Journal of Applied Phycology
https://doi.org/10.1007/s10811-023-03120-x

RESEARCH

Applications of seaweed extracts in agriculture: An Australian perspective

Tony Arioli[1,2] · Scott W. Mattner[3,4] · Md Tohidul Islam[1] · Thi Linh Chi Tran[1] · Marianne Weisser[2] · Pia Winberg[5] · David M. Cahill[1]

Received: 14 May 2023 / Revised: 5 October 2023 / Accepted: 10 October 2023

Abstract
Society depends on food production. However, agricultural productivity is greatly challenged by extreme climate events and volatility. Seaweed extracts (SWE) have a key role in food production and their use is central to improving agricultural productivity by increasing crop tolerance to stress, improving the efficiency of plant nutrient use, and by contributing to sustainable farm practices. The benefits of SWE to crops have previously been reviewed in the context of the northern hemisphere, but not since 2015 in Australia – specific to its crops and unique stressors. This review is focused on the scientific progress since 2015 and insights from Australian research related to: (i) SWE-stimulated plant responses, (ii) field research on SWE, (iii) optimising the use of SWE in agriculture. The review considers the effects of SWE (made from *Durvillaea potatorum* and *Ascophyllum nodosum*) in the field, across crops, seasons, regions, and farming systems in Australia, and research conducted in the laboratory under controlled conditions on model and crop plants at the molecular, cellular, and physiological levels. The results from the review highlight the role of SWE in plant priming responses in laboratory experiments and its association with improved plant tolerance in the field. The review discusses the field effects related to production and fruit quality. The uniqueness of the Australian research is the inclusion of the same SWE in laboratory and field research, and the characterisation of plant responses under challenged and un-challenged conditions. This information provides deeper insights into the actions of SWE and enables growers and agronomists to optimize their field application in Australian agriculture.

Keywords Agriculture · Biostimulant · Plant priming · *Phytophthora cinnamomi* · *Durvillaea potatorum* · *Ascophyllum nodosum*

Introduction

The world population is growing rapidly and relies on agriculture to produce food in productive, safe, and sustainable ways. Food production needs to be resilient to increasing climate change and weather extremes. The use of seaweed extracts (SWE) as soil drenches and crop applications is a key part of productive, sustainable, and regenerative agriculture. SWE have properties that reduce yield losses caused by abiotic and biotic stress events and improve nutrient utilization (Shukla et al. 2019; Ali et al. 2021; Deolu-Ajayi et al. 2022; Jindo et al. 2022).

The Australian experience of using SWE since the 1970s in home gardens, landscapes, and commercial agriculture provides a unique perspective (Arioli et al. 2015). Australian users of SWE are familiar with the need to counter plant stress and enhance plant vigour due to the significant impact of climate change. For example, the decade finishing in 2020 was the hottest recorded in Australia (BOM 2021). The consequences include reduced crop productivity, increased risk to Australian food security, and concerns for the survival of Australian farming communities. Australia has ancient soils that are inherently deficient in certain nutrients (e.g., phosphorus) required for agricultural production and tend to be low in organic matter (SOE 2021). Hence there is a need for SWE because of their effect in improving nutrient use.

✉ Tony Arioli
tonyarioli@hotmail.com

1 Deakin University, Geelong Waurn Ponds Campus, Victoria 3216, Australia

2 Seasol International, Bayswater, VIC 3155, Australia

3 VSICA Research, Toolangi, VIC 3777, Australia

4 La Trobe University, Bundoora, VIC 3083, Australia

5 Venus Shell Systems, NSW, Huskisson 2540, Australia

Published online: 27 November 2023

Understanding the mechanisms contributing to the beneficial effects and efficacy of SWE in the field is a priority.

The effects of SWE on plants have been comprehensively reviewed from a global perspective. These reviews include examples of SWE derived from different types of seaweed biomass and extraction processes and detail their effects on different plants (Shukla et al. 2019, 2021; Ali et al. 2021; Deolu-Ajayi et al. 2022; Jindo et al. 2022). The SWE literature is focused on research using the brown seaweed *Ascophyllum nodosum* and to a lesser extent reports about SWE made from other species; for example, *Kappaphycus alvarezii* (Kumar et al. 2020).

This review is instead focused on research for the same SWE in laboratory and field research, and the characterisation of plant responses under challenged and un-challenged conditions, related to plant priming. This review advances previous Australian publications (Abetz & Young 1983; Arioli et al. 2015) by reviewing the scientific literature on SWE since 2015 related to (i) field studies on the application of SWE under environments in Australian agriculture (Table 1), and (ii) Australian laboratory studies (Table 2) and the relevant international literature that acts as a comparator to these studies. Laboratory studies are conducted under controlled conditions, so environment or region is not a factor in these experiments.

A search of the published scientific literature since 2015 for Australian SWE studies related to agriculture has identified that the publications are concentrated on one SWE derived from two algal species (Tables 1 and 2). As a consequence, this review draws on field and laboratory studies of the SWE (designated SWE (AN/DP)) produced by alkaline hydrolysis from two brown seaweeds: *Ascophyllum nodosum* (AN, native to the northern hemisphere) and *Durvillaea potatorum* (DP, native to the southern hemisphere) (Arioli et al. 2015; Seasol®; Seasol International, Bayswater, Victoria, Australia). The analysis for the undiluted SWE (AN/DP) (concentrate) reports a total organic matter content of 8%, a soluble solid level set to 17% (w/v) (to standardize applications), alkaline concentrate filtered to below 150 µm (for commercial operations), and contains 0.2% (w/v) N, 0.02% P, 3.7% K, 0.3% S, 458 mg L^{-1} Ca, 972 mg L^{-1} Mg, 115 mg L^{-1} Fe, 2 mg L^{-1} Mn, 15 mg L^{-1} B, and 5 mg L^{-1} Zn. In addition, Wite et al. (2015) reported the undiluted extract contained 7% (w/v) total laminarins, 154 µg L^{-1} total auxins, 36 µg L^{-1} total cytokinins, and 382 µg L^{-1} total betaines.

Overall, this review highlights the scientific progress since 2015 and insights from Australian research related to: (i) SWE-stimulated plant responses, (ii) field research on SWE, (iii) optimizing the use of SWE in agriculture.

SWE-stimulated plant responses

The science supporting the plant benefits of SWE applications is extensive and convincing, and founded on studies using a broad range of extracts made from different types of seaweeds and extraction processes (Shukla et al. 2019, 2021; Ali et al. 2021; Deolu-Ajayi et al. 2022; Jindo et al. 2022). Many plant studies have demonstrated that SWE promote plant growth such as root growth, flowering, fruit set, and leaf growth (Rayorath et al. 2008; Mattner et al. 2013; Ali et al. 2016, 2022; Renaut et al. 2019; Yao et al. 2020; Hussain et al. 2021). Research using crop and model plants have demonstrated that SWE can improve plant tolerance to abiotic stresses such as salt, drought, freezing, and heat (Nair et al. 2012; Martynenko et al. 2016; Santaniello et al. 2017; Goñi et al. 2018; Jithesh et al. 2019; Cocetta et al. 2022; Repke et al. 2022), and improve nutrient uptake – for example, in crop plants such as tomato and *Brassica* (Jannin et al. 2013; Yao et al. 2020). Other research on Arabidopsis has found SWE can improve photosynthetic performance, tolerance to severe oxidative stress, and activate plant transcriptional and

Table 1 A summary of the published field research using a seaweed extract (SWE) in Australian agriculture from 2015–2023

Crop	Extract Type	SWE Rate	Number of Seasons	Number of field Trials	Number of field trial sites	Cultivars	Application Frequency	Application Method	References
Sugarcane	SWE (AN/DP)	10 L ha^{-1}	5	10	2	1	monthly	subsurface drip	Farnsworth and Arioli 2018; Arioli et. al. 2020, 2021b
Winegrapes	SWE (AN/DP)	5 & 10 L ha^{-1}	4	5	7	4	3 to 8 applications	soil drench	Arioli et al. 2021a
Avocado	SWE (AN/DP)	10 L ha^{-1}	4	3	5	2	monthly	under tree micro sprinklers	Arioli et al. 2023
Strawberry	SWE (AN/DP)	10 L ha^{-1}	2	2	3	2	monthly	overhead—drench	Mattner et al. 2018, 2023

SWE (AN/DP) is made from *Ascophyllum nodosum* (AN) and *Durvillaea potatorum* (DP)

Table 2 A summary of the published laboratory research related to plant priming and seaweed extracts (SWE) in Australia from 2015-2023

Plant Species	Extract Type	Priming Phase	Post challenge Primed State	Number of SWE Applications	Analysis	Time points	Method	Reference
Priming Phase Experiments:								
Arabidopsis	SWE (AN/DP)	Yes	N/A	1 application	GE	0,1, 3,5 days after SWE treatment	roots in sand culture system	Islam et al. 2021
					ROS	0,1, 3,5 days after SWE treatment		
Tomato	SWE (AN/DP)	Yes	N/A	1 application	GE	0,1, 3,5 days after SWE treatment	roots in sand culture system	Islam et al. 2021
					ROS	0,1, 2,5 days after SWE treatment		
Arabidopsis	SWE (AN/DP)	Yes	N/A	2 applications	M	0, 3, 5 days after last SWE treatment	roots in sand culture system	Tran et al. 2023
Strawberry	SWE (AN/DP)	Yes	N/A	up to day 4 or 5	ROS	At days 4 and 5	liquid root system	Mattner et al. 2023
Post-Challenge Primed State Experiments:								
Plant	*Extract Type*	*Priming Phase*	*Post challenge Primed State*	*Number of SWE Applications*	*Analysis*	*Time points*	*Method*	*Reference*
Arabidopsis	SWE (AN/DP), SWE (AN), SWE (DP)	Yes	*Phytophthora cinnamomi* (1 day post priming)	6 applications	T	1 day after last SWE application; 0,3,6,12,24 hpi	roots in sand culture system	Islam et al. 2020
					ROS	12hpi		
Arabidopsis	SWE (AN/DP)	Yes	*Phytophthora cinnamomi* (3,5 days post priming)	2 applications	GE	3 or 5 days after last SWE application; 0,3,6,12,24 hpi	roots in sand culture system	Islam et al. 2021

SWE (AN/DP) is made from *Ascophyllum nodosum* (AN) and *Durvillaea potatorum* (DP); SWE (DP) is made from *Durvillaea potatorum;* SWE (AN) is made from *Ascophyllum nodosum*; Gene Expression (GE); Reactive Oxygen Species (ROS); Metabolomics (M); Transcriptomics (T)

metabolic networks and the modulation of reactive oxygen species (ROS) levels (Santaniello et al. 2017; Cook et al. 2018; Islam et al. 2020, 2021; Omidbakhshfard et al. 2020; Rasul et al. 2021; Staykov et al. 2021; Tran et al. 2023). Furthermore, the effects of SWE extend beyond laboratory studies to the field, where the effects of SWE from commercial and non-commercial sources have been corroborated by a comprehensive meta-analysis of open field research with average yield increases of 16.5–18.0% (Li et al. 2022).

Despite all the science about the effects of SWE on plants, their mechanisms of action are elusive, especially the molecular processes that SWE may influence to condition plants for improved growth and tolerance to stresses. There is little evidence that the effects of SWE are based on individual nutritional factors or phytohormone compositions, but instead require the synergistic action of the components of the whole extract. In the Australian field studies the grower fertilizer programs (applied at kg ha^{-1} rate) provide significantly more nutrients than exist in SWE (AN/DP) (Mattner et al. 2013). Research on plant hormones discovered six cytokinins (up to 36.59 ug L^{-1}) and several cytokinin glucosides (up to 22.00 ug L$^{-1)}$ in the SWE (AN/DP) (Tay et al. 1985, 1987). However, Tay et al. (1987) concluded the cytokinin levels were too low to explain the effects on plants, particularly because of the high dilutions of the SWE (AN/DP). applied in the field. Other researchers confirmed nutrient levels equivalent to those found in the SWE (AN/DP), or supplementation with plant growth hormones (auxin, cytokinin and gibberellin) did not have the same plant growth stimulating effect (Yusuf et al. 2012). Overseas research using *Arabidopsis* plants insensitive to phytohormone biosynthesis identified that the phytohormone levels in a different SWE (made from *A. nodosum*) were insufficient to achieve the growth effects of the SWE application exhibited in the field (Wally et al. 2013).

Instead, Wally et al. (2013) proposed a change in thinking by suggesting components within SWE may modulate innate plant pathways involved in biosynthesis of phytohormones such as auxins, cytokinins and abscisic acid. Of note is a recent European industry review of the science on the mode of action of seaweed-based plant biostimulants, which highlighted that plant hormones are not responsible for the plant biostimulant effects observed in crops when applying seaweed-based extracts and endorsed molecular level studies for insights (EBIC 2023).

Plant priming as the basis for the action of SWE

An action that is emerging for SWE is based on the stimulation of a combination of intrinsic and systemic plant responses to achieve plant priming-like effects. Plant priming is an adaptive mechanism that enables plants to improve their defensive capacity and results in plant conditioning. The effect is manifested as a physiological state of alertness where plants respond more rapidly and intensely to different types of biotic and abiotic stresses. An intrinsic feature of the mechanism is inducibility, which bears a minimal fitness cost (relative to a constitutive mechanism) and enables a balanced trade-off between plant growth and defense responses (Karasov et al. 2017; Buswell et al. 2018). Several excellent reviews address the topic of plant priming and describe the molecular mechanisms (Balmer et al. 2015; Conrath et al. 2015; Martinez-Medina et al. 2016; Mauch-Mani et al. 2017; Tugizimana et al. 2018; Kerchev et al 2020).

The plant priming mechanism is based on the perception of varied environmental signals for plants to adapt to their changing and challenging surroundings. The priming phenomenon has two stages: (i) the **Priming Phase** is triggered by the perception of a stimulus and is characterized by responses at the physiological, transcriptional, and metabolic levels, and the enhanced activation of induced defense mechanisms such as systemic acquired resistance (SAR); (ii) the **Post-Challenge Primed State** relies on a subsequent stimulus to trigger the plant's defense mechanisms to respond faster and more intensely to effectively counter the symptoms of stress, and results in enhanced stress tolerance and/or resistance.

Priming is a plant conditioning strategy that has untapped potential for improving agricultural productivity and protection against yield loss due to environmental stress (Tiwari and Singh 2021). In the field, the plant priming mechanism can be stimulated by biotic and abiotic challenges, and the chemical priming stimuli can be applied exogenously (Aranega-Bou et al. 2014; Finiti et al. 2014). Agronomists are familiar with the actions of plant priming when using practices such as seedling hardening to prepare plants for exposure to field conditions. It is possible the effects of SWE on plants might be manifested by aspects of the plant priming mechanism. The application(s) of SWE to plants (before stress) in agriculture mimics aspects of the plant priming responses. Support for involvement of a plant priming mechanism is inherent in molecular and cellular studies incorporating a SWE pretreatment experimental design before a plant stress challenge event (Santaniello et al. 2017; Fleming et al. 2019; Rasul et al. 2021; Staykov et al. 2021; Cocetta et al. 2022).

Recent molecular research, studying the same SWE (AN/DP) applied in the Australian field trials (Table 1), supports a role for the plant priming mechanism in the way SWE (AN/DP) contribute to beneficial plant effects (Islam et al. 2020, 2021; Tran et al. 2023). In these experiments (Table 2) supporting evidence comes from studying the Arabidopsis plant model and tomato as a representative for crop plants, and an experimental design to uncouple the two stages in the plant priming phenomena: (i) the Priming Phase and (ii) the Post-Challenge Primed State.

Priming-phase: Plant gene expression, reactive oxygen species production and metabolite reprogramming

The reprogramming of plant gene expression and ROS production are responses found in (i) plant priming (Baccelli et al. 2020; Kerchev et al. 2020) and (ii) the application of SWE; for example, in Arabidopsis and tomato (Nair et al. 2012; Ali et al. 2022). However, the first reports are emerging for systematically investigating the effect of SWE (AN/DP), up to five days post-priming, utilizing two types of plants (Arabidopsis and tomato), on the distinct plant priming phases by quantitative gene expression, transcriptomics, metabolomics, and for ROS production and ROS-related Peroxidase enzyme activity (Islam et al 2020, 2021; Tran et al. 2023; Table 2). In the Priming Phase experiments, post-priming indicates the stage (in days) after the application of SWE (AN/DP) (priming phase stimulus) and without subsequently exposing plants to a stressor.

Islam et al. (2021) first treated *Arabidopsis* plants with one application of SWE (AN/DP) and then the signature systemic acquired resistance priming-related genes (*PR1*, *PR5*, *NPR1*) were assessed by quantitative gene expression. The expression of the three genes were found to be up-regulated compared to the respective control. Also, the study found the significant up-regulation of expression of other key defense priming-related genes (*AED1* and *GRXC9*) after SWE (AN/DP) treatment. In addition, the study found evidence for the up-regulation of the expression of key ROS-associated genes (*RBOHD*, *GSTF8*, *SAG21*, *TPX2*) that showed varying patterns of expression at each time point after SWE (AN/DP) application. Similarly, in tomato, priming phase-related gene expression was enhanced for two key genes *PR5* and *NPR1*.

ROS are a feature of the plant priming mechanism and have an intricate role in signaling for plants to tolerate multiple stresses (Perez and Brown 2014; Gonzalez-Bosch 2018). After one application of SWE (AN/DP) to Arabidopsis, the production of the ROS, hydrogen peroxide (H_2O_2), in Arabidopsis root tips was detected and quantified and a temporal pattern of H_2O_2 accumulation was uncovered. Peroxidase enzymes catalyse the depletion of H_2O_2 and displayed a temporal pattern mirroring the H_2O_2 levels in the root tips. Similar results were found for tomato plants. In other research, Mattner et al. (2023) found the same SWE (AN/DP) applied to strawberry plants, another commercially relevant crop, can stimulate ROS production in roots as a marker of plant priming. The ROS responses across these plants suggests ROS production is a conserved action upon application of SWE (AN/DP).

Metabolomics analysis of plant metabolite profiles and levels offers another perspective for understanding the action of SWE (AN/DP). Tran et al. (2023) reported the comparative metabolic profiling of Arabidopsis roots and leaves using an untargeted UHPLCMS (Ultra high-pressure liquid chromatography combined with high resolution mass spectrometry) approach to reveal complex response mechanisms induced by SWE (AN/DP). In these experiments, the research focused on the plant responses up to five days (post-priming) at the Priming Phase, after two applications of SWE (AN/DP). The untargeted UHPLCMS approach revealed significant metabolic changes related to: (i) response timing and (ii) plant tissue type. Across a five-day period, significant metabolite differences were identified in roots and leaf tissue profiles after SWE (AN/DP) treatment, where both metabolite accumulation and reduction occurred, and changes across diverse biochemical groups such as lipids, phytohormones, phenylpropanoids, amino acids and organic acids were evident. Enhancement in carbon and nitrogen metabolism and defense systems was supported by accumulation in TCA-cycle metabolites (such as citric acid, malic acid, and 2-oxoglutaric acid) and N-containing metabolites (such as glutamine and glutamic acid). Many of the accumulating metabolites in response to the SWE (AN/DP) treatment are important to provide energy and precursors for biological and signaling pathways. Also, metabolites involved in plant defense were found to accumulate; for example, glucosinolates. The distinct alterations in metabolic profiles in root and leaf tissue provide evidence for a systemic action and metabolomic reprogramming due to the application of SWE (AN/DP) to Arabidopsis roots.

Post-Challenge Primed State: Plant gene expression and reactive oxygen species production

The reprograming of plant gene expression and ROS production has been investigated at the Post-Challenge Primed State, after up to five days pre-treatment (priming) with SWE (AN/DP) (Islam et al. 2020, 2021). In these experiments the Arabidopsis plants were pre-treated with applications of SWE (AN/DP) (and included the testing of two other SWE; see Table 2) and then challenged one day later by inoculation with the globally distributed and destructive root pathogen *Phytophthora cinnamomi* Rands. Inoculation by the pathogen provided a convenient method to synchronize the timepoint for a stress challenge and subsequently characterize the early stages of the Post-Challenge Primed State. The plants were assessed (from inoculation) by transcriptomics analysis at five early time points in the interaction up to 24 h post-infection (hpi), and for the involvement of ROS at 12 hpi by the staining of Arabidopsis roots to detect the accumulation of H_2O_2.

The effect of *Arabidopsis* pre-treatment with different SWE (AN/DP) revealed the induction of wide-scale transcriptome reprogramming, impacting 1.3% of the genome, and included genes involved in phytohormone biosynthesis and signaling, oxidative burst, metabolic and proteolysis processes, and defense-related responses. For example, gene expression was up-regulated for the key SAR-related genes (*NPR1*, *PR1,* and *PR5*). An insight from this research is that the three SWE tested were found to induce different and overlapping genes in the plant defense pathways, demonstrating a priming-like action, and the induction was concurrent with the timing of pathogen inoculation.

The prominent effect of *Arabidopsis* pre-treatment with SWE (AN/DP) on ROS production in roots was the detection of H_2O_2 in (i) roots treated with SWE (AN/DP) alone, and (ii) more intensely in roots treated with SWE (AN/DP) and then inoculated with the pathogen. The increased intensity associated with the pathogen inoculation indicates an amplification of the ROS response (even after a longer exposure to the SWE (AN/DP)). An increase in H_2O_2 levels was not anticipated since the *Arabidopsis* ecotype *Landsberg erecta* is susceptible to the root pathogen *P. cinnamomi.* The production of ROS in roots at 12 hpi (and the modulation of plant gene expression) demonstrates a change in the plant's response to recognise and signal the stress event (in this case due to inoculation with *P. cinnamomi).* This is an important result because it supports that pre-treatment with SWE (AN/DP) may be enhancing the plant's ability to recognize stress events, in addition to, or in synergy with, the properties of the SWE (AN/DP) associated with plant priming.

Collective insights for the actions of SWE on plants

The research discussed highlights that the application of SWE (AN/DP) induces molecular and cellular plant priming responses, and the responses are more pronounced when plants subsequently encounter a stress challenge (Fig. 1). However, there are inherent challenges in characterizing

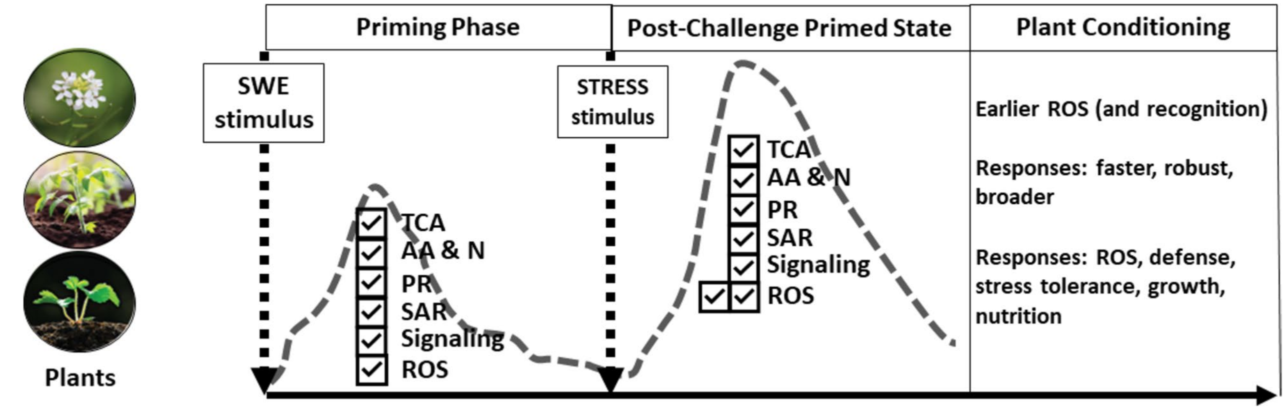

Fig. 1 Examples of plant priming-like responses initiated by seaweed extract (SWE) application. TCA: Tricarboxylic acid cycle; AA & N: Amino acid and nitrogen metabolism; PR; defense proteins; SAR: Systemic acquired resistance; ROS: reactive oxygen species (equilibrium). Figure adapted from Balmer et al. 2015

plant priming mechanisms due to their adaptive nature since plant responses at one timepoint can stochastically influence responses at other time points. This is further complicated by the cohorts of reprogramming (at transcriptomics, metabolomics and ROS levels) that are coordinated to exhibit plant priming-like responses. It is unclear how different processing methods or seaweed species used to prepare SWE may influence plant priming responses. To benefit agriculture, more research is needed to understand the role of plant priming in the way SWE achieve their benefits in the field.

Field research on SWE

Australian growers and agronomists rely on applied research to assess the benefits and relevance of production technologies, including SWE. While much has been learned from laboratory examination of SWE (see above), the effectiveness of SWE cannot be comprehensively replicated in laboratory settings, as the conditions and circumstances encountered in the field may markedly differ. In particular, field trials are essential for assessing the efficacy and resilience of SWE across diverse production systems. They provide valuable data to support the economic analysis of using SWE, and the scientific knowledge for agronomists to optimize the use of SWE in agriculture and to transition growers towards more sustainable crop production practices. Field trial information about the effects of SWE obtained in real-world conditions is endorsed by the global agricultural biostimulant industry (Ricci et al. 2019), and Australian researchers are actively contributing to this initiative. In Australia, field research testing the effectiveness of SWE (AN/DP) extends across a diverse range of crops and contrasting geographies and growing seasons (Table 1). Such science-based field research provides crucial experimental data on the effects of SWE (AN/DP) application in commercial settings, and enables crop-specific and collective insights for their application.

Wine grape

Viticultural communities in Australia are particularly concerned about climate change impacting grape yield and quality (Keller 2010). Early Australian wine grape (*Vitis vinifera*) research reported the success of using SWE in improving wine grape production (Anderson 2009; Scarlett 2009; Scarlett et al. 2011). Later Australian field research has confirmed the effectiveness of SWE (AN/DP) application in improving productivity and production economics (Arioli et al. 2021a).

Using a series of seven field experiments, the study by Arioli et al. (2021a) found that repeated applications of the SWE (AN/DP) to soil significantly increased shoot length at fruit set by 5%, anthocyanin red grape content by 10%, and wine grape yield by 15%. The economics of using SWE (AN/DP) was analyzed using a partial budget analysis method (Szparaga et al. 2019) and showed that the use of the SWE (AN/DP) increased profits and the economic benefit varied depending on the grape cultivar. The trials were conducted across an extensive number of growing seasons (2010–2017), at five different warm climate, bulk wine production areas, in three Australian states, using four red and white grape cultivars, and were located on commercial vineyards using modern Australian management practices.

The SWE (AN/DP) treatment was applied at 5 or 10 L ha^{-1}, with the number of applications ranging from three to eight, applied at different phenological stages of the crop during the growing season. The field trials encountered numerous stress events and some of the hottest average daily temperatures on record. Despite these climate variations, the

SWE (AN/DP) demonstrated its effectiveness by increasing grape vine growth, grape yield and anthocyanin content.

Crop-specific insights highlight the benefit of integrating repeated applications of SWE (AN/DP) into the grower programs. In the viticulture field experiments, the repeated applications of the SWE (AN/DP) at different phenological stages resulted in increased yield. This result is consistent with other Australian field research; for example, strawberry, sugarcane, and avocado, where repeated applications of the same SWE (AN/DP) increased crop yield and productivity (Mattner et al. 2018, 2023; Arioli et al. 2020, 2021b, 2023). The use of the SWE (AN/DP) in field trials conducted across an extended number of growing seasons and crops provides field evidence for both the resilience and efficacy of the SWE (AN/DP).

For Australian grape growers, viticulturalists, and agronomists, the comprehensive field research provides practical ways to optimize beneficial agronomic responses in wine grapes due to the versatility in application timings and frequency. Furthermore, the wine grape research provides new confidence about the feasibly and profitability of integrating SWE (AN/DP) into conventional Australian wine grape growing programs.

Avocado

Avocado (*Persea americana*) is an economically important tree crop grown in tropical and subtropical regions of many parts of the world, including Australia. However, there is a very limited number of research publications on the effectiveness of SWE on avocado production and especially fruit quality. Recent field research in Australia has found the application of SWE (AN/DP) can increase avocado production, fruit quality, and crop revenue (Arioli et al. 2023).

The avocado research is based on a series of field experiments (2016–2021) conducted on commercial farms across three different sites in northern Queensland (Australia) over four years and utilized avocado trees with different ages and cultivars (Hass and Shepard). The study evaluated the use of the SWE (AN/DP) applied monthly (at 10 L ha^{-1}) to the soil via under-tree micro-sprinklers.

The experimental results showed that the application of the SWE (AN/DP) significantly improved avocado yield (kg fruit per tree) by 38%, and after fruit storage significantly improved avocado fruit skin firmness by 4%, fruit flesh firmness by 22%, and fruit skin colour by 1° (hue). The increases in yield were associated with a larger number of fruit per tree (42% from fruit set to harvest). A partial revenue analysis found the increase in marketable yield resulted in an economically meaningful increase of 24% in the grower's return. Furthermore, the research found the regular application of the SWE (AN/DP) in an avocado pot experiment increased the root fresh weight of seedlings (cv. Hass) by 22%.

An insight from the Australian avocado research relates to the combined improvements in fruit yield and fruit post-harvest quality due to SWE (AN/DP) treatment. The action of applying SWE (AN/DP) by soil irrigation extended to crop physiology (tree yield, fruit number) and into the fruit for improved post-harvest quality. For Australian growers and agronomists, the research provides the first relevant and practical knowledge about the effectiveness of SWE (AN/DP) to improve their avocado production, fruit quality, and crop return, by integrating the regular application of SWE (AN/DP) into their growing programs.

Sugarcane

Despite the size of the industry, there are comparatively few reports about the use of SWE in Australian sugarcane (*Saccharum officinarum*) production. A review of the Australian sugarcane field research provides scientific evidence for the effectiveness of SWE (AN/DP) in sugarcane production (Farnsworth and Arioli 2018; Arioli et al. 2020, 2021b).

The field research has demonstrated SWE (AN/DP) significantly increased commercial cane yield and commercial sugar yield, each by 17%, and increased grower returns by 18% (Arioli et al. 2020, 2021b). The conclusions were based on an extended series of field trials (2014–2019) located in far north Queensland (Australia). The increased yield response was consistent across all five seasons of experimental field trials.

The SWE (AN/DP) was applied monthly at 10 L ha^{-1} and integrated into the grower fertilizer programs suited to the contrasting soil types. The SWE (AN/DP) was applied using a subsurface irrigation system and the field trials were set up at commercial scale (3.5–7.5 ha size range) to be representative of industry production practices in Australia. The sugarcane field trial results are consistent with others in the scientific literature reporting the effectiveness of SWE in sugarcane (Deshmukh and Phonde 2013; Gomathi et al. 2017; Karthikeyan and Shanmugam 2017; Chen et al. 2021). In addition, the field research found the application of SWE (AN/DP) influenced the sugarcane root microbiome profiles, which was uncovered by assessing microbial taxonomic diversity using ribosomal (S16) and nitrogen fixing (*nifH*) sequences (Arioli et al. 2021b). However, more research is needed to understand the significance of these effects at the root microbiome level.

Another field trial investigated the effect of SWE (AN/DP) application on sugarcane emergence after planting (Arioli et al. 2020). In a randomized small-plot experiment, sugarcane billets were soaked with SWE (AN/DP) for 24 h and then planted into furrows in the field. Sugarcane emergence was monitored for 10 weeks by counting the number of shoots at the different timepoints. The SWE (AN/DP) treatment significantly increased sugarcane crop emergence by 28% and the response was consistent across the 10-week emergence stage. Superior emergence is a prerequisite for maximizing commercial sugarcane yields.

Australian sugarcane research has led to the first scientific publication (Farnsworth and Arioli 2018) to demonstrate the effectiveness of SWE applied by subsurface irrigation. Subsurface irrigation is a useful practice for delivering SWE to the sugarcane root zone. This application approach leverages the other benefits such as improved production yields due to more efficient use of water and reduced weed competition (SRA 2014).

Opportunities to increase sugarcane production focus on the vulnerability of the crop to drought and adopting timely applications of SWE in rain-fed and irrigated production systems. Sugarcane requires an abundant supply of water to attain maximum productivity (SRA 2014). Irrigation reduces the dependency on rainfall for maximum sugarcane crop production and enables scheduling to avoid dry intervals that reduced crop production. In rain-fed field trials, early SWE applications were recommended to improve yield, and the yield enhancement effects were more pronounced under drought stress conditions (Chen et al. 2021). The importance of water management highlights the role of agronomists in optimizing sugarcane crop production with the integration of SWE applications into grower programs for maximum benefits.

Strawberry

Australian strawberry (Fragaria × ananassa) growers use soil fumigation in open fields to increase root growth responses and for the control of soil pests. The application of SWE may be a supplementary approach as the practice of soil fumigation is changed or withdrawn. Another concern for strawberry growers is grey mould (caused by *Botrytis cinerea*), a serious post-harvest fruit rot disease, because it reduces the quality and marketability of strawberry fruit (Hua et al. 2018). Currently, fungicides effectively manage the disease; however, there are concerns related to pathogens developing resistance to fungicides and the impact of fungicides on human health. Recent research (Mattner et al. 2023) extends support for the inclusion of SWE (AN/DP) in Australian strawberry production by demonstrating concurrent (i) increases in strawberry crop yields and (ii) reductions in the incidence and severity of post-harvest rot.

The research used a series of strawberry nursery and fruit production field trials to assess the benefits of applying SWE (AN/DP) (Mattner et al. 2018, 2023). The field trials were conducted across different years (2014/15 and 2017/18) and growing seasons and involved two cultivars of strawberries (Albion and Fortuna) predominantly planted in the Australian strawberry industry. The SWE (AN/DP) used in experiments was applied monthly as a foliar spray and soil drench at 10 L ha^{-1}. Numerous physiological, agronomic, and post-harvest fruit quality benefits were uncovered.

In the nursery sector field trials, the application of the SWE (AN/DP) significantly increased the density of feeder roots on strawberry runners by up to 22% and increased yields of marketable strawberry runners by 8–19%. Similarly in the strawberry fruit production field trials, the application of SWE (AN/DP) significantly increased marketable fruit yields by 8–10% and improved the production revenue of the crop by an average of 11%. For consumers, the SWE (AN/DP) significantly reduced the incidence and severity of post-harvest rots in marketable strawberry fruit by 52% and 87%, respectively. In these high input fertilizer trials, the application of SWE (AN/DP) did not impact the firmness, soluble solids concentration, or titratable acidity of market-grade strawberry fruit.

The strawberry field research provides crop-specific insights. For example, the experimental results confirm the efficacy of the SWE (AN/DP) in fumigated soils. The efficacy was not correlated with soil nutrient levels since there were no significant differences in the soil nutrient content between the SWE (AN/DP) treatment and control (without SWE (AN/DP)) at the beginning and end of the field experiments.

The strawberry field research discovered an important correlation between strawberry root growth and strawberry fruit yield. At the rates used, the application of SWE (AN/DP) significantly increased strawberry root length density in field grown plants at harvest. Subsequently, a strong association ($r = 0.94$) was found linking root length density at final harvest with marketable strawberry fruit yield. In addition, the strawberry research (Mattner et al. 2023) showed a reduction of post-harvest fruit rot while increasing marketable fruit yields by integrating the application of SWE (AN/DP) in grower programs. For growers, the increases in marketable yield and crop revenue are economically meaningful and therefore encourage the integration of SWE (AN/DP) in Australian strawberry production programs.

Broccoli

Growers apply high rates of nitrogen fertilizers at transplanting to promote early growth of broccoli (*Brassica oleracea* var. *italica*) seedlings (Dimsey 2009). The high nutrient inputs make broccoli production prone to nitrogen losses, so growers are seeking alternative approaches (Feller and Fink 2005; Bakker et al. 2009; Porter et al. 2012). In addition, the Australian broccoli field research extends the current review by relating SWE with contrasting soil types.

Early Australian field research by Abetz and Young (1983) showed the application of SWE made from *A.*

nodosum increased cauliflower curd size and the weight of marketable lettuce. Later, more extensive field trial research investigated whether SWE (AN/DP) stimulates broccoli establishment and growth in contrasting soil types (Mattner et al. 2013). Two field trials were conducted as randomized complete block designs at different locations in Victoria, Australia (Werribee, Boneo), harbouring contrasting soil types (clay loam/Red Sodosol and deep sand/Aeric Podosol) and utilized overhead crop drenching with SWE (AN/DP) at two rates (25 and 2.5 L ha^{-1}).

In one of the trials with clay loam soil, the application of SWE (AN/DP) to establishing broccoli seedlings was found to significantly increase broccoli leaf number by 6%, stem diameter by 10%, and leaf area by 9%, irrespective of the application rate. In addition to improved broccoli growth, the application of SWE (AN/DP) resulted in leaf suppression for white blister disease symptoms by 23%. Wite et al. (2015) reported a similar suppressive effect where the same SWE (AN/DP) suppressed *Plasmodiophora brassicae* infection of broccoli. At the trial site with sandy soil, the effect of the SWE (AN/DP) was less pronounced, and the higher rate of SWE (AN/DP) was required to significantly increase leaf area of broccoli seedlings.

An insight from the broccoli research relates to the contrasting soil types (sandy vs. clay loam) and the need to optimize the application of SWE in conjunction with soil properties. Despite the positive effects of SWE (AN/DP) application to broccoli growth when applied at the highest rate, the field trial in the sandy soil had a higher potential for leaching of water and fertilizer inputs. In addition, a dosage curve for optimal application rate defined for greenhouse production indicates that SWE (AN/DP) concentration can be adjusted for maximum broccoli total dry weight (Mattner et al. 2013). Soil properties are important aspects for agronomists to consider when tailoring grower SWE applications rates and frequencies for optimal efficacy, as few field studies have directly compared the effects of SWE in different soil types.

Collective insights about the application of SWE in the field

Insights from the Australian SWE (AN/DP) field research suggest several emerging themes about the benefit of using repeated applications of the same SWE (AN/DP) during the growing season.

SWE-activated systemic responses in the field In the field the application of SWE (AN/DP) has whole-plant responses that mimic a systemic action. The field trials demonstrate the effectiveness of SWE (AN/DP) across the plant's physiology, suggesting an underlying systemic action. For example, avocado fruit number and fruit yield were increased when SWE (AN/DP) was applied to soil, and post-harvest effects were pronounced in fruit tested for shelf life. Similarly in SWE (AN/DP)-drenched strawberry plants, effects were observed in root growth, strawberry runner physiology, and fruit yield, and in marketable strawberry fruit by reductions in the incidence and severity of post-harvest fruit rot. Physiological effects in other field crops include enhanced establishment in sugarcane and broccoli and shoot length in wine grapes. The effects of applying SWE (AN/DP) in the field are consistent with a systemic whole-plant action extending into the fruit.

SWE resilience in the field The resilience of SWE (AN/DP) across growing seasons can be demonstrated by the effectiveness of SWE (AN/DP) in improving crop yield and production economics. The economics of using a new technology is an important driver for adoption. In the case of SWE (AN/DP), the field trials showed consistent and significant improvements in crop yield which translated to improved crop revenue and profitability across diverse crops such as sugarcane, grapes, strawberries, and avocados. Results from the individual field trials were consistent with crop yield increases despite the variations in seasonal growing conditions. The crop yield results correspond with the changing seasonal growing environment, the farm management systems, and the genetic potential of the crop. The impact of seasonal variation needs to be discussed with agronomists and growers to set realistic expectations about the seasonal yield benefits when applying SWE (AN/DP) to crops in the open field. In addition, the yield results demonstrate the simplicity of integrating the application of the same SWE (AN/DP) across different real-life commercial grower programs.

Multiple SWE applications in the field The field research suggests an emerging theme about the benefit of using repeated applications of SWE (AN/DP) during the growing season. The approach of implementing multiple applications of SWE (AN/DP) to field crops could be a strategy to optimize the SWE (AN/DP) stress mitigation properties and maximize crop yield. Throughout the growing season crops encounter different and repeated abiotic and biotic stresses, and intrinsic nutrient stress at times of high developmental demands. A single application of SWE (AN/DP) has not been reported to provide season-long stress relief. For growers the inclusion of multiple applications of SWE (AN/DP) throughout the season is a practical approach to manage the ongoing exposure and unpredictable timing for crop stress occurrences. In this regard, the Australian field research provides consolidated knowledge because of the different examples implementing repeated applications of the same SWE (AN/DP).

Optimizing the use of SWE in Australian agriculture

Practical properties of SWE applications

The practical properties of applying SWE include their efficacy across plants and crops. The effects of SWE can be achieved through different application methods such as spraying canopies of plants, soil fertigation, plant and soil drenching, subsurface fertigation, under-tree micro-sprinklers, and the dipping of plant roots in diluted solutions of SWE (Arioli et al. 2015; Shukla et al. 2019, 2021; Ali et al. 2021). Cooperatively, the practical properties of SWE enable growers and agronomists to optimize their use in production by adapting their application rates, frequency, delivery methods, and timing to suit their farming soils, climate, and operations, and the crop development stage.

The economics of SWE applications

The literature supports the inclusion of SWE into grower programs for improved economic benefits. This type of information is important to share with growers and agronomists to justify the claims for improved revenue and profitability. For growers and agronomists, the proven financial gains are one of the drivers for change and reduce a firsthand concern when considering the adoption of new technologies (Cullen et al. 2013; Forbes et al. 2013). However, the absolute financial gains vary by crop and farming system. Growers and agronomists will need to optimize the application of SWE for their specific growing programs to gain maximum economic benefit and desired outcomes.

Optimization of SWE applications

The key benefits of the actions of SWE in real-world production conditions are summarized in Fig. 2. The optimization of SWE applications relies on the successful integration of SWE into production programs and farming systems. There are many aspects for agronomists to consider when recommending grower programs, including the 4R Nutrient Stewardship concept developed by the fertilizer industry to achieve best management practices for fertilizer input (Johnston and Bruulsema 2014). The nutrient stewardship guidelines recommend (i) applying the right source of nutrients, (ii) at the right rate, (iii) at the right time, and (iv) in the right place; and the principle includes matching the fertilizer applications to the crop needs and soil properties. For example, grower programs including synthetic fertilizers or manure rely on estimating the nutrient needs for growing the crop, for the right recommended amounts to be applied at the appropriate time and in alignment with the developmental needs of the crop, and for the method of application

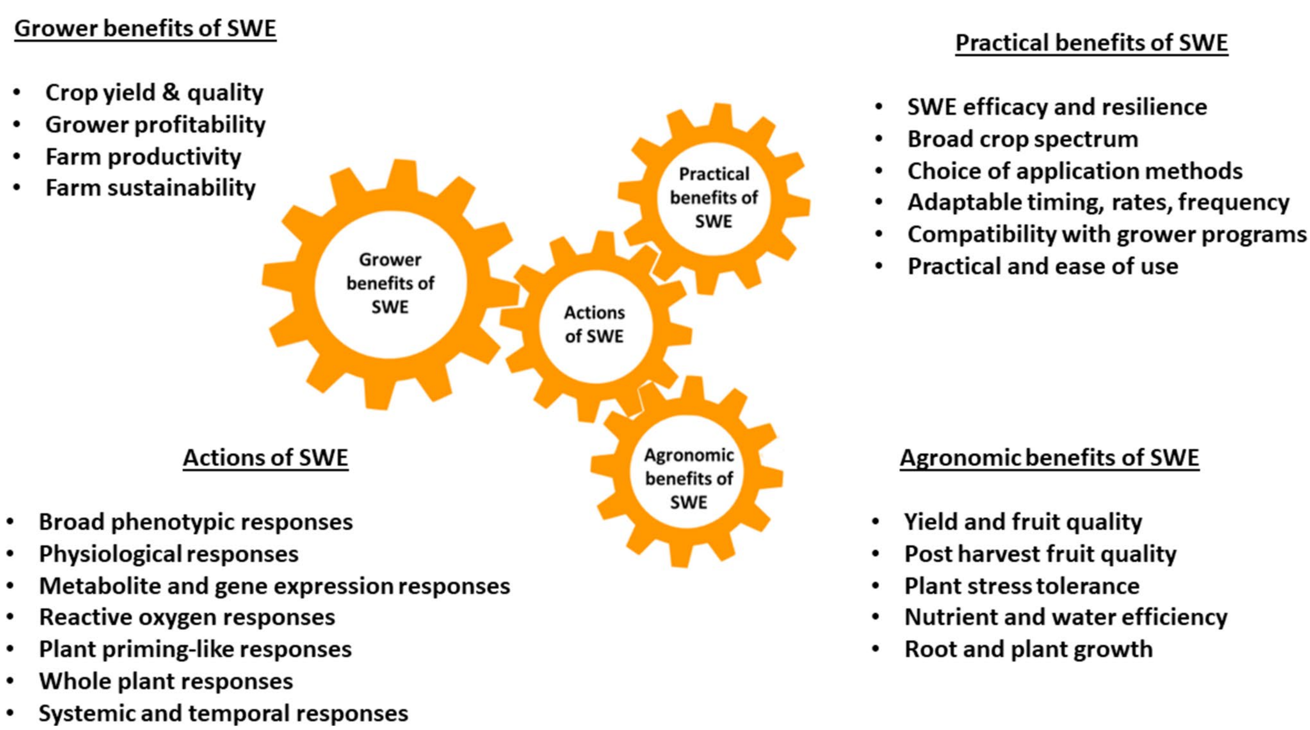

Fig. 2 A summary of the key actions of seaweed extract (SWE) in relation to grower, agronomic and practical benefits. This summary is prepared from the references listed in the review

to align with the seasonal weather circumstances. This is a simplified concept since variations in farming systems, annual yields, previous crop management, crop rotations, and grower expectations all influence the development of a grower program.

Each season the specific weather conditions vary and therefore directly impact the growth and development of crops. The practice of applying SWE on repeated occasions throughout the season is a strategy to counter the unpredictability of the growing conditions. However, there may be times where specific application(s) of SWE may be beneficial for the farm's situation. For example, in excessively cool conditions, plants may slow their growth rate, shed flowers, delay flowering time and fruit set time, impacting yield and/or fruit quality and delaying harvest. In these situations, SWE could be customized by applying SWE at times to boost growth when warmer conditions prevail and/or later as the fruit grows to advance fruit development and quality. Similarly, SWE application can be tailored for crops encountering extreme heat conditions to improve plant tolerance, improve recovery, and to reduce the impact of slowing plant growth and developmental delays in fruit quality. These types of weather circumstances can occur any time during the season and therefore the application of SWE may be adjusted to the weather patterns specific to the farm's situation and the crop's development stage.

Another aspect that needs consideration is the status of the soil properties, which are influenced by seasonal weather patterns. In Australia farmers can encounter major changes in soil properties within a growing season due to weather. For example, after flood conditions some soils can become collapsed, compacted, and hard setting; under drought conditions soils can become water repellent, microbial activity decreases, and Carbon, Nitrogen, and Phosphorus cycling is reduced (Jenkins et al. 2020; AWRI 2022). Therefore, for maximum efficacy, the timing and rates for soil applications of SWE warrant consideration of the status of the farm's soil properties. This optimization practice is understood for the fertigation of fertilizers – relationships between soil type to available water-holding capacity, and irrigation scheduling to replace readily available water, are taken into consideration for optimized fertilizer application (DPI 2014). The same considered and adaptive approach is necessary to optimize the effectiveness of SWE applications to individual farm situations. To gain the full benefits of SWE in agriculture, agronomic best practices and the fertilizer stewardship principles provide a guide for growers to tailor, adapt, and optimize the application of SWE for each farm situation. Concurrently, these principles should be validated through continued field research to ensure their use in agricultural systems remains evidence-based.

Conclusions

There is now a substantial amount of new discovery and applied published research that supports the integration of SWE (AN/DP) into Australian agricultural programs. This science is providing deeper insights for the actions that SWE stimulate to achieve improved plant growth and improved plant tolerance to stress, despite the complex composition of SWE. At the molecular level, SWE application can initiate substantial transcriptome and metabolite reprogramming in different plant parts and across diverse pathways and plant priming responses. However, we are still missing critical knowledge to decipher the actions of SWE in plants. For example, the chloroplast is a central organelle in generating metabolites for plant stress tolerance and energy from photosynthesis, therefore understanding the role of the chloroplast in the plant responses to SWE warrants research. Plants have been shown to consume microbes as a source of nutrients by a system called rhizophagy, but there is little information on how SWE affect this system.

Field research is demonstrating the capacity of SWE to perform effectively across different growing situations. There are an increasing number of SWE sold in the marketplace. For those SWE supported by discovery and/or field science there are many cogent, practical, and economic reasons to incorporate SWE into agricultural production programs. In Australia, we have reached an era in the application of SWE in agriculture where the evidence available to agronomists and growers is compelling to fully adopt, integrate, and optimize the use of SWE in their production programs. To progress we need to increase engagement with growers and agronomists about the benefits of using SWE and the science supporting their use. This can be achieved by extending to growers and agronomists the latest scientific and applied knowledge about SWE so they are best enabled to utilize, optimize, and profit by the inclusion of SWE in their conventional, organic, and regenerative farming systems.

Authors' contributions All co-authors contributed to the final version of the work and approved the manuscript for publication.

Funding None

Declarations

Conflicts of interest/Competing interests Seasol International (SI) is the manufacturer of the seaweed extract in Australia. TA and MW are employees of SI. TA is an Adjunct Associate Professor at Deakin University. The authors declare that the research was conducted in the absence of any financial relationship that could be construed as a potential conflict of interest.

References

Abetz P, Young C (1983) The effect of seaweed extract sprays derived from *Ascophyllum nodosum* on lettuce and cauliflower crops. Bot Mar 26:487–492

Ali N, Farrell A, Ramsubhag A, Jayaraman J (2016) The effect of *Ascophyllum nodosum* extract on the growth, yield and fruit quality of tomato grown under tropical conditions. J Appl Phycol 28:1353–1362

Ali O, Ramsubhag A, Farrell AD, Jayaraman J (2022) Foliar application of seaweed extracts influences the phytomicrobiome dynamics in tomato and sweet pepper plants. J Appl Phycol 34:3219–3235

Ali O, Ramsubhag A, Jayaraman J (2021) Biostimulant properties of SWE in plants: implications towards sustainable crop production. Plants 10:531

Anderson G (2009) Seaweed extract shows improved fruit quality at McLaren Vale vineyard trial. Aust NZ Grapegrower Winemaker 548:17–22

Aranega-Bou P, Leyva M, Finiti I, Garcia-Agustin P, Gonzalez-Bosh C (2014) Priming of plant resistance by natural compounds. Front Plant Sci 5:488

Arioli T, Hepworth G, Farnsworth B (2020) Effect of seaweed-extract application on sugarcane production. Proc Aust Soc Sugar Cane Technol 42:393–396

Arioli T, Hepworth G, Farnsworth B, Kasinadhuni N, Noune C, Mattner S (2021a) Effect of seaweed-extract application on sugarcane yield in Australia. Proc Aust Soc Sugar Cane Technol 42:637–644

Arioli T, Mattner S, Hepworth G, McClintock D, McClintock R (2021b) Effect of seaweed extract application on wine grape yield in Australia. J Appl Phycol 33:1883–1891

Arioli T, Mattner S, Winberg P (2015) Applications of seaweed extracts in Australian agriculture: past, present and future. J Appl Phycol 27:2007–2015

Arioli T, Villalta O, Hepworth G, Farnsworth B, Mattner S (2023) Effect of seaweed extract on avocado root growth, yield and postharvest quality in far north Queensland, Australia. J Appl Phycol

AWRI (2022) Managing waterlogged vineyards. Australian Wine Research Institute. https://www.awri.com.au/wp-content/uploads/2022/11/Managing-waterlogged-vineyards.pdf; accessed 2 July 2023

Baccelli I, Benny J, Caruso T, Martinelli F (2020) The priming fingerprint on plant transcriptome investigated though meta-analysis of RNA-Seq data. Eur J Plant Pathol 156:779–797

Bakker C, Swanton C, McKeown A (2009) Broccoli growth in response to increasing rates of plant nitrogen. I. Yield and quality. Can J Plant Sci 89:527–537

Balmer A, Pastor V, Gamir J, Flors V, Mauch-Mani B (2015) The 'prime-ome': towards a holistic approach to priming. Trends Plant Sci 20:443–452

BOM (2021) Annual climate statement 2020: issued 8 Jan 2021. http://www.bom.gov.au/climate/current/annual/aus/; accessed 18 January 2021

Buswell W, Schwarzenbacher R, Luna E, Sellwood M, Chen B, Flors V, Pétriacq P, Ton J (2018) Chemical priming of immunity without cost to plant growth. New Phytol 218:1205–1216

Chen D, Zhou W, Yang J, Ao J, Huang Y, Shen D, Jiang Y, Huang Z, Shen H (2021) Effects of seaweed extracts on the growth, physiology activity, cane yield and sucrose content of sugarcane in China. Front Plant Sci 12:659130

Cocetta G, Landoni M, Pilu R, Nolasco J, Alajarin M, Ugena L, Levy C, Scatoline G, Villa D, Ferrant A (2022) Priming treatments with biostimulants to cope the short-term heat stress response: a transcriptomic evaluation. Plants 11:1130

Conrath U, Beckers G, Langenbach C, Jaskiewicz M (2015) Priming for enhanced defense. Annu Rev Phytopathol 53:97–119

Cook J, Zhang J, Norrie J, Blal B, Cheng Z (2018) Seaweed extract (Stella Maris®) activates innate immune responses in *Arabidopsis thaliana* and protects host against bacterial pathogens. Mar Drugs 16:221

Cullen R, Forbes S, Grout R (2013) Non-adoption of environmental innovations in wine growing. NZ J Crop Hort Sci 41:41–48

Deolu-Ajayi A, van der Meer I, van der Werf A, Karlova R (2022) The power of seaweeds as biostimulants to boost crop production under abiotic stress. Plant Cell Environ 45:2537–2553

Deshmukh P, Phonde D (2013) Effect of seaweed extract on growth, yield and quality of sugarcane. Int J Agric Sci 9:750–753

Dimsey R (2009) Growing broccoli. Agnote AG0074. Victorian Department of Primary Industries, Melbourne

DPI (2014) Primefact 1364 – Irrigation scheduling principles for horticultural crops. Department of Primary Industries. https://www.dpi.nsw.gov.au/__data/assets/pdf_file/0003/534423/irrigation_scheduling_principles_for_horticultural_crops.pdf; accessed 2 July 2023

EBIC 2023 White Paper: Recent insights into the mode of action of seaweed-based plant biostimulants. European Biostimulants Industry Council. https://biostimulants.eu/publications/seaweed-whitepaper-v11/; accessed 2 July 2023

Farnsworth W, Arioli A (2018) Assessment of the yield of sugarcane following treatment with liquid seaweed extract (SEASOL®). Acta Hortic 1205:785–788

Feller C, Fink M (2005) Growth and yield of broccoli as affected by the nitrogen content of transplants and the timing of nitrogen fertilization. Hortic Sci 40:1320–1323

Finiti I, Leyva M, Vicedo B, Gomez-Pastor R, Lopez-Cruz J, Garcia-Agustin RM, Gonzalez-Bosch C (2014) Hexanoic acid protects tomato plant against *Botrytis cinerea* by priming defence responses and reducing oxidative stress. Mol Plant Pathol 15:550–562

Fleming T, Fleming C, Levy C, Repiso C, Hennequart F, Nolasco JB, Liu F (2019) Biostimulants enhance growth and drought tolerance in *Arabidopsis thaliana* and exhibit chemical priming action. Ann Appl Biol 174:153–165

Forbes S, Cullen R, Grout R (2013) Adoption of environmental innovations: analysis from the Waipara wine industry. Wine Econ Policy 2:11–18

Gomathi R, Kohila S, Ramachandiran K (2017) Evaluating the effect of seaweed formulations on the quality and yield of sugarcane. Madras Ag J 104:161–165

Goñi O, Quille P, O'Connell S (2018) *Ascophyllum nodosum* extract biostimulants and their role in enhancing tolerance to drought stress in tomato plants. Plant Physiol Biochem 126:63–73

Gonzalez-Bosch C (2018) Priming plant resistance by activation of redox-sensitive genes. Free Radic Biol Med 122:171–180

Hua L, Yong C, Zhanquan Z, Boqiang L, Guozheng Q, Shipping T (2018) Pathogenic mechanisms and control strategies of *Botrytis* *cinerea* causing post-harvest decay in fruits and vegetables. Food Qual Saf 2:111–119

Hussain H, Kasinadhuni N, Arioli T (2021) The effect of seaweed extract on tomato plant growth, productivity and soil. J Appl Phycol 33:1305–1314

Islam M, Arioli T, Cahill D (2021) Seaweed extract-stimulated priming in *Arabidopsis thaliana* and *Solanum lycopersicum*. Plants 10:2476

Islam M, Gan H, Ziemann M, Hussain H, Arioli T, Cahill D (2020) Phaeophyceaean (brown algal) extracts activate plant defense systems in *Arabidopsis thaliana* challenged with *Phytophthora cinnamomi*. Front Plant Sci 11:852

Jannin L, Arkoun M, Etienne P, Liane P, Goux D, Garnica M, Fuentes M, San Francisco S, Baigorri R, Cruz F, Houdusse F, Garcia-Mina J-M, Yvin J-C, Ourry A (2013) *Brassica napus* growth is promoted by *Ascophyllum nodosum* (L.) Le Jol. seaweed extract: microarray analysis and physiological characterization of N, C, and S metabolisms. J Plant Growth Regul 32:31–52

Jenkins A, Orgill S, Friend J, Dougherty W, Rigg J, Rose M, Beange L (2020) Primefact 367: Soil management – drought recovery. Department of Primary Industries. https://www.snowymonaro.nsw.gov.au/files/assets/public/environment-and-waste/documents/prime-fact-soil-management-drought-recovery.pdf; accessed 2 July 2023

Jindo K, Goron T, Pizarro-Tobias P, Sánchez-Monedero M, Audette Y, Deolu-Ajayi A, van der Werf A, Teklu M, Shenker M, Sudre C, Busato J, Ochoa-Hueso R, Nocentini M, Rippen J, Aroca R, Mesa S, Delgado M, Tortosa G (2022) Application of biostimulant products and biological control agents in sustainable viticulture: a review. Front Plant Sci 13:932311

Jithesh M, Shukla S, Kant P, Joshi J, Critchley T, Prithiviraj B (2019) Physiological and transcriptomics analyses reveal that *Ascophyllum nodosum* extracts induce salinity tolerance in Arabidopsis by regulating the expression of stress responsive genes. J Plant Growth Regul 38:463–478

Johnston A, Bruulsema T (2014) 4R Nutrient stewardship for improved nutrient use efficiency. Procedia Eng 83:365–370

Karasov T, Chae E, Herman J, Bergelson J (2017) Mechanisms to mitigate the trade-off between growth and defense. Plant Cell 29:666–680

Karthikeyan K, Shanmugam M (2017) The effect of potassium-rich biostimulant from seaweed *Kappaphycus alvarezii* on yield and quality of cane and cane juice of sugarcane var. Co 86032 under plantation and ratoon crops. J Appl Phycol 29:3245–3252

Keller M (2010) Managing grapes to optimise fruit development in a challenging environment: a climate change primer for viticulturists. Aust J Grape Wine Res 16:56–69

Kerchev P, Meer T, Sujeeth N, Verlee A, Stevens C, Breusegem F, Gechev T (2020) Molecular priming as an approach to induce tolerance against abiotic and oxidative stresses in crop plants. Biotechnol Adv 40:107503

Kumar R, Trivedi K, Anand K, Ghosh A (2020) Science behind biostimulant action of seaweed extract on growth and crop yield: insights into transcriptional changes in roots of maize treated with *Kappaphycus alvarezii* seaweed extract under soil moisture stressed conditions. J Appl Phycol 32:599–613

Li J, Van Gerrewey T, Geelen D (2022) A meta-analysis of biostimulant yield effectiveness in field trials. Front Plant Sci 13:836702

Martinez-Medina A, Flors V, Heil M, Mauch-Mani B, Pieterse C, Pozo M, Ton J, Dam N, Conrath U (2016) Recognizing plant defense priming. Trends Plant Sci 21:818–822

Martynenko A, Shotton K, Astatkie T, Petrash G, Fowler C, Neily W, Critchley T (2016) Thermal imaging of soybean response to drought stress: the effect of *Ascophyllum nodosum* seaweed extract. Springerplus 5:1393

Mattner S, Milinkovic M, Arioli T (2018) Increased growth response of strawberry roots to a commercial extract from *Durvillaea potatorum* and *Ascophyllum nodosum*. J Appl Phycol 30:2943–2951

Mattner S, Villalta O, McFarlane D, Islam M, Arioli T, Cahill D (2023) The biostimulant effect of an extract from *Durvillaea potatorum* and *Ascophyllum nodosum* is associated with the priming of reactive oxygen species in strawberry in south-eastern Australia. J Appl Phycol 35:1789–1800

Mattner S, Wite D, Riches D, Porter I, Arioli T (2013) The effect of kelp extract on seedling establishment of broccoli on contrasting soil types in southern Victoria, Australia. Biol Agric Hortic 29:258–270

Mauch-Mani B, Baccelli I, Luna E, Flors V (2017) Defense Priming: an adaptive part of induced resistance. Annu Rev Biol 68:485–512

Nair P, Kandasamy S, Zhang J, Ji X, Kirby C, Benkel B, Hodges MD, Critchley AT, Hiltz D, Prithiviraj B (2012) Transcriptional and metabolomic analysis of *Ascophyllum nodosum* mediated freezing tolerance in *Arabidopsis thaliana*. BMC Genomics 13:643

Omidbakhshfard A, Sujeeth N, Gupta S, Omranian N, Guinan J, Brotman Y, Nikoloski Z, Fernie A, Mueller-Roeber B, Gechev T (2020) A biostimulant obtained from the seaweed *Ascophyllum nodosum* protects *Arabidopsis thaliana* from severe oxidative stress. Int J Mol Sci 21:474

Perez I, Brown P (2014) The role of ROS signaling in cross-tolerance: from model to crop. Front Plant Sci 5:754

Porter I, Mattner S, Riches D, Edwards J, Melville P, Davies R (2012) Do nitrification inhibitors on fertilisers and manures reduce N_2O emissions and provide benefit in horticultural production systems? In: Barlow S, Kelly A, Graham A, Sullivan T, Hull L (eds) Proceedings of the Climate Change Research Strategy for Primary Industries Conference; 2012 Nov 27. Melbourne, Victoria.

Rasul F, Gupta S, Olas J, Gerchev T, Sujeeth N, Mueller-Roeber B (2021) Priming with a seaweed extract strongly improves drought tolerance in Arabidopsis. Int J Mol Sci 22:1469

Rayorath P, Jithesh M, Farid A, Khan W, Palanisamy R, Hankins S, Critchley A, Prithiviraj B (2008) Rapid bioassays to evaluate the plant growth promoting activity of *Ascophyllum nodosum* (L.) Le Jol. using a model plant *Arabidopsis thaliana* (L.) Heynh. J Appl Phycol 20:423–429

Renaut S, Masse J, Norrie J, Blal B, Hijri M (2019) A commercial seaweed extract structured microbial communities associated with tomato and pepper roots and significantly increased crop yield. Microb Biotechnol 12:1346–1358

Repke R, Silva D, Santos J, Silva M (2022) Increased soybean tolerance to high-temperature through biostimulant based on *Ascophyllum nodosum* (L.) seaweed extract. J Appl Phycol 34:3205–3218

Ricci M, Tilbury L, Daridon B, Sukalac K (2019) General principles to justify plant biostimulant claims. Front Plant Sci 10:494

Santaniello A, Scartazza A, Gresta F, Loreti E, Biasone A, Di Tommaso D, Piaggesi A, Perata P (2017) *Ascophyllum nodosum* seaweed extract alleviates drought stress in *Arabidopsis* by affecting photosynthetic performance and related gene expression. Front Plant Sci 8:1362

Scarlett N (2009) Reducing berry raisining in the vineyard: a vineyard case study in small-scale, on-farm research. Aust NZ Grapegrower Winemaker 550:25–28

Scarlett N, Needs S, Howell K, Cooley N (2011) Berry desiccation: developing pre-emptive methods to adapt to heat spikes and dry conditions. Aust NZ Grapegrower Winemaker 567:20–23

Shukla P, Mantin E, Adil M, Bajpai S, Critchley A, Prithiviraj B (2019) *Ascophyllum nodosum*-based biostimulants: sustainable applications in agriculture for the stimulation of plant growth, stress tolerance, and disease management. Front Plant Sci 10:665

Shukla P, Borza T, Critchley A, Prithiviraj B (2021) Seaweed-based compounds and products for sustainable protection against plant pathogens. Mar Drugs 19:29

SOE (2021) Australia State of the Environment 2021: Soil. Commonwealth of Australia. https://soe.dcceew.gov.au/land/environment/soil; accessed 2 July 2023

SRA (2014) Irrigation of Sugarcane Manual: Technical publication MN14002. Sugar Research Australia. https://sugarresearch.com.au/sugar_files/2017/02/Irrigation-Manual-F-LowRes2.pdf: accessed 2 July 2023

Staykov N, Angelov M, Petrov V, Minkov P, Kanojia A, Guinan K, Alseekh S, Fernie A, Sujeeth N, Gechev T (2021) An *Ascophyllum nodosum*-derived biostimulant protects model and crop plant from oxidative stress. Metabolites 11:24

Szparaga A, Kuboń M, Kocira S, Czerwińska E, Pawłowska A, Hara P, Kobus Z, Kwaśniewski D (2019) Towards sustainable agriculture – agronomic and economic effects of biostimulant use in common bean cultivation. Sustainability 11:4575

Tay B, MacLeod K, Palni S, Letham S (1985) Detection of cytokinins in a seaweed extract. Phytochemistry 24:2611–2614

Tay B, Palni S, MacLeod K (1987) Identification of cytokinin glucosides in a seaweed extract. J Plant Growth Regul 5:133–138

Tiwari M, Singh P (2021) Plant defense priming: a new tool for sustainable global food security. In: Shekhawat GS (ed) Agricultural Innovations and Sustainability. Agrobios Research, Jodhpur, pp 133–153

Tran T, Callahan D, Islam M, Yichao W, Arioli T, Cahill D (2023) Comparative metabolomic profiling of *Arabidopsis thaliana* roots and leaves reveals complex response mechanisms induced by a seaweed extract. Front Plant Sci 14:1114172

Tugizimana F, Mhlongo M, Piater L, Dubery I (2018) Metabolomics in plant priming research: the way forward? Int J Mol Sci 19:1759

Wally O, Critchley A, Hiltz D, Craigie J, Han X, Zaharia I, Abrams S, Prithiviraj B (2013) Regulation of phytohormone biosynthesis and accumulation in Arabidopsis following treatment with commercial extract from the marine macroalga *Ascophyllum nodosum*. J Plant Growth Regul 32:324–339

Wite D, Mattner S, Porter I, Arioli T (2015) The suppressive effect of a commercial extract from *Durvillaea potatorum* and *Ascophyllum nodosum* on infection of broccoli by *Plasmodiophora brassicae*. J Appl Phycol 27:2157–2161

Yao Y, Wang X, Chen B, Zhang M, Ma J (2020) Seaweed extract improved yields, leaf photosynthesis, ripening time, and net returns of tomato (*Solanum lycopersicum* Mill.). ACS Omega 5:4242–4249

Yusuf R, Kristiansen P, Warwick N (2012) Potential effect of plant growth regulators on two seaweed products. Acta Horticult 958:133–138