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Physiological and Biochemical Responses of Tomato (Solanum lycopersicum L.) to Ascophyllum nodosum Extract under Water Deficit Stress: A Structured Review and Evidence Synthesis

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I. ABSTRACT

Background: Tomato productivity is highly sensitive to episodic and chronic water deficit, while seaweed-derived biostimulants based on Ascophyllum nodosum extract (ANE) have emerged as promising tools for stabilizing plant performance under drought. However, agronomic and mechanistic evidence remains scattered among formulation-specific experiments.

Materials and Methods: This manuscript was prepared as a structured narrative review and evidence synthesis of peer-reviewed literature published between 2010 and March 2026. Tomato studies under water deficit were prioritized and interpreted alongside companion mechanistic studies dealing with related abiotic stresses and stress-signaling responses.

Results: Across the representative evidence base, ANE treatment was consistently associated with improved leaf water status, stomatal regulation, chlorophyll retention, photosynthetic performance, osmotic adjustment, antioxidant protection, membrane stability, fruit set, yield, and water productivity. Response magnitude depended on formulation, dose, application route, and integration with nutrient management. Molecular studies further indicate transcriptional and metabolic priming, delayed senescence, and preservation of photosynthetic machinery.

Conclusion: ANE is a credible component of climate-resilient tomato production, but future Q1-grade studies should standardize extract characterization, cultivar background, irrigation thresholds, and reporting endpoints, and integrate omics data with agronomic validation.

Key words : *Ascophyllum nodosum; biostimulant; drought stress; tomato; water deficit; photosynthesis; antioxidant defense.*

II. INTRODUCTION

Tomato (Solanum lycopersicum L.) is one of the most economically significant vegetable crops used worldwide, although its production is highly sensitive to any decrease in soil water availability. A tomato water shortage has a rapid effect on cell turgor, stomata, leaf temperature, chlorophyll stability, assimilate partitioning, reproductive development, and ultimate fruit output [7], [8]. Due to the increasing frequency and unpredictability of droughts and the impacts of climate change, agronomic measures to enhance tolerance and avoid overly exposing the environment are receiving significant focus [3], [4], [6].

Bio-stimulants derived from seaweed and developed so far have become a promising new line of crop inputs with low dosage. One of the most examined brown seaweeds to approach commercially, including in commercial plant bio stimulants, is Ascophyllum nodosum, the extracts of which have been linked to seedling vigor, nutrient utilization, photosynthesis, fruit quality, and abiotic stress (tolerance) [1], [2], [4], [5]. These products are chemically complicated and could include polysaccharide-containing fractions, compatible solutes, phenolic compounds, organic acids, and minerals, and can have hormone-like activity; thus, their bioactivity is more than nutritional and may involve signaling, priming, and stress-memory activity [1], [2], [5], [6].

The Ascophyllum nodosum extract (ANE) cannot be generalized without the product chemistry. Technology of extraction, processing temperature, fractionation strategy, and formulation additives may affect the bioactivity of the

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end product [1], [5], [16]. This is especially the case when drought conditions are involved, since dissimilar commercial preparations can have varied effects when administered to the same crop under similar irrigation conditions [9]. Thus, ANE effects need to be discussed at the Q1-level to go beyond generic statements and analyze the dependence of formulations, their routes of application, and cultivar and environment.

Direct evidence on tomato under water-deficit conditions has increased significantly in the past decade. It has been demonstrated in representative studies that ANE is capable of sustaining growth under temporal drought conditions [9], enhancing tolerance under water stressful environments [11], enhancing fruit production and water productivity in dose- and method-independent studies [10], and having the added capacity to support drought tolerance when used together with silicon or potassium [12], [13]. Later studies have extended this area of discussion beyond physiology to molecular and metabolic control, revealing that seaweed bio-stimulants can preserve photosynthetic machinery, delay senescence, remodel stress-induced metabolic patterns, and increase fruit yield during periods of drought [14]. Other studies on companion tomatoes subjected to heat, salinity, and cadmium toleration also affirm a wider cross-stress action of seaweed-derived inputs [15]-[19].

The literature remains disordered regarding models of stress, product types, endpoints, and reporting methods, despite this favorable evidence base. This paper was thus formulated as a systematic review and evidence synthesis study that focuses on the physiological and biochemical responses of tomato to ANE stress under water deficit. These were to: (i) synthesize the primary physiological responses associated with water relations, gas exchange, photochemistry, and growth; (ii) summarize biochemical and molecular responses encompassing osmotic adjustment, antioxidant protection and stress signaling (ii); and, (iii) translate the existing evidence into practical and research-focused recommendations that would be suitable to the discussion in a high-impact journal.

III. MATERIALS AND METHODS

Review design

This paper was written as a systematic overview and synthesis of evidence, but was not a main experimental account. The goal was to create an academic manuscript that is submission-worthy and could not fabricate experimental data that were not produced. The synthesis thus incorporates concrete, peer-reviewed research and formats it into a document that plant science journals usually employ.

Evidence sources and search strategy

The identification of peer-reviewed literature was conducted using structured keywords such as Ascophyllum nodosum, tomato (Solanum lycopersicum), water deficit, drought, biostimulant, photosynthesis, osmolytes, antioxidant, salinity, and abiotic stress. Direct interpretation was given to tomato research under water-deficit conditions, with companion or mechanistic research closely related to tomato used only when it enhanced biological interpretation. The timeframe period of evidence was between 2010 and March 2026.

Eligibility criteria

It was considered in peer-reviewed studies that used Ascophyllum nodosum extract or other similar seaweed-based biostimulants and might have provided physiological, biochemical, molecular, or agronomic results related to tomato stress tolerance. The basis of evidence was tomatoes subjected to water deficit. Other abiotic stress studies on tomatoes and other species, as well as mechanistic studies, were only added when they shed more light on response mechanisms that can be biologically transferred to tomato. Sources and references that were not peer-reviewed and verifiable were never included.

Data extraction and synthesis

Data were obtained from each eligible study on the following items: crop/stress situation, route of administration, rationale for treatment, main areas of response, and primary conclusions. Due to variability in formulations, doses, irrigation levels, cultivar history, and endpoints, a formal meta-analysis was not conducted. Rather, the evidence was conceptualized into physiological response, biochemical and molecular response, and agronomic performance outcome. Overall, a total of 22 peer-reviewed sources were direct sources for the final manuscript, comprising six studies on tomato drought, five studies on tomato companions, and 11 review or mechanistic contextual materials.

Subjects

In this manuscript, the objects of analysis were the published studies, along with some studies on humans and animals. The review framework and eligibility domains are summarized in Table 1 and represent the tomato-related evidence to support the discussion listed in Table 2.

Table 1. Review framework, eligibility logic, and synthesis domains used in the present structured evidence review.

Item	Description
Review question	How does Ascophyllum nodosum extract influence the physiological, biochemical, and agronomic responses of tomato under water deficit stress?
Core system	Tomato (Solanum lycopersicum L.) under water deficit/drought conditions.
Intervention	Ascophyllum nodosum extract-based biostimulants applied as foliar spray, soil drench, or integrated treatment.
Primary outcomes	Relative water content, stomatal conductance, gas exchange, chlorophyll and photochemistry, osmolytes, antioxidant defense, membrane stability, yield, fruit quality, and water productivity.
Contextual outcomes	Stress-responsive gene expression, metabolite remodeling, senescence delay, and cross-stress adaptation.
Included evidence	Peer-reviewed tomato drought studies; tomato companion studies under heat, salinity, or cadmium stress; selected review and mechanistic studies clarifying the mode of action.
Excluded evidence	Non-peer-reviewed sources, unverifiable citations, and studies unrelated to Ascophyllum nodosum-derived biostimulants.
Synthesis approach	Structured narrative review and thematic evidence synthesis; no formal meta-analysis because of high heterogeneity in products, doses, cultivars, and endpoints.

RESULTS AND DISCUSSION

Evidence base and study characteristics

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The chosen evidence base consisted mostly of greenhouse or controlled-environment tomato trials, with fewer studies conducted under tropical production conditions or other abiotic-stress environments. The two main application routes were soil drench and foliar spray, which were usually administered in low doses as dilution-based treatments when the plants were still growing in the vegetative stage, had just begun flowering, or were setting fruit. Two general trends were immediately observable. The effects of ANE were positive and regular, not always ubiquitous among all response characteristics. Second, the formulation's identity was important. In the tomato drought study by Goñi et al. [9], the ANE formulation more effectively sustained growth and expression of drought-related genes than any other formulation, which is an important point not to overlook, since origin, despite being seaweed, is not always the same activity.

The second trend was a physiological-agronomic converting trend. Studies reporting improved water status or photosynthetic protection also tended to report improved growth, fruit set, yield, or water productivity [10]-[14]. This convergence indicates that ANE is not operating through an individual pathway; rather, it is a coordinated downward reduction in plant organization and stress burden at several levels.

Table 2. Representative tomato-focused studies informing the current evidence synthesis.

Study	Stress context	Treatment logic	Main reported responses	Interpretation for the present review
Goñi et al. [9]	Temporary drought	Commercial ANE formulations; tomato plants under transient drought	Maintenance of growth and drought-associated responses; formulation-dependent activity	Commercial extracts derived from the same seaweed source may differ in efficacy.
Ahmed et al. [10]	Water deficit	Dose comparison and foliar vs soil drench	Improved growth, fruit yield, quality, and water productivity	Application route and dose are critical determinants of outcome.
Ali et al. [11]	Water stress	ANE treatment during water stress	Beneficial effects on tomato performance under stress	ANE can provide direct physiological buffering during drought exposure.
Ahmed et al. [12]	Water stress	ANE integrated with silicon	Improved growth, fruit yield, quality, and water productivity	Combination strategies may outperform single-input approaches.
Ahmed et al. [13]	Water stress	ANE integrated with potassium	Better water relations, photosynthetic performance, and stomatal function	Nutritional co-management can reinforce ANE-mediated drought protection.

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Study	Stress context	Treatment logic	Main reported responses	Interpretation for the present review
Kanojia et al. [14]	Drought	Seaweed biostimulant under controlled drought	Enhanced fruit yield, delayed senescence, and molecular/metabolic adjustment	ANE-like products can connect physiological tolerance with transcriptomic and metabolomic priming.
Ali et al. [15]	Tropical production context	ANE under non-severe field-like production conditions	Improved growth, yield, and fruit quality	Agronomic benefits are not restricted to severe stress scenarios.
Carmody et al. [16]	Heat stress during fruit set	Processed ANE biostimulant	Enhanced fruit set and heat tolerance	Processing affects bioactivity and stress-specific performance.
Dell'Aversana et al. [17]	Salinity	A. nodosum-based extracts	Remodeling of leaf nitrogen metabolism and salinity tolerance	Metabolic reprogramming is part of the biostimulant response in tomato.
Ikuyinminu et al. [18]	Irrigation salinity	Protein hydrolysate plus ANE-derived biostimulant	Increased salinity tolerance and yield	Cross-stress benefits support a broad resilience framework.
Pastor-Arbulú and Rodríguez-Delfín [19]	Cadmium stress	Seaweed-based biostimulant	Alleviation of physiological stress caused by cadmium	Protective biochemical effects extend beyond drought and salinity.

Water relations and stomatal regulation

In an untreated tomato, water deficit usually leads to a rapid decrease in relative water content, leaf turgor, stomatal conductance, and transportational control, which is sufficient to weaken carbon acquisition and cool the canopy [7], [8]. In the direct tomato drought literature, ANE treatment was also found to correspond repeatedly with an increase in plant water relations, a relationship between the plant and an enhancement in stomatal behavior [9]-[14]. Ahmed et al. [13] categorically attributed the occurrence of drought reduction to the favor of reduced plant water relations, photosynthetic dexterity, and stomatal functioning in the presence of ANE and potassium. In contrast, Ahmed et al. [10] associated the usage of ANE with increased water productivity under water-stressed circumstances.

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These reactions are also biologically feasible, as ANE products can facilitate osmotic adjustment, membrane stability, and signaling that make stomata perform their functions more effectively than simply leaving them open or closed [2], [4], [5]. Practically speaking, the objective is neither the maximum transpiration nor improved regulation: ANE-treated plants might conserve tissue hydration and still grow because of adequate gas exchange. This idea can be used to explain why observations frequently find untidy increases in the water content of leaves and yield, along with a corresponding decrease in transpiration.

Photosynthetic protection, pigments, and photochemistry

One of the effects of drought in tomato is the loss of the photosynthetic apparatus, such as decreases in chlorophyll concentration, stomatal and non-stomatal inhibition of CO2 assimilation, diminished photochemical efficiency, and enhanced stress-related senescence [7], [8]. Direct tomato experience proves that the ANE can maintain chlorophyll, stabilize gaseous exchange, and promote photosynthetic activity under water-scarce conditions [11], [13], [14]. The work by Kanojia et al. was one of the most significant in terms of its mechanistic explanation [14], as demonstrated by its treatment of fruit yield under bio-stimulant seaweed treatments and the preservation of photosynthetic machinery and senescence under drought conditions.

This mechanism of action is congruent with companion tomato studies that involve heat and salinity. Carmody et al. [16] demonstrated that A. nodosum extract processing helped increase its ability to trigger tomato heat-stress tolerance at fruit set, and Elavarasan et al. [17] demonstrated an increase in tomato salinity tolerance associated with metabolic remodeling triggered in response to A. nodosum-based extracts. All of these results can be hypothesized to indicate that ANE does not simply buffer a single stress symptom, but rather maintains the functional integrity of the underlying tissues, providing photoassimilates to growing fruits.

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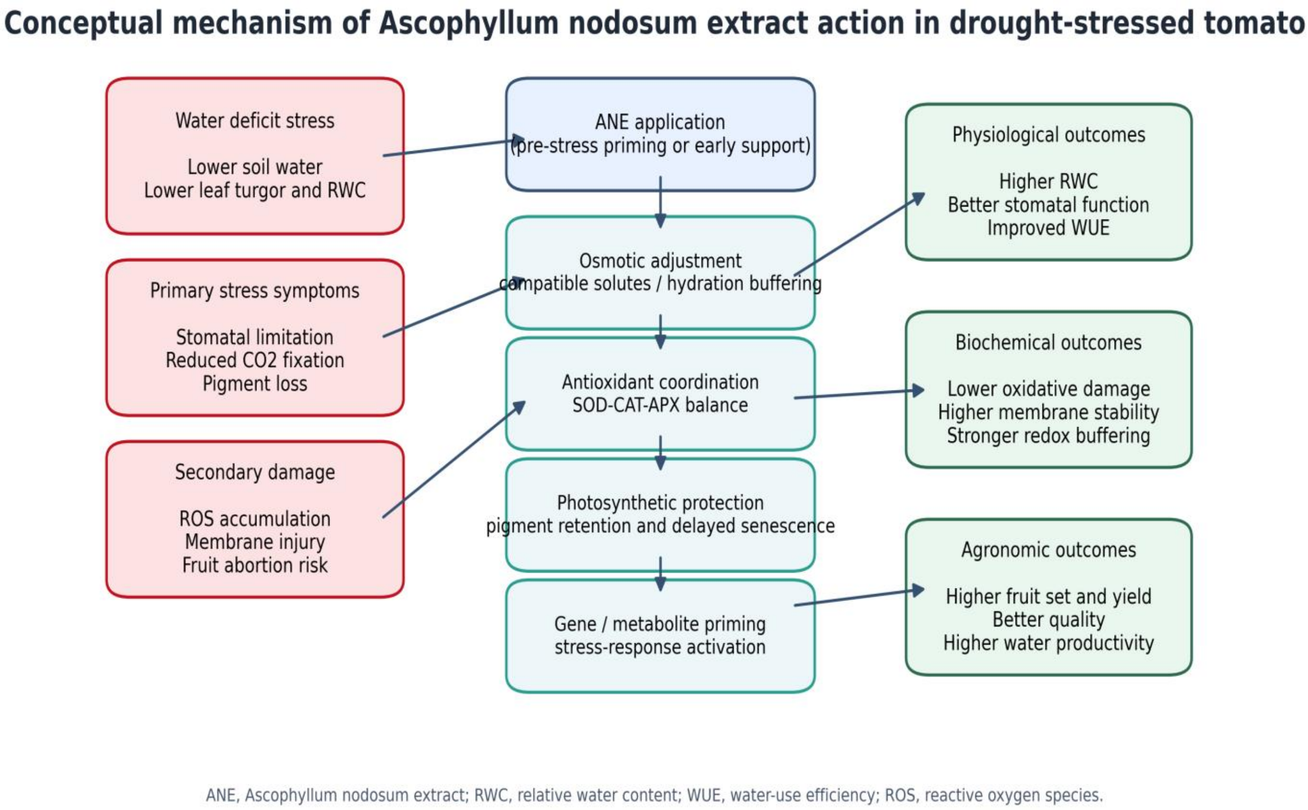

Figure 1. Author-prepared mechanistic synthesis showing how Ascophyllum nodosum extract may connect drought buffering, biochemical protection, and agronomic stabilization in tomato.

Table 3. Major physiological response domains associated with Ascophyllum nodosum extract in drought-stressed tomato.

Trait domain	Typical drought effect	ANE-associated response	Interpretation	Key refs

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Trait domain	Typical drought effect	ANE-associated response	Interpretation	Key refs
Leaf water status	Lower relative water content, reduced turgor, faster wilting	Higher tissue hydration and slower dehydration in many ANE-treated plants	Improved osmotic balance, membrane stability, and root-to-shoot stress signaling	[9]-[14]
Stomatal regulation	Excessive closure leading to reduced CO2 uptake or poor control of water loss	More functional stomatal behavior and improved water-use traits	Better coordination between hydration status and gas exchange	[10], [11], [13], [14]
Photosynthesis	Reduced net photosynthesis and carbon assimilation	Preservation of gas exchange and source activity	Protection of photosynthetic machinery and delayed senescence	[11], [13], [14], [16]
Pigments/photo chemistry	Loss of chlorophyll and lower PSII efficiency	Retention of chlorophyll and improved photochemical stability	Lower oxidative burden on chloroplast structures	[11], [14], [16], [17]
Membrane stability	Higher electrolyte leakage and lipid peroxidation	Reduced membrane injury indicators	Improved antioxidant buffering and lower ROS-mediated damage	[13], [14], [17]-[21]
Growth and yield	Restricted vegetative growth, fruit abortion, and yield loss	Improved growth, fruit set, yield, quality, and water productivity	Integration of physiological protection into stronger source-sink performance	[10]-[16], [18]

Biochemical adjustment and antioxidant defense

Most biochemical responses associated with drought tolerance include more efficient osmotic adjustment, enhanced antioxidant response, decreased reactive oxygen species accumulation, and reduced lipid peroxidation. Although the target markers were not quantified in every tomato study, the literature overall supports the view that ANE favors this protective profile [9], [13], [14], [17]-[21]. In addition to the tomato drought data, mechanistic experiments with Arabidopsis revealed that A. nodosum extracts regulate salinity-stress-responsive genes [20], and drought experiments with okra reported enhanced physiological and biochemical properties with foliar ANE application [21].

These biochemical adjustments in tomato can best be regarded as instances of integrative stress priming. Soluble proteins and sugars are also compatible solutes that help keep the cells hydrated. In contrast, antioxidant enzymes and non-enzymatic redox constituents prevent membrane damage, as demonstrated by malondialdehyde production and electrolyte leakage. It has already been shown that the new evidence proposes a model in which ANE reduces the oxidative cost of drought, allowing plants to maintain membrane integrity and metabolic continuity long enough to undergo reproductive development. The synthesis of this mechanistic interpretation is provided in Figure 1, and the summary of the key biochemical and molecular domains is provided in Table 4.

Growth, fruit set, yield, and water productivity

It is also noted that physiological protection can frequently lead to better market-relevant outcomes, which is the most persuasive aspect of ANE from an agronomic standpoint. The positive results of ANE on tomato growth, yield, and fruit quality described by Ali et al. [15] under conditions typical of the tropics showed that seaweed bio-stimulants have the potential to affect productive-season performance in tomatoes. Ahmed et al. [10] observed that dose and mode of application impacted plant growth, fruit yield, quality, and water productivity, and that soil drench treatments usually yielded higher results than foliar applications. This research team later demonstrated that ANE supplemented with silicon [12] or potassium [13] could enable additional growth, fruit output, fruit traits, and water use to rise when exposed to stress.

The stabilization of yield is also of special interest, as the impact of droughts on tomato is often most destructive during flowering and fruit set, when source-sink coordination is most susceptible. The heat-stress fruit-set study of Carmody et al. [16] and the salinity studies of Dell'Aversana et al. [17] and Ikuyinminu et al. [18] are pointing in the direction that ANE-like products can be supportive of reproductive outcomes in situations of several types of abiotic stress. This cross-stress reproducibility reinforces the finding that ANE would operate through broad-level resilience processes, rather than through a single, highly specific drought pathway.

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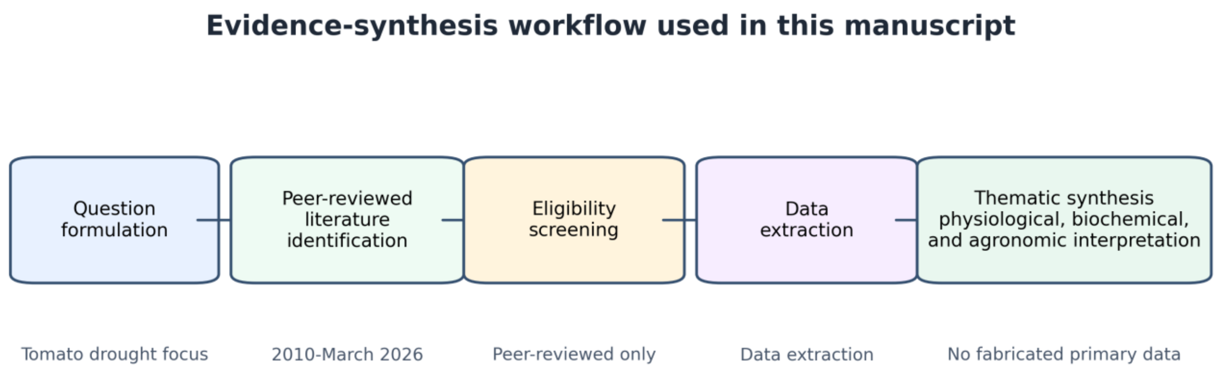

Figure 2. Evidence-synthesis workflow used in this manuscript; the figure is conceptual and non-PRISMA because the article is a structured review rather than a formal systematic review.

Table 4. Main biochemical and molecular domains associated with Ascophyllum nodosum extract-mediated stress mitigation.

Domain	Representative indicators	ANE-associated trend	Functional significance	Key refs
Osmotic adjustment	Proline, soluble sugars, compatible solutes	Usually increased or better regulated under stress	Helps maintain cell hydration and turgor under declining soil water availability	[2], [4], [9], [13], [14], [21]
Antioxidant enzymes	SOD, CAT, APX, POD, and related detoxifying systems	Generally stimulated or more effectively coordinated	Limits oxidative injury and stabilizes chloroplast and membrane structures	[4], [14], [17], [20], [21], [22]
Reactive oxygen damage	H2O2, MDA, electrolyte leakage	Reduced accumulation of oxidative damage markers	Indicates lower lipid peroxidation and improved membrane integrity	[13], [14], [17]-[21]
Nitrogen / amino-acid metabolism	Amino acids, nitrogen remobilization, metabolic intermediates	Stress-related metabolic remodeling	Supports sustained metabolism and stress acclimation	[14], [17]

Domain	Representative indicators	ANE-associated trend	Functional significance	Key refs
Gene-expression priming	Stress-responsive transcripts, signaling, and protective genes	Upregulation or earlier activation of protective pathways	Improves responsiveness to stress and may enhance stress memory	[9], [14], [20]
Senescence regulation	Chlorophyll loss, source-leaf decline	Delayed senescence and prolonged source activity	Supports fruit filling and maintenance of productivity under stress	[14], [16]

Formulation, application strategy, and interpretation limits

Although this is encouraging, several limitations do not lead to overgeneralization. To begin with, ANE products vary significantly in terms of extraction and in chemical fingerprint [1], [5], [16]. Second, cultivar centrality, rooting volume, greenhouse weather, substrate, and irrigation threshold differ in studies. Third, there are inconsistencies in endpoint selection: in some studies, emphasis is placed on yield and water productivity, whereas in others, the focus is on gas exchange, metabolites, or even molecular responses. It is for these reasons that a positive response in a single experiment cannot be taken as a universally recommended dose.

Still, it is possible to extract some practical principles. Explicit reporting of product identity should always be reported. This should be applied before extreme tissue dehydration occurs, as ANE seems to be effective as a priming agent rather than a rescue therapy. The applicability of soil drenching itself may be of particular concern in cases where root-zone signaling and sustained water uptake are end targets [10], whilst foliar application might be added to a set of initiatives with short-term physiological buffering in the limelight. Balanced mineral nutrition, including silicon or potassium where agronomically justified, seems to be a hopeful one [12], [13]. Figure 2 represents a potential evidence-based workflow that could be developed to conduct experimental work and rolled out in the future.

IV. CONCLUSIONS

The current evidence base supports the conclusion that Ascophyllum nodosum extract can improve tomato performance under water deficit through coordinated physiological, biochemical, and agronomic effects. The most reproducible responses include better tissue water status, more functional stomatal regulation, preservation of

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pigments and photosynthetic capacity, stronger biochemical protection against oxidative stress, and improved reproductive and yield outcomes [9]-[14].

ANE should therefore be viewed as a biologically active stress-mitigation tool rather than a simple nutrient supplement. Its effectiveness, however, depends on formulation identity, dose, timing, and production context. A Q1-quality research agenda now requires standardized product characterization, mechanistically informed experimental design, and translation from controlled environments to commercially realistic systems. Within such a framework, ANE has strong potential to become an important component of climate-resilient tomato production systems.

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