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Review

Hungry Plants—A Short Treatise on How to Feed Crops under Stress

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Received: 31 January 2018; Accepted: 15 March 2018; Published: 17 March 2018

Abstract: Fertilisation is as old as is the cultivation of crops. In the 19th century, plant nutrition became an area of research in the field of agricultural chemistry. *Liebig*'s "Law of the Minimum" (1855) is still the basis for plant nutrition. It states that the exploitation of the genetically fixed yield potential of crops is limited by that variable, which is insufficiently supplied to the greatest extent. With a view to abiotic and biotic stress factors, this postulation should be extended by the phrase "and/or impaired by the strongest stress factor". Interactions between mineral elements and plant diseases are well known for essential macro- and micronutrients, and silicon. In comparison, the potential of fertilisation to alleviate abiotic stress has not been compiled in a user-orientated manner. It is the aim of this chapter to summarise the influence of nutrient deficiency in general, and the significance of sodium, potassium, and silicon, in particular, on resistance of crop plants to abiotic stress factors such as drought, salinity, and heavy metal stress. In addition, the significance of seed priming with various nutrients and water to provide tolerance against abiotic stress is discussed. Underlying physiological mechanisms will be elaborated, and information on fertiliser application rates from practical experiences provided.

Keywords: drought; heavy metal pollution; no-effect value; potassium; salinity; seed priming; silicon; sodium

1. Introduction

Instinctive management practices feeding plants can be traced back to the Neolithic agricultural revolution [1]. But it was the development of mineral fertilisers, in particular nitrogen (N), after World War I which revolutionised agricultural production. *Liebig*'s "Law of the Minimum" (1855) is still the basic concept of plant nutrition. It states that the "exploitation of the genetically fixed yield potential of crops is limited by that nutrient, which is insufficiently supplied to the greatest extent" (Figure 1). This principle assumes that all other growth factors, such as water supply and temperature, are optimum. The significance of regularly occurring abiotic and biotic stress factors is neglected, but deserves attention where they significantly affect crop production. Thus, *Liebig*'s law of the minimum should be extended by the phrase "and/or is impaired by the strongest stress factor".

Though the significance of individual nutrients for maintaining or promoting plant health saw some interest in the 1960s and 1970s [2], research in the field of nutrient induced resistance mechanisms has been scarce because of its complexity and limited practical significance, due to the availability of effective pesticides. Recent omics approaches have enabled identification of underlying physiological mechanisms of nutrient induced resistance against diseases [3] and tolerance against abiotic stress [4]. Abiotic stress factors comprise nutrient and water deficiency, soil pH, temperature, oxygen supply, mechanical pressure, injury, chemical compounds, and heavy metals [5].

Figure 1. *Liebig*'s law of the minimum (diagrammatic illustration).

Sulphate and phosphate fertiliser applications have been tested to fix Sr^{90} in soil, but even excessively high rates yielded no significant effect on Sr^{90} uptake of plants in field experimentation [6]. Likewise, no data exist on a quantitatively relevant detoxification of heavy metals in plants by sulphur (S) fertilisation through the formation of phytochelatins and metallothioneins. Both metabolites are S-containing secondary compounds that bind, for instance, As, Cd, Cr, Cu, and Ni. The question remains open as to whether graded S fertiliser rates yield a parallel increase in these secondary components as has been shown, for example, for glucosinolates [7]. Rather, Ernst [8] stated that phytochelatin synthesis is an unspecific metabolic reaction to increased heavy metal concentrations, which bind only small amounts of metal, and that resistance of the biomembrane is a much more efficient mechanism against heavy metal stress. The amelioration and reclamation of acid, saline, and polluted soils by fertiliser practices are not subjects of this review, as these topics have been discussed comprehensively before [9,10].

The phenomenon that mild stress induces yield gains and quality improvements is well known from the cultivation and processing of herbal plants [11–13]. In both cases, the effect is explained by a stimulation of metabolic processes in order to defy oxidative stress. By contrast, worldwide severe stress conditions are a serious threat to crop productivity, and measures to alleviate temporal and permanent abiotic stress are an important contribution to food security. Though various essential macro- and micronutrients are involved in tolerance mechanisms against abiotic stress, only a limited number of beneficial elements proved to alleviate stress conditions under field conditions. The aim of this chapter is to compile fertiliser practices which have proved to significantly mitigate abiotic and biotic stress under field conditions. In addition, underlying physiological mechanisms have been assessed, and guidelines for fertilisation will be provided.

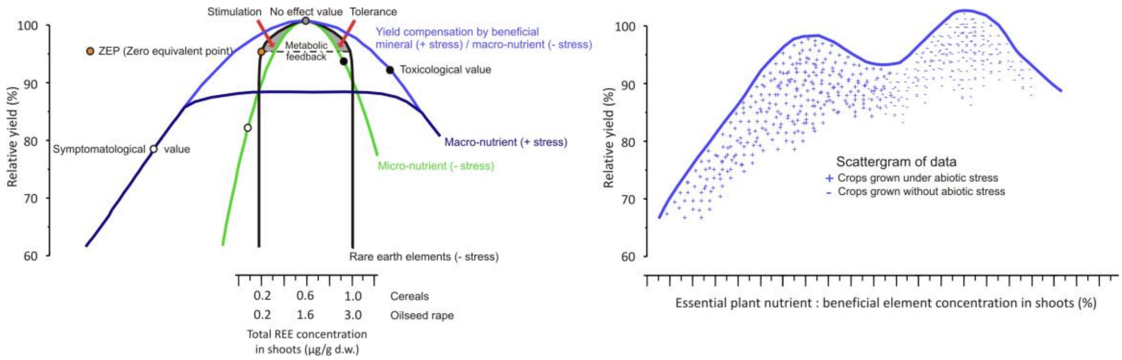
2. Balanced Nutrient Supply—Essential to Secure Productivity and Pivotal Barrier against Abiotic and Biotic Stress

A balanced nutrient supply is a basic requirement to protect plants against all forms of stress. The depletion of nutrients, soil organic matter, and erosion are the principal forms of soil degradation. Nutrient deficiency is an abiotic stress factor, whereby a limited nutrient stock needs to be distinguished from restricted nutrient availability. In the first case, the deficiency can be balanced by adequate soil-applied fertiliser rates, in the second case, the mobility can be enhanced, for instance, by increasing or decreasing the soil pH value by applying lime and acidifying fertilisers, respectively. Another alternative is the use of foliar fertiliser applications. The ideal causal chain to avoid stress induced by nutrient deficiency is assessment of the nutrient supply status–establishment of fertiliser response curves–targeted fertiliser application.

The nutrient status of plants follows the typical *Mitscherlich* growth functions from severe over moderate deficiency, to optimum supply, and finally, toxicity (Figure 2a). The so-called upper boundary lines represent the mathematical, usually, 4th order polynomial functions of the impact of increasing nutrient concentrations in the plant tissue on crop yield at defined growth stages, if no other growth factor is yield limiting [14]. The mathematical procedures to determine upper boundary line functions have been developed by Schnug et al. [15]. Boundary lines describe the "pure effect of a nutrient" on crop yield under *ceteris paribus* conditions [16–18], as the line describes the highest yields observed over the range of nutrient values measured. Data points below this line relate to samples where some other factor limited the crop's response to the nutrient. It is important to note that the slopes of the growth functions of essential macro- and micronutrients increase steeply with decreasing critical elemental concentrations in the plant tissue (Figure 2a).

So far, it is not known what impact low input systems on their own, or combined with stress conditions, have on curve progression (Figure 2). If another variable, for instance, a stress factor (drought, salinity) and stress relieving minerals, such as sodium (Na) and silicon (Si), are having a significant effect on the response to the nutrient, their presence will be indicated by two or more distinct concentrations of points, each with its own boundary line response to the nutrient (Figure 2b). Then, the data can be classified on the basis of stress factor and concentration of essential plant nutrient and stress relieving minerals; then boundary lines can be determined separately for each class (Figure 2, [14]).

The physiological nutrient demand can be higher under stress conditions than needed for high yield. This has been shown for S in order to trigger *SIR* (sulphur induced resistance) against fungal pathogens [19], and also will be shown for the application of silicon (Si) against fungal diseases in this chapter.



(**a**) (**b**)

Figure 2. Common, abstract upper boundary line progression for essential macro- and micronutrients and beneficial minerals in relation to abiotic stress, and predicted progression of upper boundary lines for rare earth elements (REEs) (**a**); scattergram showing the relationship between essential plant nutrients and beneficial elements on crop yield indicating two categories (+/−) of the discriminating variable abiotic stress (**b**) (adapted from [20]).

Minerals are rated as beneficial for plants if they promote growth and yield, replace the function of essential nutrients in plant metabolism, or strengthen the natural resistance of plants against abiotic and biotic stress. Prominent examples are, for example, Na and Si. If abiotic stress reduces crop yield, for instance, by 15%, a mineral should have the potential to compensate this gap. As a result, the boundary line progression of the essential plant nutrient will not change under stress (Figure 2a). Such stress-compensating effect has been postulated for rare earth elements (REEs), too, but data suggest that REEs yield, most likely, a hormetic effect ([20], Figure 2a). It is difficult to come to a final decision as to whether REEs are beneficial for plant growth and act as mediators against abiotic stress, as contradictory findings exist.

Critical values are indispensable for evaluating the nutritional status of a crop. Important threshold markers are the symptomatological value, which reflects the nutrient concentration below which deficiency symptoms become visible; the no-effect value, which stands for the nutrient concentration above which the plant is sufficiently supplied for achieving the maximum potential yield, the critical nutrient value for realising a yield level which is 5, 10, and 20% lower than the maximum yield [21]; and the toxicological value, which indicates the nutrient concentration above which toxicity symptoms can be observed (Figure 2a). The sufficiency range indicates the span of concentrations within which any change of the nutrient content will not influence crop yield [22].

It is important to note that there is no one exclusive critical nutrient value for each crop, as this depends on the growth conditions, the developmental stage of the plant at sampling, the specific plant part, the determined nutrient species, the targeted yield and mathematical approach for calculating it. This also implies that it is more or less impossible to compare results from different experiments, particularly as critical values are often based on not more than a single experiment [23]. Consequently, a sheer innumerable amount of critical nutrient values can be found in literature for different crops. For these reasons, Smith and Loneragan [22] stressed that it is only possible to define ranges, and not specific values, for different nutritional levels. As an example, Haneklaus et al. [7] compiled and categorised available individual data with varying experimental conditions from the literature, for the variables total S and sulphate concentrations, and N/S ratios in relation to different crop species, in order to facilitate an easy and appropriate evaluation of the S status. Plant groups were assembled by morphogenetic and physiological features. Because of the wide heterogeneity of results for similar classes of S supply and for a better comparability of results, concentrations were combined in three major categories: deficient, adequate, and high, irrespective of the sampled plant part during vegetative growth. The results of the approach chosen by [7,14] were in close agreement with individual no-effect values and ranges that the authors determined independently by employing BOLIDES ((Boundary Line Development System), Table 1). The data sets interpreted by [14] comprised several thousand entries for cereals and oilseed rape, and more than 500 for sugar beet from field surveys, field trials, or pot experiments, which cover a wide range of growth factor combinations. In Table 1, the no-effect values for macro- and micronutrients, and Na contents in cereals, sugar beet, and oilseed rape are summarised. Nutrient concentrations which equal or are higher than the no-effect values are required to achieve maximum crop yields.

Table 1. No-effect values for essential macro- and micronutrients, and Na concentrations in cereals, oilseed rape, and sugar beet (extracted from [14]).

Nutrient	Cereals	Oilseed Rape	Sugar Beet
(mg/g d.w.)			
N	35	40	46
P	4	4.2	4.5
S	4	6.5	3.5
K	35	35	42
Ca	4	22.5	4.2
Mg	1.1	1.5	1.8
Na	-	-	2.0
(µg/g d.w.)			
Fe	60	100	100
Mn	28	30	30
Zn	25	33	50
Cu	4	4.5	15
Cl	100	100	-
B	3	25	30
Mo	0.2	0.3	-

For sugar beet, the question arises as to whether the no-effect values vary in relation to the reference value of productivity, namely root and sugar yield. The sugar beet root contains, on average, 18% sugar with a range of variation from 15 to 23%, depending on soil type, cultivar, and climate. The upper boundary line analysis revealed that relevant differences in the sufficiency nutrient ranges existed for Mg and Na with respect to root and sugar yield [14]. In the case of these elements, the concentration range for a sufficient supply with respect to the sugar yield was 2.2–4.0 mg/g for Mg and 4.0–6.5 mg/g for Na. This means that for maximising the sugar yield, Mg and Na concentrations that equal the no-effect values are not sufficient for maximising the sugar yield. This fact needs to be taken into account when the nutrient status is assessed by plant analysis, and considered in fertiliser management, respectively.

Where resilient critical nutrient values, sufficiency ranges or no-effect values are not available for a specific crop species, it is recommended that these are calculated site-specifically for each location by employing on-farm experimentation techniques, such as yield monitoring and directed sampling [24]. The overall advantage is that threshold values are tailor-made. The last step is the development of algorithms for a variable rate application of nutrients and stress relieving minerals, in relation to stress. The technology for continuous, variable rate application of fertilisers is available, and the best option for realising the site-specific yield potential under stress conditions. In low input systems, in particular, including organic farming, the systematic variable rate application of farmyard manure offers a solution to the key problem of strictly limited N and phosphorus (P) sources. A local resource management will harmonise the N and P supply. Where the technology is not available, "local knowledge" may be an adequate alternative [24]. In comparison, in high input systems, the main objective of variable rate mineral and organic fertilisation is to adjust rates in such way that crop productivity is maintained, whilst negative environmental side effects, for instance, by leaching and run-off of N and P, are avoided. Independently of the land use system, variable rate application of lime seems an appropriate measure to reduce the availability of undesirable heavy metals in soils and their uptake by plants.

3. Silicon—Multifunctional Mediator against Biotic, Drought, Salinity, and Heavy Metal Stress

Amongst all minerals, it is Si which manifests significant effects against biotic and abiotic stress under field conditions. The Si content in plants varies between 0.1 and 10% d.w. [25]. Plants show an active Si uptake, a passive Si uptake by diffusion, and a rejective Si uptake. Based on this differentiation one can distinguish between Si accumulators (>1.0% Si), intermediates, and excluders (<0.5% Si). Accumulating plants are sugarcane and rice, intermediates dryland *Gramineae*, while *Brassica* crops and potatoes are Si rejective [26]. Intrinsically, positive effects of Si applications can be expected for Si accumulating crop plants. Plants take up Si in the form of the uncharged molecule H_4SiO_4 (orthosilicic acid) by roots, while no hard evidence exists that plants can absorb Si through their leaves. This implies, in the case of biotic stress, that foliar sprays with Si have a direct impact on the pathogen, for instance, an osmotic effect on spores. Alternatively, the alkalisation of condensate water in branches of the crop may yield a fungitoxic effect [27]. Comprehensive data about Si in plants, the role of Si against biotic and abiotic stress, and fertiliser recommendations have been published in textbooks and reviews, and will provide detailed information about different aspects [3,28–30].

There is a green line through the mode of action of Si in response to abiotic and biotic stress, which is a fortification of the structural integrity of cell walls, the stimulation of the synthesis of defence components, and the contribution to the osmotic adjustment together with ion balance (homeostasis). The key functions in relation to the various stress factors are summarised next.

Si proved to be highly efficient against biotrophic and hemi-biotrophic fungi, such as mildew, *Septoria tritici*, and *Fusarium*, after soil application [31]. Several modes of action of Si against fungal diseases seem to be involved in resistance to infection. Hereby, it can be seen that Si acts as a natural activator of plant disease resistance. Si increases the structural integrity of cells by incorporating Si (amorphous $(SiO_2)m \cdot n(H_2O)$) in cell walls and intercellular spaces [32]. In the shoot, orthosilicic acid is polymerised to amorphous silica ($(SiO_2)m \cdot n(H_2O)$) which is deposited in specific cells. This deposited Si in plants functions as a physical barrier. In addition, soluble silicic acid may act prophylactic against pathogens. Besides this function, Si induces resistance pathways, for instance, phytoalexin synthesis [32] and synthesis of phenolic compounds [33]. Si fertilisation at rates of 5–15 t/ha have been most efficient in reducing the disease incidence of plants infected by biotrophic, hemi-biotrophic, and necrotrophic fungi by 40–70% in Si hyper- and semi-hyperaccumulating crops [3]. The disease intensities of some diseases for Si-supplied plants were lowered to the same level achieved with fungicides [28]. A similar efficacy has been observed for elemental S applications, and the disease incidence and severity of cereals with *Fusarium* head blight [34].

Si mitigates phytotoxicity of heavy metals, such as Mn, Al, Cu, Zn, Cd, As, Cr, and Pb [29]. Most studies concentrated on the influence of Si applications on alleviating Mn and Al toxicity. In principle, two mechanisms can be distinguished. Firstly, *ex planta* mechanisms in form of a pH effect, which results in reduced availability of the heavy metal and formation of more stable heavy metal fractions. The latter involves the formation of hydroxy-aluminosilicate (HAS) and binding of heavy metals to organic matter and crystalline Fe-oxides instead of labile heavy metal pools. Secondly, are *in planta* mechanisms that inhibit Mn uptake [35], restrict root to shoot transport, and induce a more even co-distribution of Si and Mn. Other studies showed an enhanced binding of Mn in cell walls and the detoxification of apoplastic Mn by soluble Si [36], and the co-precipitation and/or co-deposition of Si and Al, which reduces the Al transport into the symplast [37].

The percentage of arable land worldwide, which is adversely affected by salinity, amounts to some 20%, so any agrotechnical measure to tackle the problem deserves attention. Si increases the tolerance against salt stress significantly [29]. Research suggests that phytoliths $(SiO_2)m{\cdot}n(H_2O))$ in the apoplast enhances water retention by reducing transpirational water loss. Next, soluble Si in the symplast is involved in the biosynthesis of hormones, antioxidant defence enzymes, H^+-pumps, and osmolytes to rebalance ion stoichiometry, reduce membrane permeability and losses of electrolytes, and improve membrane structure and stability [28,30]. Other studies showed that Si reduced Na and increased K uptake/content of shoots and roots, in vivo, through the influence of proton pumps on plasma membranes [29]. Thus, Si increased the photosynthetic activity, leaf area, chlorophyll content chloroplast structure, and biomass production.

About 30% of land worldwide is arid or semi-arid, and climate change will enforce the problem of drought in the near future. Si increases the tolerance to drought, low temperature, and UV-B radiation stress [28,29,38]. Si decreases cuticle transpiration mechanically, and is involved in osmotic adjustment in plant metabolism. Physiologically and biochemically, Si maintains membrane stability and functions, decreases oxidative damage, and increases antioxidant defence. Thus, Si improves water retention, root water uptake root growth, and increases photosynthesis and crop growth.

The positive effects of Si on plant metabolism, particularly against abiotic and biotic stress, are numerous and impressive. Next, an attempt was made to attribute the various physiological effects of Si to that of the corresponding essential plant nutrient and detrimental minerals, respectively, in order to obtain an improved overview of the reaction behaviour of Si in plants (Table 2).

Sterner and Elser [39] have provided a comprehensive overview of homeostasis in the context of stoichiometry in the animate and inanimate world. Homeostasis assumes that complex physiological processes maintain a steady state in the plant organism, unless any severe imbalance of ions taken up by the plant will impair, for instance, the functionality of chloroplasts and reduce biomass production [40]. Homeostasis is maintained most efficiently by balanced nutrient ratios in plant tissues, which then foster crop productivity, quality, and plant health, while excessive loads of minerals will reduce yield. Si seems to be able to mediate nutrient imbalances by biomineralisation and directed de-swelling of $Si(OH)_4$ after uptake by roots. A unique characteristic of Si is that it is taken up as a weak acid, $Si(OH)_4$, and by biomineralisation through a successive loss of water; heavy metals are bound in phytoliths, and SiO_2 is finally deposited in cell walls.

Table 2. Silicon, essential plant nutrients, and pollutants involved in the regulation of some stress related physiological processes.

Physiological Action	Essential Nutrient/Pollutant	Interaction	Stimulating (+) Repressive (−) Si Effect
Antagonistic uptake	As, Sb, Mn, Na, Al, Cr	$\rightleftharpoons$	−
Transpirational bypass flow change	Na, Cl	$\rightleftharpoons$	−
Biological silicification—heavy metals bound in in cell walls and phytoliths	Cd, Zn	$\rightleftharpoons$	+
Stimulation of phytoalexin synthesis	$CuSO_4$		+
Osmotic adjustment	K, Na, Cl		+
Membrane stability (physical barrier)	Ca		+
Ion homeostasis	K/Na balance (salt stress)		+
Signalling oxidative stress	K, SO_4-S, Ca		+
For references see [19,30,39,41–46]			

Debona et al. [28] concluded in their review that a minimum Si concentration in the roots and/or shoots of higher plants, especially monocots, is needed to effectively combat stress conditions that would otherwise reduce yield. The beneficial effects of Si suggest a yield increase of potatoes by 22%, rice by 30%, and sugar cane by 45% [47,48]. Si showed its highest potency to increase yield of various grasses under drought stress [49]. Similar positive effects were observed in upland rice by [50]. Favourable effects of Si on yield and oil content of canola were most probably indirectly induced through a strengthened resistance against disease, as this crop species actively excludes Si from uptake [51].

In high input systems, Si fertilisation against abiotic and biotic stress will gain relevance if suitable agrochemicals are not available and there is an augmentation of stress incidences that reduce crop productivity. Currently, the net return of prophylactic Si applications is not predictable, even if Si-containing fertiliser materials are available.

Though Si is the second most abundant element in the earth's crust [25], it is hardly available to crop plants. Basically, the following soluble Si sources are commercially available for fertilisation: Ca-metasilicate; wollastonite ($CaSiO_3$), which is an electric furnace calcium silicate slag from elemental P processing; sodium silicate (water glass) for soil and foliar application; and by-product slags (blast furnace slags, silico-manganese slags, stainless steel slags, converter slags). The major disadvantages of the three sources are the putative radon (Rn) contamination of wollastonite, the high price of water glass, and the limited solubility of by-products slags, which requires higher application rates.

4. Potassium and Sodium—Nutritional Associates against Drought

Positive yield effects of Na fertilisation are known since long [52,53]. Natrophilic crops, such as sugar beet, spinach, celery, and cabbage, contain 1–3% Na in their leaves, and the prospect of beneficial effects of Na fertilisation on crop growth are highest if the K supply is limited [54,55]. Marschner [55] and Broadley et al. [56] summarised the physiological effects of Na as follows: Na regulates the water supply by a faster closure of stomata; Na increases leaf area and number of stomata while it reduces the chlorophyll content per unit leaf area; Na stimulates the assimilate transport to roots.

NaCl fertilisation decreased the K uptake in favour of Na and Cl, which induced a higher water content in sugar beet leaves at growth stage BBCH33 and 39 ([57,58], Figure 3). Broadley et al. [56] determined thicker, more succulent leaves, which stored more water per unit leaf area after Na fertilisation.

Shabala and Cuin [59] see the maintenance of K-specific enzyme functions as the key role of an adequate K supply. With respect to drought and salinity stress, a sufficiently high K supply is indispensable for osmoregulation and stomatal functioning [43,60]. A balanced K and Na supply proved to be essential for achieving maximum yields; compensation of K by Na was obvious in the range of moderate K deficiency, but for maximum yield, a minimum K concentration in leaves of 36 mg/g proved to be necessary [58]. For maximum root yield, a concentration of 2.0 mg/g Na was required, and for maximum sugar yield, 4.0 mg/g Na was required (see Section 1). However, a higher Na uptake lowers the quality of the beet root. Haneklaus et al. [58] determined that the Na content in the beet root increased by 0.29 meq/kg f.w. per 10 kg/ha Na applied to the soil.

In 1995, a separate evaluation of the K and Na supply in northern Germany and Denmark revealed that 38% of all Danish samples and only 1% of the German samples were in the range of an insufficient K supply, with concentrations <35 mg/g K in the leaf tissue at row closing [58]. In the German samples, 4% revealed Na contents <2 mg/g, indicating a severe undersupply of this mineral. The distinctively better Na supply of Danish samples can be explained by the fact that Na fertilisation at a rate of 60 k/ha Na is a standard production technique in the country [61]. The results showed with respect to K/Na ratios that, in total, 62% of the German, but only 10% of the Danish samples showed an unfavourable nutrient relation. Highest yields could only be obtained if plants contained at least 35 mg/g K and 6 mg/g Na. Yield losses due to an imbalanced K/Na nutrition were as high as 60% or 37 t/ha [58,62]. In northern Germany, NaCl fertilisation increased beet root yield by 8.7 t/ha on a clayey soil, and 4.1 and 7.3 t/ha on loamy sand soils. The sugar yield remained unaffected on all sites [62].

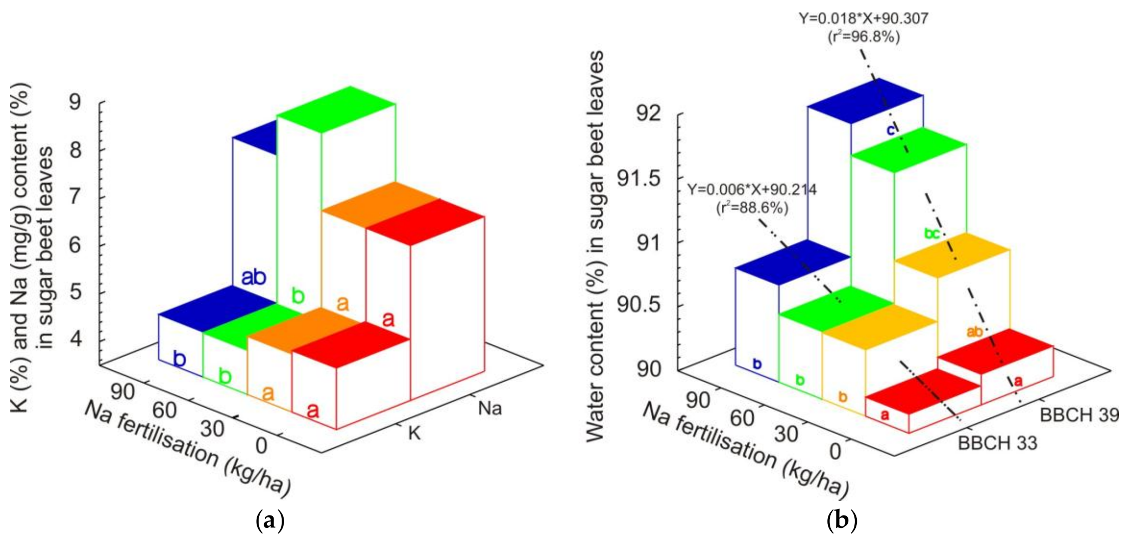


Figure 3. Influence of graded rates of Na (kg/ha) applied as NaCl on the K (%) and Na (mg/g) concentration (**a**), and water content (%) (**b**) of younger leaves of sugar beet at row closing (BBCH33 and BBCH39) at three experimental sites in northern Germany (extracted from [58,62]).

5. Seed Priming—Promoter for Improved Development at Early Stages Combats Salinity, Drought, and Nutrient Deficiency Stress

Seed priming has been applied since the 1970s, and positive effects on germination rate, plant vigour and development in early growth stages, and resistance against abiotic stress have been described under field conditions. In general, priming techniques involve imbibitions of water, hormones, chemicals, biota, and salts during the first reversible stages of germination [63]. These are summarised under the terms osmo-, hormo-, chemical, bio-, and halopriming [63]. Seed priming yields more homogenous development of seedlings and an advanced physiological status over a certain period of time [63]. Other suggested improvements are an increased efficiency of nutrient use and improved regulation of the plant water status. Seed priming not only accelerates germination, but also mechanisms which improve seed vigour. Seed priming implies an osmotic (e.g., 0.1% copper sulphate, 0.1% zinc sulphate, and 0.1% sodium sulphate) resulting in a water potential of −0.5 to −2.0 MPa, the temperature varying between 15 and 20 °C, and a duration that ranges between hours and weeks in relation to crop type. Afterwards, seeds are rinsed and dried [64]. It seems to be important during priming that the process is aerated, which improves seed performance [65]. Other factors are temperature and solution concentration. It is not possible to provide general recommendations for seed priming, as the best method varies in relation to variety, species, and seed lots [63].

Most field studies on seed priming were carried out in low input system in India and Pakistan. Varier et al. [66] suggested that priming provides extra time for the repair of damaged DNA, and an error free template for replication and transcription. Practically, the treatments improved seedling vigour, ion homeostasis (higher uptake of beneficial than toxic minerals), and starch metabolism (starch hydrolysis yields a higher content of soluble sugars) under normal and saline conditions. Primed seeds show a higher capacity for osmotic adjustment because roots take up more Na and Cl, while in leaves, the sugar and organic acid content is higher than in non-primed seeds [41]. Calcium (Ca) salts were suggested to enhance oxygen uptake and promote α-amylase activity, resulting in a higher content of total and reducing sugars [67]. Chilling stress delayed the germination of rice by more than 3 days; priming with selenium (Se) enhanced the tolerance of rice against chilling through an enhanced starch metabolism, respiration rate, anti-oxidative defence system (glutathione), and lower lipid peroxidation [68].

Main stress factors are limited soil moisture, high temperatures, and soil-crust formation in semi-arid areas, which impair germination and seedling emergence [69]. Under severe stress conditions, less than 10% of the sown seeds establish successfully [69]. Seed priming with water has been described by Wilkinson [70], and its effect on germination, crop establishment, growth, and yield has been intensely studied and reported [69,71,72]. Crop establishment in marginal rainfed areas was significantly enhanced by seed priming with water and/or nutrient solutions [69]. Seed priming with water and micronutrients was beneficial, in particular where stress affected juvenile plants [69]. As could be expected, seed priming with micronutrients enhanced their concentration in the seeds, while the content in the progeny seeds remained unaffected [73]. Calcium sulphate and calcium chloride proved to be more effective at enhancing germination of wheat under salt stress than sodium chloride [74].

Farooq et al. [75] postulate the equality of fertilisers applied to soil, foliage, and seeds, but this seems highly questionable, since under conditions of severe nutrient deficiency, particularly that of macronutrients, the rates required can only be applied to the soil. In addition, the risk of burning the plant tissue needs to be taken into account if the nutrient concentrations in foliar fertilisers are too high [76]. The same applies to in seed priming solutions, since these may result in negative yield effects [75].

The physiologically positive effects of seed priming transfer directly into yield increase. In on-farm studies, wheat yield varied between 1.2–1.4 to 4.2 t/ha in India and Pakistan, and 2.3 t/ha in Nepal [69]. Priming increased yield by 152–505 kg/ha with a mean value of 270 kg/ha. In another study, wheat grain yield increased by 200 kg/ha, and straw yield by 400 kg/ha, after seed priming with water [77]. With seed priming, 50 kg/ha N resulted in the same yield level as a crop that received 75 kg/ha N without priming [69]. These data show that seed priming enhanced N uptake of the crop plants. In addition, primed seeds showed an improved resistance to pest and diseases [69].

In the literature, results are expressed as increases in percentages, because the total yield increase is rather low, as is the yield level in general (Table 3). Maximum yield increases of 34.9 to 53.7% have been reported for seed priming of wheat with Zn, and common bean with Mo, respectively (Table 3).

To recap, it can be stated that seed priming is suitable for all crops, and proved to be effective against moderate and severe abiotic stress. Seed priming with nutrients or water seems a practical solution to alleviate nutrient deficiencies, drought, and salinity stress on marginal soils where crop production levels are low.

Table 3. Yield increase by seed priming [1].

Element	Crop	Yield Increase (%)
Zn	rice	6.8–29.6
	wheat	14.0–34.9
	chickpea	17.7–36.0
B	oats	8.4
	cowpea	37.3
Mo	chickpea	20.0
	French bean	34.8
Mn	wheat	12.8
Mo	common bean	11.6–53.7
Co.	common bean	5.0–52.5 [2]

[1] references in [75]; [2] economic yield.

6. Significance of Fertiliser Practices against Abiotic Stress in Practice—a Critical Assessment

A proven positive effect of an essential plant nutrient or beneficial element on abiotic stress factors under field conditions is a required premise for the recommendation and implementation of fertiliser practices on production fields. Another important aspect is the positive long-term performance of fertiliser applications in practice under stress conditions. For example, Na will increase yield of sugar beet under conditions of transient drought, but putatively negative side effects have to be taken into account, such as silting, and an increase in soluble salts in soils if Na is applied regularly. In addition, a regular, prophylactic application of Na will only be profitable if drought is a regular phenomenon in the production zone. In the case of Si fertiliser costs, efficacy of the fertiliser and practicability of the handling and application of the fertiliser materials are the main obstacles for being part of a routine fertiliser scheme. On-site experimentation seems the best solution for targeted fertiliser applications against biotic and abiotic stress, though the possibility of alleviating abiotic stress by fertilisation is strictly limited in high input systems. Rather, a balanced nutrient management seems important for counteracting soil degradation, maintaining the soil organic matter content on a site-specific level, and avoiding physical and chemical deterioration by regular liming. The implementation of biological know-how into fertiliser strategies, for example, a crop-specific S and Si fertilisation in combination with threshold applications of fungicides, would significantly limit the input of agrochemicals distinctly. In low input systems seriously affected by abiotic stress factors, seed priming with water and nutrients is a sensible measure to counteract drought and nutrient deficiencies.

Acknowledgments: The authors wish to express their most sincere gratitude to Mr. Herbert Daybell (Agrimedia, Bottesford, UK) for the linguistic revision of this chapter.

Author Contributions: All three authors collected the relevant literature and jointly performed the interpretation of the data including drawing of graphics and generation of tables; the first author wrote the paper.

Conflicts of Interest: The authors declare no conflict of interest.

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