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Tolerance of vegetable crops to salinity

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Abstract

Global constraints on fresh water supplies and the need to dispose of agricultural, municipal, and industrial waste waters have intensified interest in water reuse options. In many instances, the value of the water is decreased solely because of its higher salt concentration. Although quantitative information on crop salt tolerance exists for over 130 crop species, there are many vegetables which lack definitive data. Vegetable crops are defined as herbaceous species grown for human consumption in which the edible portions consist of leaves, roots, hypocotyls, stems, petioles, and flower buds. The salt tolerance of vegetable species is important because the cash value of vegetables is usually high compared to field crops. In this review some general information is presented on how salinity affects plant growth and development and how different measurements of salinity in solution cultures, sand cultures, and field studies can be reconciled to a common basis. The salt tolerance of vegetables has been condensed and reported in a uniform format based on the best available data. Discrepancies and inconsistencies exist in some of the information due to differences in cultivars, environments, and experimental conditions. For a great number of species little or no useful information exists and there is an obvious need for research. Published by Elsevier Science B.V.

Keywords: Salt tolerance; Ion composition

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1. Introduction

1.1. General comments

The intent of this review is to summarize current knowledge concerning the salt tolerance of vegetable crops. We have opted to define vegetables in a strict sense as those herbaceous species grown for human consumption in which the edible portions consist of leaves (lettuce, cabbage), swollen tap roots, (e.g. carrot), lateral roots (sweet potato), hypocotyls (radish, turnip), aboveground stems (asparagus), below ground stems (Irish potato, Jerusalem artichoke), petioles (celery), and flower buds (globe artichoke, cauliflower). We specifically exclude tomato, despite the fact that it was ordained as a vegetable by an act of the Congress of the United States in 1897. This review will not cover in detail the biochemical or molecular aspects of the responses of vegetable crops to salinity; but rather, general tolerance to salt and ions that are commonly associated with saline soils and waters. For many species we have found that the quantitative information on salt tolerance is meager; sometimes it is completely lacking. Useful salt tolerance data come from well-replicated studies conducted over an adequate range of salinities. Such studies should report data on environmental conditions, cultural practices, and especially those data related to water and salinity status of the root zone. Only a small proportion of salinity studies consist of enough critical information to satisfy the requirements of a good salt tolerance data set.

1.2. Soil salinity measurement

Usually, salinity is measured in units of electrical conductivity of a saturated soil paste extract (EC_e) taken from the root zone of the plant and averaged over time and depth. Soil paste extracts are soil samples that are brought up to their water saturation points (USDA, 1954). Electrical conductivities are measured on the vacuum-extracted and filtered water extracts from these samples in units of deciSiemens per meter ($dS\ m^{-1}$), or previously as millimhos per centimeter ($mmho\ cm^{-1}$). The advantage of using saturation extracts as a method of measuring and referencing salinity is that this measurement is directly related to the field moisture range for most soils (USDA, 1954). The soluble salt concentration in a saturation extract is roughly one half as concentrated as the soil water at saturation for a wide range of soil textures from medium to fine. Thus, a measured EC_e of 4 $dS\ m^{-1}$ would be equivalent to an EC of about 8 $dS\ m^{-1}$ in the soil water of a medium-textured soil at field capacity. For coarse, sandy soils, soil water EC would be higher (approaching 12 $dS\ m^{-1}$). Soil to water extracts of 1:1 or 1:5 can be more easily made and measured than saturation extracts and back calculations can be developed to EC_e for a given soil. New methods use electronic probes or electromagnetic pulses to calculate EC_e with even less time and effort (Rhoades, 1976, 1993).

1.3. Salinity effects

The general effect of salinity is to reduce the growth rate resulting in smaller leaves, shorter stature, and sometimes fewer leaves. The initial and primary effect of salinity, especially at low to moderate concentrations, is due to its osmotic effects (Munns and Termaat, 1986; Jacoby, 1994). Roots are also reduced in length and mass but may become thinner or thicker. Maturity rate may be delayed or advanced depending on species. The degree to which growth is reduced by salinity differs greatly with species and to a lesser extent with varieties within a species. The severity of salinity response is also mediated by environmental interactions such as relative humidity, temperature, radiation and air pollution (Shannon et al., 1994). Depending upon the composition of the saline solution, ion toxicities or nutritional deficiencies may arise because of a predominance of a specific ion or competition effects among cations or anions (Bernstein et al., 1974). The osmotic effects of salinity contribute to reduced growth rate, changes in leaf color, and developmental characteristics such as root/shoot ratio and maturity rate. Ionic effects are manifested more generally in leaf and meristem damage or as symptoms typical of nutritional disorders. Thus, high concentrations of Na or Cl may accumulate in leaves or portions thereof and result in 'scorching' or 'firing' of leaves; whereas, nutritional deficiency symptoms are generally similar to those that occur in the absence of salinity. Calcium deficiency symptoms are common when Na/Ca ratio is high in soil water.

All salinity effects may not be negative; salinity may have some favorable effects of yield, quality, and disease resistance. In spinach, for example, yields may initially increase at low to moderate salinity (Osawa, 1963). Sugar contents increase in carrot and starch content decreases in potatoes as salinity increases (Bernstein, 1959); cabbage heads are more solid at low salinity levels, but are less compact as salinity increases (Osawa, 1961). Celery has been reported to be both more resistant and more susceptible to blackheart (Osawa, 1963; Aloni and Pressman, 1987). These and other effects will be covered herein in more detail as they relate to the salt tolerance of specific species.

1.4. Definition of salt tolerance

Plant salt tolerance or resistance is generally thought of in terms of the inherent ability of the plant to withstand the effects of high salts in the root zone or on the plant's leaves without a significant adverse effect. Lunin et al. (1963) proposed a couple of ground rules for salinity studies: (1) the actual tolerance of a given crop to salinity will vary according to the growth stages at which salinization is

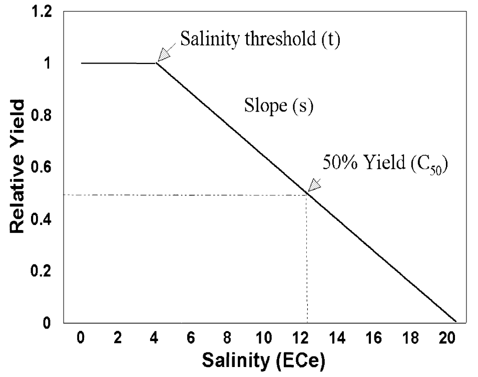

Fig. 1. Salt tolerance parameters relating relative yield to increasing salinity in the root zone.

initiated and the final level of salinity achieved; (2) Salt tolerance values should also take into consideration the portion of the plant to be marketed. Their study demonstrated that salinity caused greater reduction in beet roots than in the tops, whereas yield reductions for onion bulbs were less than those observed in the tops. In addition, salt tolerance genes function in concert with other genes that influence both quantitative traits and environmental interactions. Hence, it is not surprising that salt tolerance is a complex, quantitative, genetic character, controlled by many genes (Shannon and Noble, 1990; Shannon, 1996). In terms of its measurement, salt tolerance is described as a complex function of yield decline across a range of salt concentrations (Maas and Hoffman, 1977; van Genuchten and Hoffman, 1984). Salt tolerance can be adequately measured on the basis of two parameters: the *threshold* (EC_t), the electrical conductivity that is expected to cause the initial significant reduction in the maximum expected yield (Y_{max}) and the slope (s) (Fig. 1). Slope is simply the percentage of yield expected to be reduced for each unit of added salinity above the threshold value. Relative yield (Y) at any salinity exceeding EC_t can be calculated:

$$Y = 100 - s(EC_e - EC_t) \tag{1}$$

where $EC_e > EC_t$.

The crop salt tolerance threshold, i.e. the salt concentration at which yield first declines with increasing concentration, is very sensitive to environmental interactions. The threshold value depends upon both the accuracy of salinity measurements and the method by which salinity measurements are integrated over area, depth and time. Because of this, there is a high degree of error in evaluating the slope at salt concentrations near the threshold; few salinity studies include enough replications to precisely determine the threshold value. In addition, there is a tendency for the slope to ‘tail-off’ at the higher salt concentrations. For practical purposes, salt tolerance at high salinities has little economic importance and measurements made at high salt concentrations may disproportionately skew the salt tolerance curve. For these reasons the numerically most reliable value for crop salt tolerance response studies, and its applications, seems to be the value at which yield is reduced by 50 percent (C_{50}). The C_{50}-value may still be estimated when too few data points exist to provide reliable information on the threshold and slope (Fig. 1). The set of equations developed by van Genuchten and Hoffman (1984) takes advantage of the stability of C_{50}. The C_{50} value, together with the p-value characterizing the steepness of the response function, may be obtained by fitting van Genuchten's function to observed salt tolerance response data.

Reliable data to describe the salinity functions can only be obtained from carefully controlled and well-replicated experiments conducted across a range of salinity treatments. In order to provide information to growers concerning the potential hazards of a given saline water or soil, data of this type have been compiled for 127 crop species which includes 68 herbaceous crops, 10 woody species and 49 ornamentals (Maas, 1986, 1990). About 20 of the herbaceous crops fit our definition of vegetables. The data help growers decide if they should substitute more tolerant species in their rotations when the potential hazards indicate that expected yield reductions may be economically disastrous. A brief examination of the threshold and slope parameters gives an indication of the potential range in variability that is found among the major domesticated plant species. Although the information that comprises this database is considered to be reliable, it is significant that multiple varieties were examined in trials for only 28 of the species. Clearly, the variability for salt tolerance based on yield criterion has not been adequately explored.

Important environmental factors that show significant interaction with salinity include temperature, wind, humidity, light, and air pollution. High temperatures and low humidities may decrease crop salt tolerance by decreasing the effective value of EC_t in Eq. (1) and increasing the value of s. Thus, significant reductions in yields will be realized at lower salinities, and yields will decrease more rapidly with increasing salinity under hot, dry conditions. Two other environmental factors that can influence the measurable effects of salinity include elevated atmospheric levels of carbon dioxide and ozone. Salinity causes leaf stomata to restrict the volume of air exchanged with the environment. This usually improves plant water use efficiency somewhat, but reduces the amount of carbon dioxide that can be fixed by the plant and be used for growth. High CO_2 concentrations in the air due to the so-called 'greenhouse effect' may help maintain favorable carbon assimilation at the same time that water loss through stomates is conserved. If pollutants, such as ozone, are present, reduction in air exchange due to osmotic stress may also reduce the volume of pollutants that enter the plant, thereby decreasing the adverse effects of salinity (Maas and Hoffman, 1977).

Root zone waterlogging is another environmental hazard that can be exacerbated by salinity. Root zone salinity and waterlogging greatly increase salt uptake compared with non-waterlogged conditions (West, 1978; West and Taylor, 1984).

This effect may be due to anaerobic conditions that cause failures in active transport and exclusion processes in the root membrane. Salt tolerance in saline, drained conditions can be quite different from that in saline, waterlogged conditions.

Salinity slows germination rate and at higher levels reduces germination percentage. At low concentrations the only effect is on germination rate and not total percentage of seeds germinated. Thus reported data are dependent upon the time of observation as well as the germination conditions. Single salt solutions have differential effects on germination, but mixed salts give more uniform responses and are predominantly related to osmotic potential. In this review we will report the effects on germination as a G_{50} value as defined by the electrical conductivity of a saline solution (EC_i) that reduces germination by 50 percent at the time that the nonsalinized controls reach 100 percent of maximum germination.

1.5. Other salt tolerance parameters

Because of the difficulties in accurately measuring salt tolerance, indices other than yield have been suggested. These include tolerance during germination; conservation of shoot dry weight, root weight, or shoot number; resistance to leaf damage; maintenance of flowering, seed and fruit set, leaf size, canopy volume, or quality; and plant survival under salt stress. Some investigators have suggested using the tolerance of excised leaf or root tissues or the tolerance of tissue or callus cultures. Still other indices of tolerance have been proposed that are based on specific physiological characters; for instance, accumulation of specific ions in shoots or leaves, or the production of a metabolite. None of these artificial criteria have been unequivocally correlated with salt tolerance; however, maintenance of growth rate and leaf ion and metabolite changes that improve water balance while preserving nutrients and avoiding ion toxicities are probably the most common and universal characteristics of salt tolerant plants.

As mentioned, a nuance associated with assessment and measurement of salt tolerance is that variation occurs with ontogeny or growth stage (Lunin et al., 1963). Lettuce, for example, is sensitive during the early seedling stages and at flowering (Shannon et al., 1983); sugar beet is tolerant during later growth stages, but is sensitive during germination (Bernstein and Hayward, 1958); and turnip is more salt tolerant at germination, but is more sensitive at seedling growth than for yield (Francois, 1984). Efforts to use the criteria of salt tolerance during germination and emergence to evaluate salt tolerance at later growth stages have not generally been successful; tolerance at one growth stage usually is not related to another. In some agricultural situations, salt tolerance at only one growth stage may have a significant benefit. For instance, improved tolerance during germination in sugar beet could remove a limiting step to tolerance throughout its growth. For a large number of crops, adequate information is not available concerning salt sensitivities during development. Sometimes salt stress applied at specific growth stages may be used to advantage. Moderate salinity applied during fruit development can change the partitioning of photosynthates and improve soluble solids in melon and tomato (Shannon and Francois, 1978; Mizrahi and Pasternak, 1985; Mizrahi et al., 1988; Cornish, 1992). Any small yield decrease due to salinity might be partially offset by the higher marketable quality of the fruit.

Salinity often affects the timing of development. Flowering in onions occurs earlier under salt stress, but salinity delays flowering of tomato, *Lycopersicon esculentum* (Pasternak et al., 1979). There are many other examples; however, since this paper deals with vegetative crops, the differential effects on flowering are pertinent only to seed production.

Yield components and growth parameters also show differential responses to salinity stress. At low salinities root growth is often less affected, or sometimes even stimulated by salinity, as compared to shoot growth. Aboveground growth of turnip (Francois, 1984) and carrot (Bernstein and Ayers, 1953a) was more sensitive to salinity than root growth. Asparagus spear yield was less affected by salinity than fern production (Francois, 1987), and salinity inhibited artichoke bud growth more than shoot growth (Francois, 1995). Shannon (1980) made selections for both vegetative growth and head/frame ratio in iceberg lettuce and found that both characters were subject to selection pressure. In muskmelons, salt tolerance decreased in the order: total vegetative dry weight > total vine yield > fruit yield > marketable yield (Shannon and Francois, 1978); emphasizing not only the differences in measurement criteria, but also the importance of accounting for quality characteristics. Consequently, the degree of salt tolerance between and within species is likely to vary according to the criteria used for evaluation. In a review, Jones and Qualset (1984) assert that plant growth attributes must be measured throughout the growth period in order that particularly salt sensitive growth stages can be identified.

1.6. Tolerance to specific ions

The relative salt responses of various crops are often dependent upon soil type and other environmental factors (Levitt, 1972). Saline soils and waters include those with high concentrations of dissolved salts of many kinds, any of which may be critically limiting to plant growth. Saline soils may be sodic or acidic and cover a wide range of soil types and moisture conditions. Genotypes that show similar salt tolerance in one environment may differ in response in a different environment. Rana (1985) has cited the complexity of soils and environmental interactions as major obstacles to successful breeding for salt tolerance. He noted that crops adapted to alkali soils are usually tolerant of non-alkaline saline soils, but the converse was not true.

Most salt tolerance data have been collected based upon the effects of saline waters predominated by sodium chloride, sometimes with varying amounts of calcium as needed to avoid the development of soil permeability problems associated with soil sodicity. However, specific ion sensitivities may be critically limiting to crop growth in some geographic locations. For example, iron, aluminum, boron, selenium, arsenic, manganese or zinc may be found in toxic or growth-limiting concentrations in certain areas. Drainage waters or waters reused from agricultural processing or manufacturing operations may have high concentrations of boron, selenium, arsenic, or other ions that may pose environmental hazards (Francois and Clark, 1979; Clark, 1982). Plant species have demonstrated a wide degree of variation in their abilities to accumulate, exclude, or withstand the toxic effects of individual ions (Flowers and Yeo, 1986; Shannon et al., 1994). Even so, the potential for variability between species and varieties remains as one of the research areas that has not been adequately explored. The genetic variability associated with plant tolerance to some ions has been reviewed in detail (Vose, 1963; Epstein and Jefferies, 1964; Läuchli, 1976; Wright, 1976; Jung, 1978; Christiansen and Lewis, 1982).

1.7. Reconciliation of data

The remainder of this paper will be devoted to a review and summary of the available literature on the salt tolerance of different vegetable crop species. Due to the great number of ways to measure and describe salt tolerance information, it is very difficult to reconcile data between experiments conducted on the same crop species. Often the timing of salt application or the salt compositions differ between studies. The presence or absence of calcium (or gypsum) is an especially troublesome inconsistency. Usually, different cultivars are used between studies and very often, essential parameters are not measured or reported. This is especially true with respect to irrigation frequency, soil type, and soil water-holding capacity. All of these factors contribute to uncertainties of how one set of experimental results concerning the salt tolerance of a crop is related to results of another study. In this review, we have done as much as possible to reconcile information across experiments. Various aspects of certain studies have been either accepted or rejected based both on the general body of information on salt tolerance and our experienced opinion.

2. Monocots

2.1. Amaryllidaceae (leek, onion, garlic, chive)

Onions (*Allium cepa*) and garlic (*A. sativum*) probably originated in central Asia and leek (*A. ampeloprasum*) in the Near East. All were cultivated in Egypt by 3200 B.C. The chive (*A. schoenoprasum*) occurs wild in Europe, northern Asia, and North America and it has been cultivated in Europe since the 16th century. With the exception of chive, *Allium* species are cultivated for their bulbs and sometimes basal portions of the flattened leaf blades. Only the leaf blades of

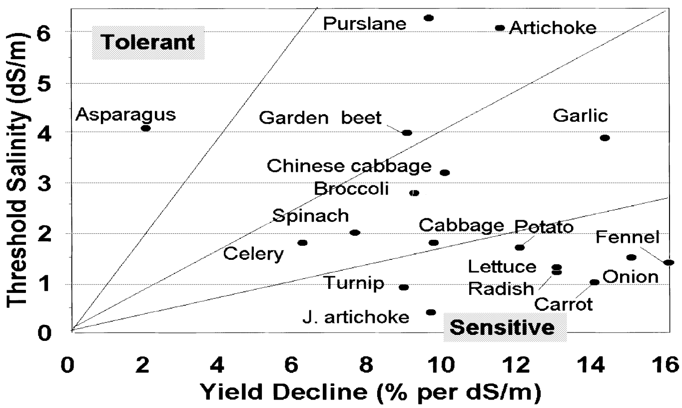

Fig. 2. Salt tolerance of several vegetable species as rated by the salinity threshold and percent yield decline.

chive are used for garnish and flavoring. Generally, onion, garlic, leek and chive are considered to be salt sensitive based on yield decline, but good data exist for only onion and garlic (Fig. 2).

2.1.1. *Onion (Allium cepa L.)*

Onions are sensitive to salt, are relative excluders of both Na^+ and Cl^-, and are sensitive to sulfate. Little genetic variation has been detected even though many cultivars have been tested. Tolerance is high at germination, very low during seedling growth and increases again at about the three- to five-leaf stage. Leaves change from rich green to dull blue-green with salt stress and leaf tips express burn symptoms typically associated with salinity stress.

Bernstein and Ayers (1953b) tested the salt tolerance of five onion cultivars (‘Yellow Sweet Spanish’, ‘Texas Early Grano’, ‘San Joaquin’, ‘Crystal Wax’, and ‘Excel’) in field plots at the U.S. Salinity Laboratory. Initial yield decline started at a threshold EC_e of 1.4 dS m^{-1} and 50% yield reduction (C_{50}) was at 4.1 dS m^{-1}. Bernstein and Ayers (1953b) noted that the osmotic potential of the expressed sap increased with salinity without a significant concomitant increase in sucrose or reducing sugar. Bulb ion content increased as a function of applied salts (Na^+, Ca^{2+}, Cl^-) and percent dry weight increased. Salinity decreased bulb diameter, bulb weight, root growth, plant height, and number of leaves per plant. Onions may mature a week earlier when grown under saline conditions.

Pasternak et al. (1984) hypothesized that sensitivity during early growth stages may be due to the small and shallow rooting system of young plants. No research has been conducted to determine whether rooting systems can be genetically modified to improve tolerance or even if variability exists for this character. If variability can be introduced, it must be done without affecting the commercial quality of the bulb.

Wannamaker and Pike (1987) studied the germination and growth response to salinity of five onion cultivars commonly grown in Texas. Using $NaCl+CaCl_2$ solutions (1:1 by weight), they found that germination was unaffected at EC_i up to 20 dS m^{-1} but was drastically reduced thereafter with no discernable cultivar difference. After 8 days, solutions of 30–35 dS m^{-1} reduced germination by 50% in all cultivars.

2.1.2. Garlic (*Allium sativum* L.)

Garlic is native to central Asia but was grown in Egypt in 2780 B.C. (Yamaguchi, 1983). In a 2-year study Francois (1994) found that the threshold salinity of garlic was 3.9 dS m^{-1} and at 7.4 dS m^{-1} yield was reduced by 50%. All yield components (bulb weight and diameter, and plants per unit area) were reduced with increasing salinity, as well as percent solids which is a major component of bulb quality. Shoot dry weight was less sensitive to salinity increases than bulb weight, but leaf tissues accumulated significantly higher Cl^-, Na^+, and Ca^{2+} concentrations than did bulbs.

2.2. Liliaceae

2.2.1. Asparagus

Asparagus officinalis is a perennial, rhizomatous plant whose fleshy stems or ‘spears’ are harvested when they are 20–30 cm high. Asparagus is native to the scrub communities of southern Europe, western Asia, and northern Africa. It was cultivated by the ancient Egyptians, Greeks and Romans, but appears to have been abandoned during the Middle Ages, except by the Arabs, until it became fashionable as a luxury vegetable in 17th century France. In North America asparagus is often found as a garden escape, frequently in subsaline waste places.

Asparagus has been considered to be the most salt-tolerant vegetable crop commercially available but it grows better in sandy, well-drained soils than in heavy-textured soils. In the first year after establishment, Francois (1987) found that spear yield was reduced by only 2% per unit increase in soil salinity (EC_e) above a threshold of 4.1 dS m^{-1}. In contrast to other plant species, ion contents of spears and ferns remained relatively stable with increasing soil salinity. As salinity increased, increases in total soluble solids contributed to increased osmotic potential in spears. Salinity reduced yields more severely during the second cropping year as a result of its carry over effects on the root mass during the first year. In the same study, salinity up to 9.4 dS m^{-1} in the soil water ($EC_e \sim 4.7$ dS m^{-1}) had no significant effect on germination, but additional salinity increases delayed rate and decreased final percentage. Based on Francois' (Francois, 1987) observations, G_{50} of asparagus occurred at about 14.3 dS m^{-1} on filter papers using mixed $NaCl+CaCl_2$ (1:1 by weight) solutions; however, studies conducted on filter paper by Uno et al. (1996), indicated a 50% reduction in germination of asparagus would occur at about 60 mM NaCl (i.e., about 6.3 dS m^{-1}). The difference between these studies may or may not be attributed to Ca^{2+} but additional research is warranted. Furthermore, studies need to be made to determine if there is sensitivity to salinity in asparagus during early stages of growth.

In vitro studies of asparagus tissues found that tolerance was directly related to cellular organization and organogenesis with rooted and unrooted plantlets showing similar levels of tolerance (Mills, 1989). In these studies, both Na^+ and Cl^- increased with salinity treatment in tissues of friable and compact callus cells, and in roots, shoots, and rhizomes of plantlets.

3. Dicots

3.1. Apiaceae (carrot, celery, coriander, fennel, parsnip, parsley)

3.1.1. Carrot (Daucus carota L.)

Carrot is valued for underground fleshy structure consisting mainly of swollen base of the taproot, but also partly derived from the hypocotyl. The species, *D. carota*, is native to western Asia, probably Afghanistan. Carrots were first used for medicinal purposes and gradually adopted as a food. Carrots were cultivated in Europe prior to the 10th century, and were introduced into North American by the first settlers to Virginia.

Carrot is rated as a salt sensitive crop (Bernstein and Ayers, 1953a; Malcolm and Smith, 1971). Root yield declines 14% for every unit increase in salinity (EC_e) beyond the threshold of $1.0\ dS\ m^{-1}$ (Maas, 1986). Both germination and seedling growth of carrot were reduced by soil moisture potentials of -0.01 MPa, although osmotic potentials as low as -0.5 MPa had no effect on these stages of growth. Root growth significantly increased at matrix potentials of -0.1 to -0.3 MPa, however, comparable osmotic potential did not have equivalent effects. From these observations, Schmidhalter and Oertli (1991) concluded that germination and seedling growth are affected differently by comparable matric and osmotic stresses and that water stress exerts a more negative effect on carrot than salt stress. The effects of salinity, soil aeration, and nutrient level on the transpiration coefficient (defined as the amount of water transpired per unit biomass produced) of carrot were evaluated under conditions of non-limiting water supply (Schmidhalter and Oertli, 1991). The authors observed no change in the transpiration coefficient at salt concentrations up to $16\ dS\ m^{-1}$ in the soil solution and suggested that in the absence of toxic ion effects and nutrient imbalances, salinity had little effect on the transpiration coefficient.

3.1.2. Celery (Apium graveolens L. var. dulce (Mill.) Pers.)

Cultivated celery was derived from wild stock which occurred naturally in marshy habitats in Sweden, Algeria, Egypt, and Abyssinia. Wild stock, which has been reported to grow in brackish marshes, by tidal waters and near the sea, might be classified as a halophyte. Consequently, during the development of celery as a cultivated crop, some degree of salt tolerance may have been retained (Francois and West, 1982). The edible portions of the plant are the young petioles, thickened at the base and conspicuously ridged on the outer face.

Growth stimulation of celery by NaCl-salinity has been reported by Lingle and Carolus (1956) and Osawa (1961). Based on field trial results, Francois and West (1982) rated celery as moderately sensitive with a threshold EC_e of about 1.8 dS m^{-1}, and a slope of 6.2% per dS m^{-1}. In contrast, Sonneveld (1988) reported a higher slope value (7.7% per dS m^{-1}) for salt-stressed celery grown under greenhouse conditions, which may reflect a difference in cultivar response or in environmental conditions. C_{50} values for trimmed shoots are 10 dS m^{-1} and for untrimmed plants, 11 dS m^{-1} (Osawa, 1961; Francois and West, 1982). Under arid conditions celery yield increased 10% in response to irrigation waters with EC_i values between 4.2 and 5.4 dS m^{-1}, but decreased 10% when EC_i was in the 6.2–8.0 dS m^{-1} range (Pasternak and De Malach, 1994).

Celery is susceptible to 'blackheart', a physiological disorder that affects young rapidly-developing leaves in the interior portions of the plant. The symptoms, tip burn and necrosis, may progress to the petioles and severely limit marketable yield. The role of calcium status in blackheart has not been irrevocably established, although its occurrence may depend on the cation composition of the saline medium. Osawa (1963) suggested that excessive Na^+ and Mg^{2+} in the root media limited Ca^{2+} uptake and caused injury. Likewise, Sonneveld (1988) observed that symptoms of blackheart were far more severe when celery was subjected to Na^+-, Mg^{2+}-, and K^+-based salinity, than when Ca^{2+} was the salinizing salt. Takatori et al. (1961) also implicated low substrate Ca^{2+} in the disorder, and found that spraying the plants with either $Ca(NO_3)_2$ or $Sr(NO_3)_2$ partially controlled the symptoms. In contrast, Aloni and Pressman (1987) reported that while Ca^{2+} levels in young, susceptible leaves were lowered by NaCl-salinity, Na^+ offered some degree of protection against blackheart and the incidence of the disorder was negligible. These investigators postulated that the cellular structure may be more stabilized in NaCl-treated plants, presumably owing to increased osmotic content and, thus, independent of Ca^{2+} concentration.

3.1.3. Fennel (Foeniculum vulgare Mill.)

Fennel is an aromatic, biennial plant of Mediterranean origin. Both wild and sweet fennel (var. *dulce*) are common in waste places (e.g. inland areas of England and Wales, southern and central California). The marketable product is primarily the anise-flavored 'bulb', which consists of the modified basal portion of the leaf petioles. The feathery leaves are also used as garnish.

Based on the response of two fennel cultivars, 'Monte Blanco' and 'Everest', Graifenberg et al. (1996) rated the crop as sensitive to NaCl-salinity. Tolerance parameters (threshold and slope) for fennel bulb yield and plant fresh weight were expressed as electrical conductivity of the irrigation water (EC_i) and saturated extract (EC_e) of a sandy soil. In terms of EC_i, threshold for bulb production was 1.15 dS m^{-1}, with a slope of 17.8–18.9%, the C_{50} value was around 3.8 dS m^{-1}. In terms of EC_e, the threshold was again 1.15 dS m^{-1}, but the slope was between 14.3 and 15.7, and C_{50} was about 4.8 dS m^{-1}. Varietal differences were slight and fennel bulbs accumulated more Na^+ and Cl^- than either the leaves or roots. The authors speculated that Na^+-induced K^+ deficiency in bulbs may have contributed to growth reduction.

3.1.4. Parsnip (Pastinaca sativa L.)

Parsnip, a native of the eastern Mediterranean region, is a common plant of roadsides and waste lands, especially on calcareous soils. It has been cultivated for the enlarged, tapered tap root at least since Roman times, but superior forms were probably only developed after the Middle Ages. Although very little quantitative data on the salt tolerance of parsnip are available, the crop has been rated as salt sensitive with significant yield losses expected when EC_i exceeds 0.8 dS m^{-1} (Malcolm and Smith, 1971).

3.1.5. Minor umbelliferous crops

Zidan and Elewa (1995) surveyed the effect of NaCl-salinity on four umbelliferous plant species. In the first 24 h, G_{50} was at 120 mM NaCl in anise (*Pimpinella anisum)*, 150 mM NaCl in coriander, (*Corinadrum sativum*, also called cilantro), and 200 mM NaCl in caraway (*Carum carvi)* and cumin (*Cuminum cuminum)*. Seedling dry weights in anise and coriander generally decreased in concert with increasing salinity, but seedling growth of caraway and cumin appeared to be stimulated by NaCl concentrations up to 80 mM. Levels of total free amino acids and proline in anise and coriander seedlings increased with increasing salinity. In caraway and cumin, however, increases in proline content occurred at the expense of the other amino acids.

3.2. Araceae (taro)

3.2.1. Taro (Colocasia esculenta (L.) Schott)

Taro, a nutritious root crop, is a major subsistence crop in many islands and countries throughout the South Pacific, Asia, and Africa. There has been interest in improving the salt tolerance of taro (*Colocasia esculenta* var. *antiquorum*), but we could not find data on the salt tolerance of field-grown taro in the literature. Taro is normally propagated vegetatively and flower and seed production is erratic in many cultivars; therefore, tissue cultures have been proposed for developing salt tolerance (Nyman et al., 1983). There is a need to develop basic data for salt tolerance of this crop.

3.3. Asteraceae (lettuce, endive, artichoke, Jerusalem artichoke, radicchio)

3.3.1. Lettuce (Latuca sativa, L.)

Lettuce was cultivated by the ancient Egyptians, Greeks and Romans. Improved forms were widely spread by the Arabs. Since the era of European colonization, lettuce has been introduced to every continent and is grown everywhere except in the hottest tropical lowlands.

In field plot studies conducted at the U.S. Salinity Laboratory in Riverside, CA, lettuce was determined to be moderately salt sensitive, with a threshold EC_e of 1.3 dS m^{-1} and a slope of 13% (Ayers et al., 1951). However, results of a field study in Israel indicated that yield and quality of iceberg lettuce was not affected by sprinkling with irrigation water salinity at 4.4 dS m^{-1} (Pasternak et al., 1986). Furthermore, it was found that romaine types were significantly more salt tolerant than iceberg types and that salt tolerance increased with age in lettuce. Finally, it was noted that no apparent osmotic adaption occurred as a result of increased salinity in the irrigation water, a finding that differed from the results reported in salinized solution cultures (Shannon et al., 1983). It is difficult to determine why there are such differences in the reported data. The data from Israel did not include a large number of salinity treatments and it is possible that the non-salinized control treatments were more stressed and that imposed salinities were not applied as early as those in the Riverside studies. Russo (1987) points out that the composition of the soils in the Israel experiment are gypsiferous and that salinity effects can be partially offset by over-irrigation. There is also ample evidence to indicate that large differences in salt tolerance exist among varieties in lettuce.

Shannon (1980) made selections for salt tolerance in the lettuce cultivar 'Empire' using the four-probe electrical conductivity device (Rhoades, 1979) as a means of decreasing the effects of field variability. In one cycle of screening, successful selections were made for significant improvement in plant fresh weight (frame) or high head to frame ratio. In subsequent studies, conducted in greenhouse sand cultures under more controlled conditions than in the field, a large number of cultivars and plant introductions of *L. sativa* were screened for salt tolerance during early seedling growth (Shannon et al., 1983; Shannon and McCreight, 1984). Plant introductions of *L. sativa* showed a wider range of salt tolerance and had a higher mean average salt tolerance than standard cultivars. Subsequent studies indicated that several wild relatives of cultivated lettuce, *L. serriola*, *L. vignata*, and *L. saligna*, had an even higher range of tolerance than the introductions (Fig. 3). Based on germination tests with NaCl the G_{50} for lettuce appears to be about 8 dS m^{-1} and is highly variable among cultivars (Odegbaro and Smith, 1969; Coons et al., 1990).

Sodium chloride salinity has been shown to result in the increase Na^{+} and Cl^{-} in tissues basal to the apical meristem in lettuce with a resultant decrease

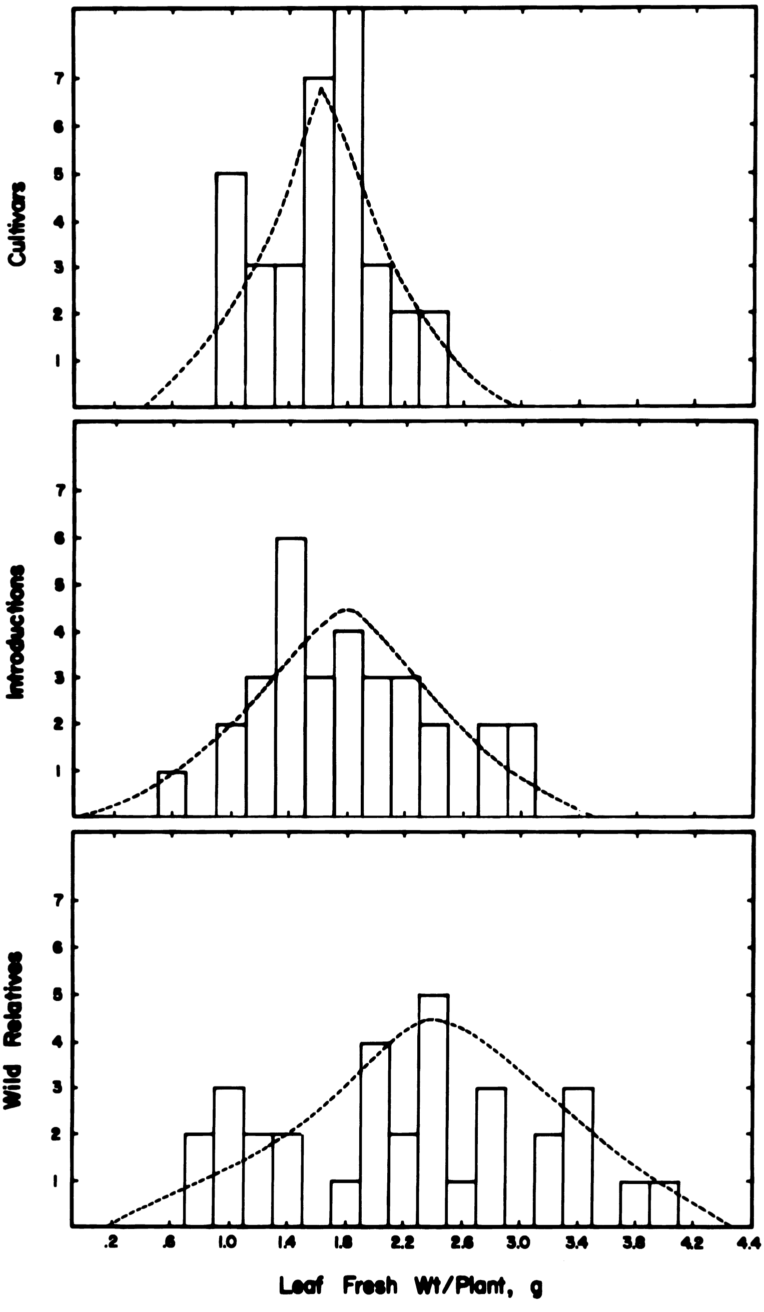

Fig. 3. Histograms showing the distributions of fresh weights among lettuce cultivars, plant introductions, and introductions of wild lettuce relatives grown under saline conditions. Plants were grown from seed in sand cultures irrigated twice daily with nutrient solutions containing 35 mM NaCl and 17.5 mM $CaCl_2$.

in Ca^{2+}, K^{+}, and PO_4^{2-} (Lazof and Läuchli, 1991). Such disruptions in ion compositions were hypothesized to affect nutrition of the apical meristem which might signal growth reduction in expanding leaves. Other studies indicate that while exogenously applied Ca^{2+} improved the nutritional levels of Ca^{2+} under salt stress and reduced Na^{+} accumulation, growth was not improved (Cramer and Spurr, 1986b). Using two lettuce cultivars that differed in salt tolerance, higher root Cl^{-} levels were found to be beneficial in maintenance of root water content (Cramer and Spurr, 1986a).

3.3.2. Jerusalem artichoke (Helianthus tuberosus)

Jerusalem artichoke, a native of North America, was cultivated in pre-Columbian times by the American Indians. The edible tubers were taken to Europe in the early 1600s where the crop became important in areas that are too dry or the soil is too poor for white potatoes.

Based on final tuber yield per plant in field trials, Jerusalem artichoke has been rated as moderately salt tolerant with a threshold EC_e of 8.3 dS m^{-1}, slope of 1.2%, and a C_{50} yield decline at an EC_e of 7.5 dS m^{-1}. The crop was rated as sensitive to moderately sensitive because salinity treatments significantly reduced plant density when tuber yield was expressed in terms of land area. On this basis, the salt tolerance threshold EC_e was 0.4 dS m^{-1}, slope was 9.62% and an expected C_{50} yield reduction was 5.8 dS m^{-1} (Newton et al., 1991). Chloride in stems increased with salinity but leaf Na^{+} remained low and was presumably under some type of control.

3.3.3. Globe artichoke (Cynara scolymus)

Globe artichoke originated in the Mediterranean region and was known as a food plant to the Greeks and Romans. The large succulent forms were probably developed during the Renaissance. It is unknown as a wild plant, but may be derived from the wild cardoon, *C. cardunculus.* Artichoke is cultivated for the immature flower head composed of the tender bases of the bracts and the fleshy receptacle or ‘heart’. Small, very immature entire heads may be used in some cuisines.

Artichoke has been rated as a moderately salt-tolerant crop based on a greenhouse study (Graifenberg et al., 1993) and a field trial conducted in an irrigated desert area (Francois, 1995). From crop performance in the greenhouse, Graifenberg et al. (1993) reported that the tolerance threshold EC_e was 4.9 dS m^{-1} and slope was 10.7%. Francois (1995) obtained similar values (threshold, 6.1 dS m^{-1}, slope 11.5%) for field-grown artichokes, but the number of marketable buds was significantly reduced by an internal browning. The incidence and severity of the disorder increased with increases in salinity level. Francois et al. (1991) postulated that under dryland conditions, decreases in root-pressure driven calcium transport to the shoot apex was impaired. The inner bracts became structurally weak due to calcium deficiency, and became susceptible to infection by species of *Botrytis* and *Erwinia*.

Two other members of tribe Cichoriae (Asteraceae) are economically-important vegetable crops: *Cichorium intybus* (chicory, witloof chicory, Belgian endive, chicon, radicchio, Italian dandelion) and *C. endiva* (endive, escarole). Plants of the two species will hybridize freely (given the chance) to produce many intermediate types, and to confuse taxonomic classification. *C. intybus* probably originated in the Mediterranean region, while *C. endiva* may be a native of the Himalayas. In the mid-18th century, chicory was introduced to North American as a garden plant. Because chicory is found as a weed, inhabiting semi-arid waste places that are probably saline, it is likely that this species may have retained some degree of salt tolerance. Salt tolerance data on members of this tribe could not be found.

3.4. Brassicaceae (cabbage, broccoli, cauliflower, mustards, radish, kale)

Brassica is a diverse genera of leafy vegetables consisting of several genome groups with a good deal of cross compatibility. *B. oleracea* is a polymorphic species of familiar vegetables which probably arose from wild sea cabbage. This edible plant has been cultivated for over 4000 years. The wide array of vegetables is produced by different modifications of the leaf or shoot system. Head cabbages were developed earlier than the more extreme morphological forms. Although the cultivated vegetables may differ widely in appearance at maturity, they scarcely differ from each other in the structure of root, fruit and seeds and cannot be distinguished as seedlings.

3.4.1. Kale (B. oleraceae, Acephala group)

Kale is very closely related to the cabbage, but instead of forming a compact head, it is open-leaved and the leaves arise from a simple, erect, stout stem. Kale appears to be the oldest variety of *Brassica* (Brouk, 1975). There is little information concerning the salt tolerance of kale, although Malcolm and Smith (1971) suggest that the crop may be productive when irrigated with waters that have electrical conductivities in the 2.3–5.5 dS m^{-1} range.

3.4.2. Broccoli (B. oleracea, Botrytis group)

Typically, broccoli produces small, loose heads that develop from buds in the leaf axils of both the central stem and side-shoots. Stems of broccoli are much thinner and longer than those of cauliflower, so that most of the edible part is formed by the broccoli stalks, in contrast to cauliflower which is formed mainly from fleshy flowers (Brouk, 1975). Broccoli is a moderately salt sensitive crop with an estimated threshold EC_e of 2.8 dS m^{-1} and a slope of 9.2% for each unit increase in salinity (Bernstein et al., 1974).

3.4.3. Cauliflower (B. oleracea, Botrytis group)

Cauliflower appears to be native to Asia Minor and was known in Europe in the 16th century, as evidenced by its oldest know description in a book published in 1559 by the Dutch botanist, Dodoeus. Edible part is the solid head formed by the racemose inflorescence composed of abortive flowers whose stalks are short, fleshy, and closely crowded. The crop has been rated as moderately salt tolerant (Bernstein, 1959) but little quantitative data is available.

3.4.4. Cabbage (B. oleracea, Capitata group)

Cabbage has been cultivated for at least 2000 to 2500 years and was introduced into Britain by the Romans. The smooth, fleshy leaves appear on a shortened stem and form a compact, hard head. Yield, as measured by head weight, is rated as moderately sensitive to salinity (Bernstein and Ayers, 1949; Osawa, 1965; Bernstein et al., 1974). The threshold salinity is 1.8 dS m^{-1} (EC_e) with a slope of 9.7% per dS m^{-1}. Under salt stress, cabbage heads are generally more compact, and leaves are fleshier than under nonsaline conditions.

3.4.5. Brussels sprout (B. oleraceae, Gemmifera group)

Edible parts are the lateral buds that appear on the stems in place of lateral branches. Brussels sprout was first recorded in 1587 and was apparently developed in the 15th century in the northern part of Europe that is now Belgium. Maas and Grattan (1998) rate the crop as salt moderately sensitive based on its phylogenetic relationships with other *Brassica* speices.

3.4.6. Kohlrabi (B. oleracea, Gongylodes group)

The edible portion of kohlrabi is the base of the stem which is thickened to form a spherical turnip-like swelling 5–12 cm in diameter. The origin of kohlrabi is obscure, but it appears to have been cultivated in Europe before early medieval times. Kohlrabi is moderately salt sensitive. Field trials have demonstrated that irrigation waters ranging in conductivity between 4.2 and 5.4 dS m^{-1} reduced yield about 30% (Pasternak and De Malach, 1994).

3.4.7. Chinese cabbage (B. campestris, Pekinensis group)

Chinese cabbage (Pe-tsai) appears to be a native of China where it has been cultivated from the 5th century A.D. Leaves and petioles are consumed. Feigin et al. (1991) studied the interactive effects of salinity and N nutrition on lettuce and Chinese cabbage. Biomass production of Chinese cabbage was not significantly reduced until soil salinity (EC_e) exceeded 3.2 dS m^{-1}. Thereafter, yield was reduced about 10% per dS m^{-1} which places Chinese cabbage in the moderately salt sensitive category, along with other *Brassica* crops, e.g. cabbage, cauliflower, Brussels sprouts (Maas, 1986). In response to salinity, some cultivars may be more susceptible than lettuce to severe tip burn disorder (Pasternak and De

Malach, 1994). Chinese cabbage is sensitive to the form of nitrogen which is supplied, particularly under saline conditions (Feigin et al., 1991). The prevalence and severity of marginal tip burn on younger leaves increased when NH_4–N was applied. In sand cultures salinized with NaCl, leaves were dark bluish green when EC_i exceeded 14 dS m^{-1} and leaf curling was noted in all salt treatments (Osawa, 1961).

Paek et al. (1988) found that sulfate salt in callus cultures was more than twice as inhibitory to growth and fresh weight:dry weight ratios than NaCl.

3.4.8. Pak choi (B. rapa, Chinensis group)

This *Brassica* is cultivated for its fleshy, white leaf petioles and green blades. It is a native of the Far East and is extensively used in China, Japan, and SE Asia. The form in which N is supplied to salt-stressed plants is important. NO_3–N was more effective than NH_4–N in alleviating injury to pak choi leaves, probably by inhibiting absorption of toxic levels of Cl (Osawa, 1955). Osawa (1966) grew pak choi and three other vegetables in sand cultures and irrigated with NaCl or concentrated solutions of nutrient salts starting at the cotyledon stage of growth. The C_{50} for yield of pak choi was calculated as 17 dS m^{-1} in NaCl and a little higher in nutrient salts. Unpublished studies conducted in outdoor sand cultures at the U.S. Salinity Laboratory indicate that the C_{50} for pak choi was about 14 dS m^{-1} when irrigated with simulated, Na_2SO_4-dominated, saline drainage waters. Yield was reduced across a range of salinities from 3 to 23 dS m^{-1} at a rate of about 4% per dS m^{-1}.

3.4.9. Mustard greens (B. juncea (L.) Czern. and Coss.)

The salt tolerance of *B. juncea* has been reported by numerous investigators (e.g. Jain et al., 1990; Ashraf and Naqvi, 1992). However, the research emphasis has been on Indian or brown mustard (*B. juncea* Czern. and Coss.), a crop valued for its seed oil production (Ashraf and McNeilly, 1990; Sharma and Gill, 1994). Little, if any, information is available on the effects of salinity on those leafy mustard varieties that are important and popular specialities in cuisines worldwide. Depending upon variety, leaves may be distinctively shaped (broadly oval or narrow and deeply notched) and highly colored (bright green, purple, or brownish red). Shoot weight of *B. juncea* decreased to less than 50% of the non-salinized controls when plants were grown in solution cultures at 50 mM NaCl (Ashraf and McNeilly, 1990). A great amount of variability exists among cultivars. Irrigation of five cultivars of *B. juncea* with 100 mM NaCl solutions in sand cultures for 4 weeks resulted in relative decreases in shoot growth from as little as 28% to as much as 72% (Ashraf, 1992).

Salt tolerance in *B. juncea* cultivars was found to be related to higher K^+/Na^+ selectivity, the ability to reduce stomata frequency in response to salt stress, and greater leaf succulence (Kumar, 1984). The salt tolerance *B. juncea* does not seem to be significantly improved by the addition of supplemental Ca^{2+} (Schmidt et al., 1993).

Certain *Brassica* species have proved to be useful model plants for research in genetics, molecular biology, and physiology because of their rapid growth and relatively small genome. Ashraf and McNeilly (1990) compared vegetative growth in four cultivated *Brassica* species grown in sand-filled pots and irrigated with NaCl solutions. They harvested the plants just before flowering and found that *B. juncea* and *B. campestris* were more sensitive to NaCl salinity than *B. napus* and *B. carinata*. In solution culture studies He and Cramer (1992, 1993a, b) evaluated the influence of dilutions of seawater salinity on relative salt tolerance, growth, and ion relations of six rapid-cycling genetic strains: *B. campestris* (Aaa), *B. nigra* (Bbb), *B. oleracea* (Ccc), *B. juncea* (ABaabb), *B. napus* (ACaacc), and *B. carinata* (BCbbcc). They confirmed the previous studies, finding that based on shoot growth of plants harvested just before flowering, the most salt tolerant species was *B. napus* and the most salt sensitive, *B. carinata*. The remaining four species were rated as moderately salt sensitive. In subsequent reports He and Cramer (1993c, 1996) compared the influence of salinity on growth and physiological parameters of the two species, *B. napus* and *B. carinata*, that represented the extremes in salt sensitivity.

3.4.10. Turnip (B. rapa L. Rapifera group)

Turnip, a crop native to Russia, Siberia and the Scandinavian countries, has been grown for several thousand years as a food for both humans and animals. The biennial, herbaceous plants are grown for the fleshy roots (hypocotyl) and the large, lobed green leaves. Turnip tops are significantly more salt tolerant than the roots (Osawa, 1961). Roots were rated as moderately sensitive. Francois (1984) found that for each unit increase in salinity above a threshold of 0.9 dS m^{-1}, root biomass production was reduced 8.9%. However, in salinized soil-filled pots Malik et al. (1983) found no reduction in fresh weight of turnip roots between EC_e of 1.1 and 2.1 dS m^{-1}. Both investigations placed the C_{50} reduction in root growth at an EC_e of about 6.5 dS m^{-1}. Turnip shoots were moderately salt tolerant with a threshold of 3.3 dS m^{-1} and a yield reduction of 4.8% for each unit increase in salinity (Francois, 1984). Turnips are more salt tolerant at germination than at subsequent stages of growth. A salinity level of 11.6 dS m^{-1} which would be expected to reduce root growth by 95%, had no effect on final germination percentage (Francois, 1984).

3.4.11. Arugula, Taramira, Rocket (Eruca sativa Mill.)

Eruca sativa is probably native southern Europe and western Asia. It is often found growing in arid and semiarid regions and on severely salt-affected soils (Deo and Lal, 1982; Ashraf and Noor, 1993). Arugula leaves are used as a salad greens and its seed is a rich source of protein and oil. Relative salt tolerance and ion relations of two *E. sativa* genotypes were compared with *Brassica carinata* or Ethiopian mustard (Ashraf and Noor, 1993). The yield and relative growth rate of the Eruca line collected from a salt-affected field was superior to the normal line as well as to Ethiopian mustard. The salt tolerance of the former line appears to be associated with exclusion of Na^+, high K/Na selectivity and high Ca^{2+} uptake. Ashraf (1994) extended the comparison of the two populations of Eruca by investigating the role of soluble sugars, proline, free amino acids, and soluble proteins in relative salt tolerance. The tolerant line accumulated significantly higher amounts of sugars, proline, and amino acids in leaves than the non-tolerant population. However, the genotypes did not differ in soluble protein. The C_{50} reduction in vegetative growth of the tolerant line occurred at about 300 mM NaCl (EC_i=30 dS m^{-1}) in salinized sand cultures.

3.4.12. Radish (Raphanus sativus L.)

Radish probably originated in western Asia. It was cultivated 4500 years ago in Egypt and Assyria, and spread at least 2000 years ago to China. Many cultivars of radish exist, including the large daikon. The most popular variety, *radicula*, may be spherical, about 2 cm in diameter or long (6–7 cm). The edible part is the swollen hypocotyl. Radish is a salt-sensitive crop (Osawa, 1965; Malcolm and Smith, 1971). Hoffman and Rawlins (1971) studied the interactive effects of salinity and relative humidity on radish yield and found that when the crop was grown under low RH (45%), root yield declined 13% per dS m^{-1} when salinity exceeded a threshold of 1.3 dS m^{-1}. However, at high RH (90%) the salt tolerance threshold was increased to about 5.2 dS m^{-1} with no change in the slope. Scialabba and Melati (1990) demonstrated that NaCl salinity caused a lack of coordination between cellular expansion and differentiation in radish seedlings. As salinity increased, structural and cellular modifications, in the form of wall thickening and metabolic aggregates inside parenchyma cells, were evident. The stage of growth at which seedlings are salt-stressed can be identified by an ontogenetic study of xylem elements. Previously, it had been noted that salinity differentially inhibited growth of different root types in radish (Waisel and Breckle, 1987). Lateral root growth was most sensitive; whereas, the initiation of new laterals was most tolerant. The G_{50} for radish as determined in NaCl solutions may be anywhere from 14 to 30 dS m^{-1} (Shadded and Zidan, 1989; Scialabba and Melati, 1990).

3.5. Chenopodiaceae

3.5.1. Spinach (Spinacia oleracea L.)

Spinach originated in Iran and has been known in Europe since the Arabs introduced it to Spain in the 11th century. Spinach, one of the glycophytic chenopods, is a moderately salt sensitive leafy vegetable. The tolerance threshold for spinach is 2.0 dS m^{-1}, and the slope 7.6% (Langdale et al., 1971). However, irrigation with saline water with an EC_i of 4 dS m^{-1} on sandy soils in Israel resulted in no yield reduction and a harvestable product of superior quality (Pasternak and De Malach, 1994). Furthermore, Speer and Kaiser (1991) reported that spinach showed little growth impairment within a 17 days period after addition of 100 mM NaCl to hydroponic cultures and Tomemori et al. (1996) found that sea water diluted to 1000 mg l^{-1} salt improved spinach growth in sandy soil. Studies in solution cultures have shown that on an osmotic basis spinach is less sensitive to NaCl salt than to other single salt formulations and that no significant growth reduction occurs up to about an osmotic potential of 0.3 MPa, or about 8 dS m^{-1} (Nieman, 1962; Osawa, 1963). Two studies have shown that there was no significant effect on the relative decrease in yield due to salinity applied at different times during vegetative growth (Lunin et al., 1963; Osawa, 1966).

Chow et al. (1990) used spinach to demonstrate that K^+ requirements for shoot growth are greater under high salinity than under low salinity conditions. Increasing substrate-K^+ can ameliorate reductions in shoot biomass that result from increasing salinity. Since spinach has a high leaf K^+ content compared to other leafy vegetables, it is conceivable that a K^+ requirement exists that may be key to the apparent sensitivity of spinach to salinity. If this hypothesis is true, selection for K^+/Na^+ selectivity could be a useful screening criteria to improve salt tolerance.

3.5.2. Swiss chard (Beta vulgaris (L.) Koch, Cicla group)

Wild sea beet (*Beta maritima*), a common seashore plant of all the coasts of Europe and western Asia, is believed to be the ancestor of both the leaf and root beets. Chard has been eaten by humans since prehistoric times in the Mediterranean region where beets are native. The leaves, with white, green, or red midribs, are eaten; the branched, stringy roots are generally discarded.

Swiss chard has been used as a test species in studies to assess the phyto-availability of potentially toxic ions such as Se (Gutemann et al., 1993) and Cd (Bingham et al., 1983, 1984; Smolders and McLaughlin, 1996a, b). In all studies, chloride-salinity increased Cd uptake by chard, and various mechanisms have been proposed to explain increased Cd availability. Growth was unaffected by 120 mM Cl^- (Smolders and McLaughlin, 1996a). In studies conducted in outdoor sand cultures at the U.S. Salinity Laboratory in 1997, Swiss chard was salinized after the development of the first true leaves with six concentrations of simulated drainage waters composed predominantly of Na_2SO_4 salts (unpublished). Dry weights increased up to 11 dS m^{-1} and then were reduced at a rate of about 5.7% per dS m^{-1}. Calculated C_{50} for yield was at an EC of the irrigation solution of about 19.8 dS m^{-1}. Osawa (1966) grew Swiss chard and three other vegetables in sand cultures and irrigated with concentrated solutions of nutrient salts starting at the cotyledon stage of growth. The C_{50} for yield of chard was calculated as 17.5 dS m^{-1} in this study.

3.5.3. Table beet (B. vulgaris L.)

Beet was known as a vegetable as early as 300 B.C. The swollen hypocotyl is eaten. It is rated as moderately salt tolerant but no reliable studies have been conducted in soils. In sand cultures salinized with NaCl and $CaCl_2$ salts, total yield of top plus roots increased up to salinities equivalent to −0.2 MPa osmotic potential (EC_i=5.2 dS m^{-1}) and decreased at −0.3 MPa (Bernstein et al., 1974). In gravel cultures irrigated with nutrient solutions and NaCl, Hoffman and Rawlins (1971) found that osmotic potentials of −0.5, −1.0, and −1.5 MPa reduced beet yields by 40, 72, and 91% respectively. These and earlier data collected at the U.S. Salinity Laboratory (Magistad et al., 1943) can be used to calculate a threshold EC_e for beet of 4.0 dS m^{-1}, and a slope of 9%. No definitive data exist on cultivar comparisons in table beets.

3.5.4. Garden Orach (Atriplex hortensis L.)

Orach is a native of western Asia and southeast Europe, where it has been cultivated for its young edible leaves since ancient times. Although it has been widely displaced by spinach, it was grown in kitchen gardens in western Europe until the 18th century and is still grown to a small extent in France and central Europe.

Jeschke and Stelter (1983) studied growth and ion relations of orach under conditions of mild (50 mM) NaCl or Na_2SO_4 salinity in solution cultures. Growth, dry matter production and leaf size were significantly stimulated at 50 mM Na-salts. In orach plants, K^+/Na^+ selectivity is established by the presence of bladder hairs which remove nearly all Na^+ from young leaf lamina, and by the recirculation of K^+ from leaves to roots. Leaf succulence of orach was stimulated effectively by Na^+ and K^+, regardless of whether the anion was Cl^-, Br^-, or SO_4^{2-}. Ca^{2+} and Mg^{2+} had no effect on succulence. At 100 mM NaCl in solution cultures (about 10.1 dS m^{-1}), growth of *A. hortensis* was reduced by about 9 and 35% after 45 and 54 days of growth respectively (Handley and Jennings, 1977). The projected C_{50} for 54 days of growth was about 300 mM NaCl (30 dS m^{-1}). In an experiment conducted in outdoor sand cultures at the U.S. Salinity Laboratory, red orach was salinized 19 days after seeding with eight levels of simulated drainage waters composed predominantly of Na_2SO_4 salts with EC's ranging from 3 to 24 dS m^{-1} (unpublished). The highest plant dry weights were harvested 70 days from seeding, from plots irrigated with simulated drainage water at 10 dS m^{-1}. Dry weights of plants were reduced by 50% with drainage water at 24 dS m^{-1}.

3.6. *Convolvulaceae (sweet potato)*

3.6.1. *Sweet potato (Ipomoea batatas (L.) Lam.)*

Sweet potato is native to South America where archeological evidence has shown that it was cultivated by at least 2500 B.C. It also forms part of the ancient agricultural complex in Polynesia and this disjunct distribution has fueled various theories about ancient migrations across the Pacific (DeRougemont, 1989). Columbus took plants to Spain and Portugal on his return voyage in 1493. The edible portion is the swollen storage root.

The crop is the seventh most important food staple in the world. It is, however, sensitive to salinity, aluminum toxicity at low pH, and low fertility (Horton, 1989). Root growth is much more sensitive to salinity than vine growth (Greig and Smith, 1962). The C_{50} of sweet potato for salinity has been reported as 11.0 dS m^{-1} (EC_e) or 4.0 dS m^{-1} in the irrigation water (Maas and Hoffman, 1977). Ekanayake and Dodds (1993) extensively tested the salt tolerance of sweet potato germplasm using salinized in vitro cultures. They measured plant growth and survival among plantlets in 38 cultivated and 17 salt-resistant clones, the latter had been selected from field sites that were highly variable in field salinity (Horton, 1989). The 55 sweet potato genotypes were reportedly representative of the sweet potato germplasm collection of the International Potato Center (CIP), and of a variety of regions across Peru, as well. NaCl concentrations as low as 0.5 to 1.0 mM in liquid media significantly reduced dry weight of plantlets, number of nodes forming roots and number of roots per node. Although significant clonal differences were found, observations did not correspond to those made in the field. Therefore, the screening procedure was modified to impose a 16 mM NaCl stress over a shortened time period. Under these conditions a significant correlation was found with field observations; however, the method was deemed suitable only for early vegetative survival and hence early generation testing.

3.7. *Euphorbiaceae*

3.7.1. *Cassava, 'Manioc', 'Brazilian arrowroot' (Manihot esculenta Crantz)*

Cassava is the most widely grown of all root crops. Starchy tubers are used to manufacture tapioca. The crop probably originated in tropical Brazil and was dispersed to other parts of Latin America thousands of years ago (Yamaguchi, 1983). Cassava is a moderately salt-sensitive crop but has been shown to have potential for improvement through screening and selection. Tuber weight of glasshouse-grown cassava was reduced by one-half when irrigated with solutions containing between 30 and 50 mM NaCl (Hawker and Smith, 1982). In long-term field experiments in Colombia, even putative tolerant cultivars showed about 50% reduction in yield at a salinity level of only 0.7 dS m^{-1} (Anon. 1976, cited in Hawker and Smith, 1982). Indira and Ramanujam (1982) used leaf-K^+:Na^+ ratio to screen and select 14 cassava genotypes for salt tolerance using soil cultures salinized with 1500 ppm NaCl. Six selections whose leaf-K^+:Na^+ was in excess of 15 were grown in the field at a soil EC_e of 3 dS m^{-1} (pH 8.65). All of the genotypes established satisfactorily and none showed disorders associated with salinity (e.g. leaf burn, necrosis).

3.8. Portulaceae

3.8.1. Purslane (Portulaca oleraceae L.)

Purslane is thought to be a native of western Asia and reportedly has grown in the Mediterranean region and central Europe since ancient times. Seeds have been found in archeological sites in the USA and southern Canada (Gorske et al., 1979). The crop is cultivated commercially in Mediterranean regions and the fleshy leaves and stems are used as salad. Purslane has been rated as moderately tolerant with an salinity threshold of 6.3 dS m^{-1} (EC_e), and a slope of 9.6% (Kumamoto et al., 1990). However, after the first cutting, the halophytic nature of purslane is expressed, and the salt tolerance of purslane increases with subsequent harvests (Grieve and Suarez, 1997).

3.9. Solanaceae (potato)

3.9.1. Potato (Solanum tuberosum L.)

The potato originated in the Andes at altitudes over 2000 m, where it was cultivated by the Incas for more than 2000 years prior to the Spanish discovery. These explorers took the potato to Europe in 1537. The only edible part of the potato plant is the tuber, a fleshy stem with buds in the axils of leaf-scars.

Potato has been classified as moderately tolerant to salinity, but is more sensitive during the period of tuber bud initiation; shortly thereafter it is more tolerant as salinity reduces the proportion of extra-large tubers in favor of smaller, more commercially acceptable tubers. As salinity duration and/or concentration increase potato is again more sensitive due to a decrease in the average tuber size. Potato is highly sensitive to drought and calcium deficiency (Abdullah and Ahmad, 1982; Bilski et al., 1988; van Hoorn et al., 1993) – two factors which add to the pitfalls of conducting salt tolerance experiments.

In a field plot study conducted at the U.S. Salinity Laboratory in 1951 (Bernstein, 1959), salinity was found to reduce tuber size and number and hasten maturity in 'White Rose' potato. A 50% yield reduction occurred at 6.2 dS m^{-1} in these studies which used frequent irrigations supplemented with NaCl–$CaCl_2$ (1:1 by weight) to give average root zone salinities (EC_e) of 0.85, 3.37, 4.85, and 6.46 dS m^{-1}. It was noted that salinity did not significantly affect quality as measured by specific gravity or percentages of reducing sugar, sucrose, and starch in tubers; nor did salinity cause any injury symptoms on potato leaves. The amounts of Ca^{2+} and Cl^{-} in leaves and stems and Na^{+} in stems increased 3- to 4-fold over the treatment range, but amounts of Na^{+} in leaves remained low. K^{+} and Mg^{2+} in leaves and stems were not significantly affected by treatment (see Maas, 1986, on crop salt tolerance to sprinkling in potato).

Levy (1992) examined the salt tolerance of 14 potato cultivars under field conditions at three salinities in the Negev desert. Irrigations were applied frequently through drippers and EC_i of the highest saline solution was 6.1–6.9 dS m^{-1} with a Na^{+}:Ca^{2+} ratio of about 2:1 by weight. Salinity retarded plant emergence, reduced growth of both haulms (shoots) and tubers, and hastened maturity. In another study conducted in the Negev, Nadler and Heuer (1995) further confirmed previous observations that salinity had the beneficial effect of decreasing the proportion of extra large tubers in favor of higher yield of large tubers (Bernstein et al., 1951; Paliwal and Yadav, 1980). In this latter study, it was noted that tuber size but not tuber number declined with increased salinity, again confirming the observation originally made by Bernstein and colleagues.

Cultivar differences in salt tolerance of potato have been documented but the relationship between tolerance and physiological or morphological characters has not been made. Levy (1992) found that the early maturing cultivars Atica and Desiree and clone LT4 were the least sensitive to moderate salinity, but among 14 cultivars, found that the relationship between maturation time and salt tolerance was not consistent. Despite the skepticism of this investigator, the body of evidence in potato and other species indicates that some portion of salt tolerance may be attributable to earlier maturity (salinity escape) as long as earliness is not associated with yield decline. This speculation is also consistent with general observations that higher growth rates allow a plant to dilute the effects of ions that accumulate in the tissues as a result of high salinity.

Levy et al. (1988) exposed seven cultivars to NaCl concentrations up to 51.3 mM and found no relationship between high proline and salt tolerance. The wild potato species *S. kurzianum* has been found to be more tolerant to salt by virtue of smaller decreases in growth with increasing salinity compared to the cultivar Alpha and Russet Burbank (Sabbah and Tal, 1995). It was found that the wild species accumulated more Na^{+} in the shoot than the cultivated species but that the accumulation of Cl^{-} and the presence of Ca^{2+} may have very significant effects on salt tolerance. Field studies also have shown the importance of gypsum applications in potatoes grown under salinity (Abdullah and Ahmad, 1982).

4. Conclusions

Although there is information on salt tolerance of several of the more common vegetables, it is interesting to note how little quantitative research on salt tolerance has been done on the majority of the vegetables species. During our literature search we also found that almost no information on salt tolerance exists for herbs, another class of vegetables not addressed in this review. Quantitative salt tolerance data are limited for several of the ‘major’ crucifers, such as cauliflower, kale, brussels sprouts, kohlrabi, cress, water cress, and rutabaga; as well as several of the minor crucifers to include horseradish and sea kale. In addition, essentially no information is available concerning the salt tolerance of the following minor or speciality vegetables: bamboo, basil, cardoon, celeriac, chayote, chervil, chicory, coriander, cress, dandelion, endive, ginger (rhizome), horseradish, jicama, leek, New Zealand spinach, radicchio, rhubarb, roselle, rutabaga, salsify, sea kale, scolymus, scorzonera, water chestnut, and yam.

Because of the high cash value potential of many vegetable and herb species, and the wide diversity of germplasm available, there appears to be a need for much research in this area. The apparent genetic diversity among vegetables to accumulate a range of different ions and combinations of ions could add to the significance and potential of these species as bioaccumulators. As high quality water becomes more scarce, there is a growing need to use poorer quality water for agriculture. Such waters will include both saline ground water, agricultural drainage, and municipal and industrial waste effluents. The challenges for using such water profitably will depend on greater knowledge of salt tolerance.

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