiment, India	Foliar spraying (extract 0.5%, 1.0%, 1.5%, 2.0%, 2.5%, and 5.0%) applied at intervals of 3 days.	[54]
Seaweed extract U. A. D. Co.	Eggplant 'Suma' F_1	Field, Egypt	Foliar spraying (extract 1,000 and 2,000 ppm), after 20, 50, 80, 110, and 140 days from transplanting.	[40]
Basfoliar Kelp SL	Pepper 'Flavio', 'California wonder'	Foil tunnel, Iraq	Foliar spraying (extract 0, 3 or 6 mL L^{-1}), the first application a month after transplanting, the second one – after 1 month.	[38]

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Wielokierunkowe działanie ekstraktów z alg morskich: wpływ na status fizjologiczny i biochemiczny warzyw z rodziny Solanaceae

Streszczenie

Algi morskie są elementem zasobów biologicznych mórz i oceanów. Obecnie wykorzystuje sie je w rolnictwie jako naturalne stymulatory wzrostu, tolerancji na stres i plonowania roślin uprawnych. Niniejsze opracowanie przedstawia aktualny stan wiedzy dotyczący mechanizmów działania i efektów stosowania ekstraktów z alg morskich (EAM) w uprawie warzyw z rodziny Solanaceae (pomidora, papryki i oberżyny). Bioaktywne składniki EAM regulują status mineralny roślin, modyfikują gospodarkę hormonalną, regulują rozwój wegetatywny i generatywny. Mechanizmy działania EAM wydają się być niespecyficzne dla pomidora, papryki i oberżyny. U wszystkich wymienionych gatunków zaobserwowano efektywniejsze pobieranie składników pokarmowych z gleby, lepszą wydajność fotosyntezy i przyspieszony wzrost. Te zmiany mogą z kolei wpływać pozytywnie na tolerancję roślin w stosunku do niekorzystnych warunków środowiskowych, intensyfikować kwitnienie i zawiązywanie owoców, zwiększać plon oraz poprawiać jego jakość. Ze względu na kompleksowy skład chemiczny i interakcje między składnikami, mechanizmy działania EAM są wielokierunkowe i trudne do zanalizowania na podstawie wyników doświadczeń rolniczych.