

HARNESSING SEAWEED-BASED BIOSTIMULANTS FOR ENHANCING ABIOTIC STRESS TOLERANCE IN FIELD CROPS: MECHANISMS, PROSPECTS AND FUTURE DIRECTIONS

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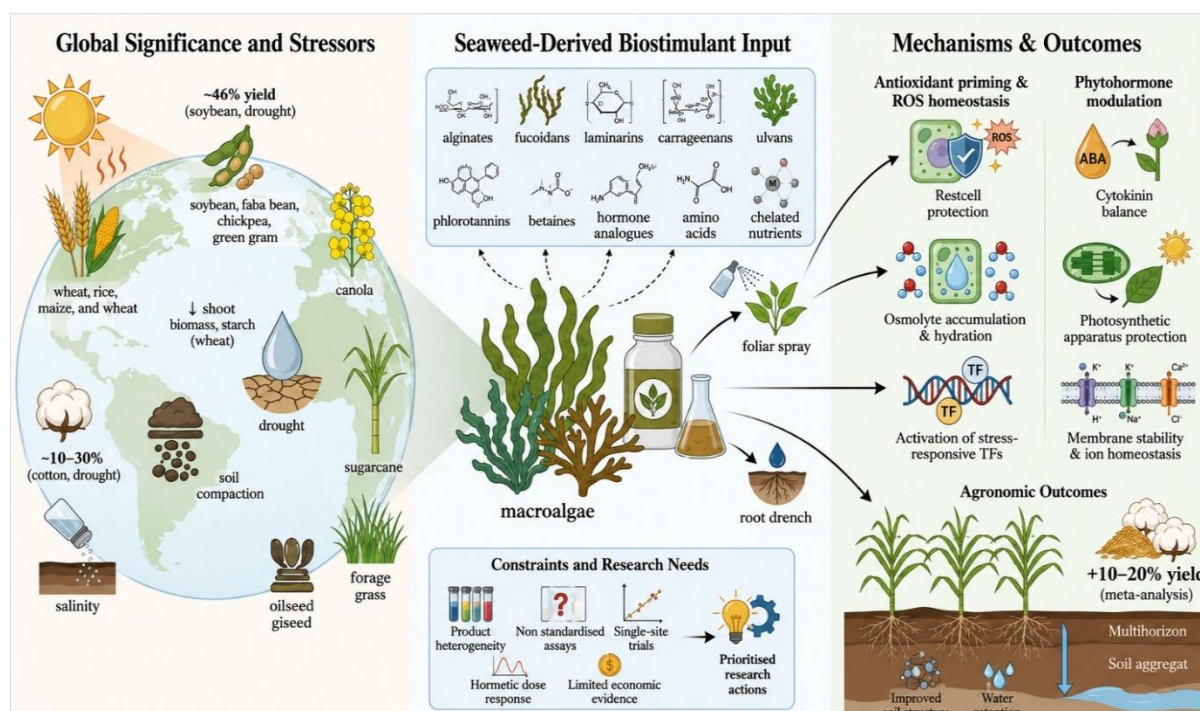
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ABSTRACT



Field crops like cereals, pulses, oilseeds and fibre and sugar crops supply the bulk of global food, feed and fibre; however, a large proportion of the area under these crops is rainfed or only marginally irrigated. Under such conditions, drought, heat, salinity and the physical constraints of heavy-textured soils depress productivity and quality. Reported penalties are substantial and crop-specific: grain yield losses approaching 46 % in soybean at 40 % field capacity, marked declines in shoot biomass, pigments and starch in wheat under terminal water deficit and yield reductions of 10–30 % in cotton under field drought. Against this background, seaweed-derived biostimulants have gained attention as low-toxicity, multi-functional inputs capable of raising abiotic stress tolerance without the regulatory and cost barriers associated with genetic or high-input approaches. This review synthesises current evidence on macroalgal biostimulants across the major field crop groups. It first characterises the chemical basis of activity alginates, fucoidans, laminarins, carrageenans and ulvans, together with phlorotannins, betaines, hormone analogues, free amino acids and chelated nutrients and relates compositional variability to taxonomy, phenology, harvest origin and extraction route. It then integrates the mechanistic literature into six converging domains: antioxidant priming and reactive oxygen species homeostasis; phytohormone modulation, particularly abscisic acid sensitisation and cytokinin-like activity; osmolyte accumulation and cellular hydration; photosynthetic apparatus protection; activation of stress-responsive transcription factor networks; and membrane stability with ion homeostasis. Crop-wise agronomic evidence is compiled for wheat, rice, maize, sorghum, soybean, faba bean, chickpea, green gram, canola, sugarcane, cotton and forage grasses, alongside soil-mediated benefits in root architecture, aggregate stability, water retention and rhizosphere function. Meta-analytical estimates converge on pooled yield gains of roughly 10–20 % under stress, but efficacy is strongly conditioned by

application strategy, formulation and extraction method. Persistent constraints product heterogeneity, absence of standardised potency assays, dominance of single-season single-site trials, hormetic dose responses and thin economic evidence for smallholders are examined and a conceptual framework with prioritised research actions is proposed for integrating seaweed biostimulants into climate-resilient field crop production.

KEYWORDS: Macroalgal extract; Osmolyte accumulation; ROS homeostasis; Rainfed agriculture; Biostimulants

1. INTRODUCTION

Field crops occupy the greater part of the world's arable land and underpin food, feed and fibre security. Unlike protected or intensively irrigated horticulture, most field crop production is directly exposed to the vagaries of the season rainfall amount and distribution, heat spells, evaporative demand and the hydraulic behaviour of the soil profile. As climatic variability intensifies, the frequency and severity of drought episodes are increasing and sustainable strategies to raise crop resilience are urgently required (Gavelienė & Jurkonienė, 2026; Ma *et al.*, 2022). The scale of exposure is considerable. In India, approximately 67 % of cotton is cultivated under rainfed conditions and comparable or greater proportions apply to coarse cereals, pulses and oilseeds grown in the semi-arid tropics (Patil *et al.*, 2024). Globally, the OECD–FAO Agricultural Outlook (2025) notes that although fibre consumption is projected to recover modestly, production continues to outpace demand and the sector faces downward price pressure, which further narrows the margin available for costly stress-mitigation inputs.

The physiological consequences of abiotic stress in field crops are well characterised and remarkably conserved across species. Water deficit lowers leaf water potential and relative water content, forces stomatal closure, restricts CO₂ diffusion and depresses carbon assimilation; heat destabilises membranes and photosynthetic electron transport; and salinity superimposes osmotic limitation and ion toxicity on an already constrained system (Anwar *et al.*, 2021; Han, J. M. *et al.*, 2024; Qamer *et al.*, 2021). Where these stresses coincide with reproductive development, the yield penalty is disproportionate, because the number and filling of grains, bolls, or stalks is set within narrow phenological windows. Yield reductions of 10–30 % under field drought are routinely reported in cotton (Patil *et al.*, 2024; Ul-Allah *et al.*, 2021), while controlled studies in soybean have documented grain yield losses of 45.6 % at 40 % field capacity (Mannan *et al.*, 2023).

Plant biostimulants are substances or microorganisms applied to plants or the rhizosphere to improve nutrient-use efficiency, abiotic stress tolerance, quality traits, or the availability of confined nutrients, irrespective of nutrient content. Among the non-microbial categories, seaweed extracts have the longest history of agricultural use and the broadest empirical base (Khan *et al.*, 2009; Rabhi *et al.*, 2025). Macroalgal biomass supplies a chemically diverse mixture of sulfated and non-sulfated polysaccharides, oligosaccharide elicitors, polyphenols, betaines, hormone analogues, free amino acids and chelated macro- and micronutrients, which together modulate nutrient dynamics, antioxidative defense and signal transduction in stressed plants (Ali, O. *et al.*, 2021; Kumar *et al.*, 2024; Tariq *et al.*, 2025). Meta-analytical evidence indicates average productivity gains of approximately 10–20 % where crops experience stress (Pei *et al.*, 2024; Staykov *et al.*, 2025) and a recent synthesis of 198 studies and 2, 021 paired comparisons confirms positive but strongly context-dependent yield responses conditioned by application strategy, formulation and extraction method (Pérez-Oñate *et al.*, 2026).

Despite this expanding literature, three problems limit the translation of research to field crop practice. First, mechanistic and agronomic evidence is scattered across model species, horticultural crops and a handful of cereals; thus, cross-crop generalisations remain fragile. Second, commercial products differ widely in feedstock, extraction route and bioactive profile, yet are compared as if equivalent and no widely accepted potency bioassay exists (Buss *et al.*, 2025; Sujeeth *et al.*, 2022). Third, dose–response behaviour is often hormetic rather than monotonic; thus, recommendations derived from one crop or environment transfer poorly (Grandin-Courbet *et al.*, 2025). Earlier reviews have addressed either single crops or single stress factors; however, a cross-crop synthesis oriented towards field production systems is lacking.

This review therefore aims to (i) characterise the composition and bioeffector chemistry of macroalgal biostimulants and relate variability to taxonomy and processing; (ii) integrate molecular and physiological mechanisms of stress alleviation into a coherent framework; (iii) compile and critically appraise crop-specific agronomic evidence across cereals, pulses, oilseeds, fibre, sugar and forage crops; (iv) examine soil- and rhizosphere-mediated contributions, with attention to Vertisols and other heavy-textured soils common in rain-fed regions; and (v) identify constraints and propose prioritised research actions for integrating seaweed biostimulants into climate-resilient field crop production.

2. THE ABIOTIC STRESS PARADIGM IN FIELD CROP PRODUCTION SYSTEMS

2.1 Magnitude and distribution of abiotic stress constraints across field crops

The dominant abiotic constraint differs by crop group and agro-ecology, but the underlying pattern is consistent: a stress episode coinciding with a critical reproductive stage produces a yield penalty far larger than an equivalent episode during vegetative growth. In wheat, terminal drought and heat during anthesis and grain filling reduce shoot height, biomass, chlorophyll and starch, with compensatory accumulation of soluble sugars, free amino acids, proline and phenolics (Ali, A. H. *et al.*, 2022; Alharbi *et al.*, 2022). In rice, salinity depresses biomass and pigment content and disturbs ionic balance, with chlorophyll deficits of the order of 26–31 % relative to treated

plants (Shahzad et al., 2023). Maize is markedly sensitive at tasselling and silking, showing reductions in fresh and dry weight, relative water content and soluble sugars, together with elevated malondialdehyde (Han, M. et al., 2024); sorghum, though genetically related, is comparatively more tolerant at equivalent water regimes (Abu-Ria et al., 2024). Among pulses, soybean loses grain yield severely under sustained deficit and legumes generally suffer flower and pod abortion when stress coincides with pod set (El Boukhari et al., 2023; Mannan et al., 2023; Sankhala et al., 2024). Canola shows progressive pigment loss and reactive oxygen species accumulation as field capacity declines from 80 % to 40 % (Shahriari et al., 2021). In cotton, drought, heat and salinity converge to cause boll shedding, shortened fibres and poor micronaire (Patil et al., 2024; Ul-Allah et al., 2021), while sugarcane loses stalk elongation and sucrose accumulation when the grand growth phase coincides with the dry season (Jacomassi et al., 2022). Table 1 summarises these constraints as documented in the cited sources.

Table 1. Dominant abiotic stress constraints, critical sensitive stages and reported stress effects in major field crops

Crop group / crop	Dominant abiotic stress	Critical sensitive stage	Reported stress effect	Reference(s)
Cereal: wheat	Terminal drought; heat	Anthesis to grain filling	Significant decline in shoot height, fresh and dry weight, chlorophyll and starch at 40 % field capacity; compensatory rise in soluble sugars, free amino acids, proline and phenolics	Ali, A. H. et al. (2022); Alharbi et al. (2022)
Cereal: rice	Salinity; intermittent drought	Panicle initiation to flowering	Reduced shoot and root biomass, disturbed ionic balance and pigment loss; chlorophyll deficit of 26–31 % relative to treated plants	Shahzad et al. (2023); Alam et al. (2024)
Cereal: maize	Drought with heat	Tasselling and silking	Significant reduction in fresh weight, dry weight, relative water content and soluble sugar; elevated malondialdehyde	Han, M. et al. (2024); Gandhi et al. (2024b)
Cereal: sorghum	Drought	Boot to grain filling	Growth reduction at 80 % and 60 % field capacity, but comparatively less responsive to stress than maize	Abu-Ria et al. (2024)
Pulse: soybean	Drought	Flowering to pod filling	Grain yield reduced by 45.6 % and water saturation deficit increased by 37.9 % at 40 % field capacity; declines in leaf water, chlorophyll, plant height and organ fresh weight	Mannan et al. (2023); Sankhala et al. (2024)
Pulse: faba bean	Drought (arid and semi-arid)	Flowering to pod set	Cascade of biochemical alterations with reduced plant growth and biomass during drought and recovery phases	El Boukhari et al. (2023)
Pulse: soybean, chickpea	Combined heat and water deficit	Reproductive phase (off-season sowing)	Yield losses in off-season sowings when temperature exceeded that of the regular season under water deficit	Mamatha et al. (2023)
Oilseed: canola	Progressive drought	Vegetative to flowering	Loss of photosynthetic pigments and reduced radical scavenging as field capacity declined from 80 % to 60 % to 40 %	Shahriari et al. (2021)

Fibre: cotton	Drought, heat, salinity	Squaring to boll development	Yield reduction frequently exceeding 10–30 % under field conditions; boll shedding, shortened fibre and poor micronaire	Patil et al. (2024); Ul-Allah et al. (2021); Zhu et al. (2023)
Sugar: sugarcane	Dry-season drought	Grand growth phase	Reduced stalk and sugar yield, impaired juice purity and technological quality, disrupted plant metabolism	Jacomassi et al. (2022)
Forage: perennial ryegrass	Drought and rehydration	Active tillering	Decline in leaf relative water content and cell membrane stability over 14 days of drought	Grandin-Courbet et al. (2025)

2.2 Physiological and biochemical changes under water-limited conditions

Water limitation triggers a connected sequence of physiological and biochemical responses that are broadly common to field crops. The earliest and most general reaction is a decline in leaf water potential and relative water content (RWC), followed by stomatal closure to restrict transpirational loss. Because stomata regulate both water efflux and CO₂ influx, closure simultaneously limits intercellular CO₂ concentration and directly restricts photosynthetic carbon uptake (Anwar et al., 2021; Han, J. M. et al., 2024). Concurrently, osmotic adjustment proceeds through the accumulation of compatible solutes proline, glycine betaine and soluble sugars which help restore cell turgor and protect macromolecules. This protection carries a metabolic cost, since carbon and nitrogen are diverted away from growth and from the filling of reproductive sinks (Singh, C. K. et al., 2021; Zhu et al., 2023).

At the biochemical level, water shortage disrupts the activity of key enzymes, including Rubisco activase and Calvin-cycle enzymes, lowers ATP generation as photochemical efficiency declines and raises lipid peroxidation as reactive oxygen species (ROS) accumulate (Qamer et al., 2021; Ul-Allah et al., 2021). The visible outcome across crops is reduced leaf area, premature senescence, poor set and retention of reproductive structures and degraded product quality (Patil et al., 2024). Importantly, the same biochemical markers RWC, proline, malondialdehyde (MDA), membrane stability index and antioxidant enzyme activity recur as the diagnostic panel in nearly all biostimulant studies, providing a common currency for cross-crop comparison.

2.3 Drought-induced limitations to photosynthesis and osmoregulation

Drought constrains photosynthesis through stomatal, mesophyll and biochemical components acting in sequence (Han, J. M. et al., 2024). Stomatal closure lowers intercellular CO₂ and as stress persists, mesophyll conductance declines and Calvin-cycle enzymes are downregulated, reducing the maximum carboxylation rate and electron transport capacity. Prolonged deficit accelerates chlorophyll degradation and destabilises photosystem II (PSII) components, lowering light-use efficiency and raising the risk of photoinhibition (Melandri et al., 2021; Zhang et al., 2021). Osmoregulation partially offsets these effects by maintaining hydration and enzyme function and osmolytes additionally act as molecular chaperones and ROS scavengers that stabilise membranes and proteins (Singh, C. K. et al., 2021; Zhu et al., 2023). However, osmolyte accumulation is genotype- and stage-dependent and while it improves short-term survival it does not fully compensate for extended carbon deficits that impair grain, boll or stalk filling (Patil et al., 2024; Zhu et al., 2023). This distinction between survival and productivity is central to biostimulant evaluation: treatments that improve stress symptoms without protecting assimilate supply to reproductive sinks will not translate into yield gains.

2.4 Heat and oxidative stress interactions in rainfed environments

In most rainfed field crop environments, heat stress coincides with water shortage and their combination is more damaging than either alone because elevated evaporative demand and accelerated ROS production act together (Chen, W. et al., 2024; Majeed et al., 2021). High temperature destabilises membrane lipids, denatures proteins and disrupts photosynthetic electron transport, promoting electron leakage to oxygen in chloroplasts and mitochondria and generating superoxide and hydrogen peroxide (Chen, W. et al., 2024; Qamer et al., 2021). Crops respond by activating enzymatic antioxidants (superoxide dismutase, catalase, peroxidases, ascorbate peroxidase) and non-enzymatic pools (ascorbate, glutathione, carotenoids, phenolics), but this capacity is finite and varies with genotype, developmental stage and prior stress history (Qamer et al., 2021; Singh, C. K. et al., 2021). Transcript and metabolite profiling under combined heat and drought shows coordinated induction of heat-shock proteins, antioxidant enzyme genes and abscisic acid-related signalling, indicating extensive crosstalk between stress response pathways (Chen, W. et al., 2024; Melandri et al., 2021). Agronomically, the heat–oxidative interaction shortens the effective duration of grain filling and reproductive maturation and degrades quality attributes (Mamatha et al., 2023; Ul-Allah et al., 2021).

2.5 Salinity, ion toxicity and combined-stress scenarios

Salinity is an increasingly important constraint in irrigated marginal and coastal field crop systems and in semi-arid regions where evaporative concentration accumulates salts in the root zone. Salinity imposes an osmotic component that mimics drought and an ionic component involving Na⁺ and Cl[−] toxicity, K⁺ displacement and

impaired enzyme function (Feng, G. et al., 2025; El-Beltagi et al., 2026). Cereals differ widely in their tolerance and the K^+/Na^+ ratio in leaf tissue has become the standard integrative indicator of ionic status (Nuruzzaman et al., 2025; Shahzad et al., 2023). Because osmotic, ionic and oxidative components overlap, salinity responses share substantial mechanistic ground with drought responses, which explains why the same biostimulant products often show efficacy against both. Combined-stress scenarios heat plus water deficit in off-season sowings, or salinity plus drought in coastal Vertisol tracts are agronomically the most relevant and least studied and evidence indicates that biostimulant efficacy is frequently greater under combined than under single stress (Mamatha et al., 2023; Trevisan et al., 2019).

2.6 The soil–plant–atmosphere continuum under stress, with emphasis on Vertisols

Soil physical behaviour determines how atmospheric demand is transmitted to the crop. Vertisols and other clay-rich soils, which dominate large cotton, sorghum, pulse and oilseed tracts, impose distinctive mechanical and hydraulic constraints on the soil–plant–atmosphere continuum (SPAC). Their high water-holding capacity buffers short dry spells, but in drying phases, they develop strong matric potentials and shrinkage cracks that restrict root penetration and reduce the effective rooting volume; under erratic heavy rainfall, the same soils become waterlogged and hypoxic (Çakir & Cangir, 2021; Melo et al., 2023). Therefore, hydraulic conductivity and matric forces govern water availability at the root surface and, through it, transpiration and stomatal behaviour, linking soil physical properties directly to canopy gas exchange (Chen, W. et al., 2024; Melo et al., 2023). Where secondary salinisation occurs in arid and semi-arid Vertisol regions, osmotic stress and ion toxicity are superimposed on these constraints (Feng, G. et al., 2025).

The SPAC perspective indicates that resilience in rain-fed field crops depends on improving water capture (deep tillage to break hardpans, mulching to reduce evaporation), root system design (genotype selection and root-promoting inputs) and soil organic matter status for aggregation and hydraulic buffering (Melo et al., 2023). This framing is important for biostimulant research because it identifies the soil-mediated pathway root proliferation, aggregation, water retention and rhizosphere function as a genuine second route to stress alleviation, in addition to the direct physiological route (Figure 1). Consequently, abiotic stress effects in field crops operate simultaneously at the molecular, whole-plant and soil system scales and integrated genetic, agronomic and biostimulant-based strategies, validated by experiments that link molecular markers to field water and soil measurements, are required to address them (Anwar et al., 2021; Kumar et al., 2024; Patil et al., 2024).

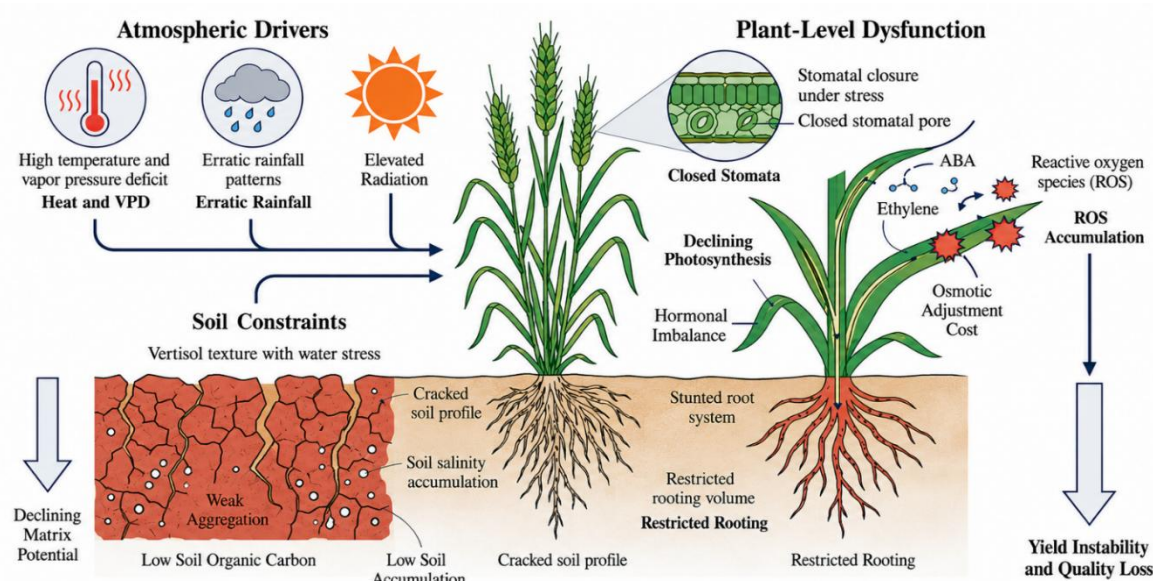


Figure 1. The abiotic stress paradigm in field crop production systems, represented across the soil–plant–atmosphere continuum. Atmospheric drivers (erratic rainfall, high vapour pressure deficit and heat spells, elevated radiation load) and soil constraints (declining matrix potential, cracking in Vertisols, restricted rooting volume, salt accumulation, low soil organic carbon and weak aggregation) converge on plant-level dysfunction (stomatal closure, photosynthetic decline, reactive oxygen species accumulation, hormonal imbalance and costly osmotic adjustment) culminating in yield instability and quality loss.

3. SEAWEED-DERIVED BIOSTIMULANTS: COMPOSITION, BIOACTIVES AND MACROALGAL DIVERSITY

3.1 Phytochemical constituents and bio-effector molecules in marine macroalgae

Marine macroalgae are rich sources of biologically active molecules that collectively account for their biostimulant behaviour. The principal cell wall and storage polysaccharides are alginates, fucoidans and laminarins in brown algae, carrageenans and agars in red algae and ulvans in green algae. These polysaccharides are widely regarded as primary bio-effectors, promoting plant immunity, conferring protection against osmotic stress and modifying microbial activity in the rhizosphere (Akter et al., 2024; Liu & Sun, 2020; Şahin, 2021; Tariq et al., 2025). Low-molecular-weight oligosaccharides derived from these polymers frequently show stronger signalling activity than their native high-molecular-weight counterparts, activating defence pathways and secondary metabolism (Sujeeth et al., 2022; Zhou et al., 2024).

Beyond carbohydrates, seaweeds contain high concentrations of polyphenols phlorotannins in brown algae and diverse phenolics in red and green species which provide antioxidant capacity and interact with plant redox signalling (Aina et al., 2022; El-Beltagi et al., 2022). Other functionally relevant classes include pigments (chlorophylls, carotenoids and phycobiliproteins), fatty acids, notably long-chain polyunsaturated fatty acids and peptides and proteins, including lectins and small signalling peptides. Inorganic macro- and micronutrients (K, Ca, Mg, Fe and Zn) contribute both nutritional and signalling functions when extracts are applied to crops (Ali, O. et al., 2021; Kumar et al., 2024). Many commercial extracts also contain measurable quantities of phytohormones or hormone-like compounds auxin-like and cytokinin-like substances, betaines and polyamines that influence cell division, senescence timing and stress responses (Ali, O. et al., 2021; Thakur et al., 2025). Detailed metabolite characterisation of commercial seaweed biostimulants confirms that this chemical breadth, rather than any single molecule, underlies observed activity (Gandhi et al., 2024a; Mughunth et al., 2024), supporting a multi-mechanism interpretation of efficacy.

3.2 Taxonomic diversity and functional metabolites of brown, red and green seaweeds

Taxonomic identity is a major determinant of biochemical composition and functional potential. Brown macroalgae (Phaeophyceae: *Ascophyllum*, *Ecklonia*, *Sargassum*, *Laminaria*) are generally rich in alginate, fucoidan and laminarin, contain substantial phlorotannins and yield alginate-derived oligosaccharides that act as elicitors and soil conditioners (Akter et al., 2024; Kergosien et al., 2023; Liu & Sun, 2020). Red algae (Rhodophyta: *Kappaphycus*, *Gracilaria*, *Chondrus*, *Corallina*) are typically higher in sulfated galactans, such as carrageenan and agar and in protein-containing fractions and several species supply bioavailable nitrogen, free amino acids and growth-promoting signals (Domingo et al., 2023; Siddik et al., 2023). Green algae (Chlorophyta: *Ulva*, *Codium*) contain ulvans and characteristic sterols with rapid biomass turnover, which makes them attractive for circular-economy biorefineries (Arias et al., 2023; Şahin, 2021).

Comparative studies confirm that this taxonomy translates into different crop responses. In faba bean under drought, extracts of *Fucus spiralis*, *Ulva lactuca*, *Laminaria ochroleuca* and *Ascophyllum nodosum* all improved biomass, but through partly distinct biochemical routes (El Boukhari et al., 2023). In maize field trials over two years, extracts of the red algae *Kappaphycus alvarezii* and *Gracilaria debilis* and the brown alga *Sargassum cinctum* each enhanced growth, cob and grain yield and grain quality, with the response depending on both source and dose (Gandhi et al., 2024b). In wheat, a red coralline alga (*Corallina elongata*) outperformed a brown alga (*Sargassum latifolium*) and two commercial products in ameliorating drought effects (Alharbi et al., 2022). Compositional differences are further modulated by season, harvest location and post-harvest handling; thus, taxonomy alone does not guarantee consistent bioactivity provenance, phenology and processing must be specified (Arias et al., 2023; El-Beltagi et al., 2026). Table 2 summarise these taxonomic and functional relationships.

Table 2. Taxonomic groups of marine macroalgae, signature bioactive constituents and documented functional roles relevant to field crops

Group	Representative genera	Bioactive compounds	Functional roles in field crops	Reference(s)
Brown algae (Phaeophyceae)	<i>Ascophyllum</i> , <i>Ecklonia</i> , <i>Sargassum</i> , <i>Laminaria</i>	Alginate, fucoidan, laminarin, phlorotannins, mannitol, betaines, cytokinin-like compounds	Elicitor priming of defence and antioxidant genes; redox buffering; delayed senescence; soil aggregation; root proliferation	Kergosien et al. (2023); Shahriari et al. (2021); Grandin-Courbet et al. (2025); Liu & Sun (2020)
Red algae (Rhodophyta)	<i>Kappaphycus</i> , <i>Gracilaria</i> , <i>Chondrus</i> , <i>Corallina</i>	Carrageenan, agar, floridoside, proteins and free amino acids, mycosporine-like amino acids	Direct supply of osmolyte precursors and organic nitrogen; abscisic acid homeostasis; osmotic adjustment; grain and biomass yield gains	Mannan et al. (2023); Sharma et al. (2019); Domingo et al. (2023); Siddik et al. (2023)

Green algae (Chlorophyta)	<i>Ulva, Codium</i>	Ulvan, sterols, glucuronic acid and rhamnose units, oligo-ulvans	Defence signalling; membrane stabilisation; antioxidant induction; rapid biomass turnover suited to biorefinery use	Li et al. (2020); El Boukhari et al. (2023); Şahin (2021); Arias et al. (2023)
Mixed and blended formulations	<i>Kappaphycus</i> with <i>Sargassum</i> ; <i>Ascophyllum</i> with <i>Laminaria</i>	Combined polysaccharide, phenolic, amino acid and hormone fractions	Broader mechanistic coverage; yield gains of 20–31 % and alleviation of salinity stress in seedling assays	Vaghela et al. (2023); Ramamoorthy & Munisamy (2025); Campobenedetto et al. (2021)

3.3 Modes of action: elicitors, signalling molecules and hormone analogues

Seaweed extracts operate through a combination of processes rather than a single mechanism. Oligosaccharide fragments and sulfated polysaccharides act as analogues of microbe- and damage-associated molecular patterns, triggering defense signalling cascades that include ROS bursts, Ca²⁺ influx and mitogen-activated protein kinase activation and enhancing systemic resistance across diverse crops (Ali, O. et al., 2021; Peng et al., 2025; Sujeeth et al., 2022). Seaweed polyphenols and carotenoids contribute to redox buffering by scavenging ROS directly and by modulating antioxidant gene expression, which is critical under drought and heat stress, where oxidative injury predominates (Aina et al., 2022; El-Beltagi et al., 2022; Xu et al., 2024).

Phytohormone-like compounds present in extracts indole derivatives, cytokinins and constituents with brassinosteroid-like activity alter hormonal balance, promoting cell division, delaying senescence and modifying stomatal regulation, thereby sustaining canopy function under sub-optimal moisture (Ali, O. et al., 2021; Thakur et al., 2025). Osmoprotectants and betaines, supplied directly or indirectly, help preserve osmotic balance and membrane integrity (Kumar et al., 2024). Seaweed biostimulants further influence nutrient mobilisation through chelation and enhanced uptake, modify root architecture by increasing root length density and fine-root proliferation and reshape rhizosphere microbial composition, all of which constitute indirect but powerful routes to stress resilience (Arias et al., 2023; Chen, D. et al., 2023). Multi-omics analyses increasingly identify consistent gene networks activated by seaweed treatment stress-responsive transcription factors, antioxidant enzymes and hormone biosynthetic genes pointing to a systems-level rather than target-specific mode of action (De Saeger et al., 2019; Kumar et al., 2024; Sujeeth et al., 2022).

3.4 Advances in extraction and formulation technologies

Extraction and formulation determine product efficacy, batch consistency and shelf life. Conventional aqueous and alkaline extractions remain the commercial mainstay and solubilise polysaccharides, small phenolics and salts, but they are relatively unselective and can degrade thermolabile constituents. Emerging approaches enzyme-assisted extraction, microwave-assisted extraction, ultrasound-assisted extraction, subcritical water extraction and pressurised liquid extraction increase the recovery of target bioactives while reducing thermal degradation and solvent use (Akter et al., 2024; Arias et al., 2023). Controlled depolymerisation using acids, enzymes, or hydrothermal treatment is widely applied to generate bioactive oligosaccharides with enhanced elicitor activity; an enzymatically produced *Ulva prolifera* hydrolysate, for example, improved root growth and antioxidant capacity in drought-stressed wheat and lowered MDA by 30.1 % at 0.1 % concentration (Li et al., 2020). At the other end of the processing spectrum, minimally processed seaweed homogenates or saps retain the full bioactive complement at low energy cost and have demonstrated substantial crop responses, with yield increases of 20–31 % reported for *Kappaphycus alvarezii* and *Sargassum wightii* homogenates (Vaghela et al., 2023). Analytical standardisation molecular-weight profiling, monosaccharide composition, degree of sulfation and phenolic fingerprinting is increasingly used to link extraction route to bioactivity and improve batch-to-batch consistency (Gandhi et al., 2024a; Şahin, 2021; Zhou et al., 2024).

Formulation science has advanced from simple liquid concentrates to concentrated extracts, encapsulated micro- and nano-carriers, slow-release granules and adjuvant-enhanced foliar sprays, improving stability, controlled release and retention on leaf or soil surfaces (Arias et al., 2023; Kumar et al., 2024). Encapsulation in alginate beads, liposomes, or polymeric nanoparticles protects sensitive bioactives from oxidation, allows targeted delivery to the root or shoot and permits co-formulation with nutrients or beneficial micro-organisms; chitosan–microalgae nanoparticle systems, for instance, have improved germination and early seedling growth in wheat cultivars with contrasting drought sensitivity under polyethylene glycol-induced osmotic stress (Gholizadeh et al., 2026; Rabhi et al., 2025; Staykov et al., 2025). Quality control and regulation, however, have not kept pace. The absence of widely accepted potency assays and labelling standards complicates comparisons across studies and products and remains a principal barrier to adoption (Buss et al., 2025; Hermans, 2024; Sujeeth et al., 2022). Progress requires standardised bioassays based on physiological and molecular markers, transparent compositional declaration and long-term validation across contrasting agro-environments (Arias et al., 2023; Kumar et al., 2024). Table 3 compares the principal extraction and formulation routes.

Table 3. Comparison of extraction and formulation technologies for seaweed-based biostimulants

Technology	Principle	Bioactives recovered	Principal advantage	Principal limitation	Reference(s)
Aqueous and alkaline extraction	Hot water or alkali solubilisation of cell-wall and cytosolic constituents	High-molecular-weight polysaccharides, small phenolics, salts, betaines	Simple, low cost, commercially established	Unselective; thermolabile compounds degraded; variable batch composition	El Boukhari et al. (2020); Şahin (2021); Kergosien et al. (2023)
Acid and hydrothermal depolymerisation	Controlled hydrolysis of polymeric polysaccharides	Bioactive oligosaccharides with enhanced elicitor activity	Markedly higher elicitor potency per unit mass	Requires control of the degree of polymerisation; risk of over-hydrolysis	Zhou et al. (2024); Peng et al. (2025)
Enzyme-assisted extraction and hydrolysis	Glycoside hydrolases and proteases release wall-bound compounds	Defined oligosaccharides, peptides, free amino acids	Mild and specific; efficacy demonstrated in drought-stressed wheat	Enzyme cost; process optimisation needed for each feedstock	Li et al. (2020); Akter et al. (2024)
Microwave- and ultrasound-assisted extraction	Cell disruption by dielectric heating or acoustic cavitation	Polysaccharides, phenolics, pigments	Shorter extraction time, higher yield, lower solvent use	Capital cost; scale-up and uniformity issues	Arias et al. (2023); Akter et al. (2024)
Subcritical water and pressurised liquid extraction	Elevated temperature and pressure alter water polarity	Phenolics, proteins, mid-molecular-weight polysaccharides	Solvent-free, high recovery, low thermal degradation	Equipment intensive; limited industrial uptake	Arias et al. (2023); Domingo et al. (2023)
Minimally processed homogenate or sap	Mechanical homogenisation of fresh biomass without fractionation	Full native bioactive complement	Low energy input; suits local manufacture; yield gains of 20–31 % reported	Short shelf life; higher application volume; standardisation difficult	Vaghela et al. (2023)
Encapsulation and nano-formulation	Entrapment in alginate beads, liposomes or polymeric nanoparticles	Protected labile bioactives with co-formulants	Controlled release, rain-fastness, targeted delivery	Cost per hectare; regulatory uncertainty for nano-carriers	Gholizadeh et al. (2026); Rabhi et al. (2025); Staykov et al. (2025)
Analytical standardisation (cross-cutting)	Molecular-weight profiling, monosaccharide and sulfation analysis, phenolic fingerprinting	Not applicable characterisation step	Links extraction route to bioactivity and improves batch consistency	No agreed potency bioassay or labelling standard	Gandhi et al. (2024a); Buss et al. (2025); Hermans (2024)

4. MOLECULAR AND PHYSIOLOGICAL MECHANISMS OF STRESS ALLEVIATION

4.1 Regulation of antioxidant enzyme machinery and ROS homeostasis

Drought, heat and salinity rapidly generate ROS in plant cells, causing lipid peroxidation, protein oxidation and DNA damage unless detoxified. Seaweed extracts and derived oligosaccharides consistently increase both enzymatic antioxidants superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and glutathione reductase (GR) and non-enzymatic pools of ascorbate, glutathione and phenolics, thereby restoring redox balance and lowering membrane lipid peroxidation, which is measured as malondialdehyde MDA (Kumar et al., 2024; Qamer et al., 2021; Sujeeth et al., 2022). The evidence spans field crops: *Sargassum angustifolium* extract enhanced pigment retention, radical scavenging capacity and SOD activity in drought-stressed canola (Shahriari et al., 2021); *Corallina elongata* and *Sargassum latifolium* extracts improved antioxidant status and metabolite content in wheat under water deficit (Alharbi et al., 2022); and an enzymatic *Ulva prolifera* hydrolysate increased CAT and peroxidase activity and reduced MDA by 30.1 % in wheat (Li et al., 2020). In rice under salinity, *Ascophyllum nodosum* treatment positively regulated the antioxidant system, with a strong negative correlation between antioxidant capacity and oxidative markers (Shahzad et al., 2023).

Mechanistically, oligosaccharide elicitors and extract phenolics act as direct radical scavengers and activators of antioxidant gene networks through MAPK and Ca²⁺-dependent signalling (Peng et al., 2025; Sujeeth et al., 2022). Several studies have shown that *Ascophyllum nodosum* extracts and alginate or laminarin oligosaccharides rapidly induce antioxidant enzyme genes, establishing a primed state in which detoxification proceeds faster when stress

subsequently occurs (Ali, O. et al., 2022; Feng, W. J. et al., 2024; Peng et al., 2025). This priming interpretation is important agronomically, because it implies that application before the anticipated stress episode should outperform application during it.

4.2 Modulation of phytohormones (ABA, cytokinins, auxins and brassinosteroids)

Alteration of hormone levels and signalling is a central route through which seaweed biostimulants influence growth and stress response. Biochemical assays and expression studies have documented cytokinin-like and auxin-like activity in extracts of *Ascophyllum*, *Ecklonia* and *Kappaphycus*, correlating with enhanced cell division, delayed senescence and better leaf area retention under moderate stress (Ali, O. et al., 2022; Kumar et al., 2024). Under drought, seaweed treatment typically adjusts abscisic acid (ABA) signalling rather than substituting for ABA, improving ABA sensitivity and stomatal responsiveness to conserve water without prolonged stomatal closure that would forfeit carbon gain (Ma et al., 2022; Sujeeth et al., 2022). Direct evidence comes from wheat, where *Gracilaria dura* extract conferred drought tolerance by modulating ABA homeostasis, with associated gains in biomass and yield (Sharma et al., 2019). In tomato under mild water stress, a formulation based on *Ascophyllum nodosum* and *Laminaria digitata* reduced ABA, malondialdehyde (MDA) and proline, while raising stem water potential and photosynthetic pigment content, indicating that a less severe internal stress state had been achieved rather than a stronger stress response (Campobenedetto et al., 2021).

Interaction with brassinosteroid and salicylate pathways is also evident: some extracts induce brassinosteroid-responsive genes associated with stress tolerance and membrane protection, while sulfated polysaccharides can activate salicylate and jasmonate pathways linked to priming and systemic response (Kumar et al., 2024; Xu et al., 2024). The resulting hormonal outcome depends on the extract composition, dose, timing and developmental stage, which is a principal reason for inconsistent field results (Arias et al., 2023; Thakur et al., 2025).

4.3 Enhancement of osmolyte accumulation and cellular hydration dynamics

Accumulation of compatible solutes, such as proline, glycine betaine, soluble sugars and polyols, is a core protective strategy under water deficit. Seaweed extracts have been shown to increase osmolyte concentrations in leaves and roots, lowering cellular osmotic potential and maintaining turgor for cell expansion and metabolic function during transient drought (Kumar et al., 2024; Pei et al., 2024; Singh, C. K. et al., 2021). In wheat, *Sargassum denticulatum* applied at 2 % increased compatible osmolytes, antioxidant compounds and yield parameters under water stress, with detectable variation in non-coding chloroplast DNA regions indicating a deeper reorganisation of stress metabolism (Ali, A. H. et al., 2022). Two mechanisms operate in parallel: direct supply of osmolyte precursors such as free amino acids and betaines, which is particularly characteristic of red algal and protein-rich extracts and indirect activation of biosynthetic pathways, including increased P5CS expression for proline synthesis (Ali, O. et al., 2022; Domingo et al., 2023; Siddik et al., 2023).

The functional consequence is improved hydration status. Field and controlled studies in cereals, legumes and sugarcane report that osmolyte accumulation following seaweed application raises RWC, maintains turgor through midday stress and sustains stomatal conductance and photosynthesis, ultimately improving biomass and yield under rain-fed conditions (Jacomassi et al., 2022; Pei et al., 2024; Zhang et al., 2021). A particularly informative demonstration comes from perennial ryegrass, where *Laminaria digitata* extract applied seven days before irrigation withdrawal increased water content specifically in the basal shoot zone housing leaf meristems, through a smaller decline in leaf RWC indicative of better osmotic adjustment (Grandin-Courbet et al., 2025). Notably, the same study found higher doses to be deleterious, confirming that the osmotic response is hormetic and that dose optimisation is not optional. Response magnitude also varies with genotype and interacts with soil moisture and application method, making crop-specific calibration essential (Patil et al., 2024).

4.4 Photosynthetic apparatus protection and chlorophyll stability under drought

Seaweed biostimulants protect photosynthetic machinery through several complementary routes: stabilisation of chloroplast membranes and photosystem complexes via enhanced antioxidant defence; delayed chlorophyll degradation through cytokinin-like anti-senescence activity; and maintenance of photochemical efficiency (F_v/F_m) and electron transport under stress (Kumar et al., 2024; Melandri et al., 2021; Santaniello et al., 2017). Foliar application of *Ascophyllum nodosum* extract or oligosaccharide fractions maintains higher chlorophyll a/b ratios, lowers chlorophyllase activity and reduces photoinhibition during drought, improving radiation-use efficiency and carbon gain through the stress period (Ali, O. et al., 2022; Santaniello et al., 2017; Zhang et al., 2021). Crop-level confirmation is available across groups: in rice under salinity, *Ascophyllum nodosum* treatment raised total chlorophyll by 26.4–31.0 % and carotenoids by 11.9–16.7 %, while improving gas exchange and PSII efficiency (Shahzad et al., 2023); in canola, *Sargassum angustifolium* extract preserved photosynthetic pigments as field capacity fell (Shahriari et al., 2021); and in sugarcane, foliar seaweed extract sustained plant metabolism and raised stalk and sugar yields during the driest period of the year (Jacomassi et al., 2022).

Transcript and protein data support increased expression of components involved in PSII repair, notably D1 protein turnover, light-harvesting complex stabilisation and modulation of the protective xanthophyll cycle, which indicates active adjustment of light acclimation rather than passive protection (Ali, O. et al., 2022; Xu et al., 2024). For field crops in which product quality depends on continuity of assimilate supply during a defined filling period grain filling in cereals, fibre elongation and secondary wall deposition in cotton and sucrose accumulation in

sugarcane protecting photosynthetic performance through well-timed application is the most direct route by which biostimulants can limit yield and quality loss (Patil et al., 2024; Ul-Allah et al., 2021).

4.5 Activation of stress-responsive gene expression networks and transcription factors

Genomic studies indicate that seaweed biostimulants prime extensive gene expression networks that underlie the observed physiological benefits. RNA-seq analyses of tomato, Arabidopsis and cereals treated with *Ascophyllum*-derived extracts showed early induction of transcription factor families, including NAC, DREB/CBF, bZIP, WRKY and AP2/ERF, which govern downstream antioxidant, osmolyte and chaperone responses (Ali, O. et al., 2022; De Saeger et al., 2019; Ma et al., 2022; Sujeeth et al., 2022). These transcriptional changes are consistent with molecular priming: treated plants mount a faster and stronger transcriptional response when stress is subsequently imposed than untreated controls (Gechev, 2025; Peng et al., 2025). Proteomic analyses have additionally reported elevated heat-shock proteins (HSP70 and small HSPs), chaperones and late embryogenesis abundant (LEA) proteins after seaweed treatment, supporting protein folding and membrane integrity under heat and drought (Melandri et al., 2021; Zhou et al., 2024). Integration across data types suggests that oligosaccharide elicitor signalling and hormone-analogue signalling converge on the same transcription factor hubs, producing coordinated metabolic reprogramming towards tolerance (Gechev, 2025; Kumar et al., 2024). Emerging omics-driven work is beginning to link these signatures to field performance, which is the necessary step towards marker-assisted product evaluation (Ateeq et al., 2026).

4.6 Membrane stability and ion homeostasis under salinity and heat stress

Membrane integrity, quantified as membrane stability index (MSI) or electrolyte leakage, is a robust indicator of stress injury. Seaweed treatments reduce electrolyte leakage and increase MSI under salinity and heat, most probably through strengthened antioxidant defence together with membrane lipid stabilisation supported by compatible solute accumulation and improved expression of membrane repair enzymes (Qamer et al., 2021; Witzel et al., 2025). In perennial ryegrass, cell membrane stability was less impaired during drought and returned rapidly to pre-drought levels after rehydration following *Laminaria digitata* priming (Grandin-Courbet et al., 2025).

Under saline conditions, seaweed extracts promote selective ion uptake and compartmentalisation. Treated plants generally show lower leaf Na^+ and improved K^+/Na^+ ratios, reflecting enhanced transporter expression through the SOS pathway and NHX antiporters and, possibly, altered ionic availability in the rhizosphere (Ikuyinminu et al., 2022; Pei et al., 2024; Witzel et al., 2025). Rice treated with *Ascophyllum nodosum* maintained ionic balance and biomass under salinity while inducing organic acids, sugars, amino acids and flavonoids (Shahzad et al., 2023) and a meta-analysis of cereal crops confirmed that aqueous seaweed extracts applied as foliar sprays increase shoot and root biomass under both normal and saline conditions (Nuruzzaman et al., 2025). Specialised formulations improve membrane protection further through targeted delivery and sustained release, which is relevant to the combined salinity–heat conditions common in rainfed and coastal systems (Rabhi et al., 2025; Staykov et al., 2025). The net outcome is improved ionic balance, preserved membrane function and better survival and productivity under multiple concurrent stresses (Feng, W. J. et al., 2024; Kumar et al., 2024).

Taken together, the evidence indicates that seaweed biostimulants act through an interconnected set of mechanisms, including antioxidant priming, hormonal modulation, osmolyte accumulation, photoprotection, transcriptional reprogramming and membrane and ion stabilisation, which jointly attenuate drought, heat and salinity injury (Table 4; Figure 2). In field crops, these mechanisms are directly mapped onto the principal points of failure: stomatal dysfunction, oxidative damage, carbon shortfall during sink filling and ionic imbalance. This provides a coherent rationale for targeted use, emphasising application before and during early stress, genotype-specific dose calibration and combination with soil management. Translating the mechanistic picture into practice requires crop-specific dose–response trials, multi-season field validation and integrated studies that connect molecular markers with yield and quality outcomes.

Table 4. Mechanistic domains of seaweed biostimulant action, diagnostic markers and representative evidence in field crops

Mechanistic domain	Diagnostic markers and traits	Direction of change	Representative evidence in field crops	Reference(s)
Antioxidant priming and ROS homeostasis	SOD, CAT, APX and GR activity; ascorbate and glutathione pools; H_2O_2 , O_2^- , malondialdehyde	Antioxidants increase; oxidative markers decrease	Canola: pigment retention, radical scavenging and SOD activity increased under progressive drought. Wheat: catalase and peroxidase increased, malondialdehyde reduced by 30.1 %. Rice: antioxidant system up-regulated under salinity	Shahriari et al. (2021); Li et al. (2020); Shahzad et al. (2023)

Phytohormone modulation	ABA content and sensitivity; cytokinin- and auxin-like activity; brassinosteroid- and salicylate-responsive genes	ABA signalling recalibrated; cytokinin-like activity increase	Wheat: drought tolerance conferred specifically through modulation of ABA homeostasis. Tomato: ABA, malondialdehyde and proline reduced with higher stem water potential and pigment content	Sharma et al. (2019); Campobenedetto et al. (2021)
Osmolyte accumulation and hydration	Proline, glycine betaine, soluble sugars; relative water content; P5CS expression	Osmolytes increase; relative water content maintained	Wheat: compatible osmolytes, antioxidants and phenolics increased with 2 % <i>Sargassum denticulatum</i> . Maize: relative water content, proline and glutathione increased. Perennial ryegrass: meristem-zone water content maintained	Ali, A. H. et al. (2022); Han, M. et al. (2024); Grandin-Courbet et al. (2025)
Photosynthetic apparatus protection	Chlorophyll a and b, carotenoids, Fv/Fm, gas exchange, chlorophyllase activity	Pigments and photochemical efficiency maintained	Rice: total chlorophyll +26.4–31.0 %, carotenoids +11.9–16.7 %, gas exchange and PSII efficiency improved. Sugarcane: plant metabolism sustained with higher stalk and sugar yield in the dry season	Shahzad et al. (2023); Jacomassi et al. (2022)
Stress-responsive gene networks	NAC, DREB/CBF, bZIP, WRKY and AP2/ERF transcription factors; HSP70, small HSPs, LEA proteins	Early induction; faster response on subsequent stress	Tomato and Arabidopsis: transcriptomic reprogramming after <i>Ascochyllum nodosum</i> application. Canola: altered stress-gene expression across three successive drought phases	Ali, O. et al. (2022); Santaniello et al. (2017); Shahriari et al. (2021)
Membrane stability and ion homeostasis	Membrane stability index, electrolyte leakage, leaf Na ⁺ and K ⁺ , K ⁺ /Na ⁺ ratio, SOS and NHX expression	MSI increase; leakage decrease; K ⁺ /Na ⁺ ratio increases	Rice: ionic balance maintained under salinity. Turfgrass: potassium and calcium composition and non-structural carbohydrates improved under saline shock. Cereals: shoot and root biomass increased under salinity	Shahzad et al. (2023); Elansary et al. (2017); Nuruzzaman et al. (2025)

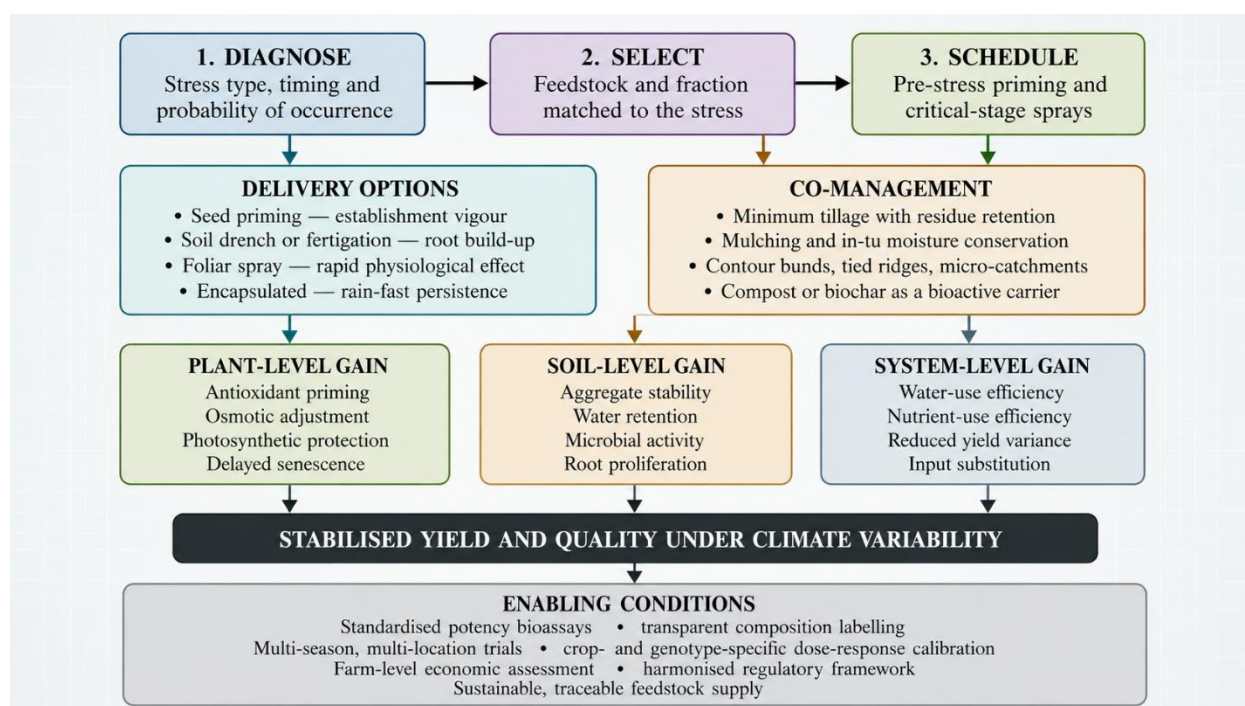


Figure 2. Integrated molecular and physiological mechanisms by which seaweed-derived biostimulants enhance abiotic stress tolerance in field crops. Oligosaccharide elicitors, phenolics and hormone analogues are

perceived through Ca^{2+} , MAPK and ROS signalling, converging on stress-responsive transcription factor hubs (NAC, DREB/CBF, bZIP, WRKY, AP2/ERF) that coordinate antioxidant priming, hormone modulation, osmotic adjustment, photoprotection, chaperone induction and membrane-ion homeostasis, thereby generating a stress-tolerant phenotype with a stabilised yield and quality.

5. CROP-SPECIFIC AGRONOMIC EVIDENCE ACROSS FIELD CROPS

The mechanistic literature is largely built on model species and horticultural crops; however, a usable body of field crop evidence now exists. This section appraises it by crop group, distinguishing controlled-environment studies from multi-season field trials, as the two carry very different weights for recommendation. A consolidated summary appears in Table 5 and the magnitude of reported responses is compared in Figure 3.

5.1 Cereals: wheat, rice, maize, sorghum and barley

Cereals accounted for the largest share of field crop evidence. In wheat, four independent lines of work converged. *Sargassum denticulatum* applied as a 2 % foliar spray under water stress at 40 % field capacity improved growth and yield parameters, as well as osmolytes, antioxidants and phenolics (Ali, A. H. et al., 2022). Comparative screening of *Sargassum latifolium* and *Corallina elongata* extracts against two commercial products at 5 % found the red coralline alga most effective, raising shoot carbohydrate by 34.6 % and protein by 51.9 % in drought-stressed plants at the first sampling (Alharbi et al., 2022). Enzymatically hydrolysed *Ulva prolifera* extract at 0.02–0.1 % improved shoot and root length and root dry weight after 120 h of stress, increased CAT and peroxidase activity and lowered MDA by 30.1 % at the highest dose (Li et al., 2020). Finally, *Gracilaria dura* extract conferred drought tolerance through ABA homeostasis, with gains in biomass and yield (Sharma et al., 2019). At the systems level, a two-season field study in durum wheat combining a biostimulant with nitrogen fertilisation improved root development, chlorophyll content and grain yield while permitting a 33 % reduction in nitrogen input and raising grain protein by 4 %, which is the clearest available demonstration of input substitution in a cereal (Rossini et al., 2025).

In rice, *Ascomyllum nodosum* application weekly or biweekly increased shoot and root biomass, maintained ionic balance, increased total chlorophyll by 26.4–31.0 %, increased carotenoids by 11.9–16.7 %, improved gas exchange and PSII efficiency and induced organic acids, sugars, amino acids and flavonoids (Shahzad et al., 2023). Extracts of *Hypnea musciformis* and *Gracilaria tenuistipitata* improved rice growth and simultaneously enhanced tolerance to drought, salinity and blast, illustrating the overlap between abiotic and biotic protection (Alam et al., 2024). A meta-analysis of cereals confirmed that aqueous seaweed extracts applied as foliar sprays increased shoot and root biomass under both normal and saline conditions (Nuruzzaman et al., 2025).

For maize, the strongest evidence is a two-year field trial comparing *Kappaphycus alvarezii*, *Gracilaria debilis* and *Sargassum cinctum* extracts, which are characterised by macronutrients, carotenoids, proline, micronutrients, phenolics, flavonoids and hormones. All three significantly improved plant growth, cob and yield attributes, grain quality and soil enzyme and nutrient status, with 7.5 % identified as the most effective dose (Gandhi et al., 2024b). Complementary greenhouse work under well-watered and drought conditions showed that foliar plant and seaweed extracts raised RWC, proline and glutathione and reduced MDA in maize (Han, M. et al., 2024). Comparative evidence for sorghum is thinner but instructive: seed priming with a biostimulant improved growth in both maize and sorghum at 80 % and 60 % field capacity, with maize being the more responsive species, consistent with its greater baseline drought sensitivity (Abu-Ria et al., 2024). Direct seaweed-extract evidence for sorghum, pearl millet, finger millet and barley under field drought remains a clear gap, which is significant given the importance of these crops in the semi-arid tropics.

5.2 Pulses and grain legumes

The largest single effect size reported for a field crop was observed in soybean. Water extract of the red alga *Gracilaria tenuistipitata* var. *liui* applied at 5 % and 10 % (v/v) under well-watered (80 % field capacity) and drought (40 % field capacity) conditions increased grain yield by 54.9 % under drought and 24.0 % under well-watered conditions at the 10 % dose, having first established that drought alone reduced grain yield by 45.6 % and raised the water saturation deficit by 37.9 % (Mannan et al., 2023). Therefore, the response represents partial recovery of a large stress-induced loss rather than an unconditional yield increase, which is the appropriate way to interpret such figures. Reviews of biostimulant use in soybean confirm improvements in water-use efficiency, antioxidant modulation and nutrient absorption across product classes (Sankhala et al., 2024).

In faba bean under arid and semi-arid drought, extracts of *Fucus spiralis*, *Ulva lactuca*, *Laminaria ochroleuca* and *Ascomyllum nodosum* all improved biomass during both the drought and recovery phases, but acted through partly different biochemical routes, demonstrating that feedstock selection changes the mechanism as well as the magnitude of response (El Boukhari et al., 2023). A concentrated blend of *Gracilaria salicornia* and *Sargassum swartzii* extracts at 0.1 % increased root growth and raised biomass by 18.9 % over the control in a green gram seedling assay under salt stress, with the product characterised for macro- and micronutrients, auxins, cytokinins, gibberellic acid, amino acids and alginic acid (Ramamoorthy & Munisamy, 2025). Under combined heat and water

deficit in off-season sowings, foliar vegetal protein hydrolysate at 2–6 mL L⁻¹ reduced yield losses in soybean and chickpea, indicating that protein-rich biostimulant chemistry a fraction also obtainable from red algae is effective in legumes under multiple stress (Mamatha et al., 2023).

5.3 Oilseeds

Oilseed evidence is limited but mechanistically detailed. In canola, seedlings sprayed with *Sargassum angustifolium* extract until the seven-leaf stage and then subjected to progressive water deficit (80 %, 60 % and 40 % field capacity in successive 20-day phases) showed improved photosynthetic pigment retention, free radical scavenging and SOD activity, with quantitative PCR confirming altered expression of stress-related genes across phases (Shahriari et al., 2021). This graded design is unusually informative because it separates mild from severe stress responses. For groundnut, sesame, sunflower, mustard and castor all major rainfed oilseeds in India and the semi-arid tropics published seaweed biostimulant evidence under field drought is scarce, representing one of the most tractable research opportunities identified in this review.

5.4 Fibre and sugar crops

Sugarcane offers the best field-scale evidence among the industrial crops. Foliar application of a seaweed extract-based biostimulant to late-harvest sugarcane during the driest period of the year, tested in three commercial field experiments in Brazil, increased stalk yield, sugar production and technological quality while enhancing plant metabolism (Jacomassi et al., 2022). A complementary study showed that seaweed extract enhanced drought resistance in sugarcane by modulating root configuration and soil physicochemical properties, thereby demonstrating both plant- and soil-mediated pathways in the same system (Chen, D. et al., 2023).

For cotton, the position is different and warrants candour. The mechanistic case is strong by extension: the failure points under rainfed stress stomatal dysfunction, oxidative injury, boll shedding, shortened fibre and poor micronaire correspond precisely to the mechanisms seaweed biostimulants influence and fibre quality depends on the timing and duration of carbohydrate supply during elongation and secondary wall deposition (Patil et al., 2024; Ul-Allah et al., 2021; Zhu et al., 2023). Reports from India indicate benefits for growth, boll retention and lint yield under rainfed conditions, with gains in boll set and fibre quality where application precedes flowering and continues through early boll fill (Kumar et al., 2024; Patil et al., 2024). However, most of these are short-term, single-location studies, product heterogeneity prevents synthesis across them and long-term Vertisol trials reporting agronomic outcomes together with fibre length, strength and micronaire are still lacking. Cotton is therefore best described as mechanistically well-supported but agronomically under-validated a conclusion that applies with equal force to jute and other fibre crops.

5.5 Forage grasses and turf: mechanistic insight from a contrasting system

Although not field crops in the arable sense, forage and turf studies contribute two findings of direct relevance. In perennial ryegrass, *Laminaria digitata* extract sprayed seven days before irrigation withdrawal, followed by 14 days of drought and 10 days of recovery, increased water content in leaves and in the basal shoot zone housing leaf meristems, limited the decline in leaf RWC, reduced membrane injury and stimulated nitrogen uptake during recovery at 2 and 5 L ha⁻¹, while higher doses were deleterious (Grandin-Courbet et al., 2025). This is one of the clearest published demonstrations of hormesis-based chemical priming in a crop system and it establishes both the value of a pre-stress priming interval and the risk of overdosing. In *Paspalum vaginatum* exposed to prolonged irrigation intervals and saline shock, *Ascophyllum nodosum* sprays at 5 and 7 mL L⁻¹ improved turf quality, photochemical efficiency, root length, dry weight, total non-structural carbohydrates and K and Ca composition (Elansary et al., 2017), reinforcing the recovery of both ionic and carbohydrate status under combined stress.

Table 5. Summary of documented seaweed biostimulant efficacy in field crops and related species under abiotic stress

Crop	Seaweed source or product	Dose and mode	Stress imposed	Key documented response	Reference(s)
Wheat	<i>Sargassum denticulatum</i>	2 % foliar	Water stress, 40 % FC	Improved growth and yield parameters; higher osmolytes, antioxidants and phenolics; cpDNA marker variation	Ali, A. H. et al. (2022)
Wheat	<i>Sargassum latifolium</i> ; <i>Corallina elongata</i> ; two commercial products	5 %	Drought	<i>C. elongata</i> most effective; shoot carbohydrate +34.6 % and protein +51.9 % at 37 days	Alharbi et al. (2022)

Wheat	<i>Ulva prolifera</i> enzymatic hydrolysate	0.02–0.1 %	Drought, 120 h	Longer shoot and root, higher root dry weight; CAT and POD increased; malondialdehyde –30.1 % at 0.1 %	Li et al. (2020)
Wheat	<i>Gracilaria dura</i> extract	Foliar	Drought	Drought tolerance via ABA homeostasis; increased biomass and yield	Sharma et al. (2019)
Wheat (durum)	Commercial biostimulant with N fertilisation	Field, two seasons	Reduced N supply	Improved rooting and chlorophyll; grain yield maintained with 33 % less N; grain protein +4 %	Rossini et al. (2025)
Wheat (seedling)	<i>Nostoc linckia</i> with chitosan nanoparticles	Seed and seedling	PEG, –2 and –4 MPa	Improved germination percentage and rate and early seedling growth in two contrasting cultivars	Gholizadeh et al. (2026)
Rice	<i>Ascophyllum nodosum</i>	Weekly and biweekly foliar	Salinity	Higher shoot and root biomass; ionic balance maintained; chlorophyll +26.4–31.0 %, carotenoids +11.9–16.7 %	Shahzad et al. (2023)
Rice	<i>Hypnea musciformis</i> ; <i>Gracilaria tenuistipitata</i>	Pot, extracts at varied pH and temperature	Drought, salinity and blast	Improved growth and simultaneous resistance to all three stresses	Alam et al. (2024)
Maize	<i>Kappaphycus alvarezii</i> ; <i>Gracilaria debilis</i> ; <i>Sargassum cinctum</i>	7.5 % foliar; two-year field trial	Field conditions	Enhanced growth, cob and yield attributes, grain quality, soil enzyme and nutrient status	Gandhi et al. (2024b)
Maize	Seaweed extract (comparative treatment)	Foliar, glasshouse	Drought	Higher relative water content, proline and glutathione; reduced malondialdehyde	Han, M. et al. (2024)
Maize and sorghum	Humic acid (comparative biostimulant)	100 mg L ⁻¹ seed priming	80 % and 60 % FC	Improved vegetative growth and reduced oxidative stress; maize more responsive than sorghum	Abu-Ria et al. (2024)
Soybean	<i>Gracilaria tenuistipitata</i> var. <i>liui</i>	5 % and 10 % (v/v) foliar	40 % FC and 80 % FC	Grain yield +54.9 % under drought and +24.0 % under well-watered conditions at 10 %	Mannan et al. (2023)
Faba bean	<i>Fucus spiralis</i> ; <i>Ulva lactuca</i> ; <i>Laminaria ochroleuca</i> ; <i>Ascophyllum nodosum</i>	Foliar	Drought with recovery phase	All extracts improved biomass; mechanisms differed by feedstock	El Boukhari et al. (2023)
Green gram	<i>Gracilaria salicornia</i> with <i>Sargassum swartzii</i>	0.1 % concentrated extract	Salinity	Increased root development; biomass +18.9 % over control	Ramamoorthy & Munisamy (2025)
Soybean and chickpea	Vegetal protein hydrolysate	2–6 mL L ⁻¹ foliar	Combined heat and water deficit	Reduced yield losses in off-season sowings	Mamatha et al. (2023)
Canola	<i>Sargassum angustifolium</i>	Repeated foliar to 7-leaf stage	80, 60 and 40 % FC in phases	Pigments retained; radical scavenging and SOD activity increased; stress genes differentially expressed	Shahriari et al. (2021)

Sugarcane	Seaweed extract-based biostimulant	Foliar; three commercial field sites	Dry-season drought	Higher stalk yield, sugar production and technological quality; plant metabolism sustained	Jacomassi et al. (2022)
Sugarcane	Seaweed extract	Soil and foliar	Drought	Enhanced drought resistance via modified root configuration and improved soil physicochemical properties	Chen, D. et al. (2023)
Cotton	Commercial seaweed extracts (heterogeneous)	Foliar at reproductive stages	Rainfed drought	Reported gains in growth, boll retention and lint yield; evidence largely single-season and single-location	Kumar et al. (2024); Patil et al. (2024)
Perennial ryegrass	<i>Laminaria digitata</i>	2 and 5 L ha ⁻¹ , 7 days before stress	14-day drought and 10-day recovery	Meristem-zone water content and membrane stability maintained; N uptake stimulated on rehydration; higher doses deleterious	Grandin-Courbet et al. (2025)
Turfgrass (<i>Paspalum vaginatum</i>)	<i>Ascophyllum nodosum</i>	5 and 7 mL L ⁻¹ at 6-day intervals	Prolonged irrigation interval with saline shock	Improved turf quality, photochemical efficiency, root length and dry weight, non-structural carbohydrates, K and Ca	Elansary et al. (2017)

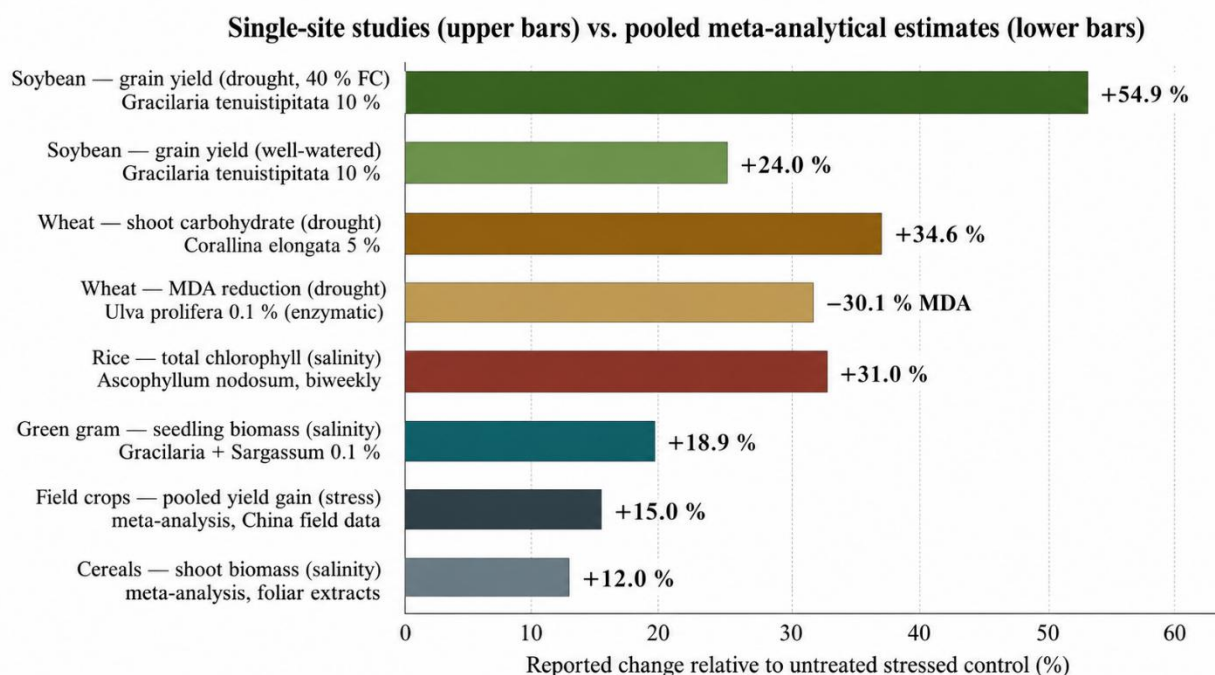


Figure 3. Magnitude of reported responses to seaweed-based biostimulants under abiotic stress in field crops. Upper bars represent single-site controlled or field studies with the seaweed source and dose indicated; lower bars represent pooled meta-analytical estimates. The metrics are not interchangeable and are stated individually for each bar; the wheat malondialdehyde value denotes a reduction, plotted as absolute magnitude. Sources: Mannan et al. (2023), Alharbi et al. (2022), Li et al. (2020), Shahzad et al. (2023), Ramamoorthy and Munisamy (2025), Pei et al. (2024) and Nuruzzaman et al. (2025).

Two patterns emerged from this cross-crop appraisal. First, the effect sizes from single-site studies at high extract concentrations substantially exceed the pooled meta-analytical estimates, which cluster around 10–20 % under stress (Pei et al., 2024; Pérez-Oñate et al., 2026; Staykov et al., 2025). The discrepancy is expected, as controlled studies impose severe, uniform stress and use doses well above economic rates; however, this means that headline figures from individual papers should not be used for extension recommendations. Second, the response is greatest where stress is genuinely limiting; under adequate water and nutrition, seaweed application produces small or

negligible gains (Velasco-Clares et al., 2024). Thus, efficacy is conditional and targeting is the principal determinant of return on investment.

6. SOIL-MEDIATED AND RHIZOSPHERE IMPACTS

Seaweed-based biostimulants influence crop and soil processes simultaneously. This dual action is particularly consequential in rainfed field crop systems, where water capture, root function and soil structural stability govern seasonal performance. Pot, lysimeter and field studies have shown that seaweed extracts alter root architecture, stimulate rhizosphere activity, improve soil physical properties and enhance nutrient delivery and that these changes support yield stability and quality during dry spells and heat (Ali, O. et al., 2021; El Boukhari et al., 2020; Kumar et al., 2024; Renaut et al., 2019; Yasmeen et al., 2025).

6.1 Root morphology and rhizosphere activity in Vertisols and heavy-textured soils

Root system architecture (RSA) determines the capacity to extract water from Vertisols, where high clay content and shrink–swell cracking create both obstacles and opportunities for root exploration (Çakir & Cangir, 2021; Melo et al., 2023). Seaweed extracts, particularly those derived from *Ascophyllum* and *Ecklonia*, stimulate adventitious and lateral root formation, increase root length density and promote fine-root development across crops (Ali, O. et al., 2021; Loconsole et al., 2024; Nunes Gomes et al., 2018; Renaut et al., 2019). Auxin-like activity and small signalling peptides in the extracts, together with improved nutrient availability, jointly drive cell division and root elongation (Kumar et al., 2024; Sujeeth et al., 2022). Quantitative confirmation is available from a green gram root assay in which a red–brown seaweed blend at 0.1 % increased measured root development and total biomass under salt stress (Ramamoorthy & Munisamy, 2025) and from sugarcane, where seaweed extract enhanced drought resistance specifically through modified root configuration (Chen, D. et al., 2023).

In Vertisols, an improved RSA expands the effective rooting volume by allowing finer roots to exploit cracks and micropores and reach stored moisture during dry periods (Çakir & Cangir, 2021; Melo et al., 2023). Seaweed application also alters root exudation and rhizodeposition, which changes microbial colonisation by mycorrhizae and plant growth-promoting rhizobacteria and modifies enzyme activities central to nutrient turnover and structural maintenance (Pantigoso et al., 2022; Renaut et al., 2019). Field observations indicate that seaweed-treated plants develop more extensive root systems in compacted or clay-rich soils and recover more completely after drought, which is directly relevant to rainfed field crops grown on Vertisols (Arias et al., 2023; Chen, D. et al., 2023).

6.2 Soil water retention, aggregate stability and microbial dynamics

Seaweed polysaccharides alginates, ulvans and laminarins contribute to soil organic matter when applied repeatedly, improving aggregate stability, porosity and water retention, all of which govern water storage between rainfall events (Akter et al., 2024; Arias et al., 2023; Tariq et al., 2025). Laboratory and field studies report increases in water-stable aggregates and infiltration rate following repeated application of seaweed extract or seaweed-based compost, attributable to greater microbial extracellular polysaccharide production and improved binding of mineral particles by seaweed-derived organic material (Akter et al., 2024; Arias et al., 2023; Chen, D. et al., 2023; El Boukhari et al., 2020). In Vertisols, where rapid wetting and drying cycles disrupt structure, even modest gains in aggregation translate into measurable increases in plant-available water (Çakir & Cangir, 2021; Melo et al., 2023).

Seaweed inputs also shift rhizosphere microbial diversity and functional group composition, favouring nitrogen cyclers, phosphorus solubilisers and saprotrophs that accelerate nutrient recycling and contribute to transient water retention through organic binding (Luo et al., 2025; Pantigoso et al., 2022; Renaut et al., 2019; Singh, A. et al., 2025). Crops treated with seaweed extracts frequently show higher soil enzyme activities, including dehydrogenase and β -glucosidase and greater microbial biomass carbon, indicators associated with improved soil functioning and greater resistance to drying (Pei et al., 2024; Rabhi et al., 2025). The two-year maize field trial cited earlier is notable in this respect because it documented improvements in soil enzyme and nutrient status alongside yield, linking the two pathways in a single experiment (Gandhi et al., 2024b). Collectively, these plant–soil–microbe interactions provide a modest but agronomically meaningful buffer during mid-season dry spells (Table 6; Figure 4).

Table 6. Soil and rhizosphere indicators responsive to seaweed biostimulant application and their relevance in rainfed heavy-textured soils

Indicator	Typical direction	Mechanistic basis	Relevance in rainfed heavy-textured soils	Reference(s)
Root length density and fine-root fraction	Increase	Auxin-like activity and signalling peptides in extracts; improved local nutrient availability	Allows exploitation of cracks and micropores, expanding effective rooting volume in Vertisols	Ali, O. et al. (2021); Chen, D. et al. (2023); Renaut et al. (2019)

Water-stable aggregates and porosity	Increase	Polysaccharide and organic colloid input; enhanced microbial extracellular polysaccharide production binding mineral particles	Counters structural breakdown under rapid wetting and drying cycles	Akter et al. (2024); Arias et al. (2023); El Boukhari et al. (2020)
Infiltration rate and plant-available water	Increase	Improved aggregation and pore continuity following repeated application	Raises capture and retention of erratic rainfall between events	Arias et al. (2023); Çakir & Cangir (2021); Melo et al. (2023)
Microbial biomass carbon and functional diversity	Increase	Altered root exudation and rhizodeposition favouring N cyclers, P solubilisers and saprotrophs	Accelerates nutrient recycling when moisture windows are short	Luo et al. (2025); Pantigoso et al. (2022); Singh, A. et al. (2025)
Soil enzyme activity (dehydrogenase, β -glucosidase)	Increase	Greater microbial activity and labile carbon supply	Serves as an early indicator of improved soil functioning under stress	Pei et al. (2024); Gandhi et al. (2024b); Yasmeen et al. (2025)
Nutrient use efficiency	Increase	Enhanced transporter activity, chelation of micronutrients, improved phloem loading	Permits reduced fertiliser rates; 33 % N saving demonstrated in durum wheat	Kumar et al. (2024); Rossini et al. (2025)

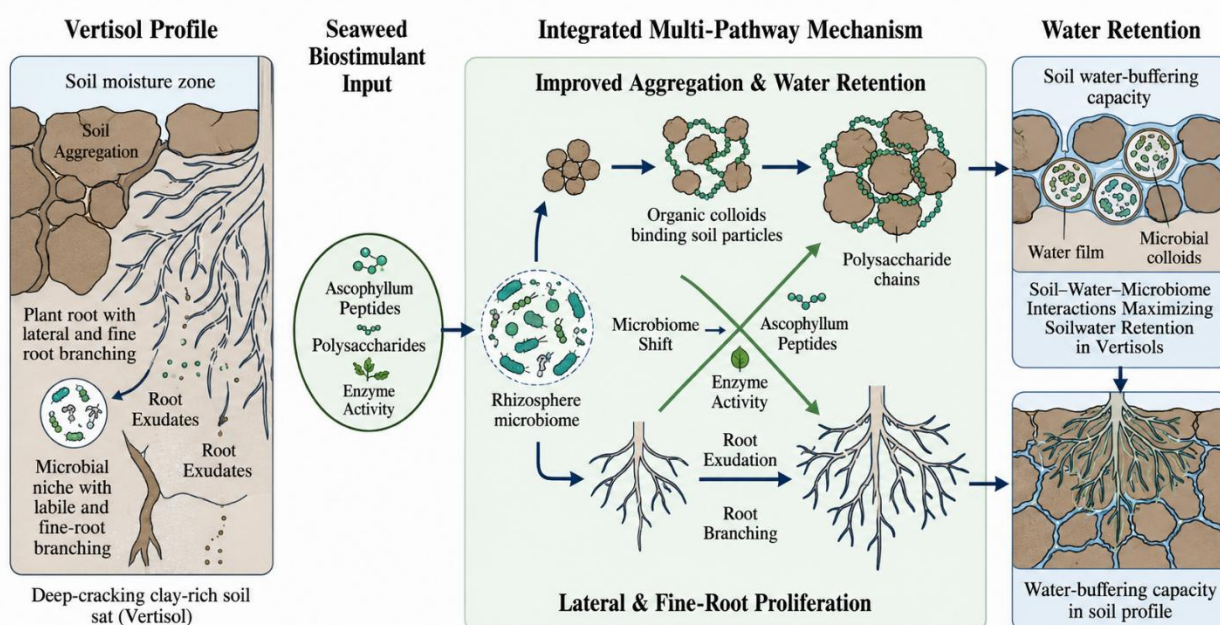


Figure 4. Soil-root-microbiome interactions mediated by seaweed biostimulants in Vertisols and other heavy-textured soils. Polysaccharide and organic colloid inputs improve aggregation and water retention, auxin-like signals and signalling peptides promote lateral and fine-root proliferation and altered root exudation reshapes the rhizosphere microbiome and enzyme activity. The three pathways interact, extending soil-water buffering and sustaining transpiration through mid-season dry spells.

6.3 Synergy with fertigation and foliar nutrient delivery under water deficit

Combining seaweed biostimulants with fertigation and foliar nutrition improves nutrient efficiency under water limitation. Seaweed extracts increase root nutrient uptake rates, enhance transporter activity and improve phloem loading and unloading, thereby raising the effectiveness of applied NPK and micronutrients (Ali, O. et al., 2021; Kumar et al., 2024; Pei et al., 2024). Foliar seaweed extract combined with low doses of nitrogen or zinc has improved photosynthesis, fruit or boll set and early retention in several crops under drought (Kumar et al., 2024; Renaut et al., 2019; Santaniello et al., 2017). The most rigorous cereal demonstration remains the durum wheat study in which biostimulant application permitted a 33 % nitrogen saving while increasing grain yield and protein content, an outcome with direct implications for input economics and nitrogen loss mitigation (Rossini et al., 2025). Complementary evidence from perennial ryegrass shows that algal extract priming stimulated nitrogen uptake specifically during recovery after rehydration (Grandin-Courbet et al., 2025), suggesting that the nutrient-efficiency benefit is partly a recovery phenomenon rather than a stress-phase one.

In fertigation systems, seaweed concentrates can improve root uptake efficiency and reduce leaching losses, which is particularly important for rain-fed farmers who apply limited fertiliser opportunistically after rainfall (Arias et al., 2023; Rabhi et al., 2025). Seaweed-derived compounds also chelate micronutrients, improving their uptake and in-plant mobility when sprayed an advantage in rain-fed systems where fluctuating soil moisture restricts root uptake at critical reproductive stages (Ali, O. et al., 2021; Siddik et al., 2023). Timing and formulation choice, specifically pre-stress conditioning and early reproductive-stage application, largely determine whether these synergies are realised (Staykov et al., 2025; Thakur et al., 2025).

6.4 Yield sustainability and quality attributes under stress

Agronomic trials across climates indicate that seaweed biostimulants stabilise yield under water stress by preserving canopy function, improving reproductive set and sustaining assimilate supply to developing sinks (Jacomassi et al., 2022; Pei et al., 2024; Ul-Allah et al., 2021). Meta-analyses report average yield improvements of approximately 10–20 % in stress-affected trials across crops (Pei et al., 2024; Staykov et al., 2025) and the most recent and largest synthesis, covering 198 studies and 2, 021 paired comparisons, confirms positive overall effects while showing that they depend systematically on application strategy, formulation characteristics, extraction method, climate, stress exposure, experimental setting, soil chemical properties, crop group and phenological timing (Pérez-Oñate et al., 2026). Quality responses are also documented: grain quality and protein improvements in wheat and maize (Gandhi et al., 2024b; Rossini et al., 2025), improved juice purity and technological quality in sugarcane (Jacomassi et al., 2022) and, for cotton, reported gains in fibre length and micronaire where application coincides with key growth stages, although the underlying evidence base is thin (Kumar et al., 2024; Patil et al., 2024).

Economic feasibility remains the weakest link. For smallholder rainfed producers, viability depends on product cost, the local magnitude of drought-induced loss and compatibility with existing soil and nutrient management (Arias et al., 2023; Kocira et al., 2020; Rabhi et al., 2025). A biochemical and economic assessment of seaweed- and amino acid-based biostimulants confirmed that agronomic and financial outcomes can diverge; therefore, both must be reported (Kocira et al., 2020). Long-term trials on Vertisols and other rainfed soils that measure agronomic performance, product quality and partial budgets are still scarce and constitute a priority for future work.

7. INTEGRATION INTO FIELD CROP PRODUCTION SYSTEMS

7.1 Compatibility with conservation and climate-smart agronomic practices

Seaweed-based biostimulants are compatible with conservation agriculture, including minimum tillage, residue retention and crop rotation and with agroforestry and other practices that increase resilience and water-use efficiency in rainfed systems (Ali, O. et al., 2021; Arias et al., 2023; Gopalakrishnan & Ghosh, 2022). The polysaccharide fraction and organic colloids can build soil organic matter and assist aggregate formation when applied regularly or blended with composts and mulches, reinforcing residue-based conservation strategies (Akter et al., 2024; Arias et al., 2023; Yasmeen et al., 2025). Applying foliar or soil-applied seaweed extract alongside mulching and minimum tillage can produce additive benefits, since mulching reduces evaporative loss while the biostimulant promotes root proliferation and microbial activity, together increasing soil water capture and access during dry spells (Melo et al., 2023; Pei et al., 2024). Field demonstrations and studies translating controlled-environment findings to the field confirm that seaweed products integrate well into organic and low-input systems because of their low toxicity and multiple modes of benefit (Ali, O. et al., 2021; Leogrande et al., 2022; Loconsole et al., 2024).

Effective adoption requires that application timing be aligned with the conservation practice in use. In residue-retaining systems, application 7–14 days before an anticipated stress episode improves root growth and antioxidant status, consistent with the priming interval established experimentally in perennial ryegrass (Grandin-Courbet et al., 2025; Kumar et al., 2024; Santaniello et al., 2017). In systems with little residue cover, an early-season soil drench helps establish a root network capable of exploiting conserved moisture. Pairing biostimulants with climate-smart water harvesting contour bunding, tied ridges and micro-catchments is logical because a biostimulant-enhanced root system can exploit conserved moisture more completely (Çakir & Cangir, 2021; Gopalakrishnan & Ghosh, 2022; Melo et al., 2023).

7.2 Formulation optimisation and delivery approaches for arid and semi-arid zones

In arid and semi-arid environments, formulation and delivery determine whether biological activity is expressed. Liquid foliar sprays, concentrated soil drenches, seed treatments and encapsulated granules confer different advantages: foliar sprays produce rapid physiological effects, such as stomatal modulation and antioxidant induction, whereas soil drenches and encapsulated products support root development and improve the root environment (Arias et al., 2023; Kumar et al., 2024). In low-rainfall areas, controlled-release formulations, including microencapsulation and polymer coating, together with adjuvant-enhanced sprays, reduce wash-off during erratic rainfall and maintain active concentrations over longer stress periods, improving the cost-effectiveness of each application (Rabhi et al., 2025; Staykov et al., 2025). Advanced extraction and fractionation,

notably enzyme-assisted depolymerisation and ultrasound- or microwave-assisted extraction, can generate oligosaccharide-enriched fractions with greater elicitor potency per unit mass, permitting lower application rates suited to resource-constrained smallholders (Gandhi et al., 2024a; Li et al., 2020; Zhou et al., 2024).

Timing is crucial in dryland conditions. Pre-conditioning sprays applied before peak evaporative demand, together with targeted applications at flowering and early sink filling, give the best return across crops (Pei et al., 2024; Santaniello et al., 2017). Soil-application strategies that combine seaweed concentrates with conditioners such as biochar or compost can retain water and release bioactives gradually into the root zone, sustaining root activity between rainfall events (Arias et al., 2023; Chen, D. et al., 2023). Formulation choices should therefore prioritise stability, targeted release and minimal labour and time demands under smallholder conditions. Where feedstock supply is a constraint, the valorization of cultivated biomass and invasive *Sargassum* accumulations offers a route to lower-cost, traceable raw materials with additional environmental co-benefits (Hermans, 2024; Martínez-Martínez et al., 2025).

7.3 A crop-stage decision framework for application

Synthesising mechanistic and agronomic evidence yields a practical decision sequence: diagnose the dominant stress and the probability and likely timing of its occurrence; select a feedstock and fraction matched to that stress; and schedule a pre-stress priming application followed by critical-stage support. Priming logic follows from the transcriptional and antioxidant evidence, which shows that treated plants respond faster and more strongly to subsequent stress than untreated ones (Gechev, 2025; Peng et al., 2025). Critical-stage logic follows from the yield physiology of each crop group: anthesis to grain filling in cereals, flowering to pod set in pulses, squaring to boll development in cotton and the grand growth phase in sugarcane. Table 7 sets out indicative windows and delivery modes by crop group and Figure 5 places these within the wider production system. These are working recommendations derived from published mechanisms and trials rather than validated prescriptions and local calibration remains essential.

Table 7. Indicative application windows, delivery modes and rationale for seaweed biostimulant use by field crop group

Crop group	Priming window	Critical-stage application	Preferred delivery	Rationale	Reference(s)
Cereals (wheat, rice, maize, sorghum, millets)	Seed treatment plus a foliar spray 7–14 days before the anticipated stress episode	Booting to anthesis and early grain filling	Foliar spray; soil drench at establishment where residue cover is low	Grain number and filling duration are set in a narrow window; antioxidant and transcriptional priming acts fastest when it precedes stress	Grandin-Courbet et al. (2025); Alharbi et al. (2022); Li et al. (2020); Rossini et al. (2025); Gandhi et al. (2024b)
Grain legumes (soybean, chickpea, faba bean, green gram, pigeonpea)	Seed priming plus foliar spray at the late vegetative stage	Flowering to early pod filling	Foliar spray; seed priming for establishment vigour	Flower and pod abortion is the dominant loss pathway; the largest documented soybean response followed reproductive-stage sprays	Mannan et al. (2023); El Boukhari et al. (2023); Mamatha et al. (2023); Ramamoorthy & Munisamy (2025)
Oilseeds (canola, mustard, groundnut, sesame, sunflower)	Repeated foliar sprays through vegetative growth to the six- to seven-leaf stage	Flowering to seed filling	Foliar spray; encapsulated soil application in low-rainfall zones	Pigment retention and antioxidant capacity are the demonstrated mechanisms and must be established before severe deficit	Shahriari et al. (2021); Pei et al. (2024); Staykov et al. (2025)
Fibre crops (cotton)	Soil application at establishment plus a foliar spray before squaring	Squaring through peak boll development	Foliar spray with soil drench or fertigation where available	Fibre length and micronaire depend on uninterrupted carbohydrate supply during elongation and wall deposition	Patil et al. (2024); Ul-Allah et al. (2021); Zhu et al. (2023); Kumar et al. (2024)
Sugar crops (sugarcane)	Soil or fertigation application at tillering	Grand growth phase, particularly if it coincides with the dry season	Fertigation or soil drench with supplementary foliar spray	Stalk elongation and sucrose accumulation are the loss pathways; field evidence derives from dry-season foliar application	Jacomassi et al. (2022); Chen, D. et al. (2023)

Forage grasses	Foliar spray approximately 7 days before an expected dry period	Repeat after each defoliation or grazing cycle	Low-rate foliar spray	Meristem protection and post-rehydration nitrogen uptake respond to low doses; higher doses are deleterious	Grandin-Courbet et al. (2025); Elansary et al. (2017)
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7.4 Field validation and meta-analytical evidence from Indian and global studies

Field evidence for seaweed biostimulants in field crops is expanding but remains uneven. Meta-analyses and multi-site studies show consistent positive effects on biomass, water-use efficiency and stress resilience across crops, with pooled effect sizes typically indicating yield increases of 10–20 % under stress (Nuruzzaman et al., 2025; Pei et al., 2024; Staykov et al., 2025). The largest synthesis to date reported positive overall yield and biomass responses but attributed much of the variability to application strategy, formulation, extraction method, crop group and phenological timing, which is a direct argument for standardised reporting (Pérez-Oñate et al., 2026). Global reviews and trials suggest that Ascophyllum-derived products and oligosaccharide-enriched fractions are among the most reliable, while outcomes vary with genotype, soil type and climate (Kumar et al., 2024; Loconsole et al., 2024; Shukla et al., 2019).

For Indian conditions, the evidence base is genuinely promising but structurally weak. Two-year field trials on maize with tropical red and brown seaweed extracts provide the most robust national-level demonstration, including soil enzyme and nutrient responses (Gandhi et al., 2024b) and characterisation of minimally processed Kappaphycus and Sargassum homogenates provides a scientific basis for low-cost domestic products (Vaghela et al., 2023). Work specifically framed around dryland and semi-arid adaptation confirms the relevance of seaweed biostimulants to Indian rainfed agriculture (Gopalakrishnan & Ghosh, 2022). Reports on cotton indicate benefits for growth, boll retention and lint yield under rainfed conditions, but these are largely short-term, single-location studies (Kumar et al., 2024; Patil et al., 2024). The dominant limitation is not the absence of positive results but the heterogeneity of products and the lack of standardised potency metrics, which prevents formal synthesis across trials (Buss et al., 2025; Pérez-Oñate et al., 2026).

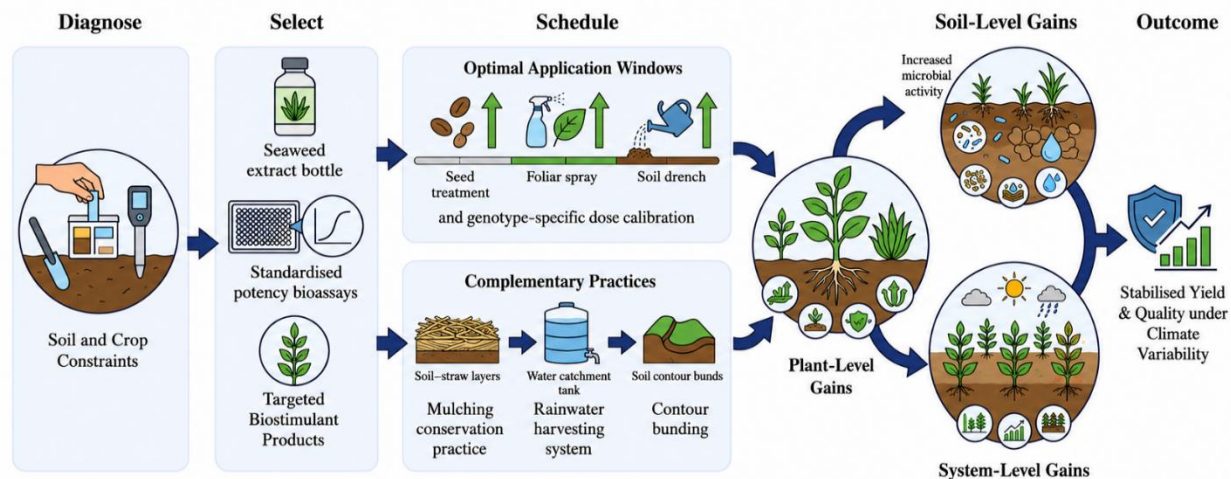


Figure 5. Conceptual framework for integrating seaweed-based biostimulants into field crop production systems. A three-step decision sequence (diagnose, select, schedule) informs choices among delivery options and is coupled with conservation and water-harvesting co-management. Plant-, soil- and system-level gains converge on a stabilised yield and quality under climate variability, conditional on the enabling conditions listed, which include standardised potency bioassays, transparent labelling, multi-season multi-location trials, crop- and genotype-specific dose calibration, farm-level economic assessment, harmonised regulation and sustainable feedstock supply.

8. CONSTRAINTS, KNOWLEDGE GAPS AND FUTURE DIRECTIONS

Five constraints recur across the literature and jointly explain why a mechanistically well-supported technology has achieved uneven field adoption. First, product heterogeneity: feedstock species, harvest season and location, extraction route and post-harvest handling all alter bioactive composition, so nominally similar products are not equivalent and cannot be pooled analytically (Arias et al., 2023; El-Beltagi et al., 2026). Second, the absence of

standardised potency assays and compositional labelling prevents dose recommendations from transferring between products and impedes regulatory harmonisation (Buss et al., 2025; Hermans, 2024; Sujeeth et al., 2022). Third, hormetic dose responses: activity peaks at low to moderate rates and declines or becomes deleterious at higher rates, as demonstrated directly under drought (Grandin-Courbet et al., 2025). Fourth, the predominance of single-season, single-site, often pot-based experiments, which cannot capture the season-to-season variability that determines the actual value of a resilience input (Patil et al., 2024; Pérez-Oñate et al., 2026). Fifth, thin economic evidence, particularly for smallholders, where labour, application logistics and product cost may outweigh modest yield gains (Kocira et al., 2020; Rabhi et al., 2025).

Crop coverage is also skewed. Wheat, rice, maize, soybean and sugarcane are reasonably represented, whereas sorghum, pearl millet, finger millet, barley, groundnut, sesame, sunflower, mustard, pigeonpea and cotton precisely the crops that dominate rainfed areas in the semi-arid tropics are sparsely covered and cotton in particular lacks multi-season Vertisol trials with fibre quality endpoints needed for recommendations. Mechanistic depth is similarly uneven: transcriptomic and proteomic evidence derives largely from Arabidopsis, tomato and a few cereals; therefore, the assumption that transcription factor networks respond identically in pulses, oilseeds and fibre crops remains untested (Ateeq et al., 2026; De Saeger et al., 2019).

The priority actions set out in Table 8 follow from these gaps. Four merit emphasis. Standardisation should combine physiological bioassays with molecular markers so that potency is defined functionally rather than by nominal concentration. Multi-location, multi-season trials should adopt common protocols, report stress intensity quantitatively (for example as field capacity or water potential) and include quality and partial budget endpoints, enabling formal meta-analysis. Dose–response and timing studies must be crop- and genotype-specific and should explicitly test for hormesis rather than assuming monotonic response. Finally, feedstock sustainability and supply chains deserve attention: transition from wild harvest to cultivated biomass, valorisation of invasive *Sargassum* and integration of biorefinery co-products can lower cost while improving traceability and environmental performance (Arias et al., 2023; Hermans, 2024; Martínez-Martínez et al., 2025). Combining seaweed extracts with microalgal, microbial and protein hydrolysate biostimulants and evaluating such combinations under realistic combined stress, is a further promising direction given the evidence that efficacy is often greatest under multiple concurrent stresses (Asif et al., 2023; Mamatha et al., 2023; Witzel et al., 2025).

Table 8. Knowledge gaps, their significance and priority research actions for seaweed biostimulant use in field crops.

Knowledge gap	Why it matters	Priority research action	Suggested endpoint or metric	Reference(s)
Absence of standardised potency assays	Products with identical labels differ in bioactivity, so dose recommendations do not transfer and trials cannot be pooled	Develop functional bioassays combining physiological response with molecular markers; couple to mandatory compositional declaration	Bioassay-defined activity units; molecular-weight profile, degree of sulfation and phenolic fingerprint	Buss et al. (2025); Sujeeth et al. (2022); Hermans (2024); Gandhi et al. (2024a)
Hormetic dose–response behaviour	Activity peaks at low to moderate rates and can become deleterious at higher rates, so extrapolation from single-dose studies misleads	Conduct crop- and genotype-specific dose–response studies with at least five rates spanning below and above the expected optimum	Dose–response curve with identified optimum and threshold of adverse effect	Grandin-Courbet et al. (2025); Velasco-Clares et al. (2024)
Predominance of single-season, single-site and pot studies	Season-to-season variability determines the real value of a resilience input and cannot be captured in one season	Establish multi-location, multi-season trials on common protocols with quantitative reporting of stress intensity	Yield stability and variance across seasons; field capacity or leaf water potential during stress	Pérez-Oñate et al. (2026); Patil et al. (2024); Staykov et al. (2025)
Skewed crop coverage	Sorghum, millets, barley, groundnut, sesame, mustard, pigeonpea and cotton dominate rainfed area yet are sparsely studied	Prioritise field trials in rainfed cereals, pulses and oilseeds of the semi-arid tropics, including Vertisol sites	Grain, lint or oil yield with quality attributes and partial water balance	Gopalakrishnan & Ghosh (2022); Abu-Ria et al. (2024); Kumar et al. (2024)
Thin fibre and grain quality evidence	Quality determines market value and is set during the same	Include quality endpoints as primary rather than secondary variables in all trials	Fibre length, strength and micronaire; grain	Ul-Allah et al. (2021); Zhu et al. (2023); Rossini et al. (2025)

	window that stress disrupts		protein, test weight and oil content	
Limited economic evidence for smallholders	Modest yield gains may not offset product, labour and application cost under low-input conditions	Report partial budgets and benefit–cost ratios alongside agronomic outcomes; test reduced-rate oligosaccharide-enriched fractions	Benefit–cost ratio; break-even yield response; cost per hectare per application	Kocira et al. (2020); Rabhi et al. (2025); Arias et al. (2023)
Mechanistic evidence concentrated in model species	Transcription factor and proteomic responses are assumed rather than demonstrated in pulses, oilseeds and fibre crops	Extend transcriptomic, proteomic and metabolomic profiling to field-grown target crops under realistic stress	Validated marker gene panels correlated with field yield response	De Saeger et al. (2019); Ateeq et al. (2026); Ali, O. et al. (2022)
Feedstock sustainability and supply	Reliance on wild harvest constrains scale, traceability and cost, particularly for domestic manufacture	Evaluate cultivated biomass, invasive Sargassum valorisation and biorefinery co-product routes	Cost per unit bioactivity; life-cycle assessment; batch-to-batch consistency	Martínez-Martínez et al. (2025); Hermans (2024); Arias et al. (2023)
Untested combination products	Efficacy is often greatest under combined stress, where multi-component products may act additively	Test seaweed extracts in factorial combination with microalgal, microbial and protein hydrolysate biostimulants under combined stress	Interaction effect size on yield and quality under combined stress	Asif et al. (2023); Mamatha et al. (2023); Witzel et al. (2025)

9. CONCLUSIONS

Abiotic stress is the dominant constraint on field crop productivity in rain-fed and marginally irrigated systems and its effects operate simultaneously at the molecular, whole-plant and soil system scales. The evidence assembled here indicates that seaweed-based biostimulants act on this constraint through a coherent and interconnected set of mechanisms: antioxidant priming and ROS homeostasis, phytohormone modulation with ABA sensitisation and cytokinin-like anti-senescence activity, osmolyte accumulation and improved cellular hydration, photosynthetic apparatus protection, activation of stress-responsive transcription factor networks and membrane stabilisation with restored ion homeostasis. In parallel, soil-mediated effects on root architecture, aggregate stability, water retention and rhizosphere function provide a second, complementary route to resilience that is particularly relevant in Vertisols and other heavy-textured soils.

Crop-level evidence now supports these mechanisms in wheat, rice, maize, soybean, faba bean, green gram, canola and sugarcane, with documented gains ranging from partial recovery of severe drought-induced yield loss in soybean to improved stalk and sugar yield in field-grown sugarcane and a demonstrated 33 % nitrogen saving in durum wheat. Pooled meta-analytical estimates of roughly 10–20 % yield gain under stress provide a realistic expectation for field conditions, well below the largest single-study effects. Efficacy is conditional rather than general: it is greatest where stress genuinely limits yield, where application precedes or coincides with the critical stage and where dose is calibrated to crop and genotype.

The principal obstacles to wider adoption are not mechanistic but methodological and institutional product heterogeneity, absence of standardised potency assays, hormetic dose behaviour, a shortage of multi-season multi-location validation and limited economic evidence for smallholders. Addressing these through standardised functional bioassays, transparent compositional labelling, harmonised regulation, common trial protocols with quantitative stress reporting, crop-specific dose–response calibration and sustainable feedstock supply would convert a promising body of laboratory and single-site evidence into dependable field practice. For rainfed field crops facing increasingly variable climates, seaweed-based biostimulants represent a low-toxicity, multi-functional and locally producible option whose realistic contribution is to reduce yield variance and protect quality rather than to raise potential yield a contribution that is nonetheless of considerable value where risk, not potential, limits farm income.

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Author contributions

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Gunasekhar Nachimuthu: Reviewing and editing.

Consent to participate

All authors consented to participate in the article (K.M.Sellamuthu- on behalf of all coauthors).

Consent to publish

All authors gave their consent for the article to be published if it was accepted (K.M.Sellamuthu, on behalf of all coauthors).

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