
19 Silicon

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19.1 INTRODUCTION

Silicon (Si) is the second-most abundant element of the Earth's surface. Beginning in 1840, numerous laboratory, greenhouse, and field experiments have shown benefits of application of silicon fertilizer for rice (*Oryza sativa* L.), corn (*Zea mays* L.), wheat (*Triticum aestivum* L.), barley

(*Hordeum vulgare* L.), and sugar cane (*Saccharum officinarum* L.). Silicon fertilizer has a double effect on the soil–plant system. First, improved plant-silicon nutrition reinforces plant-protective properties against diseases, insect attack, and unfavorable climatic conditions. Second, soil treatment with biogeochemically active silicon substances optimizes soil fertility through improved water, physical and chemical soil properties, and maintenance of nutrients in plant-available forms.

19.2 HISTORICAL PERSPECTIVES

In 1819, Sir Humphrey Davy wrote:

The siliceous epidermis of plants serves as support, protects the bark from the action of insects, and seems to perform a part in the economy of these feeble vegetable tribes (Grasses and Equisetables) similar to that performed in the animal kingdom by the shell of crustaceous insects (1)

In the nineteenth and twentieth centuries, many naturalists measured the elemental composition of plants. Their data demonstrated that plants usually contain silicon in amounts exceeding those of other elements (2) (Figure 19.1). In 1840, Justus von Leibig suggested using sodium silicate as a silicon fertilizer and conducted the first greenhouse experiments on this subject with sugar beets (3). Starting in 1856, and being continued at present, a field experiment at the Rothamsted Station (England) has demonstrated a marked effect of sodium silicate on grass productivity (4).

The first patents on using silicon slag as a fertilizer were obtained in 1881 by Zippicotte and Zippicotte (5). The first soil test for plant-available silicon was conducted in the Hawaiian Islands by Professor Maxwell in 1898 (6).

Japanese agricultural scientists appear to have been the most advanced regarding the practical use of silicon fertilizers, having developed a complete technology for using silicon fertilizers for rice in the 1950s and 1960s. Other investigations of the effect of silicon on plants were conducted in France, Germany, Russia, the United States, and in other countries.

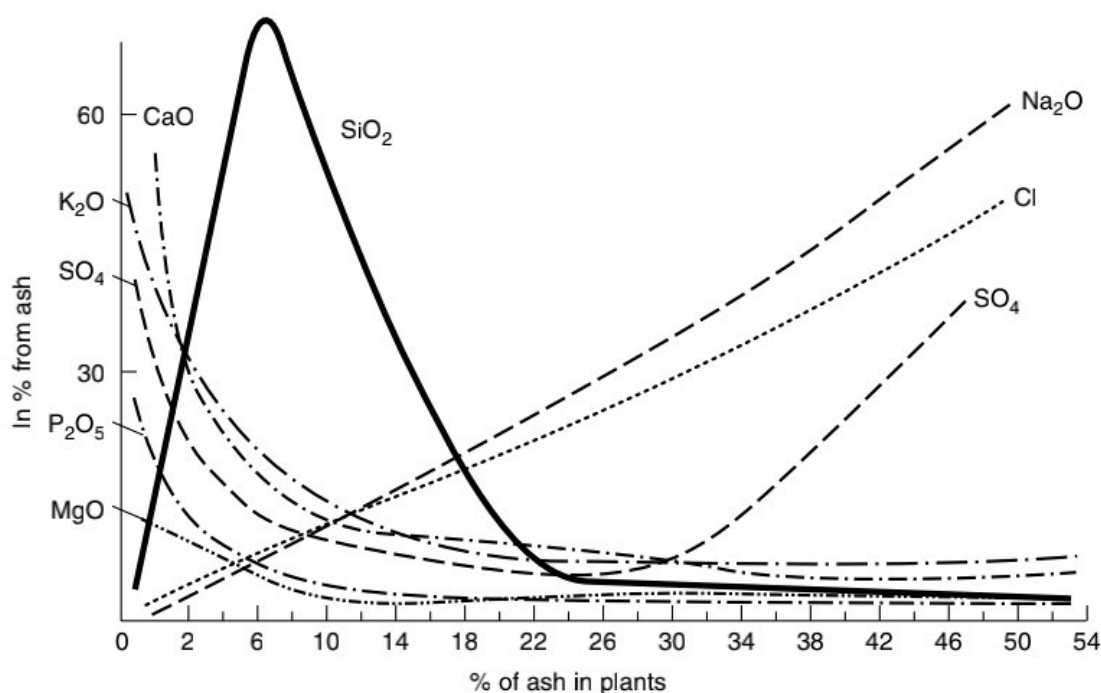


FIGURE 19.1 Silicon in ash of cultivated plants. (From V.A. Kovda, *Pochvovedenie* 1:6–38, 1956.)

19.3 SILICON IN PLANTS

19.3.1 PLANT ABSORPTION OF SILICON

Tissue analyses from a wide variety of plants showed that silicon concentrations range from 1 to 100 g Si kg⁻¹ of dry weight, depending on plant species (7). Comparison of these values with those for elements such as phosphorus, nitrogen, calcium, and others shows silicon to be present in amounts equivalent to those of macronutrients (Figure 19.1).

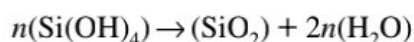
Plants absorb silicon from the soil solution in the form of monosilicic acid, also called orthosilicic acid [H₄SiO₄] (8,9). The largest amounts of silicon are adsorbed by sugarcane (300–700 kg of Si ha⁻¹), rice (150–300 kg of Si ha⁻¹), and wheat (50–150 kg of Si ha⁻¹) (10). On an average, plants absorb from 50 to 200 kg of Si ha⁻¹. Such values of silicon absorbed cannot be fully explained by passive absorption (such as diffusion or mass flow) because the upper 20 cm soil layer contains only an average of 0.1 to 1.6 kg Si ha⁻¹ as monosilicic acid (11–13). Some results have shown that rice roots possess specific ability to concentrate silicon from the external solution (14).

19.3.2 FORMS OF SILICON IN PLANTS

Basically, silicon is absorbed by plants as monosilicic acid or its anion (9). In the plant, silicon is transported from the root to the shoot by means of the transportation stream in the xylem. Soluble monosilicic acid may penetrate through cell membranes passively (15). Active transport of monosilicic acid in plants has received little study.

After root adsorption, monosilicic acid is translocated rapidly into the leaves of the plant in the transpiration stream (16). Silicon is concentrated in the epidermal tissue as a fine layer of silicon–cellulose membrane and is associated with pectin and calcium ions (17). By this means, the double-cuticular layer can protect and mechanically strengthen plant structures (18).

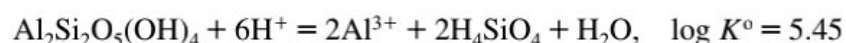
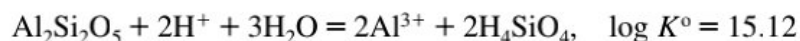
With increasing silicon concentration in the plant sap, monosilicic acid is polymerized (8). The chemical nature of polymerized silicon has been identified as silicon gel or biogenic opal, amorphous SiO₂, which is hydrated with various numbers of water molecules (9,19). Monosilicic acid polymerization is assigned to the type of condensable polymerization with gradual dehydration of monosilicic acid and then polysilicic acid (20,21):

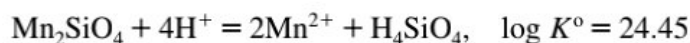
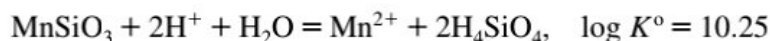
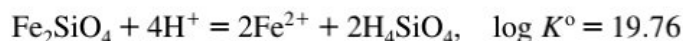


Plants synthesize silicon-rich structures of nanometric (molecular), microscopic (ultrastructural), and macroscopic (bulk) dimensions (22). Ninety percent of absorbed silicon is transformed into various types of phytoliths or silicon–cellulose structures, represented by amorphous silica (18). Partly biogenic silica is generated as unique cell or inter-cell structures at the nanometer level (23). The chemical composition of oat (*Avena sativa* L.) phytoliths (solid particles of SiO₂) was shown to be amorphous silica (82–86%) and varying amounts of sodium, potassium, calcium, and iron (24). Phytoliths are highly diversified, and one plant can synthesize several forms (25,26). A change in plant-silicon nutrition has an influence on phytolith forms (27).

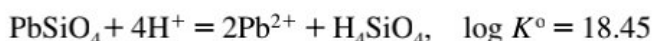
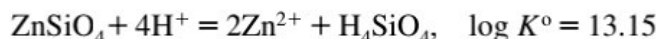
19.3.3 BIOCHEMICAL REACTIONS WITH SILICON

Soluble silicon compounds, such as monosilicic acid and polysilicic acid, affect many chemical and physical-chemical soil properties. Monosilicic acid possesses high chemical activity (21,28). Monosilicic acid can react with aluminum, iron, and manganese with the formation of slightly soluble silicates (29,30):





Monosilicic acid under different concentrations is able to combine with heavy metals (Cd, Pb, Zn, Hg, and others), forming soluble complex compounds if monosilicic acid concentration is less (31), and slightly soluble heavy metal silicates when the concentration of monosilicic acid is greater in the system (28,32).



Silicon may play a prominent part in the effects of aluminum on biological systems (33). Significant amelioration of aluminum toxicity by silicon has been noted by different groups and in different species (34). The main mechanism of the effect of silicon on aluminum toxicity is probably connected with the formation of nontoxic hydroxyaluminosilicate complexes (35).

The anion of monosilicic acid $[\text{Si}(\text{OH})_3]^-$ can replace the phosphate anion $[\text{HPO}_4]^{2-}$ from calcium, magnesium, aluminum, and iron phosphates (12). Silicon may replace phosphate from DNA and RNA molecules. As a result, proper silicon nutrition is responsible for increasing the stability of DNA and RNA molecules (36–38).

Silicon has also been shown to result in higher concentrations of chlorophyll per unit area of leaf tissue (39). This action may mean that a plant can tolerate either low or high light levels by using light more efficiently. Moreover, supplemental levels of soluble silicon are responsible for producing higher concentrations of the enzyme ribulose biphosphate carboxylase in leaf tissue (39). This enzyme regulates the metabolism of CO_2 and promotes more efficient use of CO_2 by plants.

The increase in the content of sugar in sugar beets (*Beta vulgaris* L.) (3,40) and sugar cane (41,42) as a result of silicon fertilizer application may be assessed as a biochemical influence of silicon as well. The optimization of silicon nutrition for orange resulted in a significant increase in fruit sugar (brix) (43).

There have been few investigations of the role and functions of polysilicic acid and phytoliths in higher plants.

In spite of numerous investigations and observed effects of silicon on plants and the considerable uptake and accumulation of silicon by plants, no evidence yet shows that silicon takes part directly in the metabolism of higher plants.

19.4 BENEFICIAL EFFECTS OF SILICON IN PLANT NUTRITION

19.4.1 EFFECT OF SILICON ON BIOTIC STRESSES

Silicon has been found to suppress many plant diseases (Table 19.1) and insect attacks (Table 19.2). The effect of silicon on plant resistance to pests is considered to be due either to accumulation of absorbed silicon in the epidermal tissue or expression of pathogenesis-induced host-defense responses. Accumulated monosilicic acid polymerizes into polysilicic acid and then transforms to amorphous silica, which forms a thickened silicon–cellulose membrane (44,45), and, which can be associated with pectin and calcium ions (46). By this means, a double-cuticular layer protects and mechanically strengthens plants (9) (Figure 19.2). Silicon might also form complexes with organic compounds in the cell walls of epidermal cells, therefore increasing their resistance to degradation by enzymes released by the rice blast fungus (*Magnaporthe grisea* M.E. Barr) (47). Indeed, silicon can be associated with lignin–carbohydrate complexes in the cell wall of rice epidermal cells (48).

TABLE 19.1
Plant Diseases Suppressed by Silicon

Plant	Disease	Pathogen	Reference
Barley (<i>Hordeum vulgare</i> L.)	Powdery mildew	<i>Erysiphe graminis</i>	87–89
Creeping bent grass	Dollar spot	<i>Sclerotinia homoeocarpa</i>	90
Cucumber (<i>Cucumis sativus</i> L.)	Root disease	<i>Pythium aphanidermatum</i>	91
Cucumber	Root disease	<i>Pythium ultimum</i>	92
Cucumber	Stem rotting	<i>Didymella bryoniae</i>	93
Cucumber	Stem lesions	<i>Botrytis cineria</i>	93
Cucumber, muskmelon (<i>C. melo</i> L.)	Powdery mildew	<i>Sphaerotheca fuliginea</i>	39, 94, 95
Grape (<i>Vitis vinifera</i> L.)	Powdery mildew	<i>Oidium tuckeri</i>	96
Grape	Powdery mildew	<i>Uncinula necator</i>	97
Pea (<i>Pisum sativum</i> L.)	<i>Mycosphaerella</i> leaf spot	<i>Mycosphaerella pinodes</i>	50
Rice (<i>Oryza sativa</i> L.)	Brown leaf spot	<i>Helminthosporium oryzae</i>	98
Rice	Brown spot (husk discoloration)	<i>Cochiobolus miyabeanus</i> (<i>Bipolaris oryzae</i>)	99–105
Rice	Grain discoloration	<i>Bipolaris</i> , <i>Fusarium</i> , <i>Epicoccum</i> , etc.	101, 106–109
Rice	Leaf and neck blast	<i>Magnaportha grisea</i> (<i>Pyricularia grisea</i>) (<i>Pyricularia oryzae</i>)	47, 101–103, 106, 107, 110–116
Rice	Leaf scald	<i>Gerlachia oryzae</i>	101, 106, 107, 117
Rice	Sheath blight	<i>Thanatephorus cucumeris</i> (<i>Rhizoctonia solani</i>)	52, 117–119
Rice	Sheath blight	<i>Corticium saskii</i> (<i>Shiraii</i>)	120
Rice	Stem rot	<i>Magnaporthe salvanii</i> (<i>Sclerotium oryzae</i>)	117
St. Augustine grass (<i>Stenotaphrum secundatum</i> Kuntze)	Gray leaf spot	<i>Magnaporthe grisea</i>	121
Sugarcane (<i>Saccharum officinarum</i> L.)	Leaf freckle	Probably a nutrient disorder	122
Sugarcane	Sugarcane rust	<i>Puccinia melanocephala</i>	123
Sugarcane	Sugarcane ring spot	<i>Leptosphaeria sacchari</i>	124
Tomato (<i>Lycopersicon esculentum</i> Mill.)	Fungal infection	<i>Sphaerotheca fuliginea</i>	39
Wheat (<i>Triticum aestivum</i> L.)	Powdery mildew	<i>Septoria nodorum</i>	89
Wild rice (<i>Zizania aquatica</i> L.)	Fungal brown spot	<i>Bipolaris oryzae</i>	125
Zoysia grass (<i>Zoysia japonica</i> Steud.)	Brown patch	<i>Rhizoctonia solani</i>	126
Zucchini squash (<i>Cucurbita pepo</i> L.)	Powdery mildew	<i>Erysiphe cichoracearum</i>	95

Research also points to the role of silicon in plants as being active and suggests that the element might be a signal for inducing defense reactions to plant diseases. Silicon has been demonstrated to stimulate chitinase activity and rapid activation of peroxidases and polyphenoxidasases after fungal infection (49). Glycosidically bound phenolics extracted from amended plants when subjected to acid or β -glucosidase hydrolysis displayed strong fungistatic activity. Dann and Muir (50) reported

TABLE 19.2
Plant Insects and Other Pests Suppressed by Silicon

Plant	Pest	Insect	Reference
Grape (<i>Vitis vinifera</i> L.)	Fruit cracking ^a		127
Italian ryegrass (<i>Lolium multiflorum</i> Lam.)	Stem borer	<i>Oscinella frut</i>	128
Maize (<i>Zea mays</i> L.)	Borer	<i>Sesamia calamistis</i>	129
Rice (<i>Oryza sativa</i> L.)	Stem borer	<i>Chilo suppressalis</i> <i>Scirpophaga incertulas</i>	9, 130–134
Rice	Stem maggot	<i>Chlorops oryzae</i>	135
Rice	Green leaf hopper	<i>Nephotettix bip nctatus cinticeps</i>	135
Rice	Brown plant hopper	<i>Nalaparata lugens</i>	136
Rice	White-back plant hopper	<i>Sogetella furcifera</i>	137
Rice	Leaf spider ^a	<i>Tetranychus</i> spp.	9
Rice	Mites ^a	—	138
Rice	Grey garden slug ^a	<i>Deroceras reticulatum</i>	139
Rice	Lepidopteran (Pyralidae)	<i>Chilo zacconius</i>	140
Sargent crabapple (<i>Malus sylvestris</i> Mill.)	Japanese beetle	<i>Papilla japonica</i>	141
Sorghum (<i>Sorghum bicolor</i> Moench.)	Root striga, parasitic angiosperm	Scrophulariaceae; <i>Striga asiatica</i> Kuntze	142
Sugarcane (<i>Saccharum officinarum</i> L.)	Stem borer	<i>Diatraea saccharira</i>	143
Sugarcane	Stalk borer	<i>Eldana saccharira</i>	144
Wheat (<i>Triticum aestivum</i> L.)	Red flour beetle	<i>Tribotium castaneum</i>	129
Zoysia grass (<i>Zoysia japonica</i> Steud.)	Fall army worm	<i>Spodoptera depravata</i>	126

^aNoninsect pests.

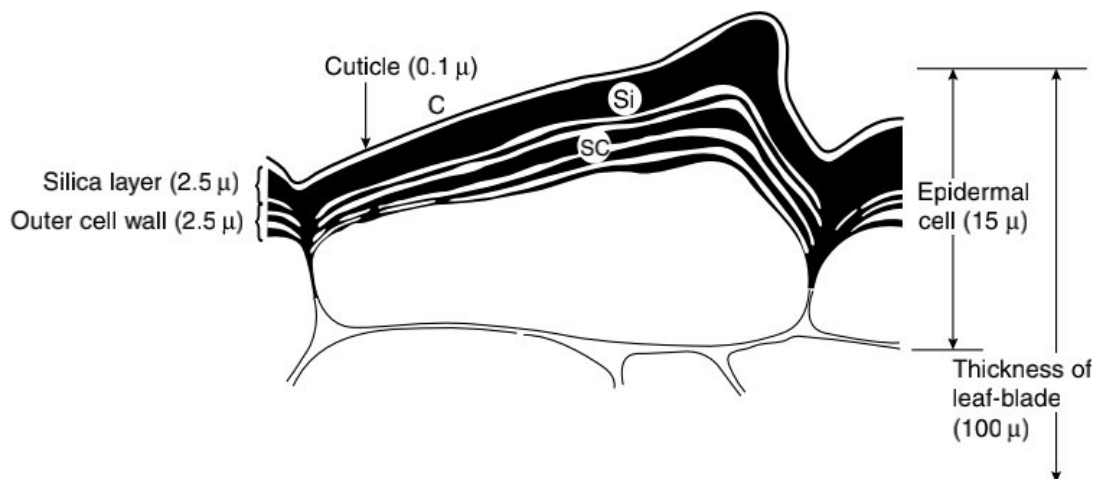


FIGURE 19.2 Schematic representation of the rice (*Oryza sativa* L.) leaf epidermal cell. (From S. Yoshida, Technical bulletin, no. 25, Food and Fertilizer Technology Center, Taipei, Taiwan, 1975.)

that pea (*Pisum sativum* L.) seedlings amended with potassium silicate showed an increase in the activity of chitinase and β -1,3-glucanase prior to being challenged by the fungal blight caused by *Mycosphaerella pinodes* Berk. et Blox. In addition, fewer lesions were observed on leaves from silicon-treated pea seedlings than on leaves from pea seedlings not amended with silicon. More

recently, flavonoids and momilactone phytoalexins were found to be produced in both dicots and monocots, respectively, and these antifungal compounds appear to be playing an active role in plant disease suppression (51,52).

19.4.2 EFFECT OF SILICON ON ABIOTIC STRESSES

Silicon deposits in cell walls of xylem vessels prevent compression of the vessels under conditions of high transpiration caused by drought or heat stress. The silicon–cellulose membrane in epidermal tissue also protects plants against excessive loss of water by transpiration (53). This action occurs owing to a reduction in the diameter of stomatal pores (54) and, consequently, a reduction in leaf transpiration (15).

The interaction between monosilicic acid and heavy metals, aluminum, and manganese in soil (discussed below) helps clarify the mechanism by which heavy metal toxicity of plants is reduced (55,56).

Silicon may alleviate salt stress in higher plants (57,58). There are several hypotheses for this effect. They are (a) improved photosynthetic activity, (b) enhanced K/Na selectivity ratio, (c) increased enzyme activity, and (d) increased concentration of soluble substances in the xylem, resulting in limited sodium adsorption by plants (58–61).

Proper silicon nutrition can increase frost resistance by plants (58,62). However, this mechanism remains poorly understood.

19.5 EFFECT OF SILICON ON PLANT GROWTH AND DEVELOPMENT

19.5.1 EFFECT OF SILICON ON ROOT DEVELOPMENT

Optimization of silicon nutrition results in increased mass and volume of roots, giving increased total and adsorbing surfaces (39,63–66). As a result of application of silicon fertilizer, the dry weight of barley increased by 21 and 54% over 20 and 30 days of growth, respectively, relative to plants receiving no supplemental silicon (67). Silicon fertilizer increases root respiration (68).

A germination experiment with citrus (*Citrus* spp.) has demonstrated that with increasing monosilicic acid concentration in irrigation water, the weight of roots increased more than that of shoots (69). The same effect was observed for bahia grass (*Paspalum notatum* Flüggé) (70).

19.5.2 EFFECT OF SILICON ON FRUIT FORMATION

Silicon plays an important role in hull formation in rice, and, in turn, seems to influence grain quality (71). The hulls of poor-quality, milky-white grains (kernels) are generally low in silicon content, which is directly proportional to the silicon concentration in the rice straw (72).

Barley grains that were harvested from a silicon-fertilized area had better capacity for germination than seeds from a soil poor in plant-available silicon (37). Poor silicon nutrition had a negative effect on tomato (*Lycopersicon esculentum* Mill.) flowering (73). It is important to note that the application of silicon fertilizer accelerated citrus growth by 30 to 80%, speeded up fruit maturation by 2 to 4 weeks, and increased fruit quantity (74). A similar acceleration in plant maturation with silicon fertilizer application was observed for corn (37).

19.5.3 EFFECT OF SILICON ON CROP YIELD

Numerous field experiments under different soil and climatic conditions and with various plants clearly demonstrated the benefits of application of silicon fertilizer for crop productivity and crop quality (Table 19.3).

TABLE 19.3
Effect of Silicon Fertilizers on Crop Production

No.	Soil, Country	Silicon Fertilizer	Dose (kg ha ⁻¹)	Regime	Plant	Crop, Grain, Mg ha ⁻¹	Straw Mg ha ⁻¹	Reference
1	Clay-with-flints chalk, Rothamsted Station, England	Sodium silicate	0	Control	Barley (<i>Hordeum vulgare</i> L.)	2.02	1.13	145
			0	N		3.03	2.32	
			448	N		5.04	4.32	
			0	N, P		6.32	5.04	
			448	N, P		6.52	5.04	
			0	N, K, Na, and Mg		3.82	3.70	
			448	N, K, Na, and Mg		5.22	4.49	
			0	N, P, K, Na, and Mg		6.42	5.08	
			448	N, P, K, Na, and Mg		7.31	5.76	
2	Clay-with-flints chalk, Rothamsted Station, England	Sodium silicate	0	N, P, K, Na, and Mg	Hay		5.98	146
			448	N, P, K, Na, and Mg			7.78	
3	Soddy podzolic soil	Amorphous silica	0	N, K	Barley	2.47	3.47	147
			870	N, K		2.88	3.57	
			0	N, P, K		2.74	3.72	
			870	N, P, K		3.17	4.00	
4	Soddy podzolic soil, Russia	Amorphous silica	0		Barley	4.6		37
			100			5.26		
			500			6.84		
5	Soddy podzolic soil, Russia	Amorphous silica	0		Com (<i>Zea mays</i> L.)	0	7.68	37
			30			4.2	11.44	
			100			6.3	13.68	
6	Soddy podzolic soil, Russia	Zeolite	0	N, P, K	Strawberry	8.9		148
			10%	N, P, K	(<i>Fragaria vesca</i> L.)	9.8		
			0			10.6		
			10%			15.3		
7	Acid podzolic soil, Sweden	Si-Mn slag	0	Lime 2000	Oats (<i>Avena sativa</i> L.)	0.6		149
			0			0.93		
			2000			1.48		
8	Alluvial soil, Russia	Slag	0		Hay		1.85	150
			1000				2.33	

9	Chernozem, Russia (mollisol)	Slag	0	N, P, and K	Beet (<i>Beta vulgaris</i> L.)	37.5	7.37	40
			0	N, P, and H+lime		40.2	7.72	
10	Chernozem, Russia (mollisol)	Zeolite	18,000	N, P, and K	Com forage	4.10	7.98	151
			0	Manure (120t ha ⁻¹)		160	202	
			120,000	Manure (120t ha ⁻¹)		280.4		
11	Chernozem, Russia (mollisol)	Sodium silicate	0	N	Wheat	2.6		152
12	Chestnut soil, Russia	Zeolite	10	N	(<i>Triticum aestivum</i> L.)	2.9		153
13	Chestnut soil, Russia	Zeolite	20,000		Sorghum (<i>Sorghum bicolor</i> Moench.)	3.72	10.5	
			0		Barley	4.3	14.7	154
14	Chestnut soil, Russia	Amorphous silica	10,000		Barley	2.66		155
			0			3.48	5.56	
			3000	N, P, and K		3.85	6.16	
15	Histosol acid, Norway	Iron slag	3000	N, P, and K	Hay	3.66	5.85	156
			0	N, P, and K		4.08	6.52	
16	Muck soil, Russia	Dunite	3600		Potato (<i>Solanum tuberosum</i> L.)	9.09		157
			0		Barley	9.97		158
17	Muck acid soil, Russia	Amorphous silica	1500	N, P, and K	Rice (<i>Oryza sativa</i> L.)	7.26		159
			0			13.05		
18	Alluvial-swamp with salt, Russia	Rice straw	8000			3.7	5.2	
			0			2.77		
19	Alluvial-swamp Chernozem, Russia	Sodium silicate	6000		Rice	4.78		160
			0			5.09		
20	Dark chestnut soil, Russia	Sodium silicate	310		Rice	5.9		161
			0			3.52		
			310			4.01		
			0	Manure		3.98		
21	Sandy loam, Sri Lanka	Rice straw ash	310	Manure	Rice	4.28		162
			0			3.9		
			1000			4.6		
			0	K		4.3		
			1000	K		5.0		
22	Ultisol, Nigeria	Sodium silicate	0		Rice	2.4		101
			0	N, P, and K		6.3		
			4.7	N, P, and K		9.3		

TABLE 19.3 (Continued)

No.	Soil, Country	Silicon Fertilizer	Dose (kg ha ⁻¹)	Regime	Plant	Crop, Grain, Mg ha ⁻¹	Straw Mg ha ⁻¹	Reference
23	Hydromorphe organic Gley, Madagascar		0	N, P, K + Mg	Rice	8.1		163
			4.7	N, P, K + Mg		14.7		
			0			2.34	4.96	
			4.7			2.48	4.86	
			0	Mg		2.04	4.58	
			4.7	Mg		3.14	6.02	
24	Mineral semi-tropic Gley, Madagascar	Amorphous silica	0	N, P, and K	Rice	3.876		163
			0	N, P, and K		5.571		
			1500	N, P, and K		6.186		
			0			3.520		
			1600			5.172		
			0	K ₁₂₀		6.1775		
25	Humic latosol, Hawaii	Calcium silicate	1600	K ₁₂₀	Sugarcane (<i>Saccharum officinarum</i> L.)	6.920	141	164
			0	P		157		
			830	P		124		
			0	pH 5.8		147		
			830			151		
			1660	pH -6.2		131		
26	Humic latosol, Hawaii	Calcium silicate	830		Sugarcane	151	166	165
			0			23.4	253	
			830			31.6	327	
			1660			20.7	262	
			0	P 280				
			4500	P 280				
27	Humic ferruginous latosol, Hawaii	TVA slag	0	CaCO ₃ (4.5 Mg ha ⁻¹) + P (1120 kg ha ⁻¹)	Sugarcane	23.4		42
			4500	P (1120 kg ha ⁻¹)		31.6		
			0			20.7		
			4500					
			0					
			4500					
28	Aluminos humic, ferruginous latosol, Mauritius	Electric furnace slag	4500	N, P, and K	Sugarcane	32.7	338	41
			0	N, P, and K		27.4	266.7	
			0	N, P, and K		26.67	256.8	
			0	+ CaCO ₃ (4.5 t ha ⁻¹)				
			6177	N, P, and K		33.84	313.7	
			0			18.1	150	
29	Histosol, Florida	Calcium silicate slag	0		Sugarcane	23.8	194	124
			6700					

Note: Response to application of silicon fertilizer is shown in bold type in the columns.

19.6 SILICON IN SOIL

19.6.1 FORMS OF SILICON IN SOIL

Soils generally contain from 50 to 400 g Si kg⁻¹ of soil. Soil-silicon compounds usually are present as SiO₂ and various aluminosilicates. Quartz, together with crystalline forms of silicates (plagioclase, orthoclase, and feldspars), secondary or clay- and silicon-rich minerals (kaolin, vermiculite, and smectite), and amorphous silica are major constituents of most soils (75). These silicon forms are only sparingly soluble and usually biogeochemically inert. Monosilicic and polysilicic acids are the principal soluble forms of silicon in soil (76).

For the most part, monosilicic acid occurs in a weakly adsorbed state in the soil (13,37). Monosilicic acid has a low capacity for migration down the soil profile (77). The chemical similarity between the silicate anion and the phosphate anion results in a competitive reaction between the various phosphates and monosilicic acid in the soil. Increasing monosilicic acid concentration in the soil solution causes transformation of the plant-unavailable phosphates into the plant-available ones (12). Monosilicic acid can interact with aluminum, iron, manganese, and heavy metals to form slightly soluble silicates (29,30).

Polysilicic acids are an integral component of the soil solution. They mainly affect soil physical properties. The mechanism of polysilicic acid formation is not clearly understood. Unlike monosilicic acid, polysilicic acid is chemically inert and basically acts as an adsorbent, forming colloidal particles (34). Polysilicic acids are readily sorbed by minerals and form siloxane bridges (78). Since polysilicic acids are highly water saturated, they may have an effect on the soil water-holding capacity. Polysilicic acids have been found to be important for the formation of soil structure (79). There is a pressing need to obtain additional information about biogeochemically active silicon-rich substances involved in soil-formation processes.

19.6.2 SOIL TESTS

Silicon forms may be defined as total, extractable, and soluble. Total silicon comprises all existing forms of soil silicon that can be dissolved by strong alkali-fusion or acid-digestion methods (80). This parameter does not provide information about plant-available and chemically active silicon because silicon in soil is in the form of relatively inert minerals (62).

Usually for determination of soil plant-available silicon, different extracts are used. Extracts remove silicon of intermediate stability that is often associated with crystalline or amorphous soil components. The most common chemical extracts used are 0.5 M ammonium acetate (pH 4.8), 0.1 or 0.2 M HCl, water, sodium acetate buffer (pH 4.0), and ammonium oxalate (pH 3.0) among others (71,81–83). Unfortunately, soil drying is a component of all these extraction methods. During drying, all monosilicic acid (plant-available form of Si) is dehydrated and transformed into amorphous silica (21). Concern has been expressed that data obtained on dried soil may not adequately describe plant-available soil silicon and may be unsatisfactory for evaluating soil previously amended with silicon fertilizer (71). Nevertheless, extractable silicon has been correlated with the plant yield (84).

To overcome problems associated with soil drying, soluble monosilicic acid can be determined in water extracted from field-moist soil samples. After 1 h of shaking and filtration, the clean extract is analyzed for soluble monosilicic acid. This method also facilitates the testing for polysilicic acid in the soil (13). It should be noted that a change in the soil-water concentration from 5 to 50% of the field capacity had no effect on the sensitivity of the method (12,13).

To fully characterize soil plant-available silicon, it appears that more than one parameter of measurement is required. The combination of data on soluble monosilicic acid, polysilicic acid, and silicon in some extracts could give more complete information about the soil-silicon status.

19.7 SILICON FERTILIZERS

Although silicon is a very abundant element, for a material to be useful as a fertilizer, it must have a relatively high content of silicon, provide sufficient water-soluble silicon to meet the needs of the plant, be cost effective, have a physical nature that facilitates storage and application, and not contain substances that will contaminate the soil (85). Many potential sources meet the first requirement; however, only a few meet all of these requirements. Crop residues, especially of silicon-accumulating plants such as rice, are used as silicon sources either intentionally or unintentionally. When available, they should not be overlooked as sources of silicon. However, the crop demand for application of silicon fertilizer generally exceeds that which can be supplied by crop residues.

Inorganic materials such as quartz, clays, micas, and feldspars, although rich in silicon, are poor silicon-fertilizer sources because of the low solubility of the silicon. Calcium silicate, generally obtained as a byproduct of an industrial procedure (steel and phosphorus production, for example) is one of the most widely used silicon fertilizers. Potassium silicate, though expensive, is highly soluble and can be used in hydroponic culture. Other sources that have been used commercially are calcium silicate hydrate, silica gel, and thermo-phosphate (85).

19.8 SILICON IN ANIMAL NUTRITION

In the last 30 years, a few studies on silicon effects on mammals, fish, and birds were conducted (33,38,86). Data have shown that active silicon (fine amorphous silica) increased the weight and quality of animals. Chicken (*Gallus gallus domesticus*), pig (*Sus scrofa*), and sheep (*Ovis aries*) with silicon-rich diets were healthier and stronger than animals without silicon supplements (33,38).

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20 Sodium

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20.1 SODIUM IN SOILS AND WATER

Sodium and potassium, being adjacent elements in Group 1 of the Periodic Table, have similar chemical properties. In the biology of higher organisms, however, these two elements have very different roles and are treated very differently by mechanisms involved in short- and long-range transport. Estimates of the percentages of sodium and potassium in the Earth's crust vary between 2.5 and 3% (by weight), with slightly more sodium than potassium (1), and these concentrations are similar to the percentages of calcium and magnesium. Much of the sodium is in seawater, to the extent of 30.6% by weight compared with only 1.1% for potassium and 1.2% for calcium. Chloride, although present at only 0.05% in the Earth's crust, makes up 55% of the mass of seawater salts. For humans and most animals, physiological solutions are dominated by sodium (around 0.8% [w/v] compared with about 0.02% for potassium, calcium, and magnesium) and chloride (0.9%), and both elements are essential for animals. Thus, when we think of sodium, we think first of common salt—sodium chloride. In soils, the situation is more complex than in bulk solutions, and concentrations of cations (as experienced by the plant root) are influenced by ion exchange, diffusion, and mass-flow processes. The osmotic effects of excessive salts are also influenced by the exact amounts and proportions of anions and cations.

Some sodium occurs in most soils, but in temperate climates, the concentrations are often similar to, or lower than, those of potassium. Excessive amounts of sodium may be present in the soil

in arid and semi-arid areas, and where evapotranspiration is similar to or greater than precipitation. The excess may be in the form of high concentrations of sodium ions in solution, usually accompanied by chloride and sulfate (saline soils), or where sodium is the main cation associated with cation-exchange sites (sodic soils). There is no absolute division of salt-affected soils into these two categories, saline or sodic, as there is a range from purely saline to purely sodic, with most salt-affected soils falling somewhere between the two extremes. The FAO estimated that in 2000, 3.1% of the Earth's land area was affected by salinity and a further 3.4% had sodic soils (2). These figures include 19.5% of irrigated land and 2.1% of land under dry-land agriculture. Detailed properties of these soils are presented in a number of monographs (3–9). A brief summary is given below.

20.1.1 SALINITY

A widely accepted definition of a saline soil is one that gives a saturated paste extract with an electrical conductivity (EC_e) of $>4 \text{ dS m}^{-1}$ (mmho cm^{-1}). Seawater is about 55 dS m^{-1} . These saline soils will also have an exchangeable sodium percentage (ESP) of <15 and a pH of <8.5 . Saline soils are a problem for most plants because of the high concentrations of soluble salts in the soil solution. Soil salinity usually involves other ions in addition to those of sodium and chloride, particularly calcium, magnesium, and sulfate. The proportions of these ions depend on the chemistry and hydrology of the soil, but all saline soils have high concentrations of salts that may be harmful in three ways. First, the high concentrations result not only in higher electrical conductivity, but also in high osmotic pressures (more negative osmotic potentials). This action makes it more difficult for plants to establish a continuous gradient of water potential between the soil solution and the atmosphere—the driving force for transpiration and water uptake by osmosis. Plants must make their own tissue solutions more concentrated (higher osmotic pressure) in order to draw water into their tissues. This response is called osmotic adjustment, and in a strict sense, it refers to an increase in solutes on a dry weight basis (a higher osmotic pressure can also be achieved to some extent by a reduction in the amount of water). The simplest and energetically the cheapest way to achieve osmotic adjustment is by the accumulation of inorganic ions (10). This action can lead to the second problem—the toxicity of high concentrations of inorganic ions in plant tissues (11). Toxicity, in this context, can result from direct interference with cellular metabolism or from an osmotic imbalance caused by the accumulation of salts in the leaf apoplast, known as the Oertli effect (12,13). The third problem is that high concentrations of salts can inhibit the uptake of other nutrients such as potassium and nitrate (see below).

20.1.2 SODICITY

In contrast, soils with little soluble sodium, and hence a low EC_e ($<4 \text{ dS m}^{-1}$), but with a substantial proportion of the exchangeable cations in the form of sodium ($ESP > 15$) and a pH of >8.5 , are called sodic soils. In purely sodic soils, a substantial osmotic problem does not occur, since the concentrations of free ions in the soil solution are low. Nutrition is a problem because of the replacement of nutrient cations (K^+ , Ca^{2+} , and Mg^{2+}) at ion-exchange sites in the soil by sodium (Na^+) and because of the high pH. Sodic soils have poor physical structure and may be impermeable to water and to plant roots, so that there are often secondary problems such as waterlogging and hypoxia.

Primary salinization is the result of geological processes such as the deposition of salt from drying lakes and seas. The large areas of salt-affected soil in parts of Hungary, Australia, and the western United States of America are the result of such natural events. Secondary salinization refers to the impact of man, mainly resulting from unsustainable irrigation for agriculture and rising water tables. Secondary salinization has played a role in the decline of several civilizations. The Sumerian civilization in Mesopotamia is probably the best known. This civilization was initially based on irrigated wheat farming, but lack of adequate drainage and excessive use of irrigation water with

an appreciable salt content led to accumulation of salts in the irrigated lands. Wheat (*Triticum aestivum* L.) was replaced gradually by the more tolerant cereal barley (*Hordeum vulgare* L.), until it was abandoned completely in about 1700 BC (6). Eventually, the salinity reached levels at which not even barley would grow. Clearly, this presentation is a simplification of a complex series of events, but the pattern of irrigation without adequate drainage or control of salt fluxes in the soil has been repeated in other civilizations such as the Hohokam of the Sonoran Desert and the Indus civilization of Pakistan. The mistakes of ancient civilizations have, unfortunately, been repeated in more modern times. Examples are the vast irrigation systems in the Indian subcontinent and central Asia. In the former case, remedial civil engineering is tackling the problem (6). In the former Soviet Union, large-scale irrigation schemes built in the 1950s abstracted water from the Amu Darya and Syr Darya rivers for the cultivation of cotton (*Gossypium hirsutum* L.) and other crops. These rivers flow into the Aral Sea, and with the reduction in river flows, the level of the sea dropped by more than 10 m; and its area decreased by over 40% in the latter half of the 20th century and is still decreasing. Even the United States of America, with all of its technological and financial resources, is not immune to the impact of secondary salinization, as in the San Joachin valley and the Salton Sea.

Secondary salinization is most severe in arid and semi-arid regions, where potential evapotranspiration rates are high, as in parts of the United States, the Indian subcontinent, Australia, the Middle East, and South America.

20.2 SODIUM AS AN ESSENTIAL ELEMENT

Some uncertainty exists about the status of sodium as a nutrient, partly arising from the semantics of 'essentiality'. The original criteria of Arnon and Stout (14) were that an essential element should be necessary for completion of the life cycle, should not be replaceable by other elements, and should be involved directly in plant metabolism. Sodium fails to meet all the three criteria for most plants and is generally regarded as a beneficial nutrient (see below). Only a few plants have any difficulty completing their life cycles in the absence of sodium, and these include some euhalophytes and some C₄ species. The osmotic functions of cations in the vacuoles of plants growing at low salinity can be performed to some extent by any of the common cations. In particular, the monovalent alkali metals can perform similar functions in generating solute osmotic pressures and turgor (1,15–18).

The term 'functional nutrient' has been suggested for sodium, and, perhaps also for silicon and selenium (19,20). It might equally be applied to some of the rare earth elements that promote plant growth in certain circumstances (21). As Tyler (21) has pointed out for the latter group, research on essentiality, even of sodium, has examined only a small proportion of the total number of species in the Plant Kingdom. Even so, it is clear that for most species, sodium is not essential in any sense.

20.3 BENEFICIAL EFFECTS

20.3.1 GROWTH STIMULATION

Halophytes. The responses of halophytes and glycophytes to salinity have been reviewed many times (4,7,22–28). One feature of the response of halophytes, and, particularly the succulent halophytes predominantly from the family Chenopodiaceae, is that maximum biomass is achieved at moderate-to-high salinity (29–33). In other species, growth can be stimulated at low salinity, compared with the absence of salt (34), but this effect may depend on the overall nutritional status of the plant and the purity of the sodium chloride.

A part of the biomass of halophytes is the inorganic ions that they accumulate, especially in the shoots (23,26,27,30). It has been argued that, for a better assessment of plant productivity, only the organic portion of the biomass should be considered—that is, the ash-free dry weight (35–37). This

consideration certainly reduces the apparent stimulation of 'growth' by sodium in the salt-accumulating, succulent euhalophytes, but a positive effect on ash-free dry weight is still apparent.

20.3.2 INTERACTION WITH OTHER NUTRIENTS

The role of potassium in generating turgor can be fulfilled by sodium and to some extent, by calcium and magnesium, particularly at low concentrations of potassium (38–41). The estimated extent to which potassium can be replaced by sodium in the edible portions of crops varies from 1% in wheat (*Triticum aestivum* L.) and rice (*Oryza sativa* L.) to 90% in red beet (*Beta vulgaris* L.) (42). The interactions among cations in terms of uptake and accumulation rates are complex. The ability of low concentrations (<500 μM) of sodium to stimulate potassium uptake when potassium concentrations are low does not appear to be of importance outside the laboratory (43). The extensive literature on the physiology and genetics of potassium–sodium interactions, especially related to membrane transport, is beyond the scope of this chapter and has been reviewed comprehensively by other researchers (44–50). Some evidence suggests that shoot sodium concentrations (altered by spraying sodium onto leaves) affects the transport of potassium to the shoots, or at least leaf potassium concentrations (51).

Interactions between sodium and other nutrients have been observed (52–54). Excessive sodium inhibits the uptake of potassium (43,55), calcium (56–67), and magnesium (53). A deficiency of calcium, or a high sodium/calcium ratio, results in enhanced sodium uptake. For most species, this calcium requirement is satisfied at a few moles per cubic meter of calcium in solution and is rarely detected in soils. It can become a problem in hydroponics if the calcium concentration in the nutrient solution is low, and no extra calcium is added. Maintaining low sodium/calcium ratios (as a general rule, not >10:1 for dicots and 20:1 for monocots) will prevent this problem. Similar considerations apply to silicon (68–75).

Nitrogen nutrition modifies the effects of sodium on Chenopodiaceae such as goosefoot (*Suaeda salsa* L.) (76). Plants of this family accumulate large amounts of nitrogen in the form of nitrate and glycinebetaine (30,77–80). The interactions among salinity, nitrogen, and sulfur nutrition have been investigated in relation to the accumulation of different organic solutes in the halophytic grasses of the genus *Spartina* (81–83). Generally, adequate nitrogen nutrition is necessary to minimize the inhibition of growth caused by excess salt, but with some differences between the ammonium- and nitrate-fed plants (84–94).

Salinity may interfere with nitrogen metabolism in a number of ways, starting with the uptake of nitrate and ammonium (87,95). Under nonsaline conditions, nitrate is an important vacuolar solute in many plants, including members of the Chenopodiaceae and Gramineae. Under saline conditions, much of the vacuolar nitrate may be replaced by chloride, possibly releasing some nitrate-nitrogen for plant growth and metabolism. On the other hand, salinity can result in the synthesis of large amounts of nitrogen-containing compatible solutes such as glycinebetaine (and in a few cases, proline) and lead to the accumulation of amides and polyamines. Changes may occur at the site of nitrate reduction from the leaves to the roots, and hence changes in nitrate transport to the shoots. Since the latter is linked to potassium recirculation (96,97) and long-range signaling mechanisms controlling growth and resource allocation (98), the implications of such changes are wide ranging. The activity of nitrate reductase may also be affected by salinity. Although toxic ions can affect all aspects of nitrogen metabolism, little evidence suggests that nitrogen supply directly limits the growth of plants under conditions of moderate salinities (99).

In comparison with the other nutrients, the interactions between salinity and phosphorus have received relatively little attention (100) and depend to a large extent on the substrate (52,53). When investigating interactions between salinity and nutrients, one has to be aware of the effects of the substrate, the environment, the genotype–nutrient balances, the nutrient and salt concentrations, the time of exposure to salinity, and the phenology of the plant. These interactions are complex and cannot be comprehended adequately from one or two experiments.

20.4 SODIUM IN FERTILIZERS

Application of sodium to many crops has been reported to stimulate growth, particularly when potassium is deficient (15,101–107). This phenomenon has been documented repeatedly with *Beta* species (red beet, fodder beet, and sugar beet) (108–126), and in a range of other crops including asparagus (*Asparagus officinalis* L.), Italian ryegrass (*Lolium multiflorum* Lam.), tomato (*Lycopersicon esculentum* Mill.), potato (*Solanum tuberosum* L.), carrots (*Daucus carota* L.), celery (*Apium graveolens* L.), and flax (*Linum usitatissimum* L.) (15,74,101,103,104,107,127,128).

There is particular interest in sodium fertilizer application to forage crops, since animals require substantial amounts of sodium (129,130). Lactating dairy cows need a concentration of about 2 g Na kg⁻¹ in forage (131). The problem is particularly evident on soils that are intensively managed and deficient in nutrients (132–134), although there are exceptions (135). Application of sodium fertilizer improves the quality of fodder crops and makes them more acceptable to animals (136–140).

20.5 SODIUM METABOLISM IN PLANTS

20.5.1 EFFECTS ON C₄ SPECIES

Sodium was reported to be necessary for the growth of some halophyte species (32,141–143); notably, bladder saltbush (*Atriplex vesicaria* Heward, Chenopodiaceae). Sodium specifically stimulates the growth of Joseph's coat (*Amaranthus tricolor* L., Amaranthaceae) (144), possibly by an effect on nitrate uptake and assimilation (145,146). Sodium appears to be essential for the C₄ grasses such as proso millet (*Panicum miliaceum* L.), kleingrass (*P. coloratum* L.) and saltgrass (*Distichlis spicata* Greene) (20,147,148) and has been found to stimulate the growth of grasses such as marsh grass (*Sporobolus virginicus* Kunth) and alkali sacaton (*S. airoides* Torr.) in some studies (149–151). Subsequent work showed that this requirement was linked with the C₄ pathway of photosynthesis (141,142,152–157) and specifically with pyruvate–Na⁺ co-transport into mesophyll chloroplasts (158–163), a step that is necessary for the regeneration of phosphoenolpyruvate and the fixation of CO₂. Not all C₄ plants require sodium for photosynthesis or grow better when it is present (161). The C₄ species of the NADP⁺-malic enzyme (ME) type have a different co-transport system for pyruvate that uses protons rather than sodium ions.

In sorghum species (*Sorghum* L.), there is a specific effect of higher concentrations of sodium (and low concentrations of lithium) on the kinase that regulates the activity of phosphoenolpyruvate (PEP) carboxylase, the primary carbon-fixing enzyme in C₄ and crassulacean acid metabolism (CAM) plants (164). The kinase also seems to be linked to the responses of PEP carboxylase to nitrate in C₃ and C₄ *Alternanthera* Forssk. species (165). There was a report that sodium was required for CAM in Chandlier plant (*Kalanchoe tubiflora* Hamet) (166), but little further work has been published on this aspect, and no relationship occurs between CAM and halophytism (167). On the other hand, salinity and other stresses are known to induce CAM photosynthesis in the facultative CAM species, ice plant (*Mesembryanthemum crystallinum* L., Aizoaceae) (168,169).

20.5.2 TOXICITY OF SODIUM

Application of sodium to recently transplanted seedlings or cuttings runs the risk of uncontrolled bypass flow of water and sodium to the shoots through damaged roots. Hence sodium is often applied in the laboratory, greenhouse, or growth-chamber experiments after the plants have become established in the growing medium. For such situations, Munns (24,25,33) has described a series of events that occurs in most plants. At its simplest, these effects start with the initial osmotic stress caused by making the external (medium) water potential more negative. Subsequently, external inorganic ions are taken up and organic solutes synthesized for osmotic adjustment of the plant cells. Failure to

properly control the influx of inorganic salts results in the direct toxicity of high intracellular (particularly cytoplasmic) concentrations of ions or to osmotic imbalances within tissues such as the accumulation of salts in the apoplast of species like rice (12,13). Although this description has been challenged in detail regarding the implications for stress-resistance breeding (11) and the point at which specific ion effects become evident (170), it is still the best model of physiological responses to applied salinity. The same concepts, with modifications of timescale and phenology, can be useful in the crop field and in natural environments, although in both cases the severity of salinity (and other stresses) is subject to fluctuations that the laboratory experiment is designed to avoid.

Important questions are what, when, and why salts are toxic to plants. The question of whether sodium or chloride is a toxic ion is still difficult to answer in most plants, though of course, this action is not important if the problem is primarily osmotic. The question of when inorganic salts (mainly sodium chloride) become toxic is a little easier to answer, at least in theory. Accumulation of salts is required for osmotic adjustment, as cellular dehydration may make a contribution, but generally perturbs metabolism by changing the concentrations of critical intermediates and signaling molecules in the cytoplasm. If salts accumulate much in excess of the concentrations needed for osmotic adjustment of plant cells, it is likely that they will become inhibitory to metabolism and growth, although this may depend on the intracellular location of the salts (see below). The cytoplasm of eukaryotic cells has evolved to work best within a limited range of concentrations of solutes, and particularly of certain ions. Exceeding these ranges for inorganic (and some organic) ions (including potassium) creates problems for macromolecular structures, and hence enzyme activities and nucleic acid metabolism (171,172).

20.6 INTRACELLULAR AND INTERCELLULAR COMPARTMENTATION

From the above, it follows that plants growing in saline environments and accumulating high concentrations of salts must have a mechanism that facilitates high rates of metabolic activity in the cytoplasm. Enzymes from halophytes were shown not to have any enhanced capacity to work at high salt concentrations compared with those from glycophytes (1,171–176). This observation led to the hypothesis that toxic inorganic salts might be preferentially accumulated in vacuoles, where they could still have an osmotic role. In this intracellular-compartmentation model (17,177–179), the osmotic potential of the cytoplasm is adjusted by the accumulation of ‘compatible’ organic solutes such as glycinebetaine, proline, and cyclitols (27,171,173,177,180–184). For the interpretation of plant-sodium contents in saline environments, it is not therefore sufficient to know how much sodium a plant tissue contains. It is also necessary to consider the relative and absolute concentrations within different parts of the tissue, both at the inter and intracellular levels (178).

20.7 SODIUM IN VARIOUS PLANT SPECIES

One has to be cautious about interpreting concentrations expressed on the basis of different units (30,185). A tissue dry weight basis is often used in the agricultural literature, but conveys no information about the osmotic effects of solutes such as sodium ions or about changes in other dry weight components such as chloride in euhalophytes. Thus, ash-free dry weight might be a more appropriate basis for measuring concentrations. Using a fresh-weight basis does not facilitate the proper assessment of osmotic contributions of solutes, nor does it provide information about changes in the amount of solute independent of the amount of solvent (water). Expressing concentrations on a plant-water basis, or as measured concentrations in cell sap, does convey information about the osmotic effects of solutes, but does not allow a distinction to be made between osmotic adjustment *sensu stricto* and changes in the water content of the tissue. An example is given in Reference (185), where sodium concentrations in the roots and shoots of mammoth wildrye (*Leymus sabulosus* Tzvel.) are compared as concentrations in sap or as concentrations per kilogram dry weight. The conclusion

TABLE 20.1
Sodium Concentrations in a Variety of Plants under Saline and Nonsaline Conditions

Species	Conditions	Sodium		Reference	Notes and Additional References
		Concentration	Units		
<i>Phragmites communis</i>	Inland saline lake, Austria	11	mol m ⁻³ water	186	
<i>Scirpus maritimus</i>	Estuarine salt marsh, U.K.	144	mol m ⁻³ water	187	Middle of the marsh
<i>Spartina anglica</i>	Estuarine salt marsh, U.K.	346	mol m ⁻³ water	187	Seaward end of marsh
<i>Salicornia europaea</i>	Estuarine salt marsh, U.K.	820	mol m ⁻³ water	187	Seaward end of marsh
<i>Avicennia marina</i>	Mangrove swamp, Australia	520	mol m ⁻³ water	188	Sodium concentrations close to, or below, that of seawater have been reported in some mangrove species by others (189–193)
<i>Triticum aestivum</i>	Hydroponics, 0 mol Na m ⁻³	1	mol m ⁻³ plant sap	194	cv. SARC1
<i>Triticum aestivum</i>	Hydroponics, 100 mol Na m ⁻³	44	mol m ⁻³ plant sap	194	cv. SARC1
<i>Triticum aestivum</i>	Hydroponics, 100 mol Na m ⁻³ , hypoxic	143	mol m ⁻³ plant sap	194	cv. SARC1
<i>Eragrostis tef</i>	Hydroponics, 100 mol Na m ⁻³	176	mol m ⁻³ plant sap	195	Salt-sensitive glycophyte

Note: Seawater has about 480 mol Na m⁻³.

about whether there are higher concentrations of sodium in the roots or shoots is reversible depending on which units are used.

Table 20.1 shows the concentrations of sodium in the healthy shoots of different species. Under nonsaline conditions, the sodium concentrations in most plant tissues are a few moles per cubic meter plant water at most. As external salinity is increased, the amount of sodium within the plant increases, but the rate at which this increase occurs varies from slow in wheat to very rapid in tef, a salt-sensitive glycophyte with little ability to control the influx of sodium. Halophytes accumulate substantial amounts of sodium, but are able to tightly control this accumulation at salinities close to or below that of seawater.

In conclusion, sodium is essential only for some C₄ species, but is undoubtedly beneficial to the growth of euhalophytes. It may stimulate the growth of some species with an evolutionary history in saline environments, and even of apparently totally glycophytic species under certain conditions. Whether there is a need to reclassify sodium as a 'functional' nutrient is open to debate. These considerations are, however, of minor importance compared with the problems caused by the secondary salinization of agricultural land.

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