THE RESPONSE OF FINGER MILLET (*Eleusine coracana* (L.)Gaertn) TO SALINITY.

By

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DECLARATION

I declare that this is my original work and that it has not been presented elsewhere for a Master of Science degree.

ONKWARE, A.O.

We, the supervisors of the work contained herein, declare that we are satisfied that the work is worth the submission for purpose of a Master of Science degree.

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ABSTRACT

In a set of experiments, both in the laboratory and in the greenhouse, two varieties of finger millet (Enakuru and EK-1) were subjected to salinity of graded concentrations; namely the control, 4, 8 and 12 mmho cm^{-1}, Ec (as measured in a conductivity bridge at $25^{o}C$).

The laboratory experiments comprised the germination of sterilized grain in paper-lined petri dishes. The salt stress effectively reduced rates and percentages of germination, the root and shoot linear growth, and the final seedling dry weight. The stress also delayed the peak α-amylase activity in the seedlings. The comparison between the two varieties showed that Ek-1 had higher rates and percentages of germination, higher linear growth, higher amylase activity and higher hydration levels than Enakuru under all experimental conditions.

The salt stress induced a significant loss of the cations; sodium, potassium and calcium from the seedlings.

The comparison between the effect of salt and that of sorbitol at equiosmotic concentrations showed that in most aspects the two solutes affected germination in a quantitatively similar way. The exception was recorded for the seedling α-amylase activity and the final seedling dry weight.

The greenhouse experiments comprised the culturing of plants in salinised soils. The soils were salinised by irrigation with saline water prepared to the specification already mentioned above.

Under the greenhouse conditions the salt stress effectively reduced the rate of heading, the final plant height and grain yield. Physiological processes such as the leaf carbon dioxide flux rates, and transpiration were effectively reduced by the soil salinity. The leaf chlorophyll content was also reduced by the salt stress, but the tissue protein content was not.

Soil salinity induced an increase in the tissue sodium content, and a decrease in the tissue calcium concentration. But the stress did not affect the potassium and chloride concentration in the tissues.

The soil salinity lowered the soil and leaf water potentials in both varieties.

In most of the aspects studied it appeared that the salt stress affected the plants primarily via water stress-like processes.

Both varieties showed moderate degree of resistance to salinity. The inter-varietal assessment showed that Ek-I had higher potential resistance to salinity than Enakuru, even though the latter variety had higher grain yield under the stress. It would be expected that the results from the greenhouse experiment would be very relevant for field trials because the conditions under the open greenhouse systems could easily apply in the field.

The implications of the results from this set of experiments are discussed in the light of the relevant literature.

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LIST OF ABBREVIATIONS AND SYMBOLS IN THE TEXT:

Ec ..... Electrical conductivity of a solution at 25°C (millimho cm^{-1}).

ECe..... Electrical conductivity of saturated soil solution extract at 25°C.

ppm ..... Parts per million (milligrams per litre).

MEQ..... Milliequivalents

PAR..... Photosynthetic active radiation ($\mu mol.m^{-2}s^{-1}$)..

ψ_π ..... Osmotic potential measured in megapascals (i.e. MPa).

ψ ..... Water potential (MPa).

M ..... Molality.

Pn ..... Net photosynthesis ($\mu mol\ CO_2 dm^{-2}h^{-1}$).

P_i ..... Net photosynthesis ($\mu mol.CO_2 cm^{-2}s^{-1}$)

E ..... Rate of transpiration

r^{CO_2} ..... Resistance to CO_2 transfer

r^{H_2O} ..... Resistance to water vapour transfer

CHAPTER ONE

1. INTRODUCTION:

1.1. Finger millet (Eleusine coracana (L) Gaertn).

Finger millet is a member of a small genus Eleusine (group chlorideae) (Kempana, 1975; Hilu, De Wet and Harlan, 1979). The taxonomic position of this genus and the constituent species form a point of contention (Purseglove, 1972; Kempana, 1975; Hilu et al., 1979). An important fact, however, is that two of the constituent species; E. coracana and E. africana are tetraploids which can, and do interbreed to produce viable hybrids (Hilu et al, 1979). Of all the eleusine species it is only finger millet (E. coracana) which is widely accepted as a crop plant, even though wild species such as E. indica may be gathered for food in times of famine (Purseglove, 1972).

Origin and domestication of finger millet has been a much debated affair. The current hypothesis is that domestication of finger millet occurred in Africa, the crop being taken, later, to the Indian Subcontinent where diversification occurred (Hilu et al, 1979).

Finger millet may grow in a variety of ecological zones but it is important as a crop in the tropics, mainly in Africa and India (Acland, 1971; Purseglove, 1972; Cobley, 1976).

In Kenya finger millet is cultivated in large amounts in Nyanza, Western and Rift Valley provinces (Acland, 1971), but some cultivation has been reported for Eastern and Coast

Provinces (Lamu District crop production-Annual report, 1977; Taita-Taveta District crop production - Annual report 1980; Mallana and Ajwang, 1981). These localities span an altitude ranging from sea level to above 2000 metres (a.s.l.*).

Finger millet is a free-tillering, small-grained annual cereal with fibrous and adventitous root system (Leonard and Martin, 1963; Thomas, 1970).

The stems are compressed and characteristically ascending to erect. The plant may grow to between 40 and 200 centimetres in height (Macharia, 1982). It has the characteristic grass leaves, with acute points (Acland, 1971). The plant is surmounted by a terminal digitate head: hence the term "finger millet" (Purseglove, 1972; Cobley, 1976). Nodal tillers may sometimes occur. (The structure and morphology of finger millet is given in figure 1).

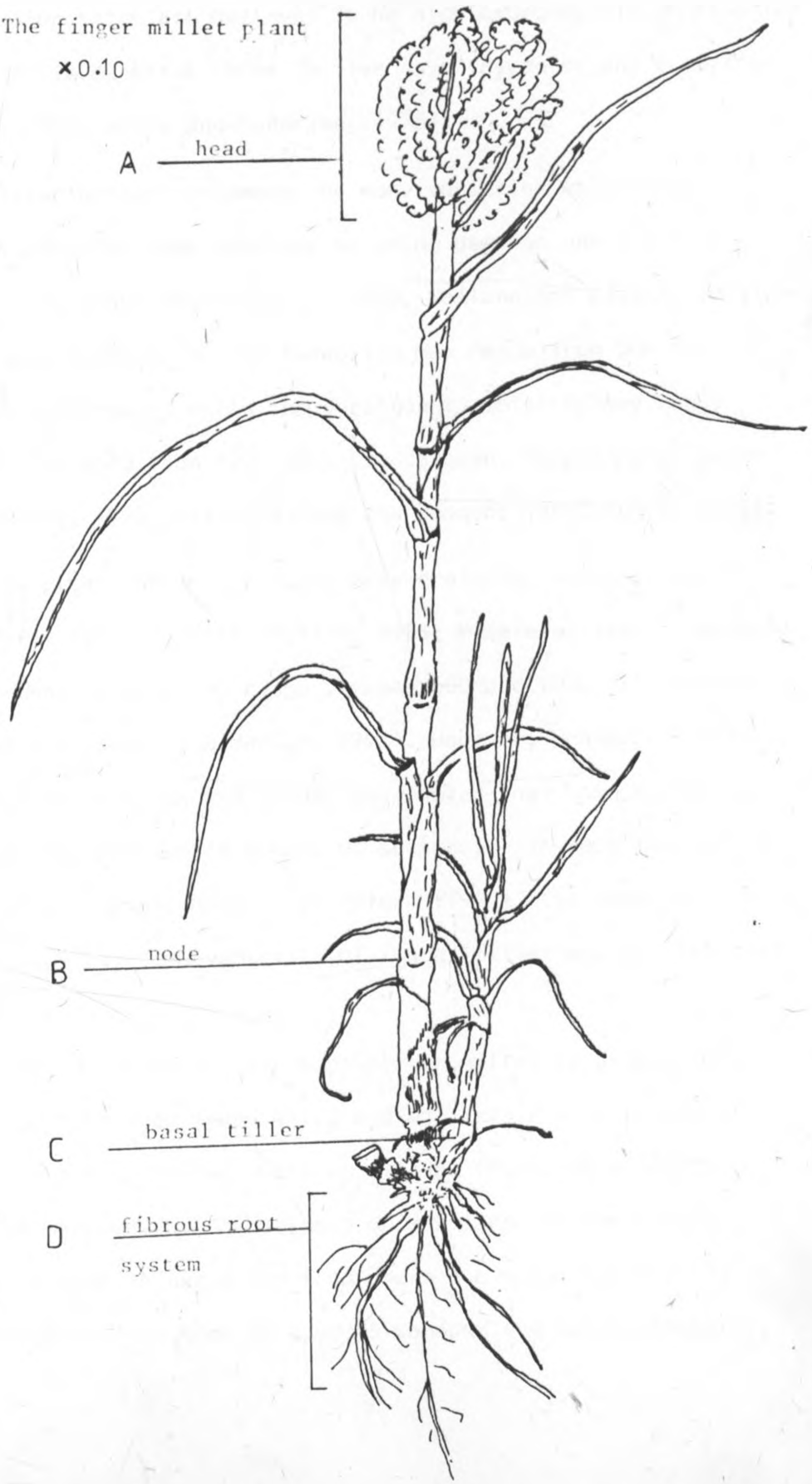
The vegetative organs as well as the grains may be pigmented differently depending on variety (Hilu and De Wet, 1976).

The head density may range from 80 to more than 85% (Purseglove 1972) and the 1000-grain weight may range from 1.92 grams to 2.79 grams (Rutto, Ajwang and Dhadho, 1980; Hulse, Lange and Pearson, 1980).

Seed germination is satisfactory; requiring a temperature range between 15°C and 30°C (Knapp, 1966). Even though Purseglove (1972) writes that no dormancy had been noted in finger millet seed at that time, it is currently believed that some varieties possess varying degrees of seed dormancy (Shimizu,

* altitude: metres above sea level

Fig. 1. The finger millet plant
×0.10



1978; Shimizu and Mochizuki, 1978; Shimizu and Tajima, 1979). The germination rates are believed to be high and complete germination may be achieved after three to five days (Ayyangar and Vijayaraghavan, 1926; Arora and Banerjee, 1978).

Tiller production among the many varieties which have been studied has been recorded as being between one and five tillers per plant (Rutto et al. 1980, Mallana and Ajwang, 1981).

Plant duration to 50% flowering may range from 50- to 80 , or more, days, while the duration to maturity may range from 9C to more than 170 days (Sundaresan, Raveendran, Thagam and Mysalmy, 1979; Rutto, Ajwang and Dhadho, 1981; Rutto, 1982).

The plant thrives on deep, free-draining, non-saline, non-alkali fertile soils (Acland, 1976; Michieka, 1980). Rainfall requirement is known to range between 600 and 1000 millimetres per annum (Leonard and Martin, 1963). However, Bhandari (1974) and Jaetzold and Schimdt (1982) have noted that some varieties can, and do, survive in areas, or seasons, with less than 600 mm rainfall per annum. Rachie and Peters (1974) cite examples indicating that some varieties of finger millet may be slightly alkali-tolerant.

Like all other cereal crops finger millet is propagated from seed. The seed keeps well, and may retain high levels of viability for up to two years in storage (Purseglove, 1972).

The seed may be sown direct on the farm. Alternatively it may be sown in nurseries from where the seedlings may be transplanted after some 25 days (Sivanapan and Balasupramanian,

1974; Rutto et al., 1980; Rutto et al., 1981).

In direct seeding, broadcasting and row-sowing may be employed (Purseglove, 1972; Rutto et al., 1980). Thorough weeding must be done early (25 - 45 days) to remove competition which might reduce the seedling vigour and the subsequent yield (Acland, 1971; Lall and Yadav, 1982). Bird damage may be very intensive, so they have to be kept away right from the filling stage to harvesting (Rutto, et al., 1980).

The finger millet grain has a high content of starch (Wakhade, Shehnaj and Rao, 1979), and may serve as a rich source of calcium and iron. It has a fair amount of phosphorus and a wide spectrum of amino acids (Pore and Magar, 1979; Wangati, Majisu, Kabuga, Karachi, Ondieki, Pirito, Potter and Matata, 1982).

The stored seed experiences little post harvest pest infestation (Rachie and Peters, 1974) but fungi may sometimes prove a problem (Ashokan, Emayavaramban and Ramabadran, 1981).

The grain may be ground into flour for making various kinds of porridges, breads, and cakes and these are said to have high sustaining power. Alternatively the grains may be malted for beer production (Bhandari, 1974; Hilu and De Wet, 1976).

Finger millet is a C_4 aspartate former (Rathnam and Rama Das, 1974; Tieszen and Imbamba, 1978). C_4 plants are so named because the primary product formed in their photosynthetic palisade cells during the process of carbon dioxide assimilation is a four carbon acid: Oxaloacetic acid (OAA). In finger millet the acid is converted into aspartic acid for translocation to the

bundle sheath cells where decarboxylation and refixation of the resultant CO_2 is carried out (Ray and Black, 1977; Bohlar-Nordenkampf, 1982).

C_4 plants require high quantum flux density (>2000 µmol $m^{-2}s^{-1}$) and high temperatures (35°C) for maximum photosynthesis (Milthorpe and Moorby, 1974; Smith 1976): finger millet has been shown to possess this property (Rathnam and Rama Das, 1974; Tieszen and Imbamba, 1978). The plants have very low (zero) carbon dioxide compensation point (Γ), and very high carbon dioxide fixation rates; up to 1818 µmol $CO_2 dm^{-2}hr^{-1}$ (Heath, 1969; Fry and Phillips, 1976; Tieszen and Imbamba, 1978).

The C_4 aspartate forming grasses are fairly drought tolerant (Ellis, Vogel and Fuls, 1980). Indeed finger millet is known to survive in areas with fairly low rainfall (Bhandari, 1974; Jaetzold and Schmidt, 1980; Western Agricultural Research Station Annual Report, 1982; Rutto, 1982).

1.2. Salinity and the salinity problem

Salinity is the occurrence of high concentration of dissolved salts in a solution.* Therefore salinity in the soil would mean a high concentration of dissolved salts in the soil solution (Richards, 1968; Arnon, 1972; Poljakaff-Mayber and Gale, 1975).

*Electrical conductivity > 4 mmho cm^{-1}

Determination of the salt status of a soil may be done in either of the two ways. The gravimetric method of salt determining involves precipitation and weighing of total salt in a soil solution extract and the units used may be percentages, grams per kilogram moles or milliequivalents per gram (Kearney and Schofield, 1936; Hayward and Wadleigh, 1949; Strogonov, 1964; Flowers, Troke, and Yeo, 1977). The alternative and preferable methods of determining the salt status of a soil is by measuring the electrical conductivity (millimho cm^{-1}) of a saturated soil extract (Ece) prepared according to the method of Richards (1968). A soil whose saturated soil extract has a conductivity of 4 m mho cm^{-1} or more is saline. In most cases the pH reaction of saline soils ranges from 7 to 8.5; never exceeding the upper mark even if the soil is saline-alkali (Richards, 1968).

The genesis of saline soils may be contributed to by many factors and events; therefore even though most of the saline soils occur in dry semi-arid areas, pockets of saline soils may also be found in wetter areas (Waisel, 1972; Chapman, 1974; Rachilo and Wataka, 1980).

The most prevalent causes of salinity in soils (and waters) include impeded drainage, infiltration by saline water and distillative precipitation* (Bernstein and Hayward, 1958; Zur and Bresler, 1973; Sheinberg, 1975; Mbuvi Wokabi, Mugai, Kanake and Muthumbi, 1976; Mahjoory, 1979). This is the reason behind the apprehension that exists about irrigation projects. These are known to have caused the problem of salinity in the past (Mahjoory,

* deposition of salt due to evaporation of water.

1979) and it is feared that the same may happen to current projects, especially where drainage is poor and the water scarce or of low quality (Arnon, 1972; Doneen, 1975; Peck, 1975; Saxena and Pandey 1981; Kingsbury, Epstein and Pearcy, 1984).

Global distribution of saline soils has been reviewed by Hayward and Wadleigh (1949), Waisel (1972), Mudie (1974), Chapman (1974); Carter (1975), among many other workers.

Kenya is not spared with the problem of both water and soil salinity and this is borne out by the Survey of Kenya (1970).

Site evaluation studies in various provinces reveal that saline waters and soils occur in various parts of the country. The evidence for this is based on the work of Muchema, Van der Pouw, Kibe, Kinyanjui and Ita (1980) and Kanake and Mureithi (1980) in Coast Province; Mugai and Bonarius (1976) and Njeru (1979) in the Rift Valley; Mbuvi, et al (1976) in the North Eastern Province and Rachilo and Wataka (1980) in Nyanza Province.

The site surveys have been carried out, mainly, in areas marked for irrigation projects or some large-scale agro-based ventures and there is every reason for guessing that the problem occurs in some of the, as yet, unsurveyed areas.

Soil salinity is important as an area of study because it impairs the growth and development of most plants except the halophytes (Bernstein and Hayward, 1958; Mudie, 1974; Flowers,

Troke and Yeo, 1977). Most of the crop plants are glycophytes (opposite of halophytes) which do not resist high salinity (>15 mmho cm^{-1} Ece) in the soil (Nieman, 1962; Strogonov, 1964; Greenway and Munns, 1980). Therefore soil salinity is a threat to food production; by reducing total acreage of arable land. However some of the crop plants have been shown to tolerate low to medium salinity (4 - 15 mmho cm^{-1} Ece). Thus, there is a nonuniformity in the susceptibility of crop plant species and varieties to salt stress; and this forms a basis for crop selection for saline soils (Nieman, 1962; Strogonov, 1964; Greenway and Munns, 1980; Epstein, Norlyn, Rush, Kingsbury, Kelley, Cunningham and Wrona, 1980).

1.3. Salinity and crop plants:

The effect of salinity on crop plants may range from impaired germination to the death of the plants at any of the stages of development (Lubach and Bondman, 1980). Therefore there has been a lot of work carried out to find out the mechanism and basis of the detrimental effects, with a view to isolation of tolerant varieties and discernment of markers.

Among the many cereal crops, those which have been intensely studied in relation to salinity include barley (*Hordeum vulgare*), wheat (*Triticum* sp.), Sorghum (*Sorghum* sp.), Pearl millet (*Pennisetum typhoides*), rice (*Oryza sativa*) and maize (*Zea mays*). In the study of these crop plants the various aspects ranging from

morphology to metabolism are assessed under salt stress.

Generally the study on plant response to salinity is divided into two major stages; germination, and growth and development.

Germination studies are mostly carried out in the laboratory using paper-lined Petri dishes irrigated with the treatment solutions (Panigarh, Misra and Misra, 1978; Varma and Poonia, 1979; Kumar, Kumar, and Shamshery, 1981; Ogra and Baijal, 1982). The growth and development may be carried in soil (Singh and Chandra, 1979; Saxena and Pandey, 1981; Gill and Dutt, 1982) and, occasionally, nutrient solution (Orton, 1980). In making treatment solutions, a mixture of salts (or diluted sea water) is preferred to single salts (Bernstein and Hayward, 1958; Gill and Dutt, 1982; Kingsbury, et al. 1984).

Several workers employing either or both of the outlined methods have observed very interesting results using the cereal crops already mentioned.

Rai (1977) observed that salt-stressed maize exhibited stunted growth, a longer duration to 50% silking and decreased yield.

Shingh and Chandra (1979) working on Pearl millet showed that salt stress depressed germination, increased the time to heading and lowered ear density and grain weight (1000 grain weight). Varma and Poonia (1979) observed the same germination effect and in addition noted a decrease in seedling linear growth in the same species. Ogra and Baijal (1982) in their experiments on sorghum showed that salt-stress impairs the synthesis

and activity of amylase in germinating seed and Saxena and Pandey (1981) noted stunting, reduced tillering and low grain weight in rice as a result of salt stress.

It is generally accepted that salt stress impairs germination and growth and development of the crop plants as Sarin and Narayanan (1968), Murthy, Ramu and Yadav (1976) and Kingsbury et al.(1984) have shown for wheat; Orton (1980), Greenway, 1965; Kumar et al. (1981); Gill and Dutt (1980); and Kumar, Singh and Sharma (1981) have shown for barley; in addition to the work of the other authors previously discussed.

Most of a plant's dry matter is accumulated by way of photosynthesis (Akunda, 1980), therefore this process plays a key role in development and yield of crop plants. This is the reason for which the photosynthetic efficiency, translocation of photosynthates and the composition of the photosynthetic pigments (mainly chlorophyll) in salt stressed plants attracts great interest.

In cereal crop plants, and grasses in general, salt stress has been shown to change chlorophyll composition (Varshney and Baijal, 1977) and the absolute chlorophyll content (Garg and Garg, 1982). This could lead to the reduced photosynthetic rates as observed by Kingsbury et al., (1984) in wheat.

The reduced photosynthetic rates may result from the above causes; alternatively it may result from reduced translocation or enzyme activity due to low water content (Shemushina, 1970;

Kaufman and Ross, 1970; Hsiao, 1973; Divate and Pandey, 1979), or closure of stomata (Hampe and Marschner, 1982; Kingsbury, et al. 1984; Gorham, McDonnel and Wyn Jones, 1984).

It is believed that plants under salt stress may suffer from either overaccumulation of mineral ions in the tissues or an ion imbalance whereby the plants absorb more of the neutral than nutrient ions. The ion excess is believed to impair enzyme activity (Helal and Mengel, 1979; Katherine, Hancock and Cavalierei, 1980; Kalir and Flowers, 1982).

Indeed, the accumulation of sodium and chloride ions, sometimes accompanied by a decrement of potassium and calcium ions, has been observed for a variety of cereal crops (Greenway, Pitman and Thomas, 1965; Orton, 1980 and Gilland Dutt, 1982, in barley; Murthy, et al 1979; in wheat; and Kurian, 1976; in Pearlmillet).

Of interest is the fact that some of the fairly drought tolerant cereal crops (barley, Pearl millet and Sorghum) are among the most salt resistant crop plants. However, Bernstein and Hayward (1958) point out that drought resistant plants may not necessarily be salt resistant and vice versa. However, former observations makes finger millet an interesting crop plant to work with in that behaviourwise it is like sorghum and pearl millet, in most aspects.

1.3.1. The physiology of salt resistance:

Salt retards the development of plants by interfering with the metabolic processes.

The plants which are under salt stress face two distinct problems. The first of these problems is connected with the soil-plant water relations. The addition of saline water to the substrate lowers the latter's water potential. Depending on the amount of water and the irrigation regime the matrix or the solution osmotic potential may have an upper hand in this process. This condition necessitates that the affected plants lower their water potential in order to continue absorbing water from the substrate. In most higher plants this is achieved by absorbing the mineral ions from the substrate (Bernstein and Hayward, 1958). Plants differ in their ability to carry out this osmotic adjustment and this may sometimes be reflected in their differences in salt resistance (Orton, 1980). The more resistant plants adjust faster than the susceptible ones. However, this may not always happen (Greenway and Munns, 1980).

The second problem that salinised plants face is that of ion excess in the protoplasm. The high ion content in the protoplasm may interfere with metabolic activities because of the agglutinating or dispersing activity of the ions on the cytoplasm components (Bernstein and Hayward, 1958). Moreover, excess univalent ions have been shown to aggravate loss of substances from the cells (Huber and Shankla, 1980).

There are several ways by which a plant may resist the high ion content in the tissues. The first of those adaptations may be the synthesis of ion-resistant enzymes. Salt resistant enzymes have been extracted from halophylic bacteria (Caldwell, 1974; Kylin and Quadrano, 1975); but <u>in vitro</u> tests of most higher

plant enzymes (halophytes and glycophytes) give results to imply that in these plants (and fungi) no specifically salt resistant enzymes are synthesised (Flowers, et al. 1977). This implies that salt resistant angiosperms are mainly ion excluders (Caldwell, 1974). Ion exclusion in plants may be effected in many ways. Some of these may be common to both glycophytes and halophytes, but others may be found exclusively among some halophytes. The ion exclusion mechanisms of the latter category may include glandular secretion (Caldwell, 1974; Thomson, 1975).

The former group of ion exclusion mechanisms may involve such processes as selective absorption, root and stem retention and dumping of the ions in the older senescing tissues (organs) or compartmenting the ions in specific organelles within the cells (Walsh, 1974). The partitioning is a process which prevents overaccumulation of ions within the cytoplasm, especially those of young active cells.

Inorganic ions have been found to accumulate in the cell vacuoles of salinised plants (Flowers, 1975; Stelzer, 1980).

Compartmentation of mineral ions in the cells may require that organic ions, especially acids and ammonium derivatives, be accumulated in the cytoplasm for ionic balance (Osmond, 1963, Storey, Ahmad and Wyn Jones, 1977; Storey and Wyn Jones, 1977).

Salt stress may change C_3 plants to carry out CO_2 fixation by CAM among some glycophytes (Ting. 1978). Such a switch has not

been proved for any C_4 plant. Research has shown that C_4 plants (halophyte or glycophyte), when compared with their C_3 counterparts, are relatively more efficient in fixing carbon dioxide under salt stress. (i.e. C_4 plants are more photosynthetically efficient than C_3 plants exposed to the same salt stress) (Caldwell, 1974; Schwartz and Gale, 1984). However, the C_4 photosynthetic enzymes have been shown to be very sensitive to salinity (Kylin and Quadrano 1975; Murata, Oshugi and Shimuzi, 1983). This is an indication that in the cell these enzymes are not exposed to high ion concentrations.

In summary, a plant under salt stress must carry out osmotic adjustment and at the same time avoid the accumulation of excess ions at the sites of enzyme activity, or alternatively synthesise salt-resistant enzyme systems in order to survive the salinity. It is apparent that most plants are ion excluders. Therefore, the resistance of a plant to salt stress will depend on how the plant carries out osmotic adjustment, and at the same time protect its sensitive enzymes from excess ions. In both cases the halophytes are better adapted than glycophytes (Flowers, et al, 1977).

1.3.2. Finger millet and salinity:

There is limited work which has been specifically designed to test the response of finger millet to salinity. This applies even to other aspects of the crop; Tieszen and Imbamba (1978) have blamed this on lack of international recognition of the crop. Even in localities where the crop is of some importance, especially in

Africa, improvement and selection of superior varieties has not advanced far because other cereals such as maize are given an upper hand in research programmes.

In Kenya, for example, the only publications available on the effect of alkalinity or salinity on finger millet is by Michieka (1980), and this was just a mention in passing!

However, from India and Japan there are a few interesting publications in which the workers show that they really were interested in this problem: the problem of the effect of salinity on development of finger millet. These publications can be divided into two groups. Those on general and the others on specific effects.

Kaliappan, Ramachandran and Rajavagopal (1967) exposed pot-grown finger millet to salinity levels between 2000 and 4000 ppm (≈ 3, and 5.4 mmho cm^{-1} Ec) in the irrigation water; and showed that these salinity levels retarded seedling linear growth.

Kaliappan and Rajavagopal (1968) stressed pot plants (finger millet) by irrigating them with water containing 8000 ppm dissolved salts (≈ 10 mmho cm^{-1} Ec). They noted that the salt stress prolonged the vegetative period of finger millet by delaying the 50% panicle emergence. The percent grain set was reduced! This must have affected the head density too.

Marachan and Rajavagopal (1971) irrigated pot plants with saline water (8000 ppm; 10 mmho cm^{-1}, Ec) and recorded a reduction of the yield in response to the salt stress.

Rachie and Peters (1974) also make a general and indirect

reference, noting that finger millet may be slightly salt or alkali resistant.

Panigarh, et al. (1978) in a laboratory experiment, germinated finger millet in salt solution containing up to 2% dissolved NaCl (≈ 3.0 mmho cm^{-1}, Ec) noted that the salt stress and reduced both the germination percentage and the root and shoot length of the seedlings.

Sundaresan, et al. (1979) point out that some particularly salt resistant varieties of finger millet have been isolated. Sarma, Reddy, Taju and Sastry (1983), in field experiments showed that irrigation with water containing medium salinity (≤ 8 mmho cm^{-1}, Ec) could reduce yield by no more than 52%. However, they recommended that irrigation with low salinity water (4 mmho cm^{-1}, Ec) may have no tremendous effect on finger millet development.

All the above authors noted genotypic differences in salt resistance..

Some work has been carried out on the response of some finger millet enzymes to salt stress. An example is the experiments by Murata et al (1983) who, in their in vitro experiments, showed that NAD-malic enzyme from finger millet leaves was inhibited by chloride ions. This inhibition was competitive in nature, because it depended on the amount of substrate available. This specificity of the ion effect on enzyme activity may be taken to be an attribute of ion toxicity. It would appear that the salt resistant variety of finger millet reported by Sundaresan et al. (1979) must protect the enzymes from excess ions by some avoidance mechanisms. It is unfortunate that these authors do not indicate the ion status

of the plants in question. Then it would have been easier to ascertain the specific avoidance mechanism employed by this variety.

Published work on mineral ion absorption and metabolism in salt-stressed finger millet include the contribution by Gopal, Rao and Rao (1983), who, working with phosphorus, showed that salt stress impaired the absorption of this nutrient element from the soil and also altered its metabolism in the plants. This observation may be extrapolated to include other nutrient elements, th ough this may not necessarily be true.

1.3.3. Hypotheses:

In view of the detailed information in the previous sections it is expected that finger millet would be affected by salinity in the typical glycophytic manner. However, some varieties may be salt resistant.

On the basis of these observations some three propositions may be advanced:

(1) the adverse salt effects may be expressed at some or all stages of finger millet development and the mechanism of effect might be purely osmotic, ionic or a combination of both.

(2) the observable morphological and structural aberrations are based on physiological abberations in the plant as a response to salt stress and

3. salt resistance in finger-millet will depend on efficient ion partitioning and maintenance of equable water status despite the salt stress. The resistance may differ between genotypes and with time.

1.3.4 Testing the hypotheses:

The effect of salt stress on the development of two finger millet genotypes (varieties) will be assessed at various stages of growth. The test solutions will comprise a series of medium concentrations of salt (or sorbitol in some cases). The salt solutions will range between 4 and 12 mmho cm^{-1} (Ec)(-0.1800 to -0.5400 MPa, ψ_π).

Germination will be assessed in the laboratory by standard seed testing methods. The parameters to be examined, in this case, include germination rates and percentages, and seedling linear growth. In vitro amylase activity will be assessed using seed and seedling extracts.

The ionic versus osmotic effects of salinity on germination will be tested by use of equiosmotic solutions containing an organic solute or salt.

Leaf photosynthetic and transpiration rates and leaf water potential will be assessed using conventional means. The photosynthetic rates will give an indication as to how salinity might affect bioproductivity and the transpiration rates and water potential will give some insight into the plant water relations.

The other biochemical assessments that will be carried out, apart from amylase activity, include leaf chlorophyll and tissue protein content. These are aspects which may be tied closely with photosynthesis and other biochemical activities.

The ion partioning abilities will be assessed by dissolution of mineral ions (sodium, potassium, calcium and chloride) from different tissues and organs and assessing their concentration by conventional means.

Cell extension growth will be assessed indirectly, by measuring the length and height of organs (and tissues) and organ formation (e.g. tillers) respectively. This will throw light upon the problem as to which of the two processes is the more susceptible to salt stress.

The translocation and partioning of resources (especially photosynthates) will be examined by assessing the weight of mature heads, the head density and the 1000 grain weight.

The data collected from the work will be analysed statistically to assess the relative resistance of the crop to salinity both within and between genotypes. The suitability (or otherwise) of the crop for saline soils will be based on final yield of crop in comparison with control (and between varieties).

CHAPTER TWO

2. MATERIALS AND METHODS:

2.1. Finger millet seed:

Two finger millet varieties were used in experiments. Both of them are Kenya locals which have not been improved. No salt-stress experiments have been carried out on the varieties before, so their response is not known. These two varieties were used because of two reasons. One was that I had plenty of seed of the varieties, and the second was that the two varieties originate from two different ecological zones in Kenya: Western and Eastern Kenya.

The variety from Western Kenya was a local Kisii variety, locally known as "Enakuru". This variety is a complex series which is thought to comprise two, more or less, distinct strains (Macharia, 1982). However, little agronomic research has been carried out on this variety. The variety has distinctively purple nodes and earheads. It is a mid-duration variety which may grow to some 180 centimetres in the field.

The variety which originated from the Eastern province of Kenya, and which I used in the experiments, is an isolate known as Ekalakala -1 (Ek-1 ; KatFM-1) (Mallana and Ajwang, 1981). This is an early maturing variety. It does not have purple nodes or heads; and this difference in pigmentation helped to ease identification during growth.

The seed had been in store for no more than six months, so the viability was high. The seed had been cleaned, so no

further cleaning was needed. Preliminary germination tests showed that the seed did not possess dormancy of any kind. Therefore no special treatments were required before sowing.

2.2 Experimental:

Two sets of experiments were conducted; one in the laboratory to test germination and the other in the greenhouse to test growth development and yield. In either case no artificial lighting, heating or air conditioning was used.

The laboratory experiments were conducted on a six day basis, while in the greenhouse the plants were raised from seed to maturity.

In both cases treatements comprised the control, 4, 8 and 12 mmho cM^{-1} (Ec) (Conductivity bridge, R C 16 B - 2, Industrial instruments). These solutions were made by dissolving salt (Kensalt)* in water. In the laboratory distilled water was used, but for the greenhouse experiments tap water (E C 0.5 mmho cm^{-1}) was used.

The laboratory experiments were carried out on the largest, undamaged sterilized seed. The seed was sterilized by immersi[illegible] in hypochlorite (20% commercial bleach - JIK) for five minut[illegible], followed by three successive rinses in distilled water.

The seed for greenhouse experiments was not sterilized, and because of the large amount of the seed needed no attempt was made to select the largest grains for experimental purposes.

* Table salt prepared from sea water by evaporation; comprising ca. Na = 30.6%, K = 1.1%, Ca = 1.2%, Cl = 55% among other ions.

All treatments and experiments were replicated eight times, unless stated.

2.2.1. Germination:

The laboratory germination tests were geared towards assessing the effect of salt stress on germination rates and percentages, weight loss, the linear seedling growth, α-amylase synthesis and activity and mineral ion status of the seedlings.

The temperatures ranged between 18°C and 23°C at time of experiments. The seeds were germinated in paper-lined petri dishes which were irrigated with four millilitres of the treatment solution. The paper used was Whatman No. 1 filter paper. This was put in the petri dishes, the treatment solution randomly allocated and applied (Fisher and Yates, 1963a) and the petri dishes labelled for treatment. Then the sterilised seeds were placed on the filter paper, ten of each variety per petri dish, and labels attached to indicate the varieties. Then the petri dishes were covered to avoid excessive loss of moisture and microorganism contamination.

Germination was observed as the exertion of the white radicle. Incidents occurred when only plumule emerged . These were counted as germination.

A further experiment was set up to assess the differences in effect between equiosmotic concentrations of salt and sorbitol (-0.18, -0.36 and -0.54 MPa) on germinating finger

millet seed. The aspects studied in this comparison exercise included percent germination, linear growth and carbohydrate metabolism.

The salt concentration (Ec) was converted to osmotic potential (MPa) by employing the method of Richards (1968).

2.2.1. A. Cumulative germination:

Cumulative germination percentage data were recorded on a 24-hour basis. The data were later used in construction of germination time curves from which duration to 50% germination was estimated according to the method of Sorensen and Campbell, (1981).

2.2.1. B. Percent germination:

The final percent germination data was based on the final count on germination, after 168 hours. The mean germination was based on data from the eight replicates per variety per treatment. Before subjecting the percentage values to statistical analyses they were given angular transformation (Fisher and Yates, 1963b).

2.2.1. C. Linear growth:

The measurement of growth was not carried out on successive period of time. The measurement was made at only one stage; 168 hours after sowing. This also marked the termination of the experiments.

The length of both the root and shoot (or whichever was present) was measured and recorded (in millimetres). This was done for every germinated seed and a mean was calculated for each replicate. This Mean was used in statistical analyses.

The length of shoot was measured from the base to the tip of the longest leaf (when present) while that of the root was measured from the base to the tip of the main root. Number of leaves or rootlets was not recorded.

2.2.1.D. Mineral ion content:

The mineral ions for which the seedlings (168 hr old) were analysed included sodium, potassium and calcium. The analyses were based on pooled seedling material per replicate. All the ungerminated seeds were discarded.

The seedlings were rinsed in distilled water, dried in an oven at 70°C for 96 hours and stored in a dessicator with self indicating silica gel.

Known weights of the seedling material were acid digested for ion analysis.

The ion content, in parts per million (ppm) was standardized to milliequivalents per 10 grams for ease of comparison. The same method was employed in analysing the ion content of leaves, stem and root of the plants grown in the green house.

2.2.1.E. Mineral dissolution and determination:

Many mineral ions in the plant tissues may not be accessible to direct elusion because the cell membranes act as a barrier to outward migration. Moreover some of these are incorporated in organic compounds which may be tightly bound in the organelles (Pitman, 1975). To get to these ions for analytical purposes the tissues have to be digested or ashed (Allen, 1974).

In my work, I employed nitric acid, perchloric acid and sulfuric acid mixture (5 ml, 1 ml and 0.5 ml volumewise) as recommended by Allen (1974).

The weighed samples were put in 30 ml Kjeldahl flasks, followed by the acids. The mixture was then heated, gently at first, then intensely later on, on a heating block. The digestion was stopped when only 0.5 ml pink or clear solution remained in the flask. This was cooled, diluted and transferred into a 50 ml volumetric flask. Two successive rinses of the Kjeldahl flask were also transferred into the volumetric flask. The solution was made to volume and stored in 60 ml polyethylene bottles. Only distilled water was used for all the dilutions and rinsing.

Each replicate for each variety was treated the same way.

2.2.1.F. Ion determination:

The determination of the cation content was based on their light emission or absorption properties. Both sodium and potassium

content was analysed in a Gallenkamp flame analyser (FGA 330-C) and the calcium content was analysed in an atomic absorption spectrophotometer (Pye Unicam SP 90A series 2)

Standards were prepared from pure analytical grade reagents as recommended by Allen (1974).

(i) Sodium:

Sodium was analysed by flame emission at 589 nm (the equipment has inbuilt filters).

Calibration was carried out by using standards containing between 0 and 20 ppm sodium. The calibration values were used to construct a standard (Calibration) curve. This was used in the conversion of sample readings to ion concentration in parts per million.

The concentration in parts per million were then converted to percentage using the equation by Allen (1974):

$$(Ca^{2+}, K^{+},), Na^{+}\% = \frac{ppm \times v}{10^4 \times W} \qquad (I)$$

ppm is the concentration, v is the volume of sample (50 ml) and W is the weight of sample digested. Then the percentage value could be converted to milliequivalents per 10 grams thus:

$$\frac{ppm \times v}{10^4 \times W} \times \frac{100}{\eta} \qquad (II)$$

where η is the equivalent weight of the ion concerned.

(n = 23 for sodium; 39.1 for potassium and 20.04 for calcium). Therefore equation (II) was employed for all the three cations.

(ii). Potassium:

The element was analysed by flame emission at 767 nm. The standard solutions ranged between 0 and 50 ppm potassium content; and these were used to construct a standard curve which was used to convert sample readings into concentration in parts per million. The concentration values were then converted to milliequivalents per 10 grams using equation (II) (section 2.2.1 (i).

(iii) Calcium

Calcium content was analysed in an atomic absorption spectrophotometer on absorption mode at 418 nm (recommended, 422.7 nm).

The standard concentrations ranged between 0 and 30 ppm calcium.

Sample readings were converted into concentration (ppm) by use of the standard curve and then to milliequivalent per 10 grams by use of equation (II).

Before analysing for calcium the sample solutions were amended by addition of Lanthanum (in form of Lanthanum chloride). Therefore calcium was determined in the sample solution after sub-samples had been drawn off for chloride

analysis, This was done only for the plant yegetative tissues.

(iv) Chloride content:

The chloride content of the samples was determined by the silver nitrate method (American Public Health Association, 1971).

All the standards were prepared from analytical grade chemicals, and distilled deionised water (Ec 0.001 mmho cm^{-1}) was used at all stages.

Standard chloride was prepared from 824.1 mg of sodium chloride dissolved in water then made to one litre (0.014IN).

The standard silver nitrate was prepared by dissolving 2.395g of silver nitrate in a little distilled deionized water then diluting to one litre.

The chromatogenic reagent (potassium chromate) was prepared from 50 grams of potassium chromate in 100 millilitres of the water. Then enough of the silver nitrate was added to form a red precipitate. The solution was let to rest for 12-hours followed by filtering and dilution of the filtrate to one litre.

In the analysis ten millilitres of sample solution was diluted to fifty millilitres and this was used directly in the titration after the addition of 0.5 ml of the chromatogenic reagent. All the titrations were carried out at pH 10.5. This was the pH at which the best colour development and hence the distinct end point, could be achieved.

Each replicate was run three times. The amount of titrant used per each run was converted to milligrams of chloride per litre of solution. This was done after standardization of the silver nitrate titrant at 0.0141N, and titration of the blank (1 ml of titrant). The equation employed for conversion is given below:

$$MgCl^{-}/L = \frac{(A-1) \times 0.0141 \times 35450}{50} \qquad (III)\ *$$

A is amount of titrant used in the titration. This values were then upgraded to reflect the actual chloride content of the samples

$$MeqCl^{-}/L = \frac{(A-1) \times 0.0141) \times (35450) \times 10^{**}}{50 \times 35.46} \qquad IV$$

* adapted from APHA (1971)

10^{**} this is the dilution factor.

2.2.1.G. Amylase activity:

Finger millet contains starch as the main food store. Therefore it is necessary that at germination α-amylase be synthesised for mobilization of these food stores. (Dunn, 1974; Terrago and Nicholas, 1976; Adams, Rinne and Fjerstad 1980). Salt and osmotic stress has been shown to reduce amylase activity of germinating cereal seeds (Sarin and Narayanan, 1968;

Armstrong and Jones, 1973). However, no publication has been made on this aspect for finger millet.

It was my aim to find out the effect of salt and osmotic stress on amylase activity in germinating finger millet seed and seedling.

In this case treatments were replicated only three times. The salt solutions were made as has already been described and the sorbitol solution concentrations have been described (see section 2.2.0).

This experiment required a large number of seeds therefore each petri dish contained seeds of one variety only.

Analysis was carried out on a 24-hour basis, using 20 seeds/seedlings of each variety per replicate, for 144 hours. Seeds were used only at the end of the first 24 hours. After the first 24 hours only seedlings were used for sake of apparent uniformity of material.

The buffer solution was based on the work of Paleg (1959), and the amylase activity was assessed using the method of Jones and Varner (1961).

The seedlings were ground in a chilled mortar containing 1 ml of chilled 0.005 M (pH 5.5) citrate buffer. The ground mixture and two rinsings were transferred into centrifuge tubes and the volume made to 5 ml. The mixture was centrifuged at 2000xg for ten minutes. Four millilitres of the supernatant were drawn off for amylase activity test.

The test involved assessing the hydrolysis of 1% starch by the extract. The 1% starch solution was prepared from soluble starch (BDH chemicals) dissolved in boiling distilled water. This stock solution was serially diluted to give standard starch solutions for calibration (we did not have pure amylase). The stock solution was used to set the spectromphotometer.

1 ml of the stock starch solution was mixed with the 4 ml extract and incubated at 25^{o}C for 10 minutes at the end of which 1 ml of 1% iodine solution was added to both stop the amylase and act as the chromatogenic reagent by combining with the starch to form a blue colour. The intensity of the colour could be proportional to amount of starch remaining in the mixture.

For blank and standards, 1 ml of the solution, in each case, was mixed with 4 ml of the buffer and incubated at 25^{o}C for 10 min at the end of which 1 ml of 1% iodine solution was added.

The optical density of the resulting blue solutions was determined at 620 nm in a spectrophotometer (Pye Unican SP 500 series 2).

The equipment was set to give an absorbance of 2(absolute) by use of the "blank" (the stock starch solution).

The absorption values for the standards were used to prepare a standard absoprtion curve which was used to quantify sample readings. The preparation of 1% iodine solution has been described by Jones and Varner (1961).

2.2.2. Growth and development

The plants were grown in pots (buckets) in a greenhouse.* Medium loam soil was used in the experiments. The soil was collected from the University botanic garden in January 1985. The soil was collected from the same area, heaped in one mound, and therefore was expected to be uniform. The soil was carried from the garden in 16-litre plastic buckets. At the site of the experiment the bigger clumps of soil were crumbled and the experimental containers were filled with the soil.

The experimental containers were of two sizes: the smaller were 18-inch flower pots with drainage holes at the bottom, and the larger were 25-litre plastic buckets, also with holes drilled in the bottom. There were 44 small and 32 bigger containers, and the two sizes were treated as separate sets of the same experiments.

It was intended to germinate the seed in already salinised soils so salinisation was started by irrigating the pots with the preallocated treatment solution. The allocation was carried out by numbering the containers, and then using a table of random numbers. The pots for particular treatment were marked and appropriately labelled. Each of the bigger pots was irrigated with 3 litres of treatment solution, and the smaller pots were irrigated with 2 litres of solution each. These amounts of liquid had been shown to completely flush through the soil column. Four such irrigations were carried out prior to sowing, so as to ensure even distribution of salt through the soil mass. Pots were irrigated at least three times a week.

* Mean temperature 18.8^{o}C; PAR 1700 µmol $m^{-2}s^{-1}$ - at mid day.

Tap water (Ec 0.5 mmho cm^{-1}) was used to make the treatment solutions (4, 8 and 12 mmho cm^{-1}), and thus formed the control. Each treatment was replicated eight times (big containers); eleven times (small).

Sowing of seed of each variety was carried out by direct seeding in rows. Each pot contained both varieties. Aldrin (a pesticide) was incorporated to take care of the soil pest problem.

The first weeding and thinning was carried out on the tenth day after sowing and the second and final thinning was carried out on the 27th day.

Data was collected on cumulative heading. Photosynthesis, transpiration and the attendant resistances were analysed by infrared gas analysis. Diffusive resistances were also determined by diffusive porometer.

The soil and leaf water potential was determined by the thermocouple psychrometry method, and a pressure chamber was employed to augment the data on leaf water potential as collected by psychrometry.

Whole plants were harvested for ion analysis and later on data was collected on tillering, ear production, plant height and number of green leaves (and nodes) per main tiller.

At maturity the heads were picked, put in labelled paper bags and dried in an oven ($50^{o}C$) for 6 days.

2.2.2.(A) Ion determination:

The harvested plants (above ground parts) were thoroughly cleaned in tap water and rinsed in distilled water. Then the plants were divided into upper, middle and lower leaves and stem. No dead leaves were used.

The separated parts were dried in separate labelled paper bags. This was done at 75°C for at least 72 hours and the samples were cooled in a dessicator (see section 2.2.1(D). The mineral dissolution was carried out by use of methods already described (section 2.2.1(E).

The determination of cations; sodium, potassium and calcium has been previously described (sections (2.2.1(i) to 2.2.1.(iii). The chloride content was determined by the method described in section 2.2.1.(iv).

2.2.2.(B) Photosynthesis, transpiration and associated resistances

The most favoured method of measuring carbon dioxide assimilation is that involving the infra red gas analyser (IRGA). The measurement is possible because of the ability of CO_2 to absorb infra red light (Long, 1982). The IRGA can be used on intact plants, thus requiring minimum disturbance on the plant (unlike, say, the oxygen electrode).

When the IRGA is coupled to other accessories it becomes possible to measure such other parameters as transpiration rates, and diffusive resistances to water vapour and carbon dioxide transfer.

An IRGA system may be calibrated on either absolute or differential mode. The latter is the preferred mode because it is cheap and easier to maintain at steady state (Long, 1982).

This work was carried out on a bench model of infra red gas analyser (The Analytical Development Co. Series 225) which was calibrated on differential mode according to Long (1982).

The leaf chamber (7.5 cm by 3 cm by 1 cm) was fitted with a fan for purpose of reducing air stagnation and boundary layer resistances. The top of the chamber was made of perspex to permit entry of light. This top could be removed and refixed by use of plasticine, after laying the leaf in place.

The temperature of the chamber was regulated by circulating water which could be heated directly by immersible coil or cooled indirectly by circulating super-cooled water from a special freezer fitted with a pump.

The leaf temperature was monitored by use of a thermocouple junction . The hot joint touched the lower surface of the leaf in the chamber and the cold joint was immersed in melting ice in a lugged plastic jar fitted with a cap. The potential output was monitored by use of a digital multimeter (Keithley 160B). The output could be converted into ^{o}C by use of a calibration curve.

The light source was one halide lamp mounted above, and separated from the chamber by a glass tank containing an eight centimetre depth of water to absorb excess heat. The power to the lamp was regulated by means of a variac meter (Dimmerstat type

150-IP). The photon flux density was maintained at 1700 μmol $m^{-2}s^{-1}$. This was monitored from time to time by use of a LICOR Quantum meter (LI-188).

The air was drawn from the top of the building (2 storeys) by use of a pump. The air was then passed through a jar of silica gel to dry it. Its moisture content was standardised before entering the chamber. Flow rates were maintained at 400 ml per minute.

The water vapour density of the air entering or leaving the assimilation chamber was monitored (in ^{O}C) by use of a dewpoint hygrometer (thermoelectric, 880).

Depletion of CO_2 from the air stream was monitored by the IRGA, whose potential output was recorded by a portable field chart recorder (TOA, EPR - I FA).

The area of the leaves in square decimeters was calculated thus:

$$A = (Wm \times 0.75)\ dm^2.$$

Wm is the mean leaf width (in dm) and 0.75 dm is the length of the chamber.

At steady state photosynthetic activity the curve on the recorder was marked and the dew point of the outgoing air was recorded.

The leaf was removed from the assimilation chamber, cut off from the plant and put in a plastic bag and stored in a deep freeze for chlorophyll analysis (2.2.2(G).

2.2.2.(C). Photosynthesis

The rate of photosynthesis is equivalent to the rate at which carbon dioxide is incorporated into organic molecules in the plant. In an IRGA system which has been calibrated on differential mode the removal of carbon dioxide from a stream of air is registered as a shift in electrical output. The shift in output will depend on the flow rate of the air stream and the rate and magnitude of CO_2 removal.

When coupled to a pen recorder, the output from the IRGA is recorded in the form of a curve which levels off at some point from the base line. The distance from baseline to the plateau of the curve is proportional to the amount of carbon dioxide removed from the air stream, hence photosynthesis, as has been outlined by Long (1982).

On basis of the relationships outlined above, and the chart calibration, an equation was employed for computation of net photosynthesis rates, (Pn):

$$\mu mol\ CO_2/dm^2/hr = \frac{(\Delta div)\ (1.13)\ (1.178 \times 10^{-4})\ (400)\quad 1000}{\text{leaf area } (dm^2) \times 44} \qquad (V)$$

(Δdiv) are the division units from baseline to the curve plateau, 1.13 the scaling factor for the chart, 400 is the flow rate of air through the system in millilitres per minute, 1.178×10^{-4} is a constant relating volumetric ppm CO_2 to weight and millilitres per minute to litres per hour and 44 is the molecular weight of CO_2.

2.2.2.(D). Transpiration

Computation of transpiration rates was based on the difference between the water vapour density of the air stream entering the assimilation chamber and that of the air leaving the chamber, the flow rate (400 ml min^{-1}) and leaf area in square decimeters.

The water vapour density was a value arrived at after conversion of the dewpoint (^{o}C) data from the hygrometer by use of the Smithsonian Meteorological Chart.

The equation which was used in all our transpiration (E) calculations is given below:

$$\mu Mol\ H_2O/dm^2/hr = \frac{(H_2O\ (out) - H_2O\ (in) \times 400}{\text{leaf area } (dm^2) \times 18} \quad 1000 \qquad (VI)$$

H_2O (out) and H_2O (in) are the water vapour density of the air coming out of the assimilation and that of the air stream entering the chamber respectively. Hence "in" and "out" define the direction in which the air is flowing in relation to the chamber and 18 is the molecular weight of water.

2.2.2.(E). Resistances to diffusive transfer:

The two gases of greatest interest in this case are carbon dioxide and water vapour. Resistance to transfer of the two is complex in C_4 plants but may ultimately be tied with the stomatal movement (Heath, 1969; Long, 1982). The flux of water

through plants and the flux of CO_2 into the leaves are closely intertwined at the stomatal level where they may together or individually effect closure or opening.

The resistance to water vapour transfer was calculated by use of the equation given below:

$$rH_2O \text{ sec/cm} = \frac{H_2O(\text{leaf}) - H_2O\ (\text{out})}{E_i} \qquad (VII)$$

H_2O(leaf) is the water vapour density at the leaf surface (30.38) based on temperature of the leaf (30^oC). The temperature was converted into water vapour density by use of Smithsonian Meteorological Chart, as has already been explained. "H_2O (out)" is the same as in (II) and E_i is a value derived from (II) thus:

$$E_i = \frac{E}{10^2 \times 360} = \text{Transpiration, } \mu\text{mol } H_2O\ cm^{-2}s^{-1} \qquad (VIII)$$

2.2.2.(F). Resistance to CO_2 transfer:

Calculations for resistances to CO_2 transfer was based on the equation given below:

$$\gamma CO_2\ (\text{sec cm}^{-1}) = \frac{CO_2\ (\text{air}) - \Gamma)}{P_i} \qquad (XI)$$

CO_2(air) is the CO_2 concentration of the ambient air (mg CO_2 cm^{-3}). Computation of this value is given by the equation:

$(1.977 \times 10^{-3}$ mg $l^{-1}) \times (CO_2$(out) ppm) $\times 10^{-3}$ s $cm^{-1})$.

CO_2 (out) is the CO_2 concentration (ppm) in the air leaving chamber.

Γ is the carbon dioxide compensation point (assumed to be zero for C_4 plants - Heath, 1969).

P_i is the conversion of P_n into µmol $CO_2/cm^2/sec$ thus:

$$P_i = \left(\frac{P_n}{10^2 \times 360}\right) \qquad \text{(XII)}$$

2.2.2.(G). Chlorophyll

The chlorophyll content of the leaves was assessed by the method of Arnon (1949) as modified by Witham, Blaydes and Devlin (1971) to give values in milligrams of chlorophyll per gram of plant tissue. The analysis is based on light absorption properties of the major chlorophyll at λ 645 nm and 633 nm.

The material was ground in 5 ml of 80% acetone. The resulting slurry was filtered through one layer of Whatman No. 1 filter paper by use of vacuum pump (electrical). The mortar and pestle were rinsed three times with 2 ml of extract for each sample. The final volume of filtrate was made to 20 ml.

The optical density of the filtrate was determined (absorbance) at λ645 and 663 nm in a spectrophotometer (Pye Unican SP 500, series 2) after blank calibration (extractant absorbance = 0). The calibration was made before each reading.

The equations given below were used to convert absorbance reading to chlorophyll content.

$$\text{Mg chlorophyll a/g tissue} = \frac{(12.7\ (D_{663}) - 2.69\ (D_{645}) \times v}{1000 \times W} \qquad \text{(XIII)}$$

$$\text{Mg chlorophyll b/g tissue} = \frac{(22.9\ (D_{645}) - 4.68\ (D_{663}) \times v}{1000 \times W} \qquad \text{(XIV)}$$

$$\text{Mg total chlorophyll/g tissue} = \frac{20.2\ (D_{645}) - 8.02\ (D_{663}) \times v}{1000 \times W} \qquad \text{(XV)}$$

D. stands for optical density (absorbance) at the given wavelength (either 645 or 663 nm). v is the volume of extract and W is the fresh weight, in grams, of the tissue from which the extract was made.

2.2.2.(H) Water potentials

Water in soils and plants is under some tension due to reduced chemical energy (Slavik, 1974, Akunda, 1980). This reduction in the chemical energy of the water is a sum total of solute concentration and capillary attraction. Water potential of a system is an intergrated value which takes into account all those factors which reduce the chemical activity of water in the system and has been found to be the most relevant parameter in

the study of water status - physiological activities in plants (Akunda, 1980). I assessed both the leaf and soil water potential. In the former both thermocouple psychrometer and pressure chamber methods were employed, and in the latter only the psychrometers were used. Measurements were carried not more than 24 hours after irrigation. Analysis samples comprised discs punched out of the leaves or small sample of undisturbed soil from at least two centimeters below the soil surface.

Psychrometer measurements

This study was based on the guidelines of Ludlow (1982). Wescor psychrometer chambers (C-52) were used and the potential output (μv) and temperature was read off a WESCOR dewpoint microvoltmeter (HR - 33T). The output was standardized at 25°C using the equation of Savage, Cass and Jager (1981), as given below:

$$V_{25} = \frac{V_{t_1}}{0.325 + (0.027 \times t_1)} \qquad \text{(XVI)}$$

V_{25} is the standardized voltage output at 25°C,

V_{t1} is voltage output at t_1 (temperature of experiment as read from the microvoltmeter).

The water potential was calculated as the product of the corrected voltage (V_{25}) and the reciprocal of the psychrometer constant of the particular chamber used in each case,

i.e. $V_{25} \times 1/_{C}$). (XVII)

The Psychrometer constants were calibrated by use of dilute sorbitol solutions of known osmotic potential (-MPa). The osmotic potential was calculated from known molal concentrations by use of Van't Hoff equation:

$$\psi_{\pi} = \frac{-MiRT}{10} = \quad \text{(XVIII)}$$

where ψ_{π} is the osmotic potential in Megapascals, M is the molal concentration, i is the dissociation constant, R the gas constant and T the absolute temperature (^{O}K)

The Psychrometer constants were calculated thus:

$$C = \frac{V_{25} \times 1}{\psi_{\pi} \text{ (i.e. MiRT)}} \quad \text{(XIX)}$$

The constants were very close to those supplied by the manufacturers.

Samples were left to equilibrate for at least 15 minutes and this was carried out in eight replicates.*

Pressure Chamber

The pressure chamber works on the principle that a pressure applied on a plant twig or leaf to force a water bubble to appear on the cut end is equal to (but opposite in sign) to the water potential of the plant material (Scholander, et al., 1965; Sutcliffe, 1977).

* Vapour pressure equilibration depends partly on the size of the psychrometer chambers. 15 minutes have been found to be enough for the chambers used in this experiment.

A pressure chamber was used and pressure was supplied in form of cylinder nitrogen.

The sample leaves were sealed in the chamber with the cut end protruding. Pressure was increased slowly till a droplet of water was observed to form on the midrib at the cut end. This (with a negative sign) was adopted as the leaf water potential. This was replicated eight times.

2.2.2.(I) Leaf diffusive resistances

To supplement the diffusive resistance measurements mentioned in section 2.2.2. which were carried in the laboratory, I measured the leaf diffusive resistance (to water vapour) in the green house using a LI-COR autoporometer (LI-65) fitted with a Li-sensor cup. The assessment was replicated eight times per treatment.

The sensor cup was calibrated using a calibration plate and distilled water by the method outlined in the Li-COR autoporometer manual.*

2.2.2.(J) Days to 50% heading:

Cumulative counts of emerged heads were recorded for the plants grown in small pots, every pot being represented. The count was made on daily basis till there were no more heads emerging. The counts were converted to percent of the final count. The percent values were plotted against the day (from sowing) and cumulative heading curves were constructed. The curves were used to obtain the time to 50% heading.

2.2.2.(K). Height, nodes and green leaves at heading

Salt treatment is known to reduce the final height of plants (Lubach and Bondman 1980); and increase leaf senescence. The reduction in height may result from impaired cell division and organ differentiation or from cell expansion or both. Node formation depends on the process of differentiation. Hence when this is compared with height a measure of impaired cell elongation may be glimpsed.

The height (in centimeters) of the main tiller (from soil level to tip of the head) was measured by use of a metre ruler and recorded. The number of nodes and green leaves on the same tiller were also recorded. The number of green leaves was taken as a measure of senescence. The data were analysed for statistical differences. This was replicated eight times, using plants from different buckets.

2.2.(L) Tiller production and productive tillering

Optimum tillering is a property very much sought in crops growing under stress condition (Arnon 1972). However, tillers can only contribute to productivity if they are able to head and form grain (productive tillers). Tillers which do not produce grain are just a waste of precious energy under stress conditions.

Tiller counts and productive tillering were recorded from same plants as in (2.9). Only basal tillers were recorded, also those with heads were recorded (number) for that particular plant.

2.2.2.(M). Head density and 1000 grain weight

The ready heads were individually picked before they were dead dry. This was done to avoid extensive bird damage and shattering at harvest. Thirty heads per variety per treatment were randomly selected and tagged.

The heads were put into paper bags according to variety and treatment and the bags were labelled. The heads were dried in an oven at $50^{o}C$ for six days.

The labelled heads were carefully weighed and then threshed on a sieve and the clean grain was weighed. The weight ratio of clean grain to that of whole head (given as a percentage) formed the head density (Sing and Chandra, 1979).

Then all the heads were threshed and the grain was cleaned. The grain was pooled on basis of variety and treatment. Sub-samples of the pooled grain, composed of 50 grains per sub-samples, were drawn and their weight determined. This was repeated twenty times per pool. The weight per each subsample was standardized for 1000 grains and then subjected to statistical analysis.

2.3. Protein content

The protein concentration of the grain, upper - middle - and lower leaves, the stem and the root samples was assessed by the Lowry method (Coombs, 1982).

The protein in plants is made up of two components, the soluble component which is usually found in the cytoplasm and the bound component which may be found in combination with the membrane systems (Lundborg, 1979; Ellis, Blair and Hartley 1973). Therefore the extraction of both components from tissue material without too much of other substances, which might interfere with the colorimetric determination is not easy. Such contaminating substances would include chlorophylls which are really difficult to separate from proteins by centrifugation (Lundborg, 1979).

In the Laboratory all the samples, except the grain, were ground in a mill to increase the surface-to-volume ratio, thus making more efficient the extraction.

Weighed samples (50 mg) were put in glass vials. 4 millilitres of absolute acetone were added per vial and the vials were closed. The samples were left in the acetone for 48 hours. This was done for purpose of extracting the chlorophyll from the leaves and stem. Grain and root samples were similarly treated for the sake of standardization of conditions.

At the end of the 48 hours the acetone was decanted off and discarded. Then to each vial was added 4 mls of IN NaOH

and the samples were allowed to rest for 24 hours at room temperature. The IN NaOH solution is a good solvent for proteins, especially when the protein is not easily soluble, such as when it has to be extracted from plant tissues (Lowry, Rosebrough, Farr and Randall, 1951).

At the end of the 24 hours the solution was decanted into 10 ml test tubes. The residues were washed with 0.5 ml of distilled water. The washing was added to the sample solution which was then made up to 5 ml (in a graduated cylinder) by addition of distilled water. A 0.5 ml subsample of the final solution was used in determining protein concentration.

The quantification of sample optical densities was carried out by calibration curve prepared from the optical densities of standard bovine serum albumin concentrations. The BSA concentrations ranged between 50 and 800 µg ml^{-1} of protein.

The optical densities of the samples and standards, after appropriate blank setting, were determined at λ 750 nm in a Unicanm spectrophotometer (SP 500 series 2). Final data was given in mg protein/gram.

2.4. Statistical methods

In the analysis of data a complete randomisation was assumed. The uniformity of the values in any one given instance was tested by the F-max. method of Parker (1977):

The F-max was computed thus:

$$\frac{\text{Highest variance in a set of data}}{\text{Lowest variance in same set}}$$

The values were compared with the tabulated critical F-max values for the given degrees of freedom.

All percentage values were given angular transformation before being analysed.

The statistical tests of the data were by ANALYSIS OF VARIANCE using a computer program. (ANOVAR)*.

Since the experiments sometimes involved two-variables and sometimes three (or even four) the analysis was always geared to meet these conditions.

That is, when the data to be analysed involved the treatment and varieties only, two-factor ANOVA with replicates was used. However, when a third factor such as solutions (salt or sorbitol), time, or tissues had to be incorporated, three-factor ANOVA without replicates was used.

Least significant difference values were computed to quantify any significant differences that could be detected during the analysis.

*ANOVAR: a computer programme
written by Long, S.P. for the UNEP Bioproductivity
programme. I.R.L. Press, Oxford.

CHAPTER THREE

3.0 RESULTS

3.1 Germination

3.1.1. Germination rates

The germination rates were determined from the cumulative germination curves in figure 2. The rates were determined on basis of the time taken to attain a mean of 50% germination in each treatment.

Salt stress delayed germination, thus increasing the time to 50% germination. Both varieties were affected and the delay was in proportion to the salinity of the treatment solution.

In Enakuru the 50% germination was attained after 72, 84, 90 and 144 hours for control, 4, 8 and 12 mmho cm^{-1} (Ec) salinity respectively. This made the delay due to the salinity to range between twelve and seventy-two hours considering the 4 and 12 mmho cm^{-1} (Ec) salinity respectively.

The Ek-1 seeds attained 50% germination in 66, 72, 84 and 108 hours for control, 4, 8, and 12 mmho cm^{-1} (Ec) salinity respectively. The delay ranged between six and fourty-two hours considering the 4, and 12 mmho cm^{-1} (Ec) salinity.

Treatment brought about less delay in the germination of Ek-1 than in Enakuru. At all salinity levels, control included, Ek-1 had higher germination rates than Enakuru.

Figure 2. Cumulative germination percentage of finger millet seeds under salt stress.

(a) Enakuru .(b) Ek-1.

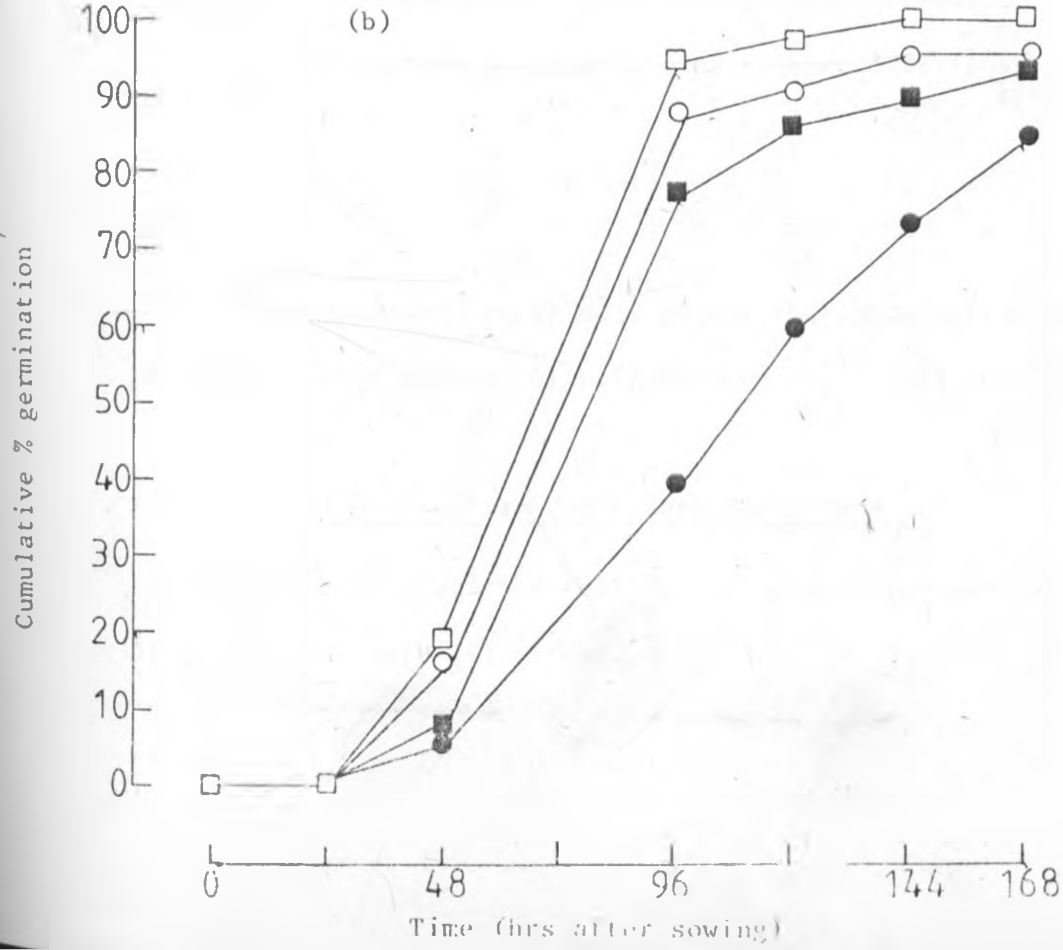
LEGEND:

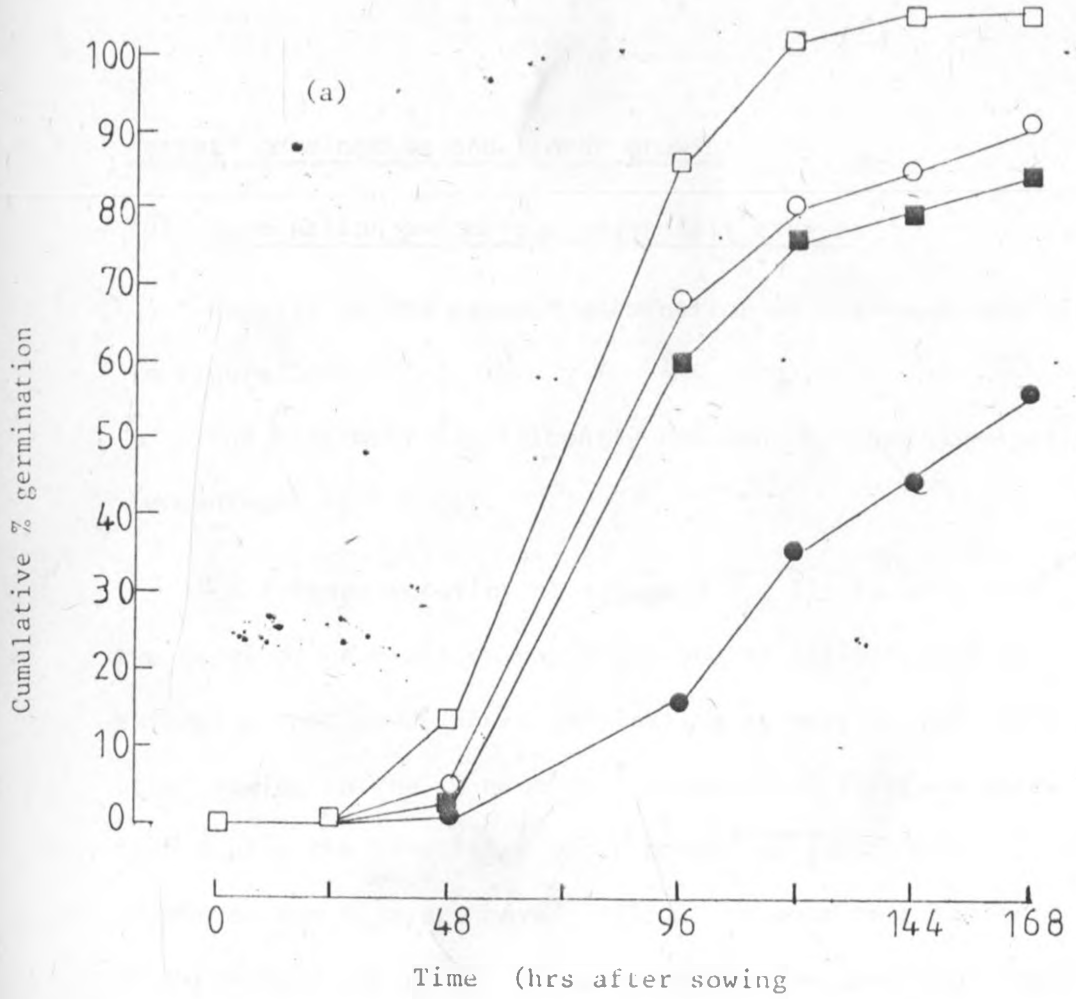
Control

4 mmho cm^{-1} (Ec) salinity

8 mmho cm^{-1} (Ec) salinity

12 mmho cm^{-1} (Ec) salinity


(b)
100
90
80
70
60
50
40
30
20
10
0
Cumulative % germination
0
48
96
144
168
Time (hrs after sowing)


(a)
Cumulative % germination
100
90
80
70
60
50
40
30
20
10
0
0
48
96
144
168
Time (hrs after sowing

3.1.2. Percent germination and linear growth:

(a) Germination percentage under salt stress:

Results of the percent germination of the seeds are given in Figure 3(a).

The treatment significantly reduced the seed germination percentages ($P < 0.01$).

A further scrutiny of figure 2 (pg 52) reveals that the delay of germination substrate due to salinity was so extensive that seeds where germinating as many as 168 hours after sowing in the 12 mmho cm^{-1} treatment. This was more than double the time taken under normal curcumstances (Ayyangar and Vijayaraghavan, 1926). However termination of experiment was a must because some of the seedlings had started dying, most probably from waterlogging and fungal contamination. Therefore the per cent germination values may not be the maximum attainable under those conditions.

Inter-treatment comparisons showed that germination was not affected by the lowest salinity (4 mmho cm^{-1}, (Ec) ($P < 0.05$).

(b) Percent germination under sorbitol stress

Figure 3(b) gives the results for germination percentage of seeds under sorbitol stress.

For the purpose of comparing the solute and stress level effect the data was analysed by analysis of variance; three factors without replication. The data for the control did not form part of this particular analysis.

The osmotic stress reduced the seed germination percentage ($P < 0.05$) and each of the lowest stress levels had a distinctly different degree of effect compared with the others.

The germination percentage of Ek-I was not affected much by the sorbitol stress. The seedlings in the 0.18 MPa germination medium attained 96 percent germination, while 98% germination was attained under 0.54 MPa osmotic stress by the same variety.

On the other hand the percent germination in Enakuru was severely reduced by the higher stresses: The variety attained 95% and 73% germination under 0 and 0.54 MPa, osmotic stress due to sorbitol, respectively.

These results call to mind that the same trend had been recorded for salt-stressed seeds.

Neither of the solutes (salt or sorbitol) had greater effect on germination than the other nor was either of the varieties more susceptible to either of the solutes.*

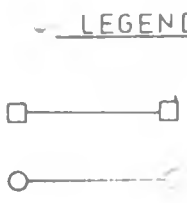
(c) Seedling dry weight:

The results of the seven day old seedling dry weight are given in figure 3b(i) and b(ii)

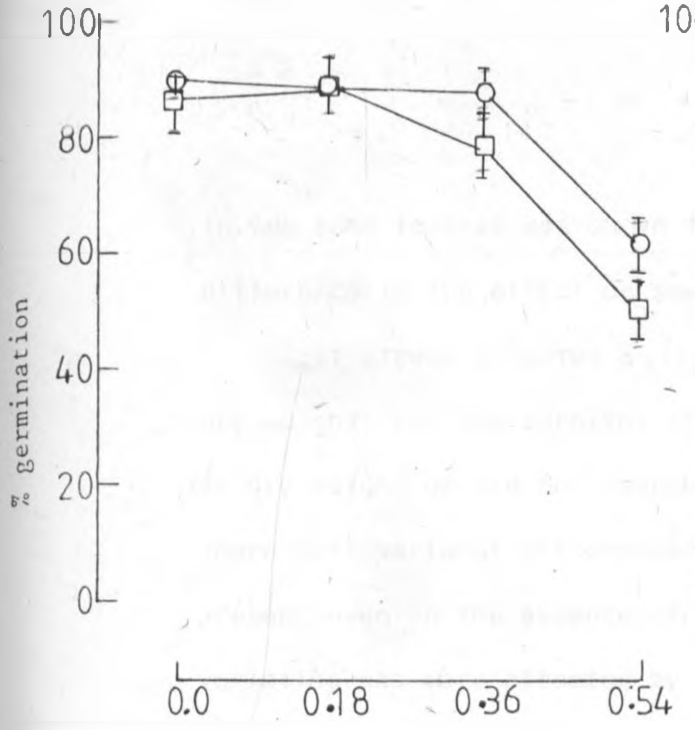
*Refer next page: 54A

(I) Figure 5a(i) and 5 a(Iiii). The two figures visually indicate that the salt effect on the seed germination percentage was much higher than the sorbitol. This apparent (common sense) difference attributable solely to the 12 mmho cm^{-1} salinity. On the other hand the varietal difference in the response to the stress appears greater in the two highest sorbitol concentrations than any of the salt concentrations. However this subjective observation had to be subjected to objective statistical tests. Thus it was demonstrated that the standard deviation of the mean became larger with higher solute concentration in the substrate(the error bars in Fig. 3) a(i) and a(ii). Secondly the graphical differences could not be found to be of statistical significance ($P < 0.05$). There was no other way of quantifying the differences except by statistical tests and the results of the tests form the basis of the argument put forward in the discussion on the germination performance of the two varieties of finger millet under either of the solute stress.

Figure 3. The effect of (i) salt and (ii) sorbitol stress (equiosomotic concentration) on (a) germination % and (b) seedling dry weight.

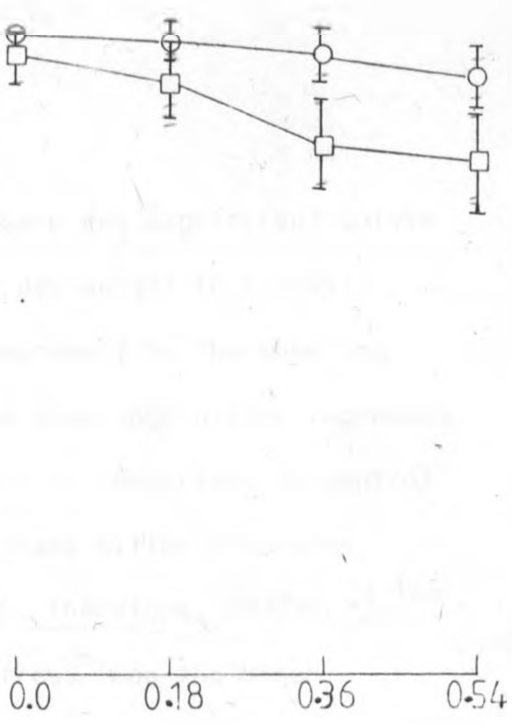


Statistics	Figure (a)	Figure (b)
Treats (Tr).....	31.8*	679**
Variety (VA).....	36.8*	88.9*
Solute (So)	11.5 ns	4206*
Tr x VA	3.2 ns	158.9*
Tr x So	15.8 ns.	446.7*
VA x So	7.7 ns.	40.3*
LSD(Tr)	1.66	0.32
LSD (VA)	5.84	0.264
LSD (So)	-	0.264
	0.2 ≤ SE ≤ 1.0	0.7 ≤ SE ≤ 3.8



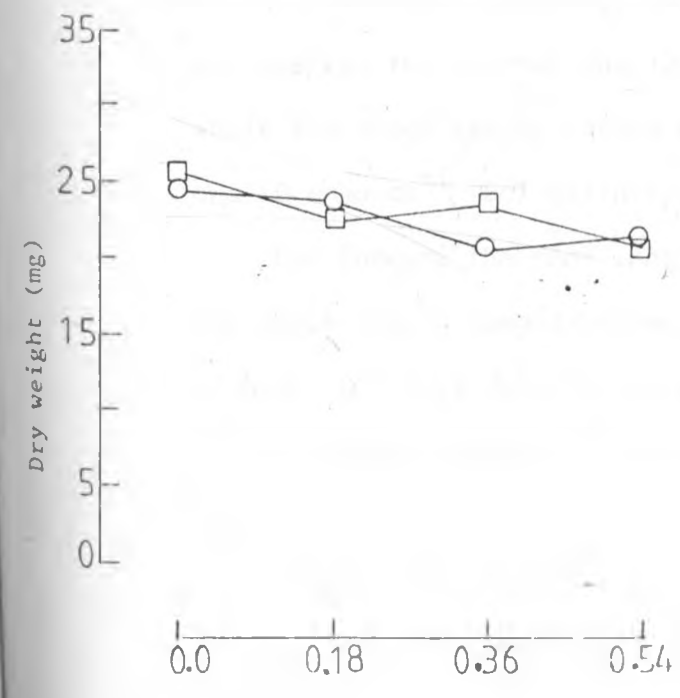
Osmotic potential (- MPa)

a(i)



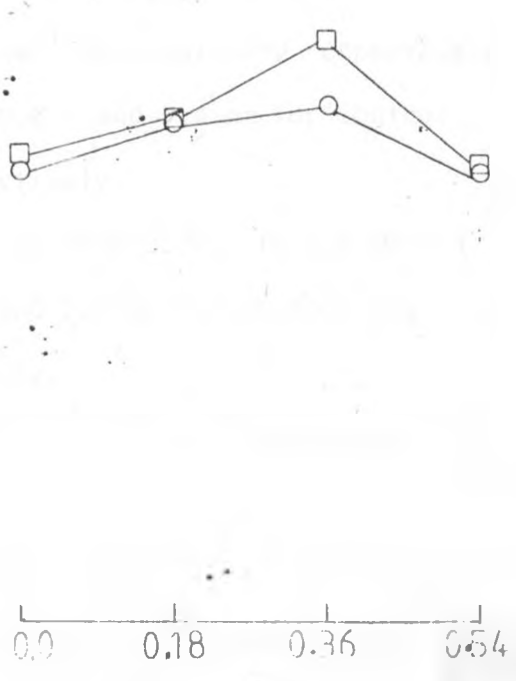
osmotic potential(-MPa)

a(ii)



osmotic potential (-MPa)

b(i)



osmotic potential (-MPa)

b(ii)

In the same test it was shown that there was significant solute difference in the effect on seedling dry weight ($P < 0.05$).

Salt stress effected a slight decrement on the seedling dry weight; but the sorbitol stressed seedlings either increased in dry weight or did not change at all in comparison to control. There were varietal differences but these differences were present even in the absence of stress. Therefore, neither of the varieties was more affected by the stress than the other.

(d) The seedling linear growth under salt stress:

The root and shoot lengths of seven day old salt-stressed seedlings are given in figure 4(a) and (b). salt stress effectively reduced the seedling linear growth ($P < 0.5$). There were significant inter-varietal differences in both the root and shoot length, with Ek-1 having higher values ($P < 0.05$). The shoot growth was significantly reduced only by the highest salinity $P < 0.05$).

For the Ek-1 seedlings the mean root length was 30 and 10.3 millimetres for control and 12 mmho cm^{-1} (Ec) salinity respectively while the shoot length ranged between 8.1 and 5.4 mm for control and 12 mmho cm^{-1} (Ec) salinity respectively.

For Enakuru the root length ranged from 23.2 to 5.2 mm and the shoot length ranged between 7.3 and 2.8 mm for control and 12 mmho cm^{-1} (Ec) salinity respectively.

The lowest salinity (4 mmho cm^{-1} (Ec) did not have effect on seedling linear growth.

The two varieties had significantly different linear measurements ($P < 0.05$). Ek-1 attained higher growth measurements than Enakuru.

Figure 4.

The linear growth of (a) root and (b) shoot of finger millet seedlings under the stress of equiosmotic concentrations of (i) salt and (ii) sorbitol.

LEGEND

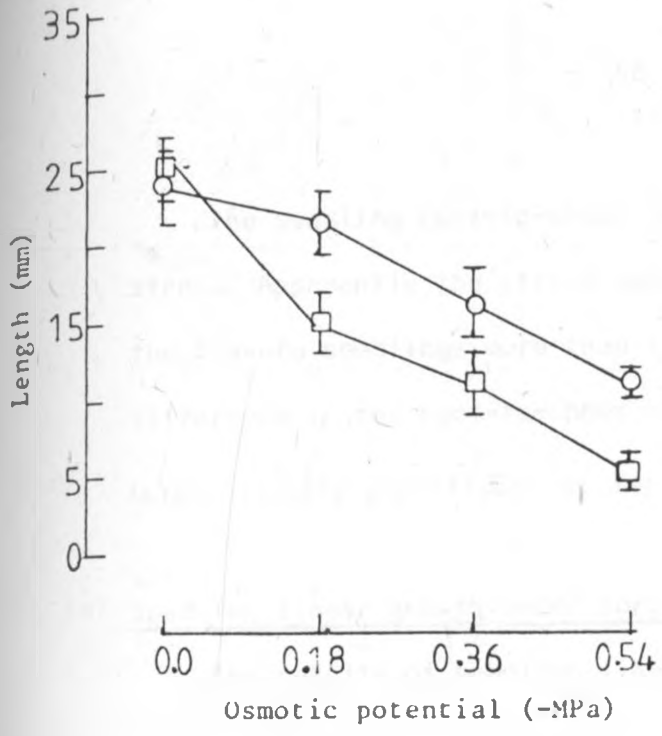
□——□ Enakuru

○——○ Ek-1

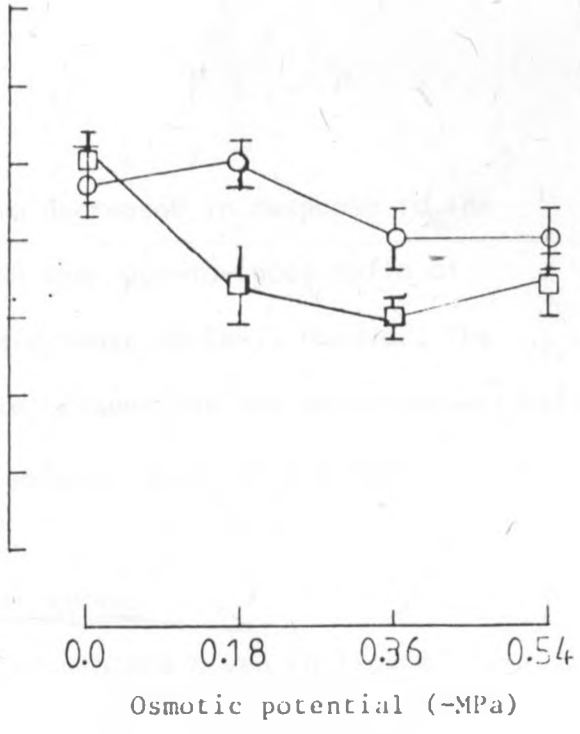
Statistics (ANOVA)

	Figure (a)	Figure (b)
Treatment (Tr)	29.5*	24.6*
Variety (Va)	8.6 n.s.	2.7 n.s.
Solute (So)	0.7 n.s.	0.2 n.s.
Tr x Va	0.3 n.s.	0.05 n.s
Tr x So	0.1 n.s.	1.4 n.s
Var x So	0.4 n.s.	0.5 n.s
LSD (Tr)	2.59	0.73
LSD (Va)	-	-
LSD (So)	-	-

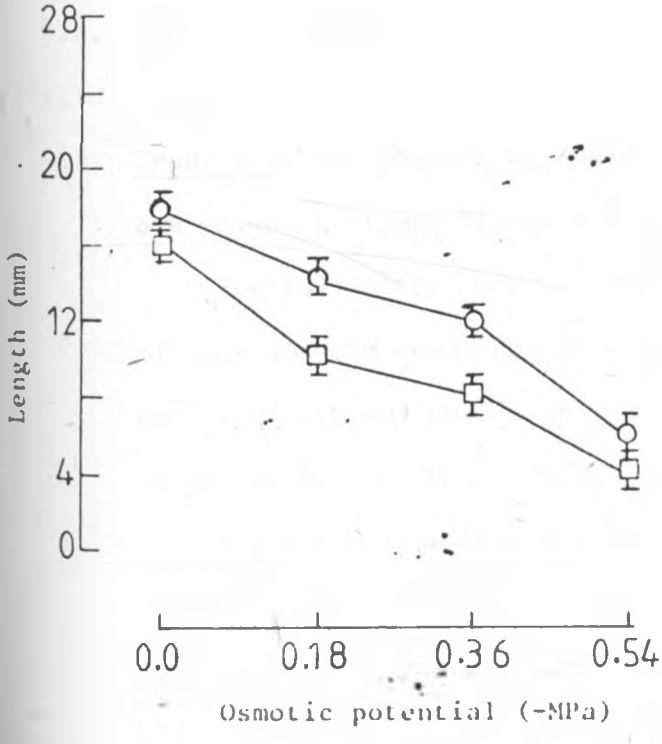
Vertical bar on graph points stand for standard error of the mean.


35
25
15
5
0
Length (mm)
0.0
0.18
0.36
0.54
Osmotic potential (-MPa)

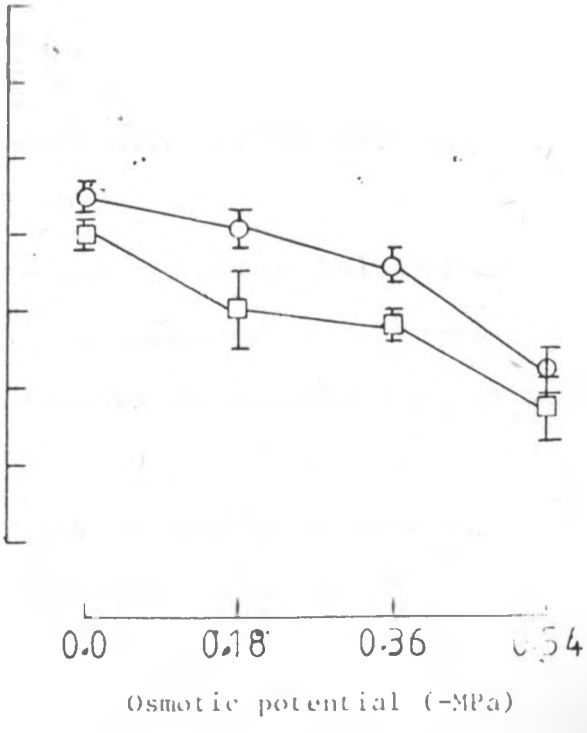
a(i)


0.0
0.18
0.36
0.54
Osmotic potential (-MPa)

a(ii)


28
20
12
4
0
Length (mm)
0.0
0.18
0.36
0.54
Osmotic potential (-MPa)

b(i)


0.0
0.18
0.36
0.54
Osmotic potential (-MPa)

b(ii)

The seedling root-to-shoot ratio decreased in response to the stress. Apparently the stress reduced the root-to-shoot ratio of the Enakuru seedlings more than it did those of Ek-I. However, the difference in the root-to-shoot ratio between the two varieties was not statistically significant at any treatment level ($P < 0.05$).

(e) Seedling linear growth under sorbitol stress:

The results of seedling linear growth are given in figure 4(a) ii and (b) ii.

The linear growth was significantly reduced by the treatment ($P < 0.01$). The lowest osmoticum concentration had no effect on seedling linear growth.

The stress reduced the root length from 23.2 to 15 mm in Enakuru and from 30 to 20 mm in Ek-I at 0 and 0.54 MPa osmotic stress (sorbitol) respectively.

3.2. Ion Concentration:

3.2.1. Sodium

A. Seedlings: The results of sodium concentrations in the seedlings are shown in figure 5(a).I and (a)ii

The salt stress significantly reduced the sodium concentration of 168-hour old seedlings ($P < 0.01$)*. The lowest salinity (4 mmho cm^{-1} (Ec) did not have significant effect on the sodium concentration in the seedlings ($P < 0.05$).

There was significant inter-varietal difference in seedling sodium content ($P < 0.01$). Ek-I had higher sodium concentration than Enakuru at all treatment levels.

*Refer appendix VII.

The treatment-variety interaction was highly significant ($P < 0.01$) with Ek-1 being more affected by treatment than Enakuru. The sodium concentrations ranged between 5.7 and 3.7 meq/100grams in Ek-1, and 4.3 and 3.0 meq/100 grams in Enakuru, for control and 12 mmho cm^{-1} (Ec) salinity respectively.

B. Vegetative tissues

The results are given in figure 5(b)i and ii. The salt stress increased the sodium concentration in the various vegetative tissues of the finger millet ($P < 0.01$). All treatments were mutually different in this effect ($P < 0.05$).

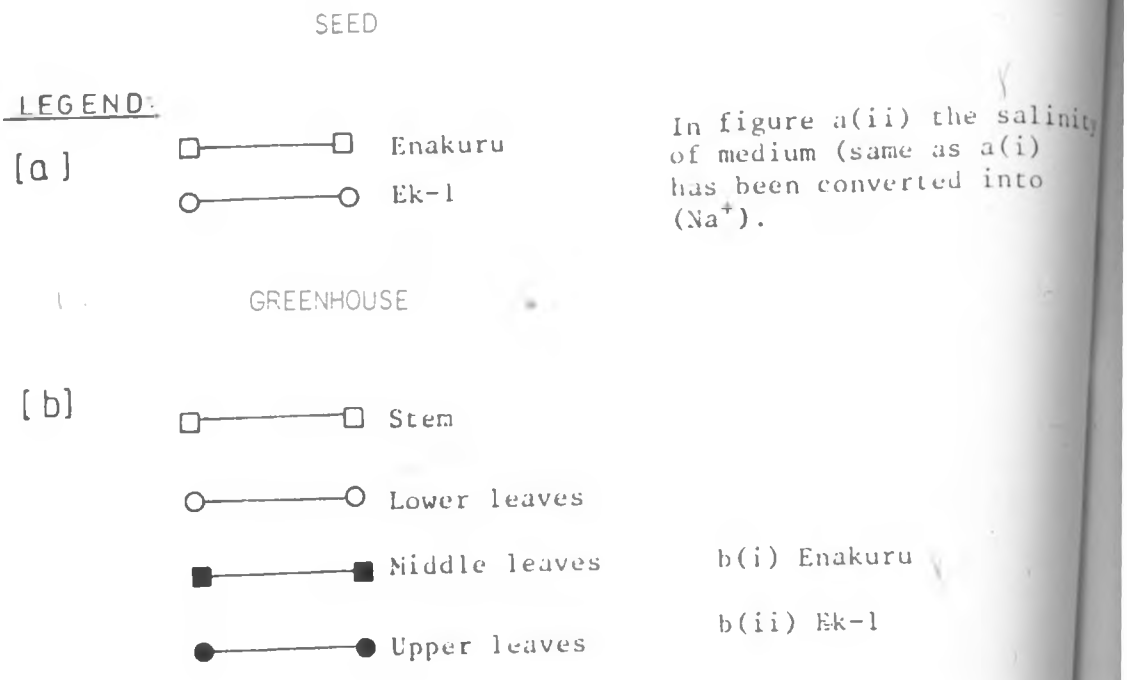
The inter-varietal differences in sodium concentration were not significant ($P < 0.05$), even though the Enakuru was more responsive to treatment than was Ek-1 ($P < 0.05$).

There was significance difference among tissue in their sodium concentration ($P < 0.05$).

The highest combined mean sodium concentration was registered for the lower leaves, and the lowest mean concentration was registered for the upper leaves.

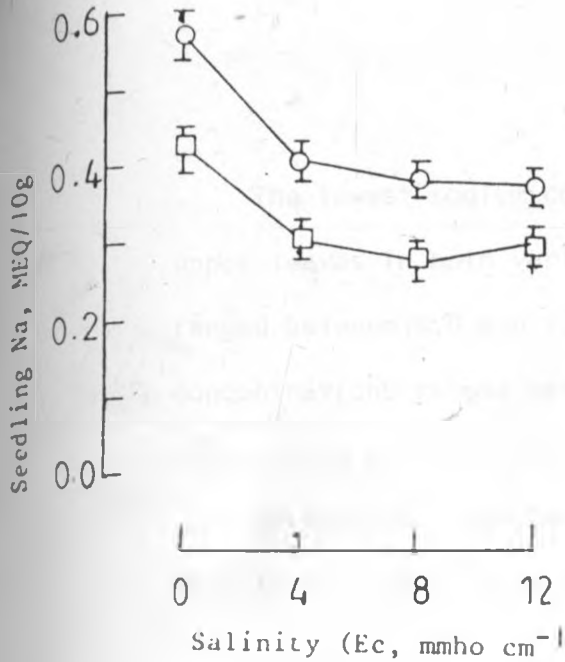
On the basis of individual variety the highest mean sodium content was registered in the stem for Enakuru and the lower leaves for Ek-1. In Enakuru the mean sodium concentrations ranged between 2.7 and 29 meq/10 grams; for control and 12 mmho cm^{-1} (Ec) respectively. In Ek-1 the concentrations ranged between 4 and 29 meq/10 grams for control and 12 mmho cm^{-1} (Ec).

Figure 5: The influence of salinity of the substrate on the sodium ion concentration in (a) the seedlings and (b) greenhouse plant tissues.

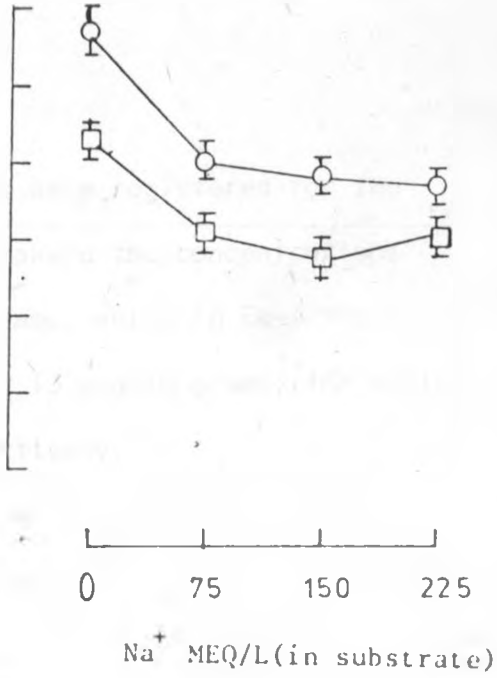


Statistics

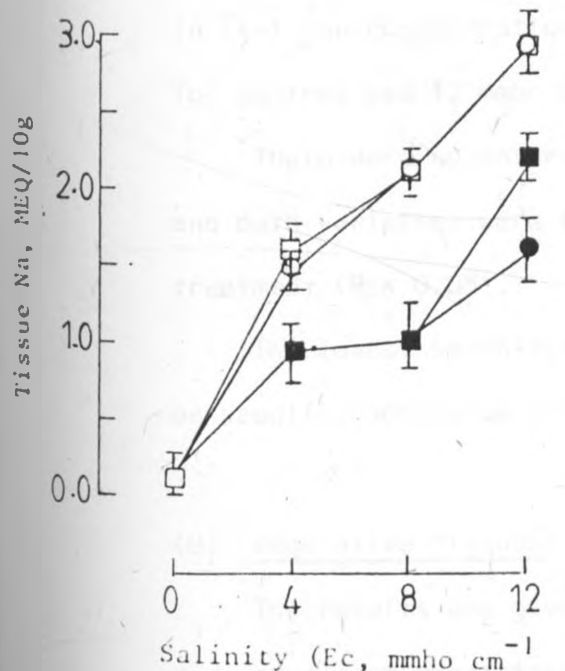
	Figure (a)	(b)
Treatment (Tr)	114*	41.7*
Variety (Va)	98.9*	0.56 n.s.
Tissue (Ti)	-	6.21*
Tr x Va	9.6*	4.78*
Tr x Ti	-	1.3 n.s.
Va x Ti	-	0.4 n.s.
L S D (Tr)	0.165	11.5
L S D (Va)	0.12	-
L S D (Ti)	-	11.5


Seedling Na, MEQ/10g
0.6
0.4
0.2
0.0
0
4
8
12
Salinity (Ec, mmho cm^{-1}

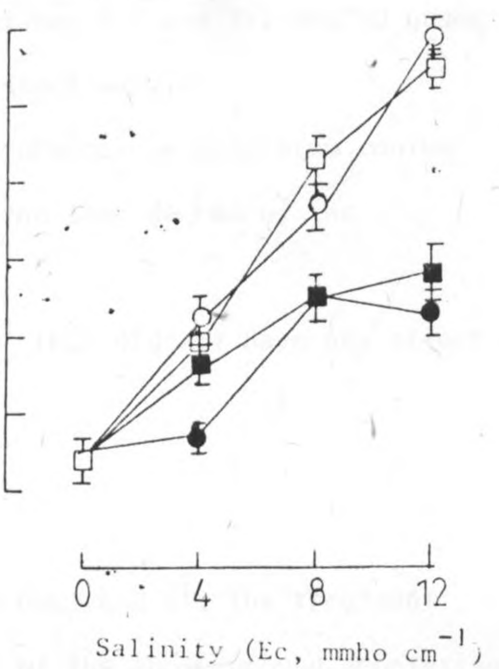
a (i)


0
75
150
225
Na^{+} MEQ/L(in substrate)

a (ii)


Tissue Na, MEQ/10g
3.0
2.0
1.0
0.0
0
4
8
12
Salinity (Ec, mmho cm^{-1}

b (i)


0
4
8
12
Salinity (Ec, mmho cm^{-1})

b (ii)

The lowest sodium concentrations were registered for the upper leaves in both varieties. In Enakuru the concentrations ranged between 4.0 and 17.0 meq/10 grams, while in Ek-1 the concentrations ranged between 3.7 and 13 meq/10 grams; for control and 12 mmho cm^{-1} (Ec) salinity respectively.

Neither the treatment - tissue nor the variety - tissue interactions were significant ($P < 0.05$).

3.2.2. Potassium

(A) Seedlings

The results of seedling potassium concentration are given in figure 6(a).

Treatment induced significant decrement of seedling potassium content ($P < 0.05$).

In Enakuru the potassium concentrations ranged between 4.5 and 3.0 meq/10 grams for control and 12 mmho cm^{-1} (Ec) respectively. In Ek-1 the concentrations ranged between 4.1 and 3.2 meq/10 grams for control and 12 mmho cm^{-1} (Ec) respectively.

There were no intervarietal differences in potassium content and both varieties were affected to the same degree by the treatment ($P < 0.05$).

The lowest salinity (4 mmho cm^{-1} (Ec) did not have any effect on seedling potassium content.

(B) Vegetative tissues:

The results are given in figure 6(b) i and ii. The treatment did not affect the potassium content of the above-ground vegetative tissues of finger millet ($P < 0.05$). There were significant inter-

varietal differences in tissue potassium content ($P < 0.05$) with Ek-I having a higher combined mean content than Enakuru.

The inter-tissue differences in potassium concentration were significant ($P < 0.05$). Middle leaves contained the highest potasium concentration among all the tissues. In Enakuru the potassium concentration for these leaves ranged between 120 and 132 meq/10 grams while in Ek-I the concentration ranged between 120.3 and 129 meq/10 grams for control and 12 mmho cm^{-1} (Ec) salinity respectively.

The lowest potassium content was registered for the lower leaves whose concentrations ranged between 111 and 102 meq/10 grams in Enakuru and 123 and 111 in Ek-I, for control and salt-stress respectively.

The treatment-variety interaction was significant ($P < 0.05$). The effect of treatment on Ek-I potassium concentration was shown as reduction of the latter, while in Enakuru treatment induced a slight increase in tissue potassium content.

In Enakuru, the tissues which apparently registered an increase in the potassium concentration in response to salt-treatment included the upper and middle leaves.

None of the tissues, however seemed to have been preferentially affected by the treatment ($P < 0.05$).

3.2.3. Calcium:

(A). Seedlings

The results are shown in figure 7(a). The treatment decreased

Figure 6: The Potassium concentration in salt stressed (a) seedlings and (b) greenhouse plant tissues for (i) Enakuru and (ii) Ek-1.

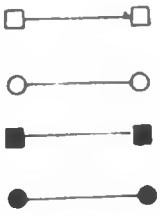
LEGEND:

[a]

Enakuru

Ek-1

[b]



Stem

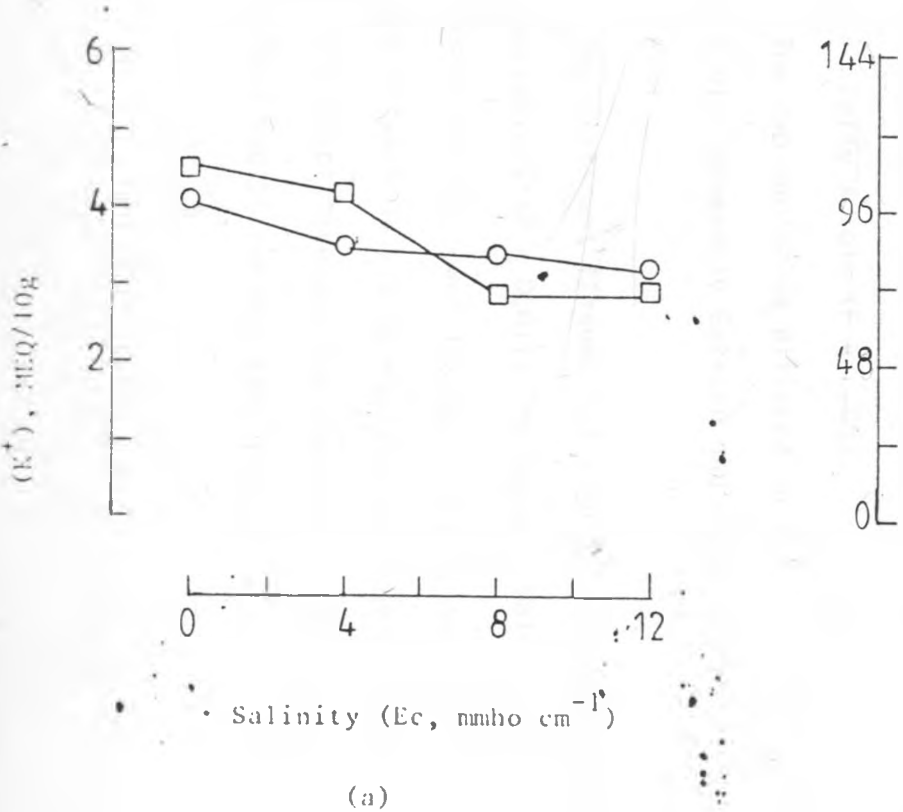
Lower leaves

Middle leaves

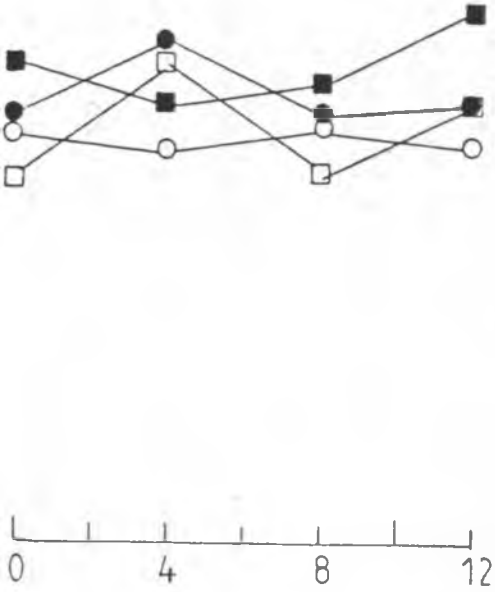
Upper leaves

Statistics:

	Figure (a)	(b)
Treatment (Tr)	3.3*	1.57 n.s
Variety (Va)	0.05 n.s	8.1*
Tissue (Ti)	-	6.5*
Tr x Va	0.6 n.s	.5.1*
Tr x Ti	-	1.8 n.s
Va x Ti	-	2.5 n.s
L S D (Tr	6.39	9.1
L S D (Va)	-	-
L S D (Ti)	-	12.9
S.E	$0.2 \leq SE \leq 0.7$	$2 \leq SE < 4$

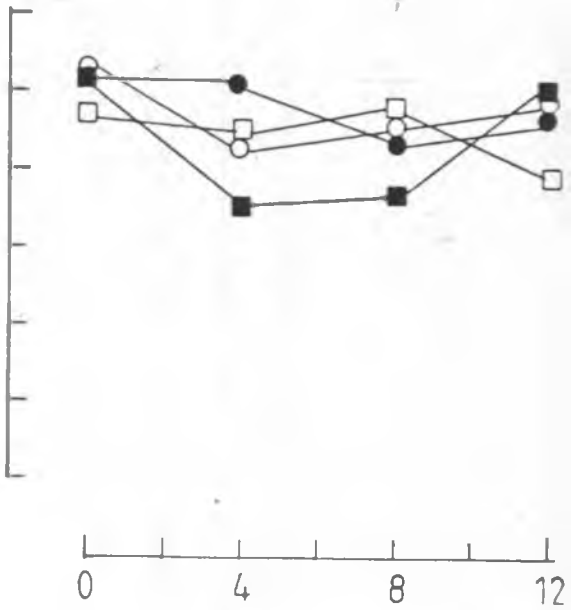


(a)



Salinity (Ec, mmho cm^{-1})

b (i)



Salinity (Ec, mmho cm^{-1})

b(ii)

the seedling calcium concentration ($P < 0.01$). In Ek-I the concentration was decreased from 6.6 to 5.1 meq/10 grams for control and 12 mmho cm^{-1} (Ec) salinity respectively. In Enakuru values ranged from 8.3 to 4.1 meq/10 grams for control and 12 mmho cm^{-1} (Ec) respectively.

There were no varietal differences in calcium concentration. Both varieties were affected in the same way by treatment ($P < 0.0$[illegible].

The 8 and 12 mmho cm^{-1} (Ec) salinities affected the seedling calcium content to the same degree.

(B). Vegetative tissues

The results are given in figure 7(b) I and II.

Treatments induced reductions in the tissue calcium content ($P < 0.05$). The analysis indicated that the reductions, in comparison to control, were significant for only the 4- and 8 mmho cm^{-1} (Ec) salinity levels ($P < 0.05$).

The two varieties differed in their tissue calcium concentration ($P < 0.01$). Generally Enakuru had higher mean calcium content than Ek-I.

The different tissues had significantly different calcium concentrations ($P < 0.01$). The highest calcium concentrations were recorded for the lower leaves. In Ek-I the concentration ranged between 39 and 32 meq/10g for control and the highest salinity respectively. The corresponding values for Enakuru were 39.7 and 31 for the same tissue.

Figure 7: The calcium content of salt stressed (a) seedlings and (b) greenhouse plant tissues of (i) Enakuru and (ii) Ek-1.

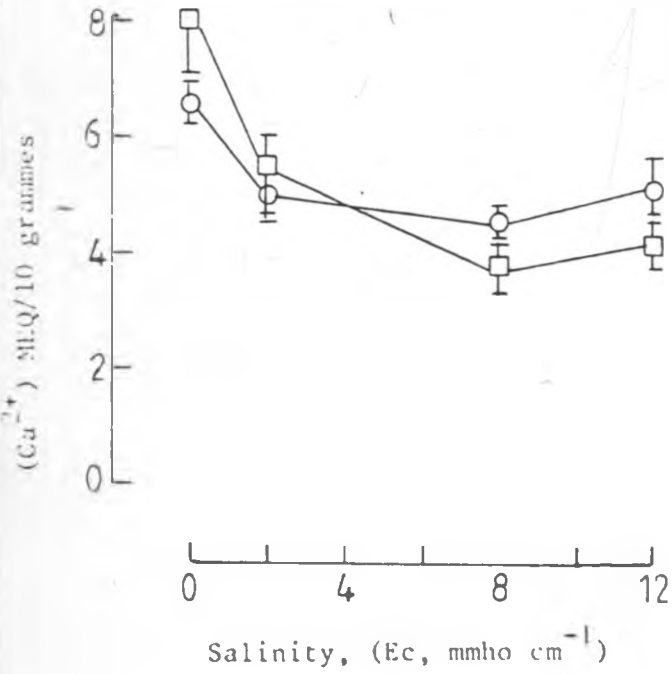
LEGEND:

[a]
- Enakuru
- Ek-1

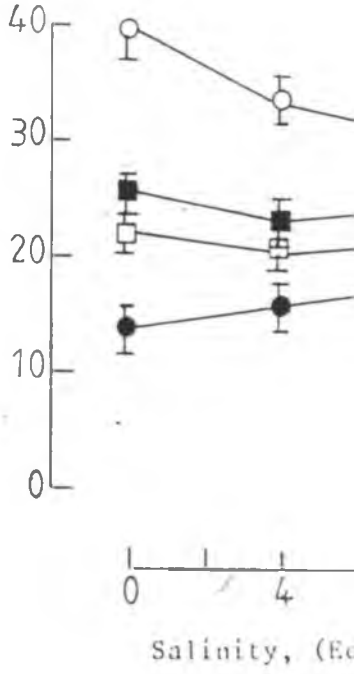
[b]
- Stem
- Lower leaves
- Middle leaves
- Upper leaves

Statistics (ANOVA)

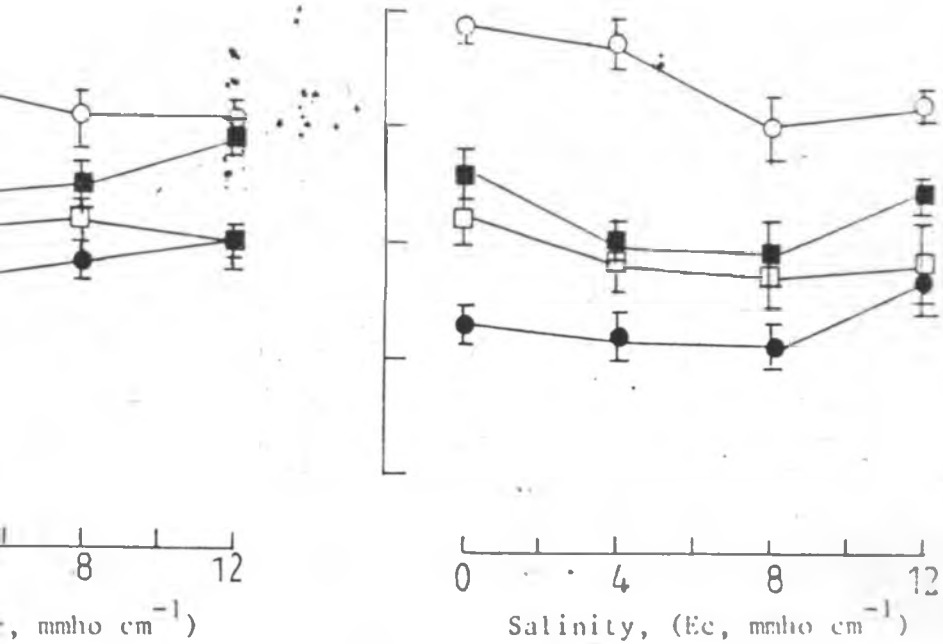
	Figure (a)	(b)
Treatment (Tr)	14.7*	5.4*
Variety (Va)	1.1 n.s	48.8*
Tissue (Ti)	-	191*
Tr x Va	2.2	0.80 n.s
Tr x Ti	-	3.0 n.s
Va x Ti	-	3.4 n.s
L S D (Tr)	0.76	1.31
L S D (Va)	-	0.93
L S D(Ti)	-	0.58


8
6
4
2
0
0
4
8
12
Salinity, (Ec, mmho cm^{-1})
(Ca^{2+}) ME/10 grammes

(a)


40
30
20
10
0
0
4
Salinity, (Ec

b(i)



b(ii)

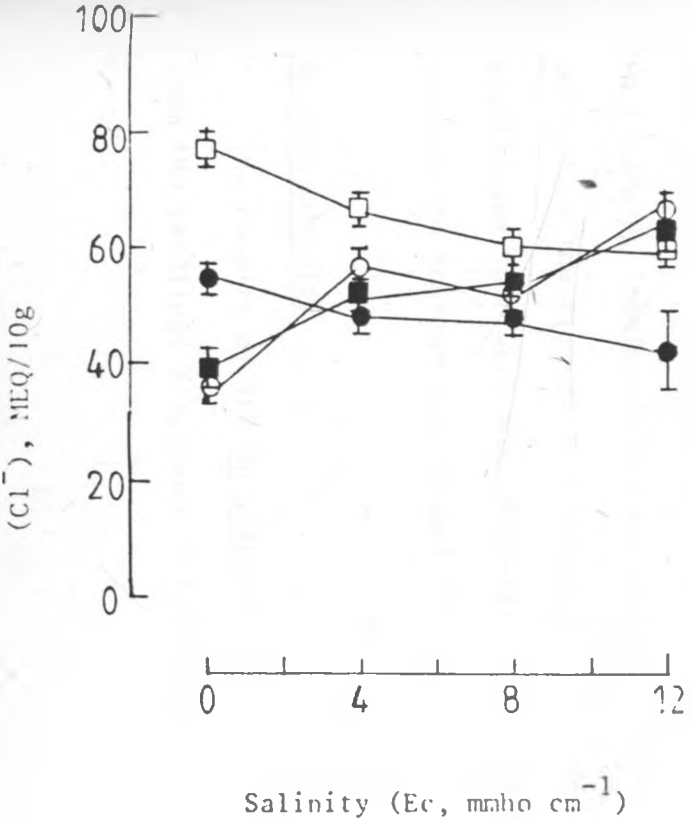
Figure 8: The chloride concentration in salt stressed plant tissues of (a) Enakuru and (b) Ek-1

LEGEND:

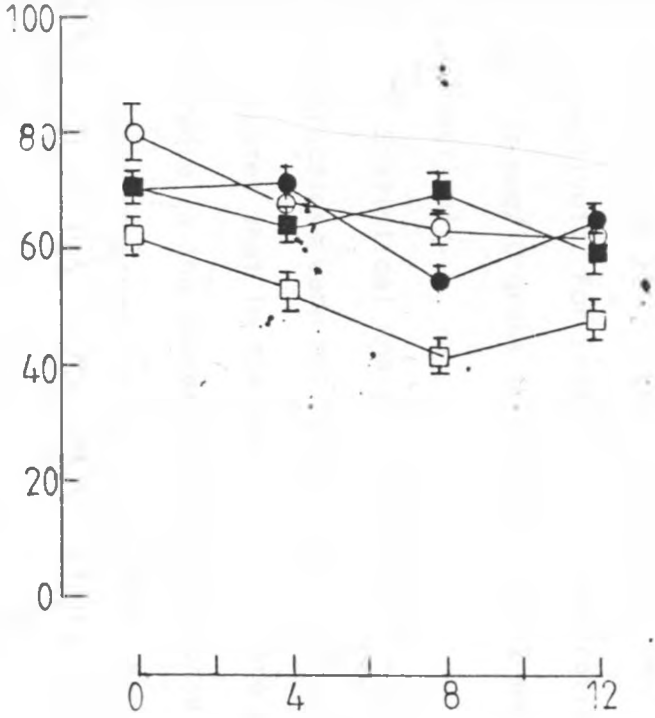
- Stem
- Lower leaves
- Middle leaves
- Upper leaves

Statistics (ANOVA

Treatment (Tr)	1.2 n.s
Variety (Va)	4.3 n.s
Tissue (Ti)	0.2 n.s
Tr x Va	1.8 n.s
Tr x Ti	0.5 n.s
Va x Ti	3.6 n.s



(a)



(b)

The lowest calcium content was encountered in the Upper leaves. The Ek-I values for this "tissue" ranged from 13 to 16 meq/10 grams for control and 12 mmho cm^{-1} (Ec) salt treatment respectively. For Enakuru the concentrations ranged between 14 and 20 meq/10 grams for control and 12 mmho cm^{-1} (Ec) salinity respectively.

Statistical analysis indicates that the treatment-variety interactions were not significant. However, closer examination indicates that in the upper leaves there occurred an apparent increase in the concentration in response to salt treatment. This was observed for both varieties. Another apparent increase was registered in the middle leaves of Enakuru, whose values ranged between 26 and 29 meq/10 grams for control and 12 mmho cm^{-1} (Ec) salinity respectively.

3.2.4. Chloride

The seedling extracts were not analysed for chloride content. The results on the vegetative tissue concentrations are given in figure 8. Treatments did not have any effect on the chloride content of the tissues ($P < 0.05$). None of the interactions were significant; nor were the inter-tissue or inter-varietal differences in chloride content significant ($P < 0.05$).

3.3 Amylase activity

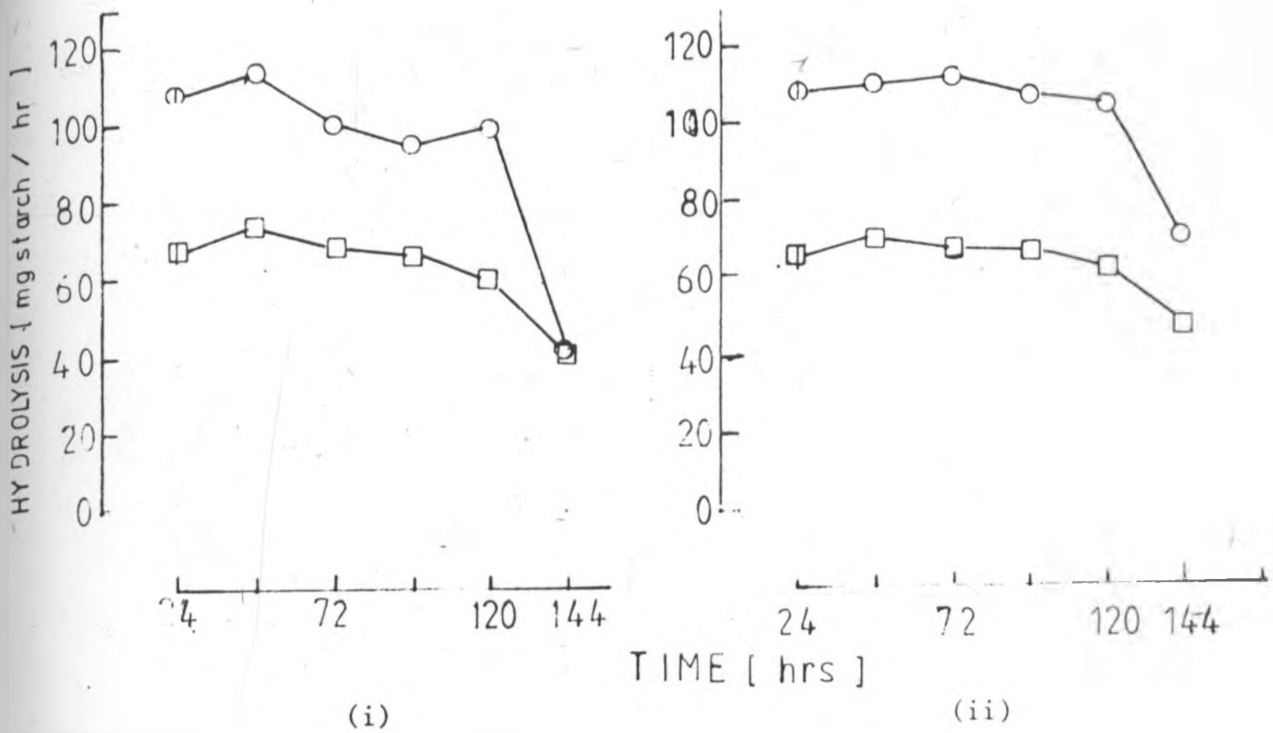
The results of the *in vitro* activity of amylase extract from the seedlings are given in figure 9.

Figure: 9(a): Time series activity of α-amylase in germinating seeds and seedlings. (i) control (ii)-0.18 MPa (salt) (iii)-0.36 MPa (salt) and (iv) -0.54 MPa (salt).

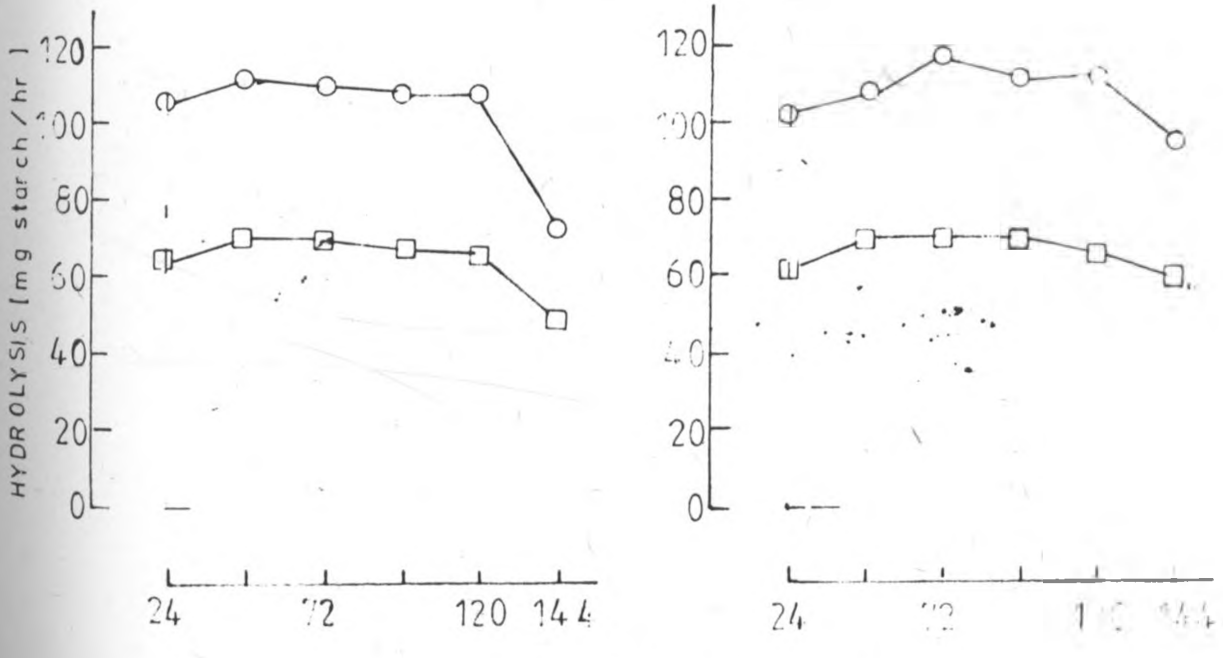
LEGEND:

Enakuru

Ek-1.


HYDROLYSIS [mg starch / hr]
120
100
80
60
40
20
0
24
72
120
144
TIME [hrs]

(i) (ii)


HYDROLYSIS [mg starch / hr]
120
100
80
60
40
20
0
24
72
120
144
TIME [hrs]

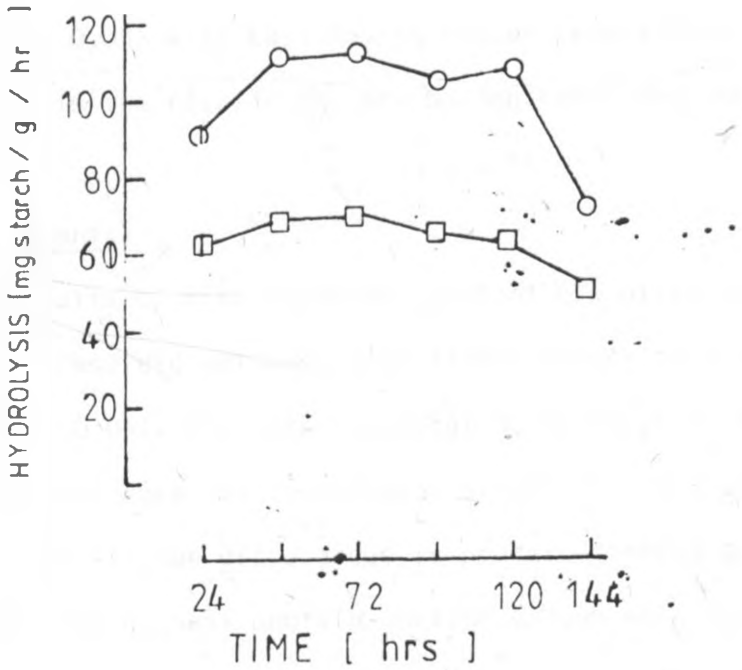
(iii) (iv)

Figure 9(b) : Time series activity of α-amylase in germinating seeds and seedlings: (i)-0.18 MPa (sorbitol) (ii)-0.36 MPa (sorbitol), (iii)-0.54 MPa (sorbitol).

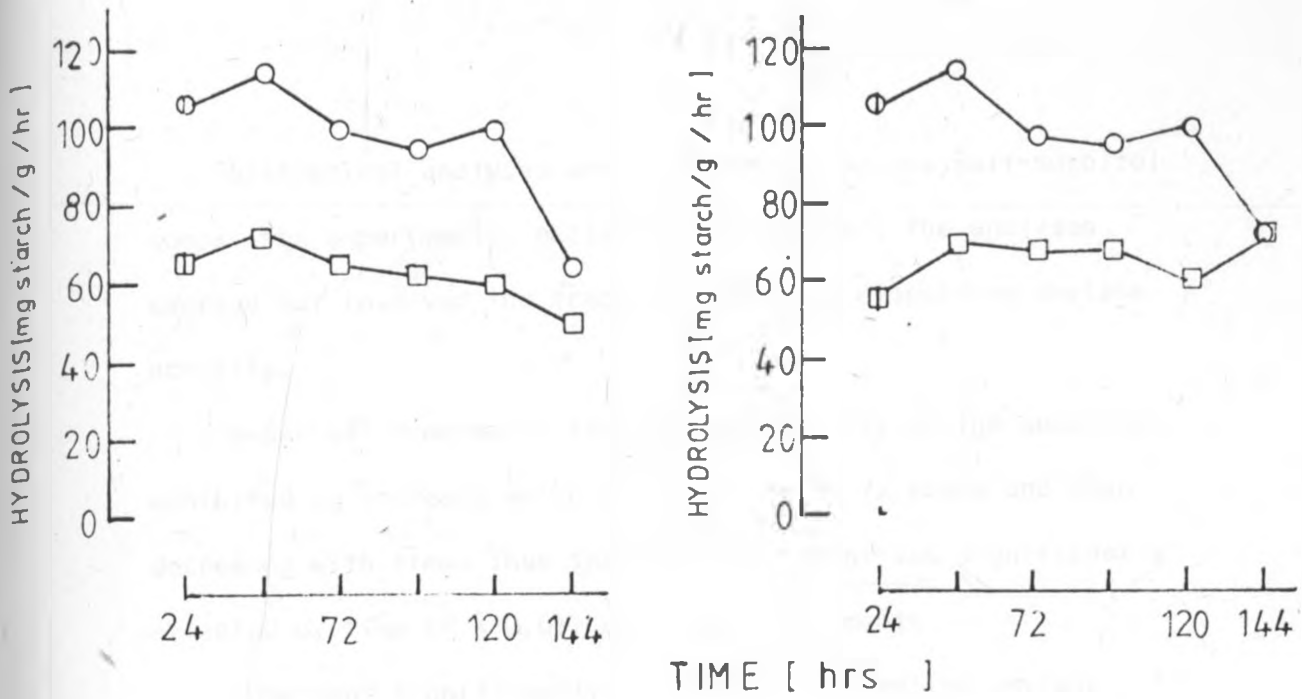
LEGEND

□——□ Enakuru

○——○ Ek-1


HYDROLYSIS [mg starch / g / hr]
120
100
80
60
40
20
24
72
120
144
TIME [hrs]

(iii)


HYDROLYSIS[mg starch / g / hr]
120
100
80
60
40
20
0
24
72
120
144
TIME [hrs]

(i) (ii)

Statistical analyses were carried out on the salt-sorbitol comparison experiments, excluding the control. The analyses carried out involved the treatment and time effects on amylase activity.

Under all treatments the amylase activity of the seedlings exhibited an increase which peaked at 48 to 72 hours and then decreased with time. Thus the amylase content was significantly affected by time ($P < 0.01$) under all treatments.

Treatment significantly increased the seedling amylase content at 24 hours, ($P < 0.05$). However, at 48 to 72 hours treatment significantly lowered the seedling amylase content ($P < 0.05$), but treatment was ineffective in the later periods of time. At 48 and 72 hours salt-treated seedlings had more amylase than "sorbitol seedlings" ($P < 0.05$).

There was significant inter-varietal differences in amylase content ($P < 0.05$) with Ek-I having higher levels than Enakuru. This parallels the results on germination rates and percentages.

3.4. Protein content:

The results of tissue protein content are given in table I.

Salt stress did not have significant effect on tissue protein content ($P < 0.05$). The inter-varietal differences in tissue protein content were not significant either ($P < 0.05$).

The inter-tissue differences in protein content were significant ($P < 0.01$). The highest protein content values were registered for the upper leaves. In Ek-I the mean values ranged between 425 and

Table 1: Effect of salinity on tissues protein content (mg/g) in two varieties of finger millet: (EN-Enakuru; Ek-1).

Tissue	Salinity (mmho cm^{-1}, Ec)							
	0		4		8		12	
	EN	EK	EN	EK	EN	EK	EN	EK
Grain	35 ± 5	73 ± 2	53 ± 10	63 ± 7	42 ± 6	38 ± 6	52 ± 4	48 ± 6
Upper leaves	383 ± 98	426 ± 15	413 ± 29	458 ± 17	483 ± 33	453 ± 9	363 ±10	430 ± 7
Middle leaves	270 ± 30	255 ± 29	270 ± 29	359 ± 46	383 ± 62	355 ± 79	313 ± 50	278 ± 17
Lower leaves	330 ± 58	253 ± 9	277 ± 33	250 ± 23	367 ± 62	308 ± 57	416 ± 33	293 ± 32
Stem	253 ± 14	195 ± 29	360 ± 20	225 ± 14	267 ± 4	280 ± 6	235 ± 25	267 ± 65
Root	265 ± 14	210 ± 11	195 ± 26	290 ± 12	205 ± 20	292 ± 51	207 ±53.6	133 ± 4.4

Treatment (Tr)	1.31 n.s	Tr x Va	0.5 n.s.
Variety (Va)	0.62 n.s.	Tr x Ti	1.0 n.s
Tissue (Ti)	57.8*	Va x Ti	0.8 n.s.
L S D (Ti)	6.92		

450 mg/g, and in Enakuru the values ranged between 385 and 425 mg/g.

The lowest protein content registered for vegetative tissues were for the stem. These, in Ek-I, ranged between 195 and 280 mg/g, and in Enakuru the values ranged between 225 and 255 mg/g.

However, the seed had the lowest protein content of all tissues of the plants, both above and below-ground. In Ek-I the values ranged between 48.5 and 73.5 mg/g and in Enakuru the concentration ranged between 36.5 and 56.5 mg/g.

None of the interactions were significant ($P < 0.05$).

3.5. Chlorophyll

The results of leaf chlorophyll concentration are given in figure 10(a).

The salt stress significantly reduced the leaf chlorophyll concentration ($P < 0.05$). This effect could be attributed to the 8 and 12 mmho cm^{-1} (Ec) salt treatments.

In Ek-I the highest chlorophyll concentration was registered 1.2 mg/g, and for Enakuru the highest chlorophyll concentration was 1.5 mg/g. The lowest chlorophyll concentration registered was that of 0.95 and 0.98 mg/g for Ek-I and Enakuru respectively.

Enakuru had significantly higher mean chlorophyll concentrations than Ek-I ($P < 0.05$).

Both varieties were affected by salt treatment in a parallel fashion ($P < 0.05$).

3.6. Photosynthesis:

The results on rates of photosynthesis in the leaves are given in figure 10(b).

The salt stress significantly reduced the leaf photosynthetic rates at the quantum flux density of 1700 mol $m^{-1}s^{-1}$ and, 30°C.

In Ek-1 these rates ranged between 872.7 and 340.9 µmol CO_2 $dm^{-2}hr^{-1}$ and in Enakuru the values ranged between 1127.3 and 368.2 µmol $CO_2dm^{-2}hr^{-1}$ for control and 12 mmho cm^{-1} (Ec) salinity level respectively. The inter-varietal differences in rates of photosynthesis were not significant ($P < 0.05$) even though Enakuru tended to have apparently higher rates than Ek-1.

The treatment-variety interactions were not significant ($P < 0.05$).

3.7. Carbon dioxide transfer:

The results of resistance to carbon dioxide diffusive transfer in the leaves during photosynthesis are given in figures 10(c) and (d).

Salt stress significantly increased the leaf resistance to carbon dioxide transfer. The effect of 4.0 mmho cm^{-1} (Ec) salinity in comparison to control, was not significant. The effect could be attributed to only the 8 and 12 mmho cm^{-1} (Ec) salt treatment levels ($P < 0.05$).

In Ek-1 the resistance to CO_2 transfer was increased from 6.5 to 15.5 sec cm^{-1} and in Enakuru from 4.2- to 14.3 sec cm^{-1} for control and the highest salinity level (12 mmho cm^{-1}, Ec) respectively.

Figure 10: The effect of salt stress on (a) leaf chlorophyll content (b) net photosynthesis (c) total resistance to CO_2 transfer and (d) the mesophyll resistance to CO_2 transfer in green house grown finger millet.

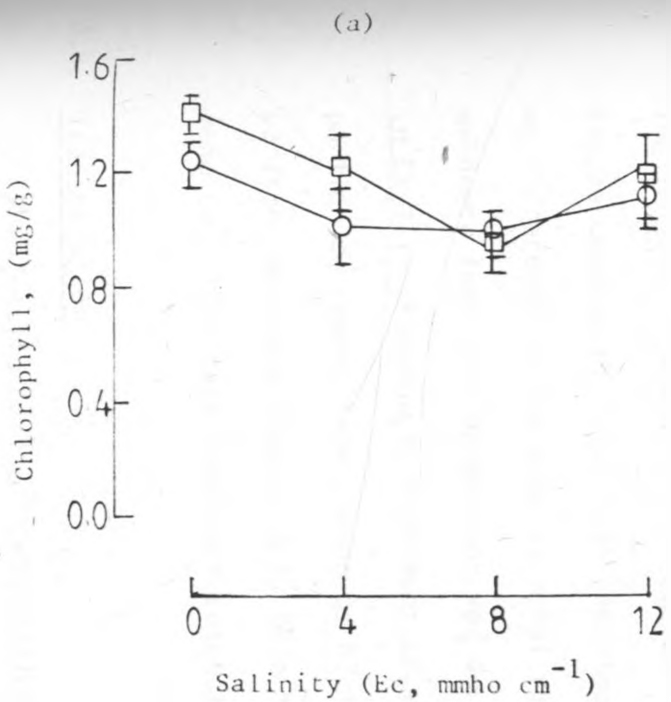
LEGEND

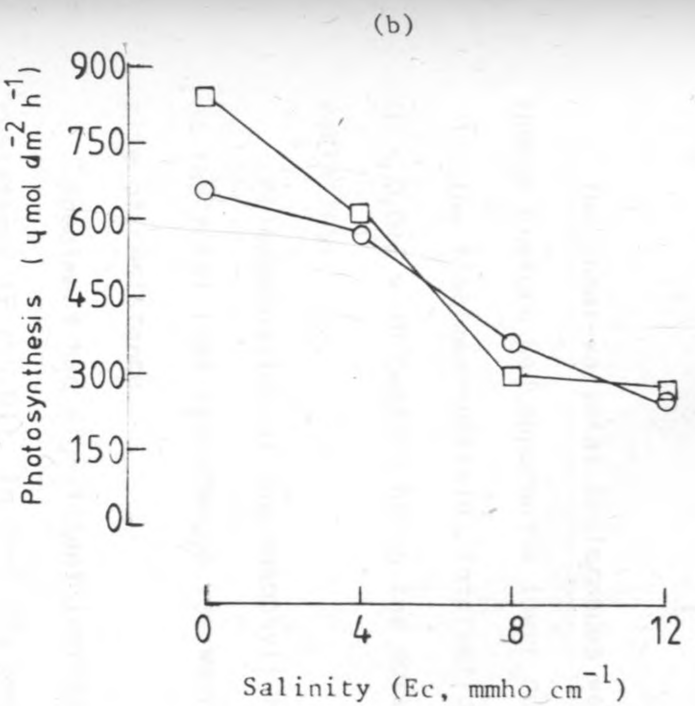
□——□ Enakuru

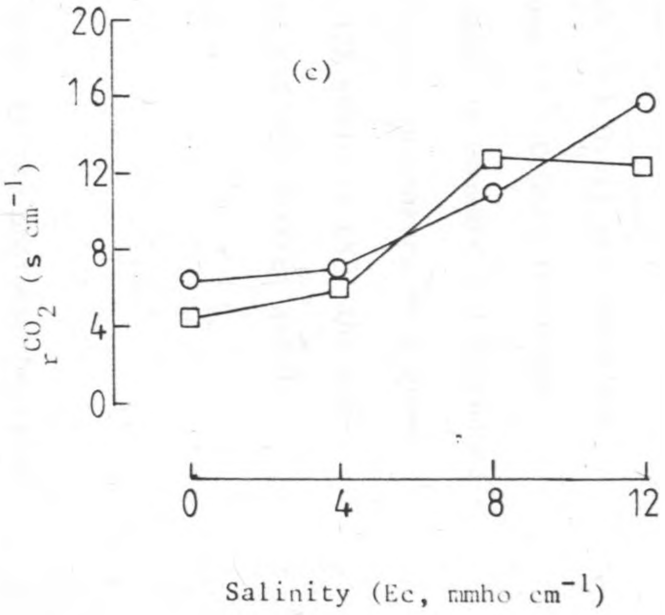
○——○ Ek-1

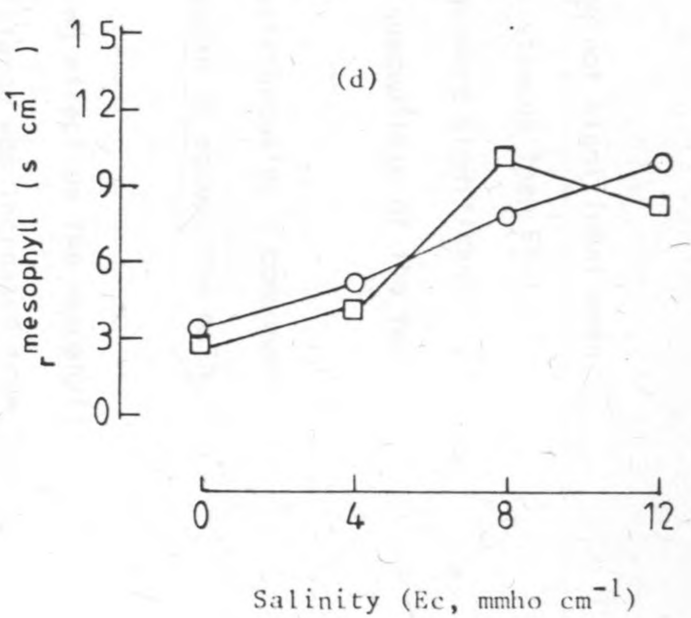
Statistics (ANOVA)

	Figure			
	(a)	(b)	(c)	(d)
Treatment (Tr)	4.7*	35.9*	65*	32.7*
Variety(Va)	6.4*	1.6	0.03 n.s	2.5 n.s
Tr x Va	1.4 n.s	1.9 n.s	5.3*	7.2*
L S D (Tr)	0.16	4.6	1.2	1.03
L S D (Va)	0.1	-	-	-
S E	-	$0.01 \leq SE \leq 0.02$	$0.02 \leq SE \leq 1.4$	


(a)
Chlorophyll, (mg/g)
1.6
1.2
0.8
0.4
0.0
0
4
8
12
Salinity (Ec, mmho cm^{-1})


(b)
Photosynthesis (μmol dm^{-2} h^{-1})
900
750
600
450
300
150
0
0
4
8
12
Salinity (Ec, mmho cm^{-1})


(c)
r_{CO_2} (s cm^{-1})
20
16
12
8
4
0
0
4
8
12
Salinity (Ec, mmho cm^{-1})


(d)
$r_{mesophyll}$ (s cm^{-1})
15
12
9
6
3
0
0
4
8
12
Salinity (Ec, mmho cm^{-1})

The inter-varietal differences were not significant even though Enakuru had apparently lower resistances than EK-1.

The treatment-varietal interactions were significant ($P < 0.01$) with Enakuru being the more susceptible of the two varieties.

An examination of the mesophyll resistances as a component of the total leaf resistances was warranted to assess the main site of resistance.

Treatment had significant increasing effect on the mesophyll resistance ($P < 0.01$). In Ek-1 the resistance was increased from 3.3 to 9.95 s cm^{-1} while in Enakuru the resistance ranged between 2.8 and 6.0 s cm^{-1} for control and 12 mmho cm^{-1} (Ec) salinity (Fig. 9(d).

When the mesophyll resistance was converted into percentage of total resistance another revealing evidence came into light. The treatment increased the combined mean of the mesophyll resistance (as percentage of total leaf resistance) ($P < 0.01$) and there was no difference in the mean varietal values ($P < 0.05$). There was evidence that this proportion was decreased in Enakuru and increased in Ek-1 in response to treatment ($P < 0.05$). In Enakuru this proportion decreased from a mean of 67 to 42%, while in EK-1 the proportion increased from 51.4 to more than 64% for control and 12 mmho cm^{-1} (Ec) salt treatment respectively.

3.8. Transpiration

The results of the transpiration rates in the photosynthesising leaves are given in figure 11(b).

The leaf transpiration rates decreased in proportion to the salinity of the substrate ($P < 0.01$), even though the lowest salinity level (4 mmho cm^{-1}, Ec) did not have a significant effect ($P < 0.05$).

In Ek-I the transpiration rates decreased from about 19.0 to 9.0 mmol H_2O $cm^{-2}hr^{-1}$ and in Enakuru the values ranged between 20.5 and 11.1 mmol H_2O $cm^{-2}hr^{-1}$ for control and 12 mmho cm^{-1} (Ec) salinity respectively.

Inter-varietal differences in transpiration were not significant. The treatment-variety interactions were not significant ($P < 0.05$).

3.9. Water vapour transfer

The results of leaf resistance to water vapour transfer are given in figure II(a)i and II(a)ik. Figure II(a)i is based on diffusive porometer data. Therefore it is only figure II(a)ii which may have direct relationships with transpiration as outlined in section 3.8.

The salt stress induced progressive decrement in leaf water transfer ($P < 0.01$) (i.e. there was progressive increase in the resistance to water vapour transfer in response to treatment). In Ek-I the mean diffusive resistance to water transfer increased from 1.4 to 3.5 s cm^{-1} and in the Enakuru the corresponding values were 1.3 and 5.2 s cm^{-1} for control and 12 mmho cm^{-1} (Ec) salinity respectively.

Figure 11: The effect of salinity on (a)i porometer diffusive resistance measurements, (a)ii leaf resistance to water vapour transfer (IRGA) and (b) the leaf transpiration rates of finger millet under open green house conditions.

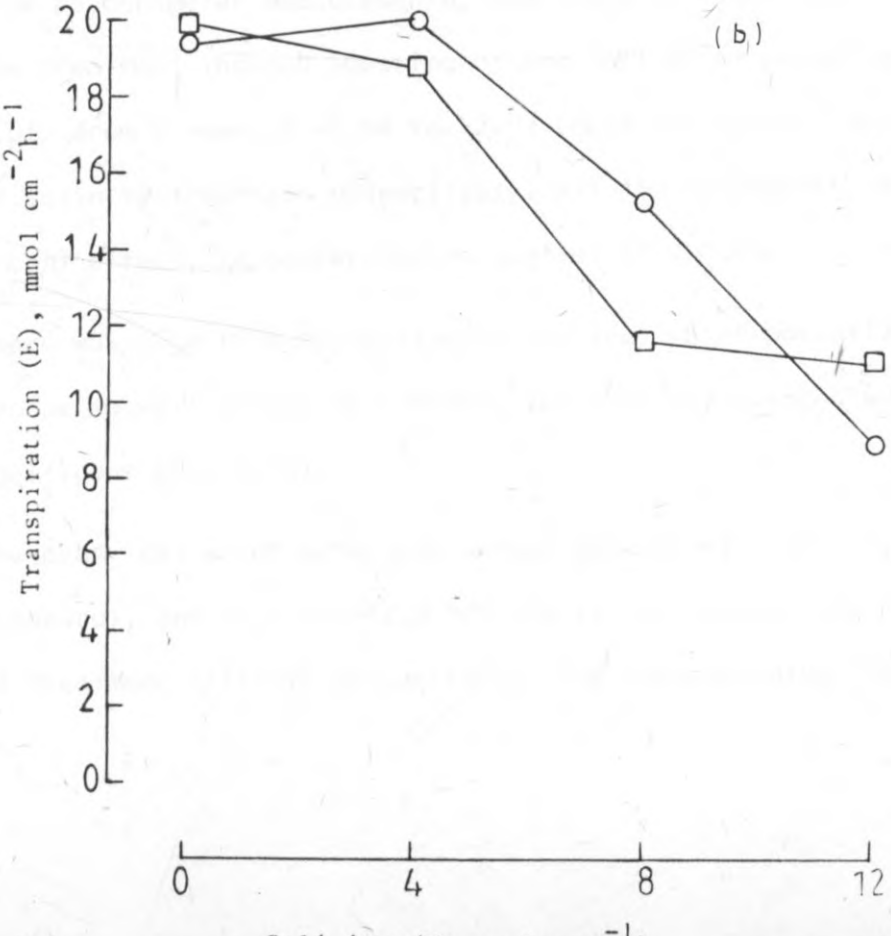
LEGEND:

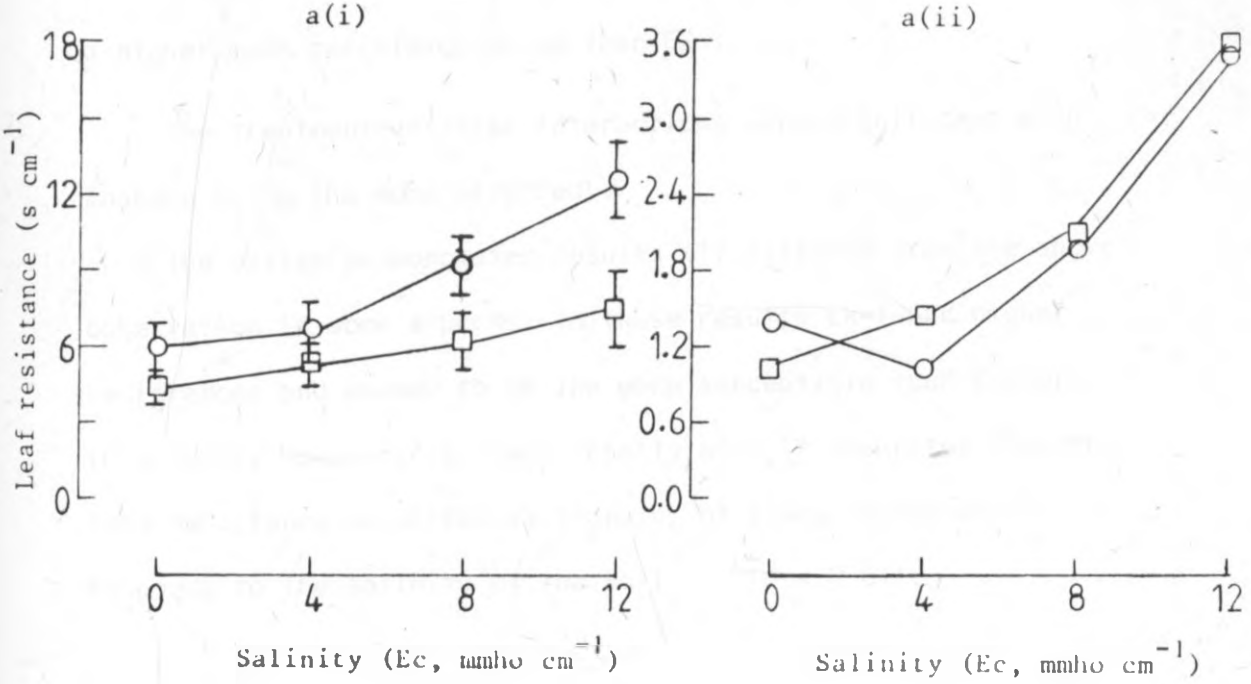
Enakuru

Ek-1

Statistics (ANOVA)

	Figure		
	(a)	(b)	(c)
Treatment (Tr)	31.6*	83.2*	13.0*
Variety (Va)	20.3*	9.1*	0.65 n.s
Tr x Va	3.8*	7.6*	1.36 n.s
L S D (Tr)	0.88	0.33	5.47
L S D (Va)	0.63	0.24	-
SE	-	$0.2 \leq SE \leq 0.4$	$0.03 \leq SE \leq 0.2$


(b)
Transpiration (E), mmol cm^{-2}h^{-1}
20
18
16
14
12
10
8
6
4
2
0
0
4
8
12
Salinity (Ec, mmho cm^{-1})


a(i)
a(ii)
Leaf resistance (s cm^{-1})
18
12
6
0
3.6
3.0
2.4
1.8
1.2
0.6
0.0
0
4
8
12
Salinity (Ec, mmho cm^{-1})
Salinity (Ec, mmho cm^{-1})

The mean varietal differences in diffusive resistances to water vapour transfer were significant ($P < 0.01$) with Enakuru having a higher mean resistance value than Ek-1.

The treatment-varietal interactions were significant with Enakuru being the more affected.

The diffusive porometer results (i) differed from the above observation in some aspects. In these results Ek-1 had higher resistances and seemed to be the more susceptible than Enakuru ($P < 0.05$). However, in these results, also, it was noted that the leaf resistance to diffusive transfer of gases increased in response to the salinity of the soil ($P < 0.01$).

3.10 Leaf and soil water potential:

The results of the soil and leaf water potential, based on data from psychrometer measurements, are given in figure 12.

The treatment induced lowering of the soil water potential ($P < 0.01$) from a mean of -0.64 to -2.57 (MPa) for control and highest salinity treatment respectively. All the treatments had significant effect, in comparison to control ($P < 0.05$).

There was significant lowering of the leaf water potential in response to salt stress ($P < 0.01$). Varietal differences were not significant ($P < 0.05$).

The mean leaf water potential ranged between -2.2 and -2.9 MPa(Enakuru), and -1.7 and -2.8 MPa (Ek-1) for control and the highest treatment salinity respectively. The corresponding results

Figure 12: The effect of irrigating with water of different salinities on (a) leaf water potential (Psychrometry); (b) leaf water potential (Pressure chamber) and (c) soil water potential (Psychrometry).

LEGEND:

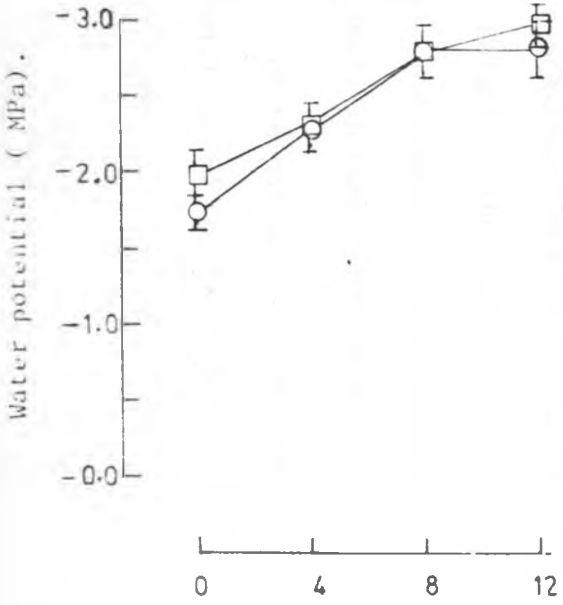
Enakuru (ψ_l)

Ek - 1 (ψ_l)

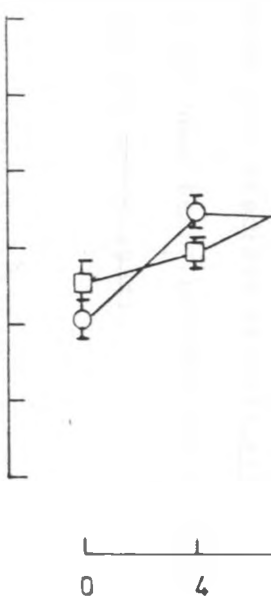
ψ_{soil}

Statistics

	ψ_l		ψ_{soil}
	(a)	(b)	(c)
Treatment (Tr)	13.8*	35*	21.7*
Variety (Va)	1.6 n.s	2.1 n.s	-
T x Va	2.4 n.s	5.9*	-
L S D Tr	1.98	1.2	3.7
L S D Va	-	-	-

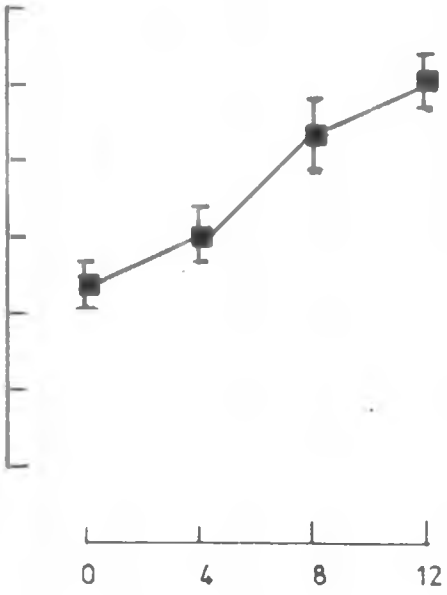

Water potential (MPa).
-3.0
-2.0
-1.0
-0.0
0
4
8
12
Salinity (Ec, mmho cm-1)

(a)


0
4
Salinity (E,

(b)

mmho cm^{-1})



Salinity (Ec, mmho cm^{-1})

(c)

from pressure chamber data were -1.29 and -2.14 MPa and -1.03 and -1.80 MPa respectively.

On the basis of psychrometry data, inter-varietal differences were not significant and this was confirmed by data from the pressure chamber work ($P < 0.05$).

Psychrometer data showed that the two varieties were affected in a parallel fashion but the pressure chamber data indicated that Enakuru was more affected by treatment than Ek-1 ($P < 0.05$).

The two pieces of equipment gave slightly different values because of their distincty different methodology.

The data collected on leaf water potential comprised distinctly low values. The values could not have resulted from error; because the same instrument gave credible results with soil samples. Moreover such low values have been recorded for other cereal crops (Garrity, Sullivan and Watts 1984).

3.11 Height, nodes and leaves:

A. Height

The results are shown in fig. 13(a). There was registered decreasing mean height of the main tiller in response to salt stress ($P< 0.05$). The lowest salinity treatment (4 mmho cm^{-1}, Ec) did not have effect, in comparison to control.

The mean tiller height was reduced from 123 to 106 cm (Enakuru) and 104.7 to 93 cm (Ek-1) for control and the highest salinity respectively.

The inter-varietal differences in height of the main tiller were highly significant ($P < 0.01$) with Enakuru being the taller.

(B) Nodes

The results are given in figure 13(b). Treatment did not affect the mean number of nodes per main tiller ($P < 0.05$).

The inter-varietal differences in number of nodes were not significant nor were the treatment-varietal interactions ($P < 0.05$). Therefore the inter-varietal difference in height was mainly due to differences in internodal lengths.

(C) Green leaves:

The mean number of green leaves per main tiller are given in figure 13(c).

The treatment did not affect the number of green leaves on the main tiller ($P < 0.05$). The mean number was 7.5 and 6.5 for Enakuru and Ek-1 respectively.

The inter-varietal differences in number of green leaves per main tiller was highly significant ($P < 0.01$) with Enakuru having the higher number. The differences, apparently, are attributable to higher leaf senescence rate in Ek-1. However, the two varieties might have been at different physiological ages; because Ek-1 matures earlier than Enakuru.

The treatment-variety interactions were not significant ($P < 0.05$).

Figure 13: The effect of soil salinity on finger millet (a) height (b) nodes per tillers and (c) leaves per tiller at dough stage.

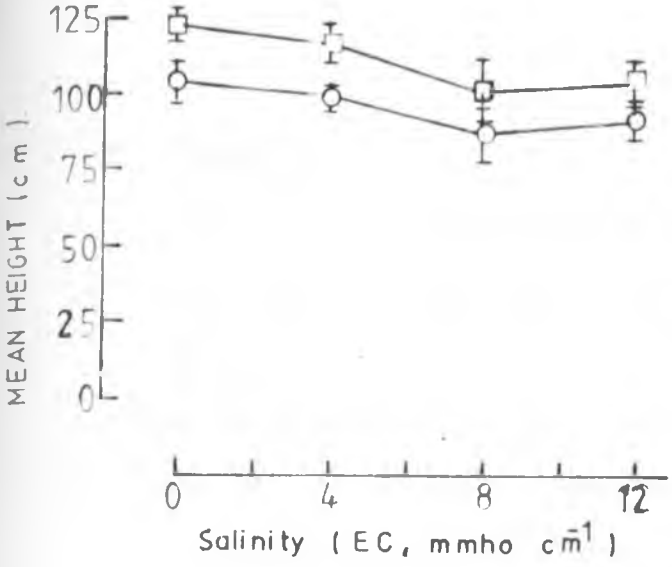
LEGEND:

Enakuru

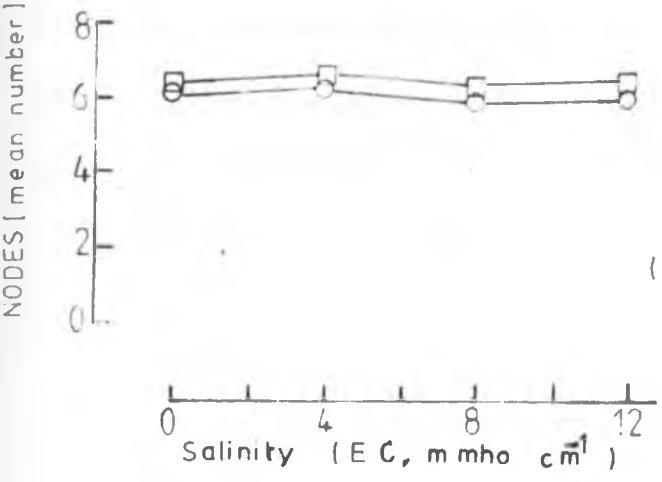
Ek-1

Statistics (ANOVA)

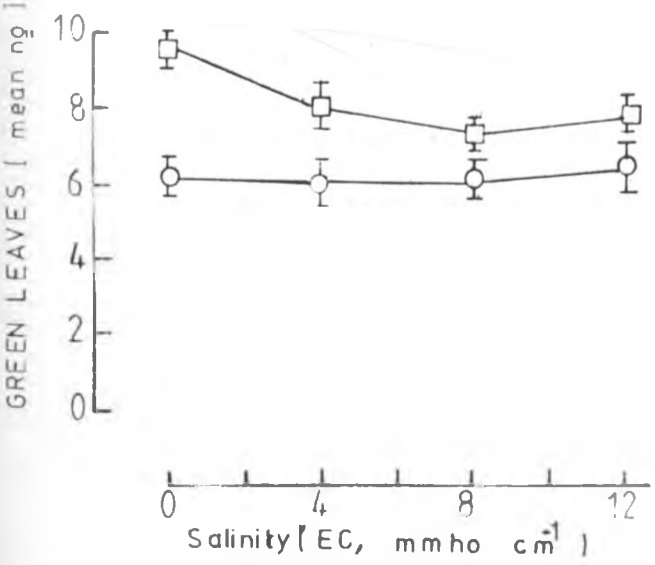
	Figure		
	(a)	(b)	(c)
Treatment (Tr)	9.5*	1.3 n.s	1.94 n.s.
Variety (Va)	24.5*	3.7 n.s	17.3 *
Tr x Va	0.3 n.s	0.15 n.s	1.6 n.s.
L S D (Tr)	5.96	-	
L S D (Va)	4.22	-	0.4
S E	-	$0.2 \leq SE \leq 0.4$	-


MEAN HEIGHT (cm)
125
100
75
50
25
0
0
4
8
12
Salinity (EC, mmho cm⁻¹)

(a)


NODES (mean number)
8
6
4
2
0
0
4
8
12
Salinity (EC, mmho cm⁻¹)

(b)


GREEN LEAVES (mean no.)
10
8
6
4
2
0
0
4
8
12
Salinity (EC, mmho cm⁻¹)

(c)

3.12 Ear emergence

The results are shown in figure 14. Salt treatment delayed emergence (heading) in both varieties.

The controls attained 50% ear emergence in 76 and 84 days. In Ek-1 and Enakuru while the highest salinity increased these to about 84- and 96- days for EK-1 and Enakuru respectively.

Ek-1 had earlier heading dates than Enakuru.

3.13 Tillering and ear production:

The results are shown in figure 15. The treatment had no significant effect on either tiller production or tiller fertility ($P < 0.05$). The varietal differences in either of the parameters were not significant ($P < 0.05$) nor were the treatment-varietal interactions.

The mean tiller number per plant was 2.2 for Enakuru and 1.9 for Ek-1.

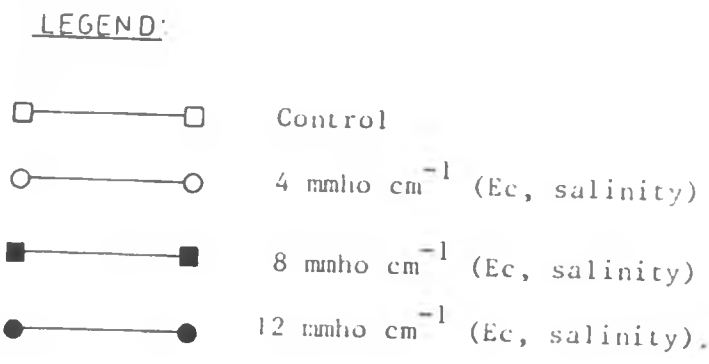
The mean ear number per plant was 1.6 for both Enakuru and Ek-1.

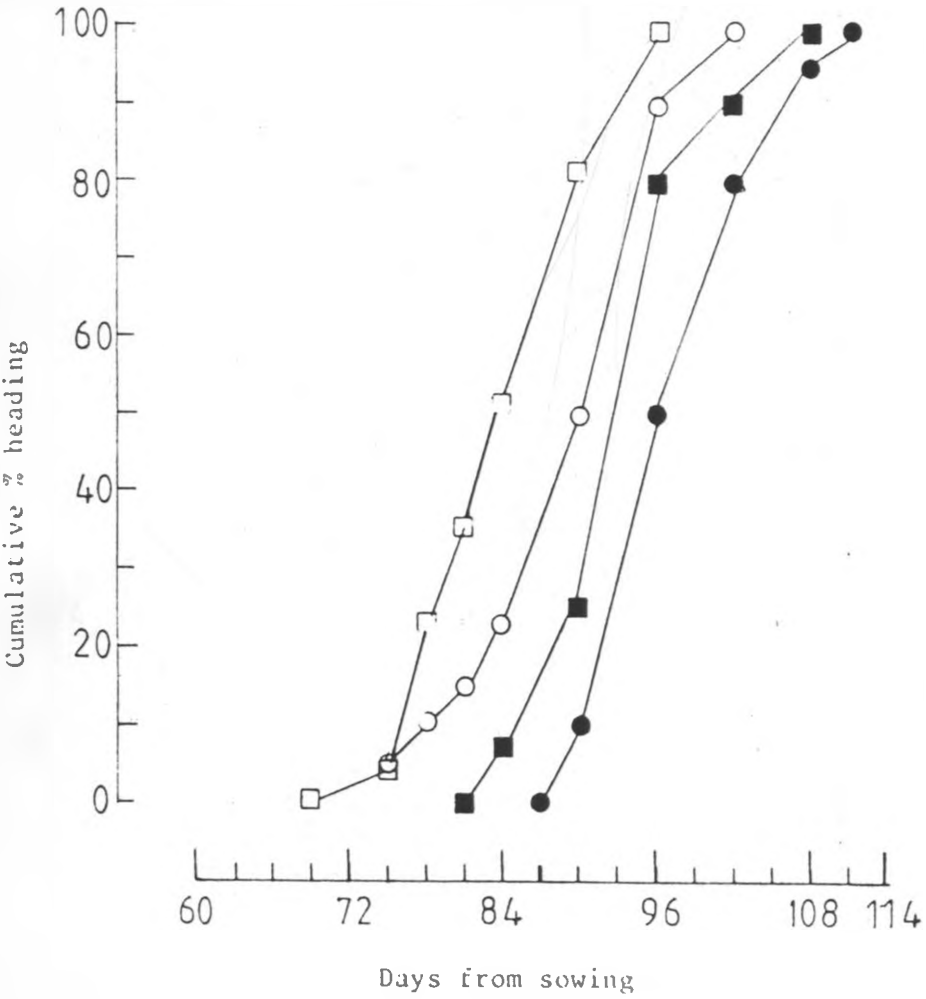
3.14 Yield

The yield results based on the data collected on the head weight, percent head density and 1000 grain weight are shown in figure 16.

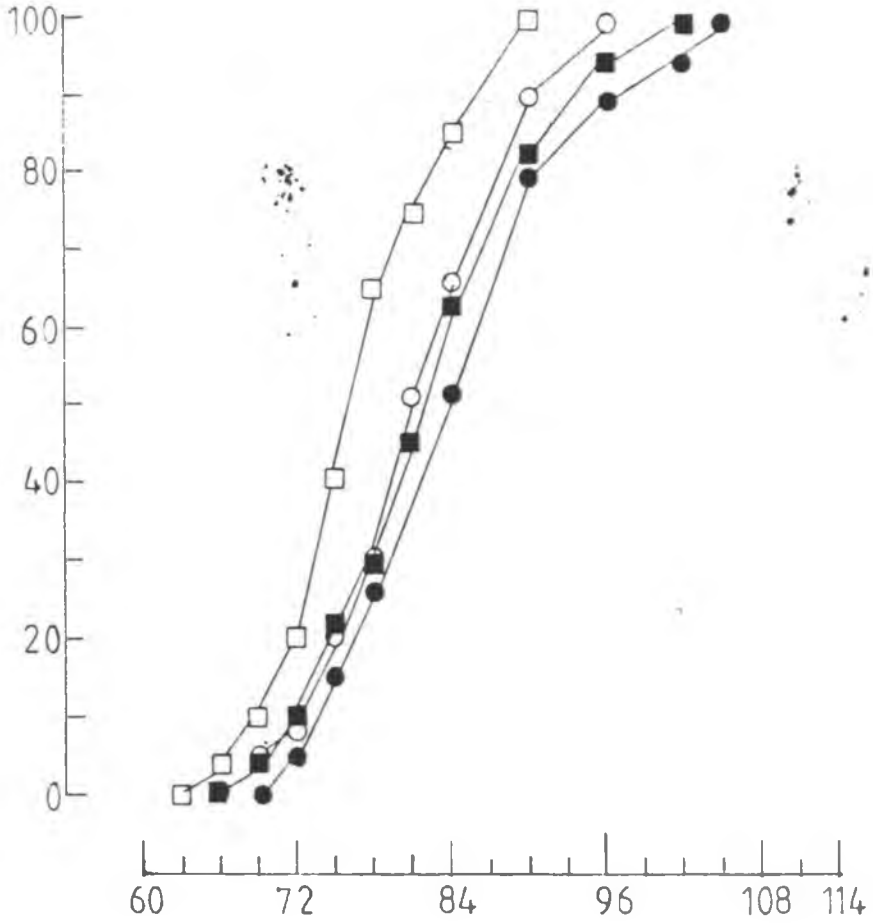
Treatment had significant reductive effect on head density head weight and grain weight per head ($P < 0.01$).

Figure 14: The effect of salt stress on the rate of flowering in two varieties of finger millet (a) Enakuru and (b) Ek-1.




100
80
60
40
20
0
Cumulative % heading
60
72
84
96
108
114
Days from sowing

(a)



(b)

Figure 15: The effect of salinity on (a) degree of tillering and (b) number of productive tillers per plant in two varieties of finger millet.

LEGEND:

Enakuru

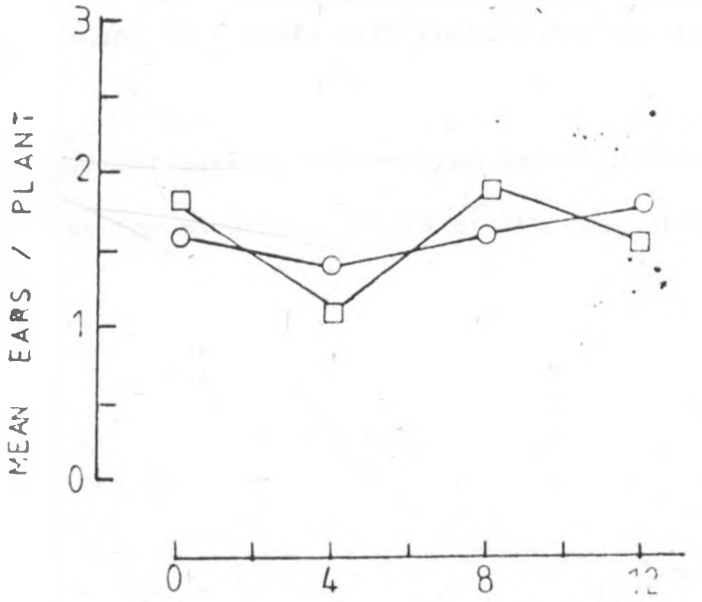
Ek-1

Statistics: (ANOVA)

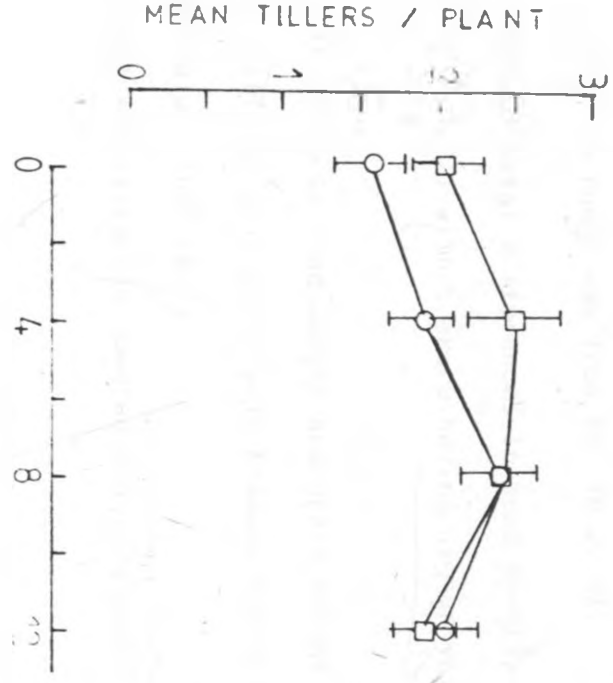
	Figure (a)	(b)
Treatment (Tr)	0.89 n.s	1.61 n.s
Variety (Va)	3.23 n.s	0.0 n.s
Tr x Va	0.42 n.s	0.71 n.s
L S D (Tr)	-	-
L S D (Va)	-	0
S E	-	$0.1 \leq SE \leq 0.3$

Salinity (Ec, mmho cm^{-1})

(a)



(b)


MEAN TILLERS / PLANT
0
3
0
4
8

The varieties differed significantly in their head density ($P < 0.01$).

In Ek-1 the head density ranged between 80.3 and 72.9%, while in Enakuru the range was from 84 to 72.8%.

The inter-varietal differences in head density were highly significant ($P < 0.01$) with Enakuru having higher values than Ek-1.

The difference in head weight and grain weight per head were also significant ($P < 0.01$) with Enakuru having higher combined mean values than Ek-1.

Treatment significantly lowered the 1000 grain weight ($P < 0.01$).

The mean values, Ek-1, ranged between 2.6 and 1.61 grammes, while in Enakuru the values ranged from 3.6 to 2.0 grammes for control and 12 mmho cm^{-1} (Ec) salinity respectively.

The inter-varietal differences in 1000 grain weight were highly significant ($P < 0.01$) with Enakuru having the higher values.

The treatment-variety interaction was significant ($P < 0.01$) and Enakuru was the more susceptible of the two varieties.

Figure 16: The effect of salinity on yield in two varieties of finger millet: (a) mean head weight (b) mean 1000 grain weight and (c) mean head density.

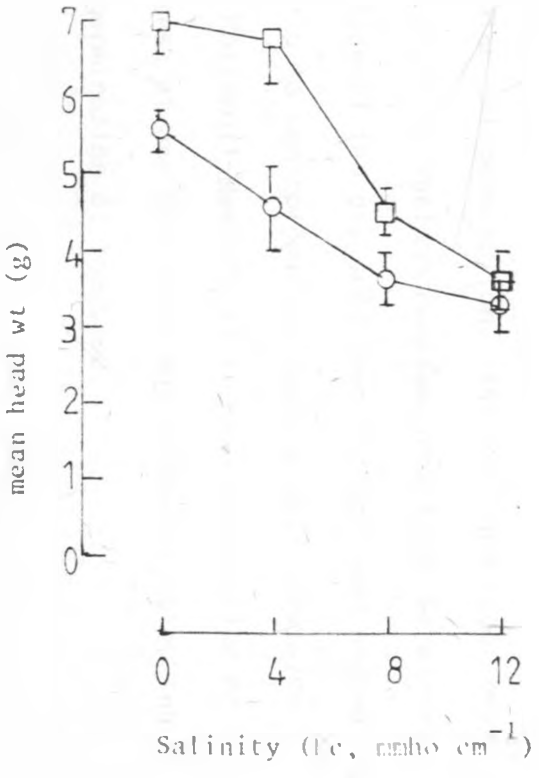
LEGEND

Enakuru

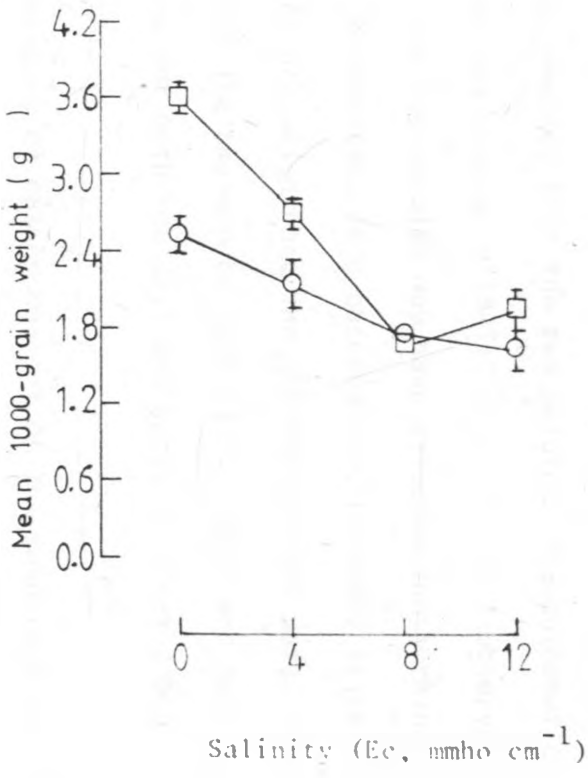
Ek-1

Statistics (ANOVA)

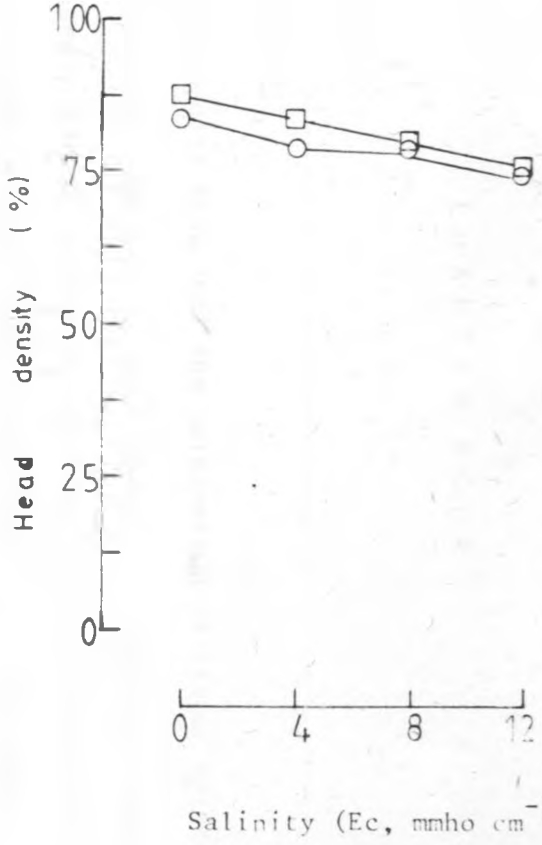
	Figure (a)	(b)	(c)
Treatment (Tr)	15.3*	171.5*	19.69*
Variety (Va)	10.32*	81.2*	7.9*
Tr x Va	2.72 n.s	18.0*	0.84 n.s
L S D (Tr)	0.66	0.10	1.86
L S D (Va)	0.46	0.07	1.32
SE	-	-	0.5 ≤ SE ≤ 1.0


mean head wt (g)
7
6
5
4
3
2
1
0
0
4
8
12
Salinity (Ec, mmho cm^{-1})

(a)


Mean 1000-grain weight (g)
4.2
3.6
3.0
2.4
1.8
1.2
0.6
0.0
0
4
8
12
Salinity (Ec, mmho cm^{-1})

(b)


Head density (%)
100
75
50
25
0
0
4
8
12
Salinity (Ec, mmho cm^{-1})

(c)

CHAPTER FOUR

4.0 DISCUSSION

4.1. Germination:

The results show that the germination of finger millet seeds was reduced by exposure to salt stress. The inter-varietal differences were purely genotypic and had nothing to do with the stress. The two varieties of finger millet were affected in a parallel manner by the stress in both the rate and percentage of germination.

The comparison between salt and sorbitol effect on seed germination revealed that the two solutes, at equiosmotic concentrations, had similar effects on seed germination. This observation would imply that the two solutes may have affected the germinating seeds by similar mechanisms. This observation, however, is belied by the seedling dry weight and the amylase content data. The results indicate that the amylase content of the seeds and seedlings was not the same for both the salt and sorbitol treated seeds at all times.

The analysis of cation content of the seedlings indicated a substantial loss of sodium, potassium and calcium from the seedlings in response to the salt stress.

The botanical germination, (the root and shoot emergence) is an end result of various complex processes. Germination starts with hydration of the dry seed then hormonal and enzymatic activities set in to control metabolism and cell extension growth (Mayer and Poljakoff-Mayber 1975). Any interruption or retardation of the process at any one level may either delay or inhibit the botanical germination of the seed.

Dry seeds have very low water potentials (Sutcliffe, 1977) whose main component is the matrix potential due to the seed proteins (Mayer and Poljakoff-Mayber, 1975). Therefore once seeds are exposed to a moist environment they take up water from the environment by imbibition, a purely physical process. In quiescent seeds, (as were the finger millet seeds) imbibition may soon be overridden by controlled water absorption when membrane reconstitution and metabolic processes have been established in the seeds (Bewey and Black, 1978).

The rate at which imbibition takes place and the amount of water that an imbibing seed may take up will depend upon the absolute or relative water content of the environment. The presence of solutes or matrices in the environment lower the outside water potential and hence the potential gradient between the inside and the outside of the seed is reduced (Durrant, Draycott and Pyne, 1974; Kingsbury, et al., 1984). The consequential low hydration of the seed may lead to other problems such as low enzyme activity (Armstrong and Jones, 1973), irreversible loss of metabolites and macromolecules (Bewey and Black, 1978) or hormonal imbalance (Walton, 1977; Bozcuk, 1984).

In this work, the introduction of solutes (salt or sorbitol) into the germination medium lowered the relative water content (the water potential in this case) by a magnitude of between -0.18 and -0.54 MPa. It is highly probable that the seeds may have had much lower water potential but this would increase with imbibition while that of the medium may, at best, have remained the same or even decreased due to leaching of solutes from the seeds, and the

matrix potential due to the paper. This diminishing potential gradient may have had further detrimental effects on the imbibition, and loss of substances. That loss of substances occurred, can be inferred from the results of seedling ion content. Even though the loss of other substances was not monitored, it is very likely that this loss might have been substantial.

Apart from the osmotic effects, mineral salts are believed to interfere with seed germination by way of the "toxicity" of their ions (Hayward and Wadleigh, 1949; Bernstein and Hayward, 1958; Manohar, 1966; Heydecker, 1977; Pandey and Kanan, 1979).

The toxicity of the ions may accrue from the specific interactions between the ions and protoplasm constituents. In germinating seeds salt stress may reduce enzyme synthesis and activity (Sarin and Narayanan, 1968; Ogra and Baijal, 1979) and aggravate membrane permeability (Huber and Shankla, 1980; Greenway and Munns, 1980). The mechanism by which the ions affect the cell integrity will depend on such properties as the nature of the charge and the valency. In this experiment the sodium and chloride ions were the most abundant in the media (>85%). Sodium as a univalent cation may have had two specific effects on the cells. The ion may have dispersed protoplasm constituents, thus reducing metabolic activities. Such dispersive effects of univalent cations have been reported by Bernstein and Hayward (1958). Alternatively, the cation could have increased membrane permeability. The increased membrane permeability would aggravate solute loss, far and above

the loss due to osmotic stresses.

Of these two possible mechanisms of ion effects only the latter can be backed, indirectly, by data collected. Ions do not have to be within the cells in order to make cell membranes leaky but for dispersion of protoplasmic constituents the ions have to be in the cells. The evidence adduced from seedling ion content indicates clearly that the concentration of univalent cations decreased with the increasing salinity of the germination medium.

It has already been noted that leaky membranes would result in substantial loss of cell constituents into the medium. Such a loss would be an energy and reserve loss from the seeds because the medium may act as a sink. When such losses are severe not only would low germination rates result, but the final germination percentages would also be low.

Therefore, the stress, in this experiment, may have acted as a form of selection where the seeds which were better endowed (genotypically and physiologically) to withstand the stress germinated, even though with reduced vigour. Those seeds which were not well endowed to resist the selection due to stress succumbed and did not germinate. This principle has been well expounded by Pollock and Roos (1972), and it forms the basis for the reduction of germination in response to the stress that is indicated in the results.

The loss of substances from within the seed may also affect the rate of certain metabolic processes; such as food reserve

hydrolysis and mobilization. The finger millet grain has large starch stores (Wakhade, Shehnaj and Rao, 1979). Therefore at germination the mobilization of the food stores would require α-amylase as the hydrolysing enzyme (Adams et al, 1981).

Mobilization of food stores accompanied by high respiration rates and leaching may result in drastic loss of the dry weight of both the remains of the seed and the seedling (Ramana and Rama Das, 1978; Varma and Poonia, 1979; Ogra and Baijal, 1979).

The examination of amylase activity in the seeds and seedling and the final recorded dry weight may give much insight about store utilization in the germinating seed, especially in such a case as where the seedlings had not had an opportunity to photosynthesise.

The results of the in vitro amylase activity experiments indicate that treatment (with either sorbitol or salt) delayed peak production of α-amylase in the germinating finger millet seeds. Further observation was made to the effect that peak amylase production in the seedlings differed with the solute. Peak production was achieved earlier in sorbitol treated seedlings. This difference between salt and sorbitol effects is not expressed at the gross botanical germination level. This swamping effect may have resulted from higher amylase levels in the salt-treated seedling at later times, especially from 72 to 96 hours. In this argument it is assumed that the results obtained in vitro were a correct reflection of the processes taking place in vivo, which should have been the case.

The one problem that seemed to be insurmountable was that of being completely unbiased in the experiment. The selection of only the germinated seeds after the first 24 hours of the experiment was for purpose of standardising all the sub-samples which were extracted. However, this selection left out one important aspect: that of determining whether α-amylase content was essential for emergence of either radicle or coleoptile. In this way the essence of α-amylase production in finger millet seed is not resolved. Therefore trying to relate α-amylase with rate or percentage of germination may not be justified.

During germination utilization of reserves in respiration, and loss of substances from the seeds may lead to rapid loss of dry weight. Rapid losses of dry weights may also be expressed in rapid germinating seeds because of the high respiratory requirement.

The experimental results of seedling dry weight showed that salt-treated seedlings incurred higher losses than sorbitol treated seedlings. Yet, linear growth data does not show any difference between sorbitol-stressed and salt-stressed seedlings. Therefore, the recorded differences in dry weight loss must have resulted from either higher respiratory requirement or greater leaching in the salt-stressed seedlings. The leaching of substances has been discussed already, so what remains is to discuss the respiration requirement.

In this work the effect of salt stress on the respiration of germinating seeds was not tested. However, some other workers

(Nieman, 1962; Caldwell, 1974), have shown that salt stress increases the respiration rates of plant tissues. The high respiration rates may be a result of high energy requirements for ion exclusion and retranslocation for purpose of osmotic adjustment (Caldwell, 1974). Alternatively the high respiration rates may result from uncoupling of the energy conversion or an abnormal increase in the ATPase activity (Waisel, 1972).

Ek-1 showed higher germination rates, higher per cent germination, higher amylase activity and higher seedling relative water content than Enakuru. The difference was noticed for seedling linear growth too.

Varietal differences in finger millet seed germination have also been reported by Panigarh et al. (1978) who also found out that salt-stress reduced the germination percentage. However, it is not explicit from their work whether the differences stemmed from the response to stress or in spite of it.

In this work the results indicate that the ability of Ek-1 seedlings to take up water excee ded that of Enakuru. Most probably this hydration level was the basis for the higher germination, the higher enzyme activity and the higher linear growth.

Even though it has been argued previously that in this experiment it would be difficult to relate amylase activity and seed germination, it is probable that there might have been some relationship.

In the literature there is evidence for enzyme synthesis

being a prerequisite to radicle and plumule emergence in germinating seeds (Jann and Amen, 1977; Bewey and Black, 1977).

In these results it is observed that Ek-1, the variety with high enzyme content also had higher rates and percentages of germination than its counterpart. This may have been coincidental but is unlikely because such differences in amylase activity have been shown to occur in salt-stressed sorghum varieties by Ogra and Baijal (1982).

The above authors noted that under salt stress, the varieties with higher amylase activity also had higher germination rates and percentages.

In my results Ek-1 gave results which were qualitatively similar to those of the authors mentioned above. Therefore, this would be a case to support to proposal that the seed and seedling amylase activity may be used as a marker for salt resistance in germinating finger millet seeds.

The germinating of seeds in paper-lined petri dishes is an accepted standard method of seed testing (Arora and Banerjeee, 1978). In such tests, sometimes there is need to select the seed for sake of uniformity (Ramana and Rama Das, 1978), unless the seed had been graded under standard conditions (Mackay, 1972; Heydeker, 1972).

Selected seeds were used in the laboratory experiments. This may have favoured the use of the most vigorous seeds (Pollock and Roos, 1972). The relevancy of the vigour in the experiments is not easily ascertained. It may be argued that the seeds had not been

selected for resistance to salt stress. Therefore, despite the size of the seeds their resistance to salt stress might not have been abnormally high.

In field practice there is no selection of seed from batches. But over-seeding in such conditions is a normal practice. The practice, therefore, evens out any bias.

In the greenhouse experiments, the germination of seeds was excellent under all treatment condition. The crop was weeded and thinned twice to maintain the required stand (Rutto et al. 1980). The seeds were sown in saline soils, and the excellent germination is an indication that the two varieties of finger millet may resist medium salinity ($\leq$12 mmho cm^{-1}, Ece) in the germination substrate even under field conditions.

In the experiments, I maintained short irrigation regimes. Such irrigation regimes may impose other restrictions on the soil process. Conventional methods of rescheduling irrigation may not work when dealing with saline soils. This is so because plants on saline soils may suffer from water stress, even though they may not droop, and the soils may look and feel moist (Bernstein and Hayward, 1958).

The problems which accompany the use of saline irrigation water are much amplified under field conditions where such parameters as method of irrigation, amount of water available and the nature of the soil play very important roles. It is because of these that overseeding with finger millet has been recommended for saline soils (Sarma, et al., 1983).

The specific problems may include salt retention, reduced hydraulic conductivity, and the limited rates and levels of soil water depletion by plants, evaporation or percolation.

Salt retention in soils irrigated with saline water is a big problem which actually threatens some irrigation projects and is thought to have caused some of the current salines (Mahjoory, 1979). The risk is highly reduced if the soils have a high sand composition (Kurian, 1976) or if enough water is flushed through the soil profile to leach the accumulated salts (Richards, 1968). The latter technique is widely employed: it was used in this experiment.

The soil water potential is a sum of the matric and osmotic potential. When a soil is being irrigated with saline water the matric potential should not be permitted to exceed the osmotic potential. This is done by employing short irrigation regimes (Zur and Bresler, 1973), as was done in this experiment. However, short irrigation regimes may be counterproductive. The reduced hydraulic conductivity of the soil (Sarma et al., 1983) may encourage evaporative loss of the water thereby increasing the soil salinity by capillary rise of salt solution and concentration and the problem is compounded by the low water depletion in saline soils. Apparently salinity may be maintained at a steady state only in sandy soils.

Despite those limitations that accompany the use of soil in testing the response of plants to salt stress the method has several points to its credit in comparison to sand and solution

culture methods.

The solution culture and the other methods that are sometimes preferentially employed in laboratory and some greenhouse experiments are highly artificial set-ups. These may be tolerated only because of the more accurate regulation and measurement that can not be carried out if soil culture methods were used.

It has been recognized that such processes as seed germination, may vary greatly depending on the susbstrate that is employed (Manohar, Bhan and Prasad, 1968; Hadas and Stibbe, 1973). The root system may also be affected by the medium. On the other hand the use of soil in the greenhouse experiments gives results that may be extrapolated into the field. The problems that accompany the soil culture methods under open greenhouse conditions would also accompany the field experiments. This may be to such an extent that the plant response to salt treatment in such greenhouse experiments would be reflective of what would happen in the field.

The contention implies that the results from these experiments are quite valuable in that they may relate better to field conditions than if I had used the more precise, but less relevant, solution culture method.

The timing of seed germination in the life cycle of a plant is very important. If seed germination took place at the wrong time or in an unfavourable environment the seedling or plant may perish before maturity (Bernstein and Hayward, 1958).

At germination the embryo is poorly prepared to exploit the resources offered by the environment, and moreover its activity

is very much limited in space (Carter, 1975). It is for this reason that germination is considered to be the most susceptible stage of plants which are under salt stress (Hayward and Wadleigh, 1949; Bernstein and Hayward, 1958; Richards, 1968; Ogra and Baijal, 1982). In some cases, however, germination has been shown to be more resistant to environmental stresses than other stages, for example flowering (Bernstein and Hayward, 1958; Rachie and Peters, 1974).

In crop plants germination means more than just the start of a life cycle. Good germination in a crop means good cover and stand formation, and if all other conditions held constant, subsequent good yields (Strogonov, 1964).

In the results there is enough evidence to show that finger millet, not only germinates well, but also forms good stand on soils of medium salinity ($\leq$12 mmho cm^{-1}, Ece). This relates fairly well with the laboratory tests where more than 50% germination was attained at 12 mmho cm^{-1}, (Ec).

4.2. Plant water status and allied processes:

In this experiment it was intended that the osmotic potential of the irrigation water should be the major component of the water potential of the substrate. However, maintaining this state is very difficult when the water is introduced into some form of matrix (paper or soil) (Richards, 1968). Such ideal conditions may exist only in circulated liquid cultures; with frequent replacement.

In this case it would be more appropriate to talk of water potential than of osmotic potential. In both the laboratory and the greenhouse the water potential of the substratum would be lower than that of the irrigation water (or solution) because of the added matrix.

Apart from any other effects the introduced solutes would lower the substratum water potential in proportion to the quantity of solute and this would greatly affect imbibition or regulated water uptake (Jarvis, 1965; Zur and Bresler, 1973; Maliwal, Manohar and Paliwal, 1976; Kurian, 1976). The problem is made worse if matric potential is permitted to exceed the solution osmotic potential as the major water potential componet (Kaufman and Ross, 1970).

One way of overcoming such problems would have been germinating the seeds in the liquid or maintaining a very short irrigation regime. These "solutions" to the problem would have been counter-productive in that immersed seeds may be so soaked that only abnormal seedlings may emerge, at best (Bewey and Black, 1978); and too much water in the soil would have resulted in poor aeration (Gur, Dasberg, Schkolnik, Sapir and Peled, 1978).

Plants which are faced with a low soil water potential have to adapt or perish (Jones and Turner, 1977). When such low soil water potential is due to salinity the best way to adapt is to absorb the mineral ions (Waisel, 1972; Flowers et al., 1977). However, accumulation of mineral ions in the cell cytoplasm may impair metabolic activities. Therefore ion absorption for osmotic

adjustment must be accompanied by ion compartmentation. Apparently the greater resistance to salinity that is exhibited by halophytes lies in their ability to absorb ions for osmotic adjustment but at the same time sequester the ions away from sites of enzyme activity. The ability to compartment the ions is limited in glycophytes (Greenway and Munns, 1980). Therefore some of these plants may carry out perfect osmotic adjustment and yet die from ionic stress (toxicity) (Bernstein and Hayward, 1958). Hence among glycophytes exclusion of ions such as sodium and chloride rather than their accumulation is an indication of salt resistance (Orton, 1980).

This argument may imply that among glycophytes, osmotic adjustment may be brought about by accumulation of organic solutes.

The results on relative water content of the seedlings indicate that treatment did lower their relative water content. Generally Ek-1 had higher relative water content than Enakuru. It is not clear whether this had any clear role to play in the higher germination recorded for the variety. Singh and Singh, (1982) working with osmotically stressed wheat, showed that degree of hydration may not be proportional to germination or linear growth.

It is very probable that the high amylase content recorded for Ek-1 may have played an indirect role in the high hydration recorded. The sugars resulting from the amylase activity would have acted as the cell osmotica. Bewey and Black, (1979) have pointed out that during germination the products of hydrolysed food stores (especially sugars) are the primary cell osmotica.

If the seedlings employed starch hydrolytic products for osmotic adjustments, then the amylase activity could be, indirectly, tied with germination. Osmotic adjustment would have led to cell extension growth with the resultant exertion of radicle and coleoptile (Bewey and Black, 1978). This same process would have happened during the seedling linear growth.

Therefore it may not be surprising that Ek-1, the variety with higher amylase activity also had the higher seedling linear growth.

On the basis of this train of thought, it would appear that the impairment of osmotic adjustment by combined osmotic and ionic effects would really impair seedling extension growth, as it actually happened.

The greenhouse plant water status was assessed by leaf water potential (ψ_l) methods and the water flux by examining the leaf transpiration (E) rates.

The leaf water potentials were low for the controls and were made even lower by the treatment. Such a phenomenon has also been reported by Hanks et al, (1978).

Low leaf water potentials may have adverse effects on the growth and development of plants (Akunda, 1980). Hsiao, (1973) and Sutcliffe (1977) have pointed out that the cell extension growth may stop when the leaf water potential goes down to -0.3 MPa (-3 bars). However, salinised plants may have very low osmotic potentials, and this may contribute to low leaf water

potentials while actually the cells themselves may be turgid (Flowers, et al., 1977). But the data collected on height of main tiller clearly shows that cell extension growth must have been impaired by the treatment, which indicates that the turgidity of the cells may also have been reduced by salt stress.

The water potential gradient between the plant leaves and the soil was maintained at relatively high and steady values for most levels of treatment. The exception seemed to be for the Ek-1 leaf water potential at 12 mmho cm^{-1}, (Ec).

This potential gradient would favour uptake of water from the soil. However, the potential gradient between the leaves and the soil is not all that matters in water absorption, especially in saline conditions. The primary site of water absorption is the root system, and in the long term it is the potential difference between the root and the soil that will determine water absorption (Greenway and Munns, 1980). The leaf water potential is usually lower than the root water potential, therefore the potential difference between the latter and the soil is smaller than it is for leaf and soil. Therefore, those plants which have rapid root osmotic adjustment may be better prepared to counter any osmotic snock (Dehan and Tai, 1978).

Leaf water potential is the most appropriate way of assessing the water status of a plant (Jarvis, 1965; Akunda, 1980). But, as has been pointed out, the measurement may be very confusing when dealing with salt-stressed tissues. Whereas low leaf water

potential may be an indication of reduced turgidity in plants which are growing in normal soils, this may not be the case for plants under salt stress. The low water potential, as has already been argued, may result from low osmotic potential of the cell or xylem sap.

However, whichever way one may like to look at it, the low water potential of the tissues may still hinder cell extension growth. Extension occurs in the newly divided cells. Unfortunately, these cells are not endowed with low enough osmotic potential to facilitate uptake of water from the older cells and the xylem. The resultant reduction in turgidity will limit growth. Even though stress may extend the period in which the cell wall may remain plastic (Black, 1968), still this may not compensate for the lack of adequate cell turgidity. It has already been pointed out that cell turgidity stimulates growth and this has been reported by Hsiao (1973) and Flowers et al. (1977).

Under normal conditions low plant water status (low leaf water potentials) is closely linked with stomatal closure (Sutcliffe, 1977; Edwards and Meidner, 1978; Fischer, Neil and Turner, 1978; Akunda, 1980). The stomatal closure is usually indicated by low transpiration rates and low stomatal conductance (i.e. high diffusive resistance) under normal temperature conditions (Jamieson and Willmer, 1984).

Salt stress also causes changes in stomatal rhythms and diffusive resistances(Hasan and Vardar, 1977; Huber and Shankla, 1978; Devi and Rao, 1980; Hampe and Marschner, 1982; Schwartz and

Gale, 1984).

In the experiments the data on leaf diffusive resistances and transpiration, agree with the contention presented in the previous paragraphs.

The recorded reductions on transpiration rates in response to treatment indicate reduced loss of water from the leaf per unit time. In the leaves the major portion of transpiration is through the stomata (Beardsell, Mitchell and Thomas, 1973). Therefore, reduced transpiration may indirectly be construed to indicate stomatal closure.

In finger millet stomata occur on most of the aerial organs. These stomata may have differing sensitivity to stress. To get meaningful data as to what might happen in stressed finger millet the leaf stomatal conductance should be measured because these are quite sensitive and have a finer regulatory mechanism than, say the inflorescence stomata (Tieszen and Imbamba, 1978).

During transpiration, the major component of total resistance to water vapour transfer is stomatal. Therefore the increasing resistances must be attributed to this one source. This also agrees well with the results on general transpiration.

Another piece of evidence which lends support to this argument comes from the results of diffusive resistances to carbon dioxide transfer. This will be discussed in detail in a subsequent section.

4.3. Mineral ion concentration and distribution:

Sodium, potassium, calcium and chloride are the major ions that occur in the saline soil, and consequently in the soil solution (Hayward and Wadleigh, 1949; Bernstein and Hayward, 1958). These ions may have a variety of effects on the plants growing in such soils.

The named ions are essential plant nutrients but when excess concentrations occur in the plant, the death of the plant may occur.* The ions which are most blamed for such toxicity under saline conditions are sodium and chloride (Richards, 1968; Greenway and Munns, 1980). The toxicity of the two ions is not well understood, but may involve effect on enzymes (Kylin and Qudrano, 1975, Murata et al., 1983), membranes (Greenway and Munns, 1980) or hormonal balance (Bozcuk, 1981). In addition sodium may cause an imbalance in the plant mineral nutrition by reducing the ability of the plants to select for such macronutrient cations as calcium and potassium (Poole, 1976; Stassart, Neirinckx and Dejaegere, 1981).

It is mainly for this reason that the absorption and distribution of these ions forms the backbone for most of the studies on the response of plants to salt stress.

In this work the concentration of the four mineral ions was assessed because of three major reasons.

Firstly it was necessary to examine the selectivity of the finger millet varieties in the absorption of the ions and ascertain whether salt stress interfered with this process.

Secondly I had to examine the distribution of the ions among

*Refer to discussions on individual ions (pp 108 - 118).

the plant tissues in order to know how the ions would have affected the metabolic process, and if salt stress would interfere with the retranslocation of the mineral ions from older to younger tissues.

And lastly there was the task of relating the ion selectivity and accumulation with some of the biochemical processes that were actually examined and those that could be inferred from other results.

Because of their small size, the seedlings were not dissected into their various component tissues. Each replicate was considered as a unit, so the initial seedling ion concentration data were based on pooled seedlings for each replicate. The concentration of chloride in the seedlings was not determined, so only the three cations would be discussed in this aspect, unlike in the greenhouse plants.

In the seedlings the concentration of all cations decreased in response and in proportion to the salt stress. However, in the green house plants the effect of salt stress on the tissue ion content was different with the different ions.

Because of these marked differences between the seedlings and the greenhouse plants a comparison is likely to be fallacious. Therefore separate discussions should be made for the two separate entities.

4.3.1. The seedling ion content:

The concentration of all the three cations decreased in response to treatment. This loss must have occurred because of high membrane

permeability due to either the effect of high concentrations of univalent cations (especially Na^+) or the osmotic potential of the germination medium or both. The mechanism by which such membrane permeability and leaching of substances occur has already been discussed.

More important, however, are the consequences of such losses. For this to be made clear each of the cations will be dealt with separately.

(a) Potassium:

Potassium is an essential macronutrient. The element is not metabolised in the plants but it forms the main inorganic osmoticum (Cram, 1976). The ions are also needed as prosthetic groups for activation of certain enzymes (Noggle and Fritz, 1977). Loss of potassium from the seedlings may, therefore, have had an effect on osmotic adjustment and enzyme activity. However, it is not easy to determine the enzymes whose activity may have been affected by the decrease in potassium content. The effect on osmotic adjustment can be visualised as outlined below.

The loss of this cation would have necessitated production of large amounts of organic solutes; mostly sugars. It is for this reason that Ek-1 which had higher amylase activity may be taken to have been genotypically adapted to counter such great loss of the major osmotica.

(b) Sodium:

Sodium is an essential micronutrient in C_4 plants (Bollard and

Butler, 1966; Bowling and Ansari, 1971; Epstein, 1972; Carkirlar and Bowling, 1981). Under normal conditions sodium is only a very minor component of the plant tissues, but the sodium concentration of plant tissues may vary depending on the availability of sodium in the substrate (Cram 1976).

Excess sodium in tissues may be toxic (Doneen, 1975) and it is thought that high sodium content of the substrate may interfere with the plants selectivity for potassium (Poole, 1976, Gorham et al., 1984).

The effect that the recorded losses of sodium may have had on the seedling development is obscure. However, the fact that the seeds had relatively high sodium content implies that somehow this element may be important in germination of finger millet seed. The differences between the two varieties is indicated by the different concentrations that were recorded.

(c) Calcium:

Calcium is an essential macronutrient for all plants. The ions are not mobile in plant tissues because they are bound up in organic matrices to form the cell lamellae (Pitman, 1975). The ions are also essential for membrane integrity (Poovaiah and Leopold, 1976). Calcium is also known to be involved in enzyme activation in a rather an unknown manner (Noggle and Fritz, 1977).

The loss of calcium that was recorded must have greatly affected the integrity of the cells; apart from any effects

on enzyme activation. Such loss of calcium would have led to accelerated loss of substances from the seedlings by leaching. This proposal has already been discussed.

The loss of calcium must have had a profound effect on cell growth in that formation of lamella between the cells must have been interefered with. The specific effect this would have on germination or linear growth remains obscure.

4.3.2. Greenhouse plants:

The tissue ion content of the greenhouse plants was affected in different ways depending on the ion as response to salinity of the soil.

(a) Potassium

As has been pointed out in the previous section, potassium is an essential plant macronutrient. In growing plants its role as cell osmoticum is put into some other use apart from cell extension; namely stomatal movement (Smith, 1967; Raghavendra, Rao and Rama Das, 1976; Sutcliffe, 1977).

The uptake of potassium from the substrate by the roots is an active process (Epstein, 1972). The uptake is selective, but the selectivity is disturbed if the sodium content in the same substrate is too high (Poole, 1976).

The salt stress did not have a significant effect on the tissue potassium content. The genotypic differences in tissue potassium content were significantly expressed, with Ek-1 having

higher mean concentration than Enakuru. The mean Enakuru tissue potassium content apparently increased with increase of soil salinity while that of Ek-1 showed a slight decrease along the treatment range.

This marked difference between the varieties in the response to salt stress must be based on genotypic differences.

It is apparent that Enakuru absorbed more and more potassium in response to either the increasing potassium content of the substratum with the increasing salinity, or perhaps as a way of counteracting the high tissue sodium content as a result of salt stress.

The uptake of potassium is a complex process whose mechanism has not yet been unequivocally proved (Dalton, 1984), but the increasing salinity must have led to increase of the soil potassium content and it would be expected that total absorbed potassium might increase as a response even though the rate of absorption may be low.

The other important aspect of plant mineral nutrition concerns the partitioning among the plant organs and tissues.

Potassium is a very mobile ion in plants and may be expected to be distributed in such a way that older tissues may have lower concentrations than the younger tissues (Pitman, 1975). This is so because the younger tissues get the potassium from the older tissues by retranslocation.

The selectivity of potassium absorption and retranslocation from older tissues to younger ones in salt-stress plants is a sign

of salt resistance in some cereal crops (Greenway et al., 1965).

Apparently such selectivity was maintained by Enakuru which maintained high potassium content in the middle and upper leaves than in the lower leaves and the stem.

In such circumstances the osmotic adjustment of the growing cells and the stomata of the most actively photosynthesising tissue could be maintained within safe limits.

(b) Sodium

The uptake of sodium is a plant process which may sometimes interfere with uptake of potassium and calcium (Stassart et al., 1981). Therefore among glycophytes salinity may result in reductions of both calcium and potassium (Poole, 1976).

In C_4 plants sodium is an essential micronutrient even though its specific activity is, as yet, not known (Bollard and Butler, 1966).

Salt-stressed plants usually show an increase, of varying degrees, in the tissue sodium content. This happens when pots (soils) are irrigated with salts whose major component is sodium (Epstein, 1972).

The sodium ion is not as mobile in plant tissues as potassium is, therefore, the higher concentrations of sodium are found in the older tissues (Pitman, 1975). For this reason the younger tissues get their sodium supply from the roots via the xylem.

In both varieties the tissue sodium content increased with

treatment. Just as for potassium, Enakuru showed greater increase response than Ek-I. This may indicate that Enakuru had a higher cation uptake capacity than Ek-I; or that Ek-I had higher cation selection efficiency.

The increase of the tissue sodium content was coupled with an increase in the inter-tissue differences in sodium content (i.e. the inter-tissue differences in sodium content increased in response to treatment).

In Enakuru the highest mean sodium concentration was recorded for the stem and the lowest for the middle and upper leaves. This distribution contrasted with that of potassium. Even though sodium concentration for stem and lower leaves was expected to be high, yet the salinity of the soil should have resulted in even higher concentrations in the younger tissues than those recorded. While it may be argued that there must have occurred sodium retention and binding in the stem and lower leaves it has been proposed that what was recorded here, and has been recorded by many other workers is not an expression of selectivity or retention as such but just a natural result of progressive dilution up the plant shoot (Greenway et al., 1965).

Whatever the mechanism, apparently Enakuru maintained equable Na/K ratios in the upper and middle leaves.

In Ek-I the highest mean sodium concentration was recorded for the lower leaves and the lowest was for the upper leaves. Therefore, the distribution was qualitatively similar for both varieties.

The retention of sodium in older tissues is not well understood.

The retention may be effected by sequestering the sodium in the cell vacuoles from where retranslocation may be difficult (Strogonov, 1964; Greenway, et al., 1965; Flowers, et al., 1977).

What direct effect the increase in sodium concentration had on the tissue metabolism can not be explained. But the increase may have increased the role of sodium as cell osmoticum. This may imply that the ions may have started to be involved in such processes as stomatal movements as reported (Raghavendra, et al., 1976) The increase in the univatent cation (K^+ + Na^+) concentration that was recorded may in itself had dispersive effect on the protoplasmic systems. This may have had disruptive effects on metabolic efficiency unless the ions were not accumulated in cytoplasm.

The tissue Na/K ratio for both varieties increased significantly in response to salt stress. The increase of Na^+ in relation to K^+ is attributable to its being the majority cation in the substratum. Such changes have been recorded by many other authors (Kurian, 1976; Orton, 1980; Gill and Dutt, 1982). In most instances it is proposed that very high Na/K ratios in salt stressed plants could be used as specific marker for susceptibility to salinity (Joshi, Qadar and Rana, 1980; Murthy et al., 1979). In some cases this has been shown not to apply (Gill and Dutt, 1982).

(c) Calcium

The tissue calcium content decreased in response to salt stress. This observation was in line with that of Orton (1980) on Hordeum.

The two varieties differed in their tissue calcium content

with Enakuru having the higher mean amounts. This contrasts with the seedling calcium content where neither variety had higher calcium concentration than the other.

The lowest calcium concentration was registered for the upper leaves and the highest in either the lower leaves or the stem. This is generally the normal distribution order of calcium in plants (Epstein, 1972; Arjunan and Gopalkrishnan, 1981).

Closer examination reveals an apparent increase in the calcium concentration of the upper and middle leaves in Enakuru and the upper leaves in Ek-1. This observation may be connected with the observed rise in the K^+ content in the upper and middle leaves of Enakuru.

The cell selectivity for K^+ depends upon the integrity of the membranes and the calcium content of either the surrounding solution or the cell cytoplasm (Stassart et al., 1981). It is most probable that the high concentration of calcium in the upper and middle leaves may have enhanced selective accumulation of potassium in the same tissues in response to salt stress. The combined force of relatively high K^+ and Ca^{2+} content in these tissues would probably enhance the resistance to high sodium concentration. Indeed these same sentiments have been proposed by Bernstein and Hayward (1958) and Gill and Dutt (1982).

The mobility of calcium from older to younger tissues in plants is limited (Pitman, 1975). This implies that most of the calcium supply to the growing points comes from the soil via the xylem.

In the results there was an apparent increase in the concentration of calcium in the middle and upper leaves. Even though the apparent calcium increase in the younger tissues did not raise the calcium levels in these tissues to par with the older leaves and stems, still it was remarkable that the calcium concentration in the latter tissues decreased in response to the salt stress.

Apparently the calcium increase in the younger tissues was concomitant with the decrease in the older tissues. Therefore, these apparent changes in tissue calcium content in response to salt stress did not involve increased absorption from the soil. The changes may have stemmed from enhanced retranslocation from the older tissues. The retranslocation may have been triggered by the increasing tissue sodium content. The retranslocation process may have been slightly higher in Enakuru than in Ek-1.

(d) Chloride:

The seedlings were not assessed for this ion. All the results recorded, and to be discussed, came from analysis of greenhouse plant tissues.

The concentration and distribution of this ion was not affected by the treatment. The inter-varietal differences were not significant too.

Closer observations revealed that in Enakuru the chloride content of the upper leaves apparently decreased in response to salt stress while those of the older tissues increased. In Ek-1 all tissues registered more or less steady content of chloride

despite the treatment.

These observations imply that both Ek-I and Enakuru have mechanisms by which chloride is excluded from the tops. This would call for a bias against chloride ions at absoprtion, or retention in the root cells or both of these processes. In Enakuru the retention process must be extended to include the stem and the older tissues. The retention processes must involve some form of binding.

The chloride is an essential plant micronutrient (Trebst and Avron ,1977; Malkin, 1977; Noggle and Fritz, 1977). However the same ion is proposed to be toxic to plants where present in excess amounts (Kurian, 1976; Greenway and Munns, 1980).

Among the glycophytes the uptake of chloride is limited (Cram. 1976) but under salt-stress the same plants may accumulate high amounts of the ion (Strogonov, 1964). Such chloride concentrations may be followed by death of tissues or the whole plant (Bernstein and Hayward, 1958). Therefore exclusion of the ion from the tops of crop plants may enhance resistance to salinity (Greenway and Munns, 1980); though Rai (1977) has recorded high resistance in some chloride accumulating Zea mays varieties.

The within-plant chloride distribution is an intriguing subject. Greenway et al, (1965) recorded higher chloride content in younger tissues than older ones. The observation does not concur with the results in my experiment. It is most probable that the increase in $K^+ + Na^+$ which was concomitant with steady levels of Cl^- must have made it necessary for the plants to synthesize increasing

amounts of organic counter-ions.

In this experiment no assessment was made on any possible organic counter-ions which might have been synthesized in the plant in response to salt stress. However, workers in this field have recorded that in cereals salt (or water) stress results in the accumulation of quaternary ammonium derivatives, especially glycine betaine (McDonnell, Coughlan, and Wyn Jones, 1983). It is proposed that these ammonium derivatives may enhance the resistance to the stress due to salinity (Storey, Ahmad, and Wyn Jones, 1977; Storey and Wyn Jones, 1977). This is an area where adequate information is lacking.

However, on the basis that no data was collected on any anionic species other than chloride, any discussion of probable counter-ions to the cations would be speculative and based on publications by other workers. The exact mechanism of the organic anionic species is not known, nor is their accumulation unequivocally known to confer resistance.

4.4. Enzyme and protein content

The seedling enzyme activity and the tissue protein content of the greenhouse plants are discussed in one section because most of the plant proteins (except in seed) are enzymatic in nature, even though their activity was not examined in this particular works.

4.4.1. Seedling α-amylase activity

The effect of stress on the seedling α-amylase activity varied with time. At 48 hours the stress effectively lowered the seed α-amylase activity, but at 72 hours the stress inhibitive effect was not expressed.

Thus the stress delayed the peak enzyme activity from 48 to 72 hours. α-amylase is essential for the hydrolysis of native starch grains in seeds (Adams et al., 1981). The activity of this enzyme results in the formation of soluble sugars which may be used in osmotic adjustment and respiration.

Apparently the effect of treatment on α-amylase activity was most pronounced between 24 and 72 hours of the experiment time. This, incidentially, was the time when the enzyme activity was highest.

Several other workers have shown that the salt stress delays the peak activity of α-amylase in germinating cereal seeds (Sarin and Narayanan, 1968; Ogra and Baijal, 1982). The same authors also recorded a significant reduction of α-amylase activity in response to treatment.

The delayed peaking of enzyme activity and the reduction recorded in this experiment may have various implications.

In most cereals the germinating seeds perform de novo synthesis of α-amylase (Chrispeels and Varner, 1967). It is most probable that the process may involve translation and not transcription (Armstrong and Jones, 1973). Therefore it is

probable that at early stages of germination the polysome formation may have been affected by salinity. However, this situation may have been reversed as time went on. This reversal may have resulted from either the actual inhibition of polysome formation or from the need to synthesize more ribosomes in the cells. The latter option is the most probable. This would then imply that there occurred excessive loss of the residual ribosomes by leacning. This process has already been discussed in connection with other substances.

Impaired polysome formation has been reported for germinating seeds which are under osmotic stress (Armstrong and Jones, 1973). Therefore, it is fairly difficult to pinpoint the specific ionic effect on this process. Such impairment could lead to low rates of enzyme synthesis and the accompanying metabolic processes would be impaired too. Such conditions may result in delayed germination for the mild cases or cessation of germination for the more severe cases. This is based on the assumption that enzymes, other than α-amylase, were similarly affected. Indeed, Sheoran (1980) has reported a similar trend of events in legumes. However, cases are reported where such enzymes as ATPases (Flowers et al., 1977) and peroxidases (Shukla and Baijal, 1978) are stimulated by salinity. Enhanced activity of some of these enzymes would only contribute to growth retardation due to energy losses.

It is worth noting that α-amylase synthesis and activity may be under the influence of such other factors as hormones. Hence care is needed to interpret the results in this experiment.

Ek-I had higher α-amylase activity and the rate and percentage of seed germination were higher in Ek-I than in Enakuru. Ogra and Baijal (1982) have reported that high sugar concentrations could be positively correlated with high germination percentage in sorghum. Since sugars in the germinating sorghum could only result from the activity of α-amylase on the native storage starch it is probable that high amylase activity in salt stressed seeds may lead to high germination percentage. This is how the α-amylase would have indirectly affected the germination of the two varieties in this experiment.

The high relative water content of the Ek-I seedling may or may not have played part in the high amylase activity. However, because of what has been noted on osmotic stress and amylase activity, it is possible that the high hydration level of Ek-I seedlings may have enhanced α-amylase activity, or the reverse might have been the case; the hydration level may have depended upon α-amylase activity which made possible the osmotic adjustment of the cells.

4.4.2. Tissue protein content

The salt stress did not have a significant effect on tissue protein content. The inter-varietal differences in tissue protein content were not significant either. The tissues had significant differences in protein content. However, all tissues can not be included in a general comparative study because of the time difference at harvest. For this reason all the vegetative tissues

are discussed together while the seeds are given a separate discussion. It is worthwhile to note that while the extraction and preservation processes may not have been perfect (Batra, Deshmukh and Joshi, 1976) the method of determination was fairly sensitive (Lowry, Rosebrough, Farr and Randall, 1951). Thus the results may be regarded with confidence.

(a) Vegetative tissues:

The highest protein content was registered for the upper leaves (42.5%) and the lowest was for the stem (26%).

The major protein component of the green leaves is the photosynthetic enzyme system (Ellis, Blair and Hartley, 1973). Structural and other enzymatic protein fraction would form a minor component.

The results in this experiment indicated that those leaves (or tissues) in which most of the photosynthetic activity would take place also had high protein content. These extremely high figures must have accounted for by the enzymes of the two carboxylating systems that are encountered in C_4 plants. It is expected that these values may be higher than for C_3 plants, even legumes (Stahmann, 1968), because C_4 plants have 2 carboxylating systems to the C_3's one.

The absorption and metabolism of nitrogen in salinised plants is a controversial issue. Kumar, Singh and Sharma (1981) have suggested that salinity may enhance the absorption of nitrogen and the subsequent protein synthesis. However, Strogonov (1964)

noted a reduction in protein content in salinised plants. Apparently the metabolism of nitrogen in salt-stressed plants differs in different plant species. Furthermore the authors do not explain their results in relation to nitrogen availability in the soil. The loss of nitrogen from heavily irrigated saline soils is rapid (Richards, 1968). So plants may end up absorbing little nitrogen because of the availability problem.

In this work the supply of nitrogen was abundant in the soil. This might account for the results. However, the non protein nitrogen component was not assessed and it may be argued that incorporation of nitrogen into proteins may have proceeded at the expense of the other nitrogen pools in the plant. If such processes occurred then protein content, would not change even if nitrogen absorption were impaired.

Such an argument may not be valid because most workers have recorded an increase in the other nitrogen pools at the expense of the protein pool in salinised plants (Poljakoff-Mayber and Gale, 1975).

The protein in the roots may have been made of two components too (enzymatic and structural). As carboxylation may not be taking place in the roots, the major enzyme systems may have differed from those of the stem and the leaves. Apart from the ordinary metabolic enzymes, the roots might have contained substantial amounts of the specific enzymes which are involved in ion absorption, translocation and retention.

(b) The seeds:

The seed protein content averaged 6.9% and compares well with the results from the work of Joshi and Joshi (1979). Most of this protein component must have been for storage purposes. This is based on the observation that dry cereals may have only limited amount of enzymes (Bewey and Black, 1978). During germination such storage protein may be converted into enzymes and structural proteins.

The seed storage proteins (and enzymes) are synthesized in the endosperm of the cereal seeds (caryopses) (Bewey and Black, 1978). Therefore the results indicate that salt stress did not have signficant effect on both the translocation of non-protein nitrogen from the other plant parts and the incorporation of the translocated nitrogen into proteins in the seeds.

Even though the individual amino acid content was not assessed, the results on crude protein content of the seeds is an indication that the salt-stress did not have any adverse effect on the finger millet grain nutritive value (concerning protein, at least).

The final point to note is that of the differences between the seed protein content and that of the vegetative tissues. Even though there was a time factor, and the comparison of the two plant components may not be fair, it is worth pointing out that such differences have actually been recorded by many authors for example, Stahmann,, (1968).

Always the green vegetative tissues have higher crude protein content than the grains.

The recorded normal tissue protein content despite the salinity is an indication that enzyme synthesis in the stressed plants may have remained stable. This would be expected to result in undisturbed plant development.

However, I am not in position to know whether there was a switch in the kind of protein synthesized, and, moreover, there might have been other processes which might have either been more sensitive to salinity than enzyme synthesis, or might have retarded enzyme activity.

4.5. Chlorophyll and CO_2 fluxes:

Salt stress lowered the leaf chlorophyll content and the photosynthetic(and CO_2 flux)rates.

Enakuru had significantly higher mean chlorophyll content than Ek-1: Differences, though not as significant, were also recorded for CO_2 flux (and photosynthetic rates). In both cases Enakuru had higher rates than Ek-1. These results compare well with those of Kingsbury, et al. (1984) and Schwartz and Gale, (1984) who also observed reduction in CO_2 flux in salt-stressed cereals.

The mean maximum rates of photosynthesis recorded in this experiment (873 and 1127 µmol $CO_2/dm^2/hr$ for Ek-1 and Enakuru respectively falls far short of the maximum potential photosynthetic rates recorded for finger millet (1818 µmol $CO_2/dm^2/hr$ - Tieszen and Imbamba, 1978).

The higher figures are reported to have been recorded at optimum temperatures, 35°C, and maximum mid-day like light conditions (2000 µmol $M^{-2}s^{-1}$ PAR). In this experiment less than optimum temperature and maximum light intensity were used (30°C, 1700 µmol $M^{-2}s^{-1}$, PAR).

In the analysis for chlorophyll, and CO_2 flux the leaves were employed because at that stage they should have been the main organs of CO_2 fixation (Sayi, 1977; Tieszen and Imbamba, 1978).

Akunda (1980) has indicated that the photosynthetic process accounts for the major portion of the plant biomass. Single leaf photosynthesis may not represent a true net CO_2 assimilation in a whole plant or in a canopy because of such variables as light interception and mutual shading, and respiration of the non-photosynthetic tissues (Tieszen, 1982). However, net productivity has positive correlation to apparent rates of leaf photosynthesis. Therefore measurement of the latter would be expected to indicate a general trend in productivity.

Photosynthesis is dependent upon processes which may be enhanced or retarded by various internal or environmental conditions .

Atmospheric carbon dioxide has to diffuse into the leaf and at the site of carboxylation it is biochemically removed. This source-sink relationship will depend upon two main factors; the rate at which the gaseous CO_2, is removed at site of carboxylation, and the resistance offered to the diffusing carbon

dioxide from the source to the site of fixation (Long, 1982).

The three major types of resistances encountered in the transfer processes are the boundary layer, stomatal and mesophyll resistances (Long, 1982). Of these resistances the boundary layer resistance is normally a minor component but the other two are very important.

The types of resistances to CO_2 flux are interdependent. The stomatal resistance is dependent upon the size of the stomatal aperture. The stomatal movement (opening or closing) is under the influence of many leaf and environmental processes.

The leaf processes which are known to influence stomatal aperture include the plant water status, potassium ion translocation, hormonal balance and substomatal CO_2 concentration (Jarvis, 1971; Sutcliffe,1977). High mesophyll resistance may indirectly lead to stomatal closure. In such cases it may be difficult to determine which of the two resistances was initially paramount.

Mesophyll resistance comprises two components: the purely physical diffusion through the cell walls, and the biochemical carboxylation. The tissue water status plays a big role in these two components because any biological diffusion and enzyme activity must take place in watery environments.

Carboxylation in green plants require the participation of chlorophylls. The chlorophylls are important in harvesting solar energy thus facilitating the reduction of carbon dioxide.

The experimental results showed that the salt stress induced

an increase of the total resistance to CO_2, lowered the leaf chlorophyll content and lowered the leaf water potential. These are factors which may have formed the basis for the reduction in leaf photosynthetic activity which were recorded.

A detailed analysis of the total resistances to CO_2 transfer revealed that in Ek-1 the contribution by mesophyll resistance overwhelmed the contribution by stomatal resistance in response to treatment, while in Enakuru the same contribution declined with treatment. This implies that stress aggravated mesophyll resistance in Ek-1, but in Enakuru it was the stomatal resistance which was the more affected.

The observation may be connected with the one made on chlorophyll content. It was noted that even though the two varieties suffered to the same extent under salinity, yet the chlorophyll content of Enakuru remained relatively higher than that of Ek-1. The lower chlorophyll content of Ek-1 may have been the limiting factor in CO_2 incorporation. The stomatal closure may have been of a similar magnitude in both varieties, considering the data on transpiration. But the stomatal conductance became the limiting factor in Enakuru because the chlorophyll content (and the carboxylation) was relatively high.

Chloride ions inhibit the *in vitro* activity of some finger millet enzymes (Murata *et al.*, 1983). However, my results show that the tissue chloride content did not increase in response to salt stress. Therefore, such inhibition as reported by Murata

and others could not have occurred. This argument does not in any way invalidate possible effects of the sodium on enzyme systems: the concentration of sodium ion in the tissues increased in response to treatment.

The distribution of chloride within the cells was not examined. Therefore, the effect of salt stress on this aspect is not known. If treatment changed the inter and intracellular chloride distribution then enzyme activity would have been affected, even though the overall tissue concentration did not change in response to salt treatment.

4.6. Growth and Development:

Plant development is a process which comprise such other processes as cell division, cell differentiation and cell linear extension (Wareing and Phillips, 1970). Therefore, the development may outwardly be perceived as linear growth and tissue and organ formation.

When plants are subjected to salt stress some aspects of the development process may be impaired. The aspects which have been observed to be affected by salt stress in cereals include linear growth, tillering, heading and seed formation.

In the following sections the effect of salinity on the plant development is discussed considering the various aspects individually for sake of clarity. In the discussion an attempt will be made to indicate which of the various aspects of development seemed to have been most affected in the experiments.

4.6.1. Seedling linear growth:

The ultimate organ length in the seedlings was decreased by the salt stress in proportion to the salinity of the medium. The stress reduced the root-to-shoot ratio of the seedlings. Apparently Enakuru was the more affected in this aspect, even though there were no statistical inter-varietal differences.

The decreasing root-to-shoot ratio is an indication that the salt stress interferred with the root linear growth to a greater extent than it did the shoot linear growth.

The results on linear growth are basically similar to those of Panigarh et al., (1978). These workers also observed that salt stress reduced the finger millet seedling linear growth, but they do not say what effect the stress had on the root-to-shoot ratio. The reduction of the root-to-shoot ratio in salt stressed seedlings has been reported for cereals other than finger millet. Among such publications is one by Varma and Poonia (1979). Such a decrease, if it occurred in soil grown plants, may be detrimental to the plants because the supply of such essential requirements as water and mineral salts may be impaired. It is no wonder that Bernstein and Hayward (1958), considered the maintenance of the root-to-shoot ratio within small limits as a marker for resistance in salt stressed plants.

The mechanism by which the root growth is more affected by salt stress is not well understood; but the process may be based on the seedling resource partitioning.

The results showed that Ek-1 seedlings had higher linear

measurements than Enakuru.

These genotypic differences were not influenced by the salt stress. The growth differences may have been based on the differences in germination rates. Personal observation on seedlings which were exposed to salt stress after germination showed that salt stress reduced the root and shoot length in this case too. This implied that the stress may have influenced the ultimate seedling length by interfering with both the speed of germination and the actual cell extension growth. Apparently the differences in the ultimate seedling length between the two varieties may have been contributed to,partly, by the differences in germination rates and, partly, by differences in the organ extension rate.

The effects of both salt and sorbitol stress (at equiosmotic concentrations) were statistically similar. The observations support the contention that the salt stress may have effected the seedling linear growth largely via the osmotic stress. Apparently Lk-1, which had higher α-amylase activity, was able to carry out osmotic adjustment more efficiently than Enakuru.

However, the observation made on the seedling dry weight is a bit perplexing. The seedling dry weight decreased slightly with the increasing salinity of the medium; an observation similar to one made on barley by Kumar et al, (1981). In contrast the "sorbitol seedling" either underwent an increase in dry weight or the weight remained the same as in control; in response to stress. Probably the seedlings were able to metabolise the sorbitol.

Differentiation, as outwardly expressed in organ formation was not quantified; and so cannot be competently discussed in my work.

4.6.2. Greenhouse plants:

(a) Height

The linear growth in the greenhouse plants depended upon cell division and extension; just like the seedling linear growth.

The results show that the main tillers of the plants were shorter than the control in response to the salinity of the soil. Such a response has also been reported by Kaliappan, et al, (1967) in finger millet, by Varma and Poonia (1979) for pearl millet, and Saxena and Pandey, (1981) for rice. Indeed Bernstein and Hayward (1958) contend that retarded plant growth is the first observable reaction of glycophytes to salt stress.

There are two ways by which growth may have been impaired. The first of this may have been the reduction in the rate of mitotic division of cells, and the second could be the reduced extension growth of cells. These processes may have acted singly or together in response to metabolic or physical processes. The pertubation may have been a response to just the imposed osmotic stress or ion toxicity or both. The last of the alternatives is the most probable; bearing in mind that even in the seedlings where growth seemed to have been controlled by the osmotic status of the medium, such biochemical processes as α-amylase activity showed preferential response to either salt (osmotic-ionic) or

sorbitol (osmotic), in time.

Apparently the osmotic effects must have exceeded the ionic effects; when all the work is taken as a unit.

The ions that would have been considered for their toxicity in this experiment included sodium and chloride. Chloride was not accumulated in response to treatment, therefore, toxity due to this ion may be ruled out. The sodium ions may have been toxic to the seedlings only if they enhanced membrane permeability. The loss of sodium from the seedlings in response to salinity is a pointer to the fact that the cell cytoplasm was relatively free from the sodium menace. Hence sodium toxicity in this case may also be ruled out. In the greenhouse plants the sodium concentration increased in response to treatment. However, Enakuru, the variety which preferentially accumulated the ion in response to treatment, did not have its growth preferentially affected by the treatment, hence sodium increment did not lead to toxicity symptoms. The ions may have had their subtle influences but statistically the plant growth must have been mainly affected by osmotic stress.

Hsiao, (1973) has reported that cell expansion growth is reduced at around -0.300 MPa water potential (ψ). A similar observation has been made by Sutcliffe, (1977). The same authors point out that cell division may not be as sensitive to osmotic stress as the extension is. However, this has not been unequivocally proved.

The relationship between the water potential and the turgor pressure of a water-stressed tissue has been discussed. The

relationship may not hold for salt stressed plants because of the observed ions and the activity of these in the tissues. However, any osmotic adjustment in salt stressed plants should be reflected in transpiration and stomatal conductance. The results on the two processes show that transpiration rates and leaf stomatal conductances were lowered in response to treatment. This could be an indication that the leaf cells had low turgidity. Indeed Hsiao (1973) has stated that plant tissues with a water potential of lower than -1.200 or -1.600 MPa may have negligible turgor pressure. The water potential results in this work reveal that salt-treatment lowered the leaf water potential well below this mark. Even though cells may adapt to grow at very low water potentials (Hsiao, 1973), such low values as are recorded in this work must have retarded the extension growth.

The low rates of photosynthesis (already discussed) may have played some part in the reduction of plant growth in that there would have been only small amounts of metabolites for the growth processes (Schwartz and Gale, 1984).

As salinised plants have high tissue respiration rates (Nieman, 1962) the low supply of metabolites would be used mainly in respiratory activity at the expense of growth processes.

There is also a likelihood that the loss of metabolites from roots would have been aggravated by the osmotic stress. This has been discussed in the case of seedlings, but it should be noted that even soil growing (established) plants may lose up to 25% of total photosynthates (Barber and Martin, 1976, Bowen, 1980), if they are exposed to water stress, and that this loss

may contribute a great deal to impair linear growth.

It is my hypothesis that reduction in growth in response to salinity must have resulted from the water stress like conditions imposed by salinity and that I could not record specific ion effect in my work.

(b) Differentiation and senescence

Under this subsection the formation of tissues and organs, as a morphological demonstration of cell differentiation is dealt with.

Salinity did not interfere with the processes of differentiation: the number of nodes per the main tillér, number of tillers per plant and ear number per plant remained statistically the same for all plants.

Rachie and Peters, (1974) have cited examples to show that finger millet is also resistant to alkalinity at the tillering stage, and Kumar and Garg (1981) have evidence to show that cell differentiation in peas (and thus formation of organs) is not as sensitive to salinity as organ growth is.

Cell differentiation is known to be under the control of hormones, and other metabolites (Nanda, 1978). The formation of normal organs (of given mean number) under salt stress would imply that the salt stress did not interfere with the critical hormonal and resource distribution, in as cell differentiation and organ formation was concerned. It is for this same reason

that whereas the height of the main tiller was significantly reduced by stress, the number of nodes (hence internodes) was not changed. The implication of this is that reduced plant height resulted from low mean internodal lengths.

The salt stress delayed panicle emergence without affecting the final percentage of emergence. This must have resulted from the low growth rates of the salinised plants. Similar observations have been made by Singh and Chandra (1979) in pearl millet and Saxena and Pandey (1981) in some rice varieties.

Ek-1, true to its early maturity characteristics, headed earlier than Enakuru.

The data on number of green leaves revealed that salt stress did not aggravate death of the leaves. This resistance may be quite beneficial to finger millet, a crop which depends on photosynthates from most of its leaves for grain-filling (Sayi, 1977). Senescence in plant organs is a hormone-controlled process (Wareing and Phillip, 1970) and the fact that salinity did not aggravate senescence implies that the stress did not interfere with the critical hormonal balance for this process. However, this is an inference which may not be accurate because the process of leaf senescence in finger millet is not well understood.

One important observation however, is that the apparently higher sodium concentrations in the older leaves did not lead to accelerated senescence. This may be taken to indicate that

finger millet, unlike some other plants, may not be sequestering sodium in older tissues for purpose of dropping these tissues off later on, rather the accumulation is not followed by rapid death. Apparently, these older tissues, unlike the younger tissues, may have mechanisms for avoiding the toxicity of the accumulated cations (especially sodium).

4.7. Grain yield:

Salinity reduced the grain yield of both varieties of finger millet. The mean head weight of the main tiller, the amount of grain per ear (Weight), the head density and the mean 1000 grain weight were all reduced by the stress. In all these weight measurements Enakuru had higher mean values than Ek-1.

The yield of the local (Kenyan) finger millet varieties has been shown to have positive correlation with the duration of the particular variety (Macharia, 1982). However, among the improved varieties from India the correlation may not be very strong (Mallana and Ajwang, 1981).

The varieties used in this work were from a local collection, therefore, they would be expected to differ in grain yield because the two did not have the same field duration. Therefore the heavier weight values that were recorded for Enakuru were just a direct result of the longer duration of this variety in vegetative stages, in comparison to Ek-1. This could also be said for the higher heights attained by this variety (Enakuru).

The final grain yield is an end result of several metabolic and physiological processes that work in series or concurrently. The more important of these include flowering, grain set (as a result of fertilization), photosynthesis resource translocation and grain filling.

These processes which take place in the plant are subject to modification by environmental conditions such as water or salt stresses, among several others (Moss and Musgrave, 1971; Sing and Chandra, 1979). I have also noted that data collected from the experiments indicate a reduction in plant linear growth, leaf photosynthetic rates and plant water potential. I have also proposed that the water stress-like effects of the salt treatments exceeded any probable ion toxicity on the impairment of development.

Even though these water stress-like effects did not interfere with ear-head production yet the grain yield per head was affected.

It is probable that the stress may have interfered with flowering and the subsequent grain set. Even if this has not been quantified for finger millet, Saini and Aspinall (1981) have documented such evidence for wheat, Such reduced grain set would result in fewer grains per head and this would lower the values of such parameters as head weight amount of grain per head and head desntiy, though the 1000 grain weight may actually increase due to larger and heavier grain (Reddy and Lal, 1976).

Finger millet is a crop which lays down little reserve for retranslocation to the grain later on. So the post emergence

photosynthetic activity is very important as a determinant of grain yield (Sayi, 1977). This implies that impaired photosynthesis after ear emergence would result in poor grain filling because of the scarcity of photosynthates from the leaves. Under such conditions the proportion of the contribution from the ear-fixed photosynthates to the grain may increase, but because the ear has low rates of photosynthesis the grain-filling may still be poor (Tieszen and Imbamba, 1978; Perumal, 1980).

During the grain filling stage of finger millet, the grains form the major sink for food. However, under water stress finger millet may change its food partitioning with less food being allocated to such sinks as growing points and grains, and more being translocated to the roots (Udayakumar, Rao and Sastry, 1981). Under such effects the total amount of food allocated to the ears may be quite small because the total photosynthates are small in quantity.

Not all of the photosynthates translocated to the head will be used in grain-filling. Some of the photosynthates may be used in respiration (Tieszen and Imbamba, 1978), some may be used in laying down the non-seed (non-grain) parts of the head. The partitioning of resources between the grain and non-grain parts is reflected in such parameters as head density and 1000 grain weight.

In wheat it has been shown that water stress may interfere with grain filling due to impairment of biochemical activities in the grain themselves. In this case the biochemical processes,

rather than the supply of photosynthates, is the limiting factor (Aggarwal and Sinha, 1984). It is highly probable that such limiting biochemical processes were involved in the finger millet grain filling under salt stress. Evidence for this is derived from the results on head density and 1000 grain weight.

The decreasing head density in response to salt stress may reflect either poor grain set, poor grain filling or both. The reduction in 1000 grain weight is an indication of poor grain filling. When these parameters are used side by side, the results indicate the stress resulted in using more of the translocated photosynthates to lay down non-grain parts of the head. Otherwise fewer grains should have resulted in higher 1000-grain weight because of reduced sink competition (Reddy and Lal, 1976).

The grain protein content was not affected by the salt stress. Aggarwal and Sinha (1984) also noted that water stress did not affect the seed protein content of wheat. Their explanation for the observation was that unlike for photosynthates most of the nitrogen pool in cereal plants is built up prior to ear emergence, therefore, later retranslocation to grains is not limited by low supply. Apparently the explanation could apply in the case of finger millet.

The apparently higher grain yield by Enakuru would make it the better variety, of the two, to grow on saline soils. However, the statistical analyses show that Ek-1 was comparatively more resistant to the salt stress than Enakuru. Therefore the lower

yields recorded for Ek-1 were mainly a result of genotypic attributes in spite of treatment.

The argument has been based on the observation that salt-treatment affected the development of finger millet by water stress-like processes. Apparently Ek-1, true to its place of origin, is relatively more resistant to the stress than Enakuru. Any specific ion effects that may have resulted from the increase in tissue sodium, and a decrease in tissue calcium concentration remain obscure.

4.8. Summary:

This work has answered a few questions regarding the growth and development of finger millet (Eleusine coracana (L) Gaertn). It has been shown, for example, that salinity affected the germinating seeds and the green house plants primarily by water stress like processes.

However, other questions emerged to which I had no ready answers. This may form material for further research.

The perturbation of the developmental processes resulted from the effect of the stress on physiological and biochemical processes. The evidence for this could be adduced from the data collected on the α-amylase activity of the germinating seed, the apparent stomatal movements and net carbon dioxide fixation.

The salt stress reduced both the rate and percentage of germination. This was accompanied by loss of cations, and possibly organic solutes too.

The linear growth was reduced by the stress in both the seedlings and green house plants. However, no death of either the seedlings or the greenhouse plants was recorded as a response to salt stress. This implies that in none of the salinity levels employed was the stress lethal to the plants.

Apparently the salt stress did not impair cell differentiation; tiller production, for example, was not impaired by the stress. The effect of the stress on cell extension growth was not assessed nor was the rate of mitotic division. But because Hsiao (1973) has documented evidence to show that the cell extension growth may be more sensitive to water stress than the mitotic division, I concluded that the impaired growth may have resulted from impaired cell extension growth.

The salt stress interfered with leaf chlorophyll content, but had no effect on protein metabolism. The stress increased the tissue sodium content while that of calcium decreased. The tissue chloride and potassium content was not affected by the salt treatment.

In most of the developmental, physiological and biochemical aspects that were studied there were significant varietal differences. Most of these differences were inherent in the varieties and could be expressed even in the absence of treatment.

However, in a few aspects the response of the varieties to salinity differed significantly. In such cases the difference between the two varieties was either increased or nullified by the treatment. In most of the cases where the intervarietal

differences in the response to salt stress was significant Enakuru was the more responsive. Because most of these responses were connected with impaired plant processes, Enakuru, because of its higher response, was found to be less resistant to the salt stress than Ek-1. However, because Ek-1 is naturally a lower yielder than Enakuru, it ended up that Enakuru had higher grain yield than Ek-1, despite its higher susceptibility to salinity.

The lowest salinity level (4 mmho cm^{-1}, Ec) did not have significant impairment on most of the finger millet developmental processes; but even at the highest salinity no mortality was recorded, either in the laboratory or in the greenhouse. Successful flowering and grain yield was achieved under all levels of salt treatment. Hence it follows that the two varieties offinger millet could survive a salinity of up to 12 mmho cm^{-1} (Ece) in the substrate.

4.9. Suggestions

This work was not exhaustive, and only forms a base from which further and more detailed and specific work may be built. Indeed so much remains to be done, but a few prominent aspects are worthy noting.

At germination various processes and substances may influence emergence. The process which is most salient in salinity studies at this stage is the imbibition rate and level of the germinating seeds.

It is important that this process be quantified in finger millet seed. The other aspects which need attention include respiratory rates, hormonal status and the loss of organic molecules into the medium.

In the seedlings and growing plants there are a few aspects which need examining too. They included the effect of salt stress on growth rates, biomass accumulation (and the root-to-shoot ratio) and leaf area index.

As indicated earlier the results on ion concentration showed a general increase in the univatent cations without a concomitant increase in the chloride concentrations. There is need to find out what substance(s) would assume the role of a counter ion in the place of chloride in finger millet.

There is also need to examine the process of grain filling in salt-stressed finger millet.

Studies on the aspects which have been pointed out will help clarify the response of finger millet to salinity stress, particularly under field conditions.

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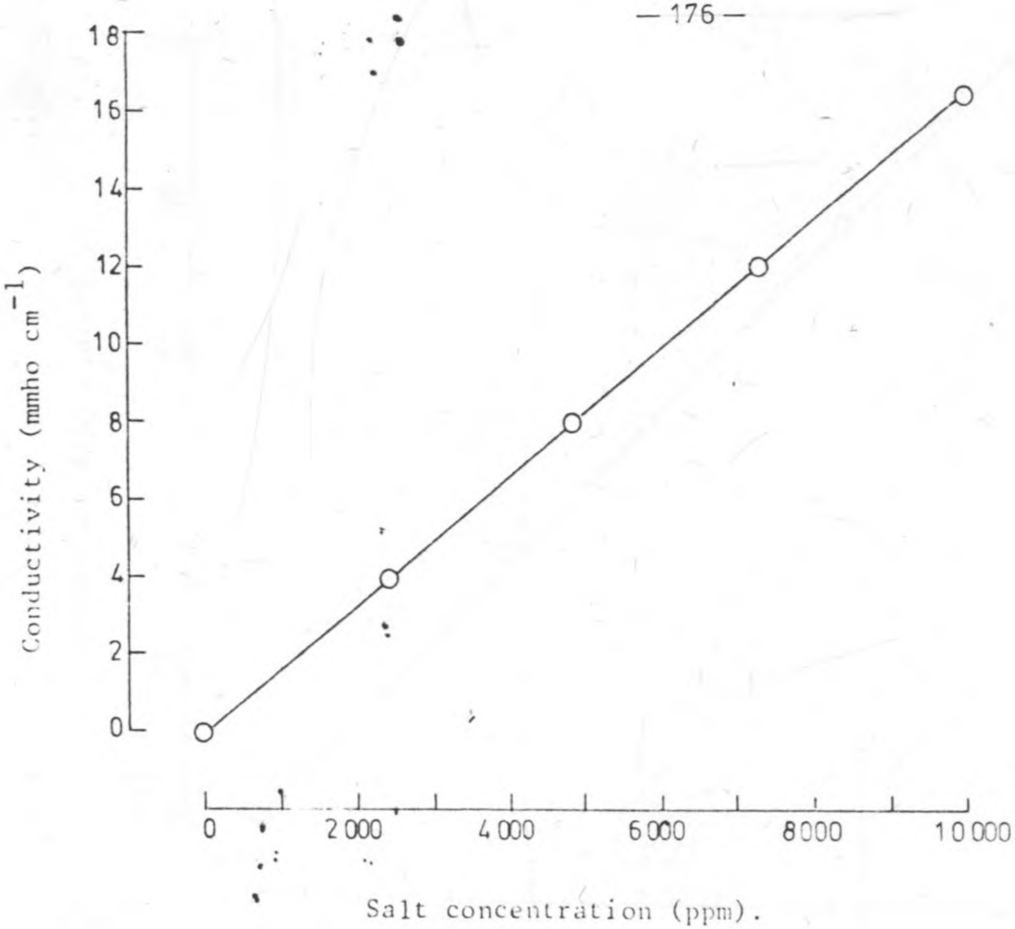
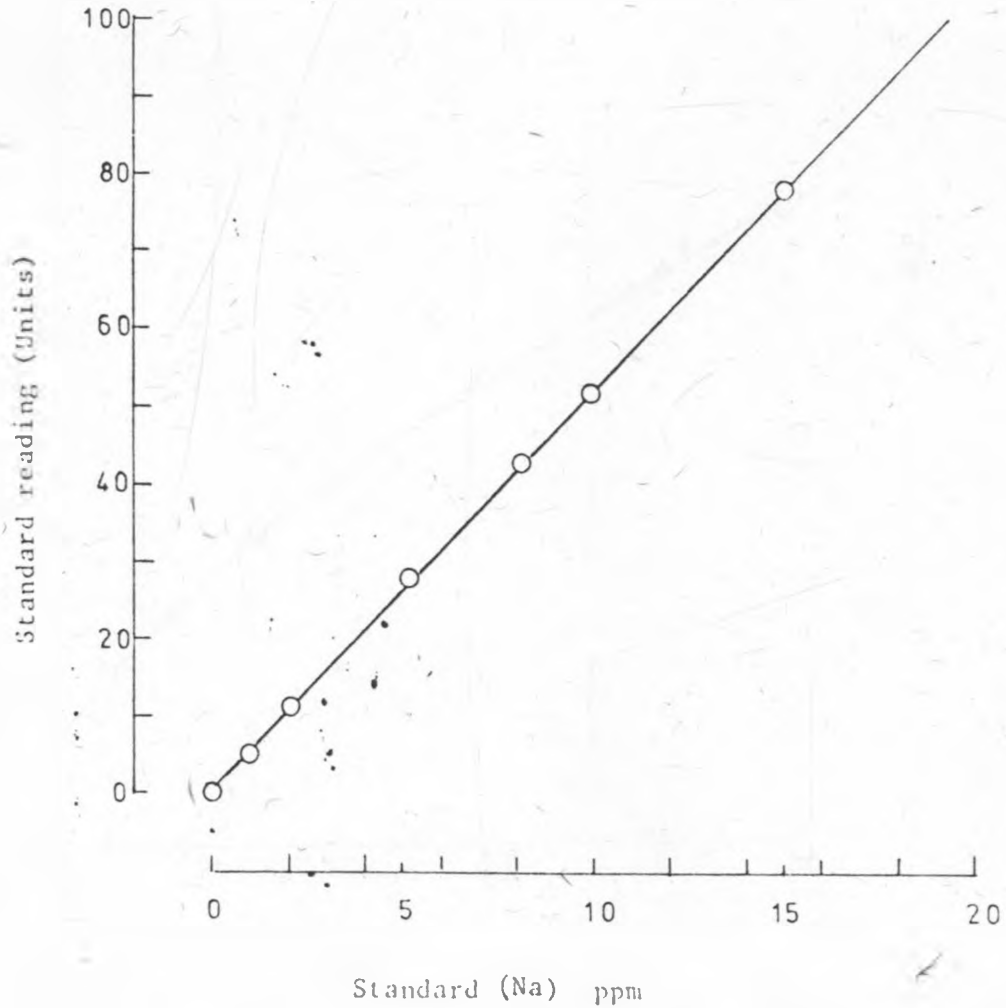
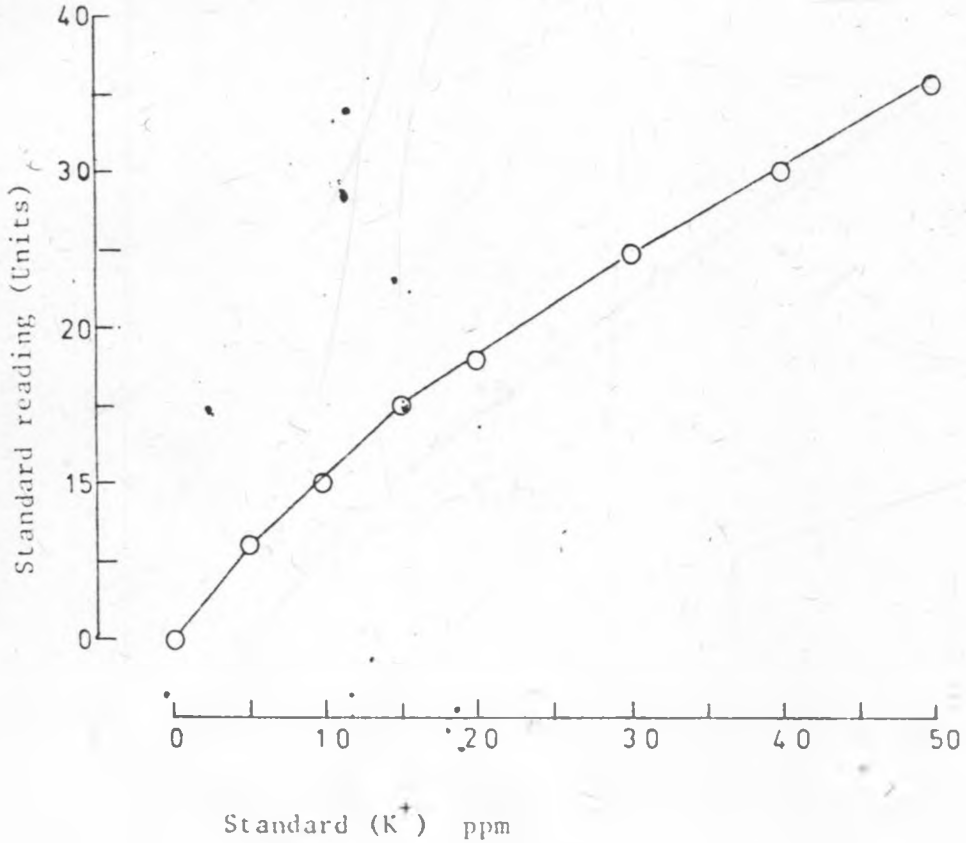


Appendix I. Standard Conductivity curve for table salt at 25°C.

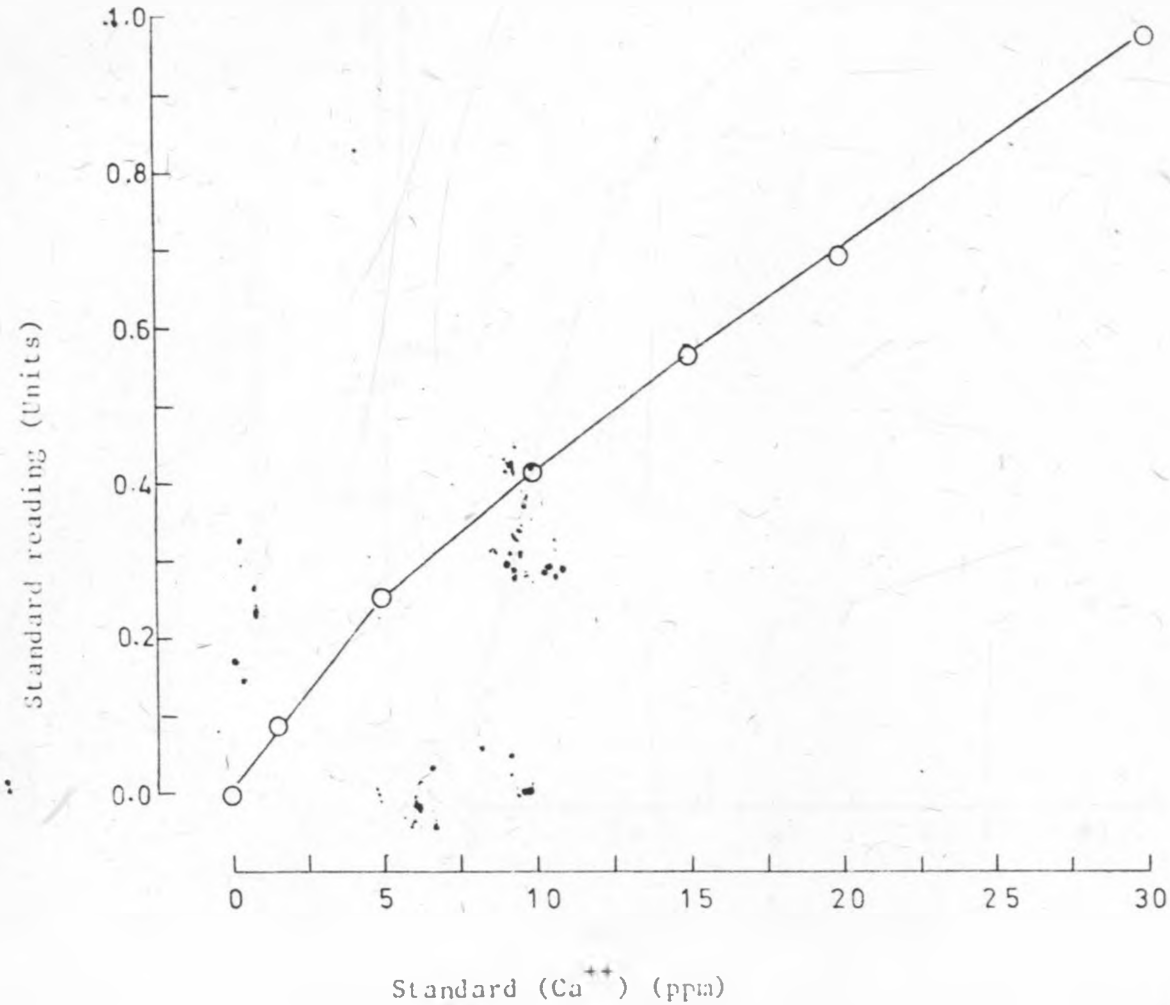


Appendix II: The sodium standard curve. This curve was prepared as outlined in Materials and Methods. (Ref. Allen, 1974).

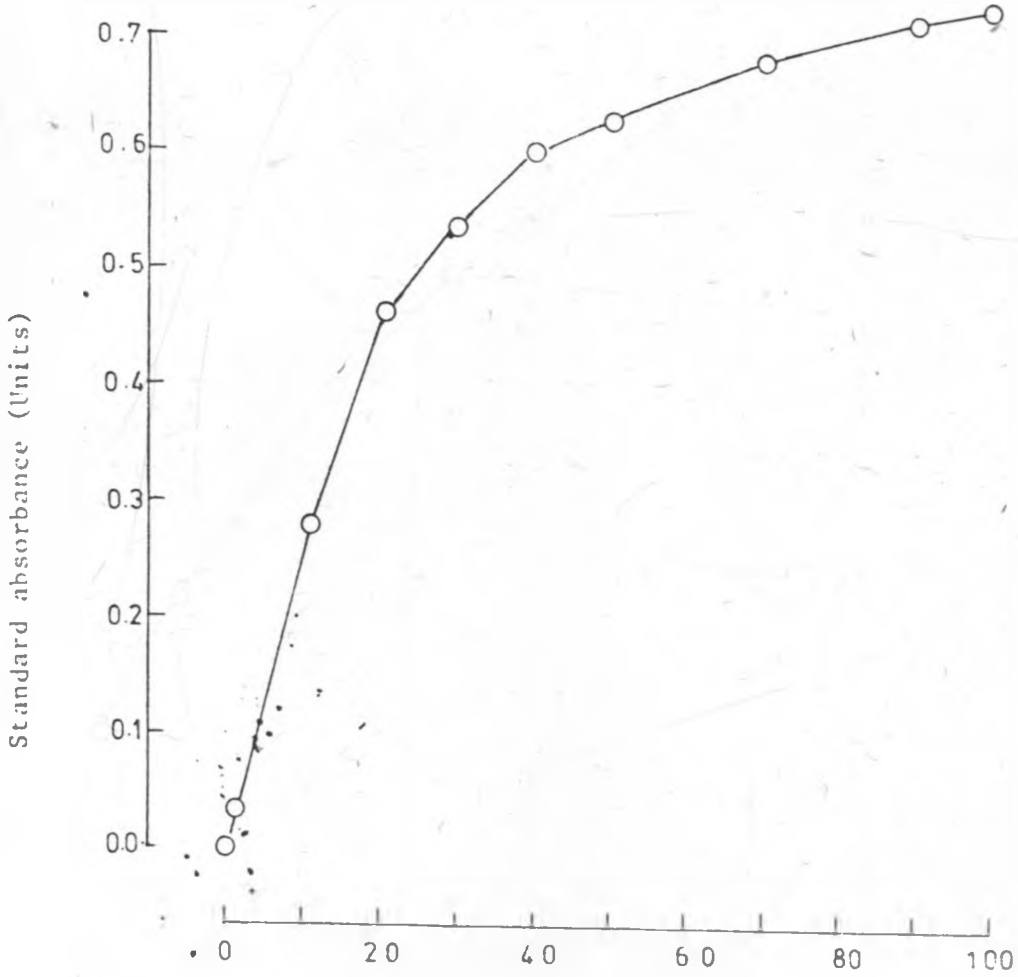


Appendix III: The potassium calibration curve. The curve was used to quantify the analyser readings for the tissue extract. The curve was constructed from the readings for standard potassium concentrations in a flame analyser.

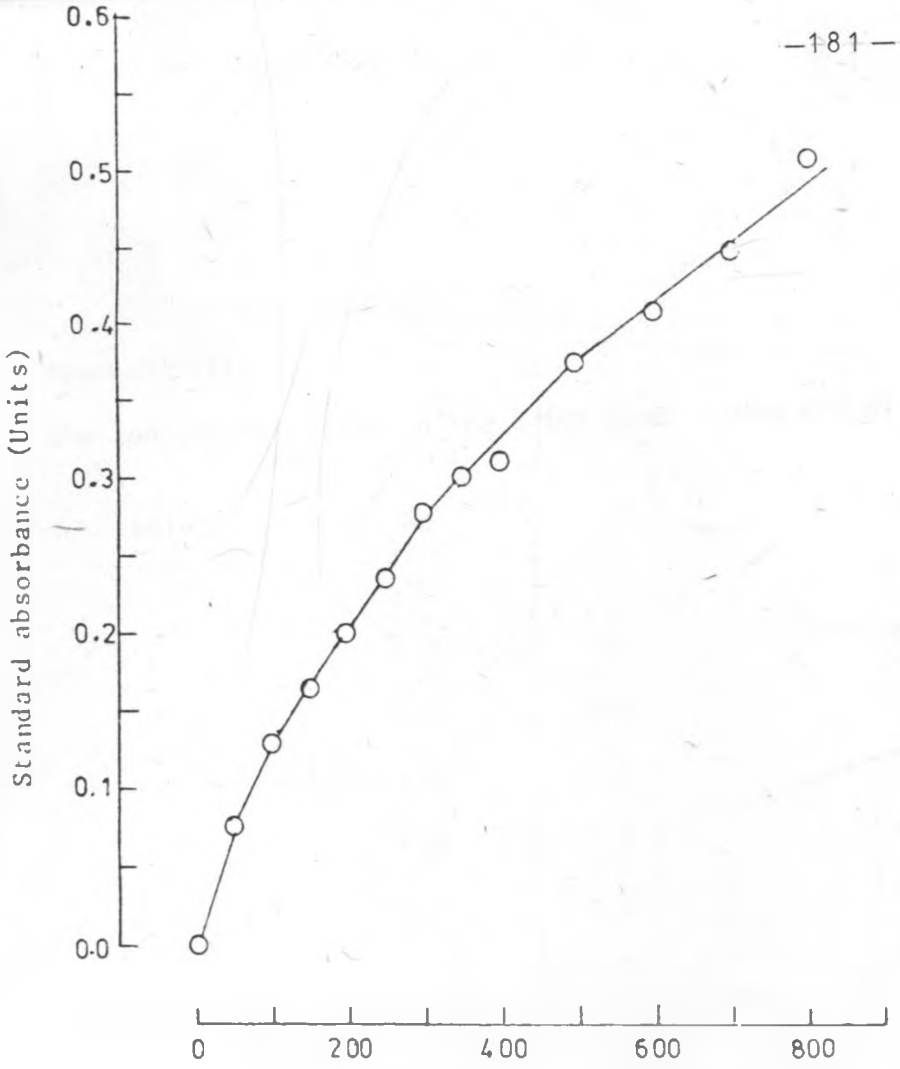
(Ref. Allen, 1974).



Appendix VII. The calcium calibration curve, prepared from standard instrument readings as outlined in Materials and Methods. (Ref. Allen, 1974).



Appendix V: Standard curve for starch: Constructed as outlined in Materials and Methods.



Appendix VI: Protein calibration curve. (Ref. Long, 1982).

Appendix VII.

The ion concentration in the stock seed (Meq KIO g).

ION VARIETY	Na		K		Ca	
	Ek-1		K	Ek-1	K	Ek-1
	1.4	0.9	5.1	4.9	3.0	2.8
	1.5	0.9	5.3	4.9	2.8	2.9
	1.2	1.2	5.0	5.3	2.7	2.8
	1.0	1.4	4.8	5.0	2.9	3.0
	1.3	1.3	5.6	4.6	2.8	2.8
	1.2	1.0	5.1	4.7	2.8	2.9
$\bar{x}$	1.2±	1.1	5.1	4.9	2.8	2.9
SE	0.06	0.09	0.04	0.2	0.04	0.03

Plate 1. General outlay of green house experiment.

Plate 2. A close-up of the small pot experimental plants as appeared in the green house.

Plate 3. A. close-up of the small pot plants showing the effect of soil salinity. The figures on the white cards show the salinity of the irrigation water (mmho cm^{-1}).