Chapter 1

General introduction

Irrigated agriculture and salinisation

The fast increase of the world's population rises concerns about the ability of the world's farmland to produce sufficient food. Irrigation gives higher potential yields per unit area and increases yield stability. An adequate supply of irrigation water is therefore important for agricultural production. However, the resources of good quality water do not meet the increasing demand. Ground water is a major water resource, but 55% of it is saline (Yeo, 1999), with Na^+ and Cl^- as the most abundant ions. For example, water resources in China, my home country, especially on the arid and semiarid loess plateau, have a high salt content. In some areas, even drinking water may taste salty. In coastal regions, there is a risk of seawater intrusion. For example, around Murcia (Spain), 55% of the irrigation water has an electrical conductivity (EC, deciSiemens per meter, dS m^{-1}) higher than 3.5 (Flower, 1999). Soil salinisation tends to increase after the start of irrigation. In the Shanxi province (China), more than one-third of the total area of irrigated land became salinised (Qiao, 1995). On a global scale, it was projected that, due to excess soil salinity, the productivity of currently irrigated cropland would at least be halved (Buras, 1992). Salinity has become the most severe agricultural problem in many parts of the world, and will be a significant issue in world agriculture during the twenty-first century (Flower, 1999). For this reason, plant response to salinity is one of the main research topics in agriculture, as inferred from the number of citations in plant science journals. In popularity, it comes second only to photosynthesis (Garfield, 1987).

Greenhouse production and salinity

Greenhouse horticulture has developed into a separate, economically significant agricultural activity. Year-round high yields of good quality are possible with modern techniques and new cultivars in intensive greenhouse horticulture. However, in greenhouse soil culture, secondary salinisation, caused by high input of fertilisers, is also a big problem. Irrigation with excess water or crop rotation with non-food crops could solve this problem, but only at the expense of efficiency. In this respect, a transition from soil culture to soilless cultivation represents an appealing challenge.

There are many advantages in soilless cultivation: more suitable growing conditions (*e.g.* suitable temperature, good aeration of the root zone, uniform and suffi-

cient supply of water and nutrients); reduced labour requirement (less weed and cultivation management); less problems with soil borne diseases, *etc.* all leading to increased profit and higher product quality. Moreover, the growing season can be extended and growers may specialise on certain crops. In a soilless cultivation system, nutrients are supplied to plants dissolved in irrigation water. The concentration of the nutrient solution is closely related to the electrical conductivity (EC). However, when in soilless cultivation, abundant and fresh nutrient solution should be supplied to maintain the nutrient balance. For example, in rockwool cultivation, normally 30% more nutrient solution (Van Os, 1995) or *ca* 10 to 25% more salts (van de Vooren *et al*., 1986) are needed to meet the water demand and prevent solute accumulation. The additional water and salts drain out into the soil, and pollute the soil and the surface water. To solve this problem, Dutch growers have to adopt re-circulation of the nutrient solution.

A growing system with re-circulation of the nutrient solution ('closed system') ensures a total reuse of water and nutrients, and links savings of water to a decreased emission of nutrients. The uptake concentration of single nutrients is not necessarily equal to the concentration in the solution (Steiner, 1984). Therefore, nutrients will accumulate after a certain period of re-circulation. In addition, non-nutrient salts, such as Na^+ and Cl^-, may accumulate in the nutrient solution, since these ions are not readily absorbed by most plant species. That is, poor water quality can cause salinity problems also in closed growing systems. The EC of the nutrient solution is very important for crop production, since EC affects the quality and quantity of crop production.

Yield response to salinity

Salinity research has been done with many greenhouse crops (Shannon and Grieve, 1999), especially with tomatoes (Cuartero and Fernández-Muñoz, 1999). It is well established that crop yield decreases with increasing salinity (Maas and Hoffman, 1977; Maas, 1986). In general, salt tolerance or salt resistance is described as a function of: the salinity level at which the initial yield decline is observed (threshold EC value), and the yield decrease per EC unit (Maas and Hoffman, 1977). Both parameters differ among crops (Maas and Hoffman, 1977; Shannon and Grieve, 1999). The response of vegetative growth and growth of storage organs to salinity is not always the same (Maas and Hoffman, 1977). With tomato, fruit yield is mainly decreased because the uptake of water into the fruit is reduced and fruit size decreases (Adams and Ho, 1989, Sonneveld and Wells, 1988). However, whether and how the accumulation of dry matter per fruit is affected at high EC is a matter of controversy in the literature. Both no effect (Ehret and Ho, 1986a; Adams and Ho, 1989) and negative effects (van Ieperen, 1996; Petersen *et al.*, 1998) are reported. Dry matter content in the fruit crops increases with EC (Ehret and Ho 1986a; Awang *et al.* 1993b; Savvas and Lenz, 2000), which is a very important pa-

rameter of produce quality. Other parameters of fruit quality, *e.g.* acidity, concentration of sugars and of total soluble solids, are also highly increased in tomato by salinity (Mitchell *et al.*, 1991; Petersen *et al.*, 1998). Increased salinity, however, may also cause the incidence of physiological disorders, such as blossom-end rot (BER) in tomato and pepper (Adams, 1991; Sonneveld and Van der Burg, 1991). Physiological fruit disorders affect fruit quality adversely, may significantly reduce fruit yield, and cause considerable economic losses. The application of a high EC to improve fruit quality goes along with a big reduction of yield. Therefore, it would be attractive to take advantage of the quality-effect of saline water, while finding ways to limit yield reduction, what is the scope of the present study.

Response to salinity is modulated by the shoot environment

It has been reported that a humid atmosphere may modulate the effect of salinity. Sonneveld (1988) found in greenhouse experiments a lower salt sensitivity for several species than that reported by Maas and Hoffman (1977) in field experiments. The difference was attributed to the higher humidity in a greenhouse, compared to outdoors. With bean, onion and radish, Hoffman and Rawlins (1970, 1971) observed that a high humidity significantly raised the salinity level at which the yield was reduced to 50% of the yield under non-saline conditions. O'Leary (1975) reported that high humidity overcame lethal levels of salinity in red kidney bean. Salim (1989) concluded that plant growth on a saline root medium could be improved by exposure of the plants to a high relative humidity, which resulted in a decreased accumulation of ions in the plant.

Importance of water relations

Salinity increases the osmotic pressure of the nutrient solution. Plants respond to salinity with osmotic adjustment (Munns, 1988) though growth is reduced (Yeo, 1983). A possible reason for growth reduction mentioned in the literature (Hoffman *et al.*, 1980; Greenway and Munns, 1980; Munns *et al.*, 1982) is water stress. Hsiao (1973) stated that lower water potential due to water stress restricted the expansion growth of plant cells. High salinity may also result in a too-high internal ion concentration (ion excess or ion toxicity) or in ion deficiency (nutritional imbalance), thus causing growth reduction (Bernstein, 1975; Greenway and Munns, 1980; Blum, 1986). In addition, the stomatal conductance may be affected, which results in a decrease of photosynthesis (Yeo, 1983; Xu *et al*., 1994).

The counteracting effect of salinity and of air humidity is usually explained by their effect on water stress within a plant (Hoffman and Rawlins, 1971; O'Leary, 1975; Salim, 1989). Therefore, in the framework of this research, it is postulated that water stress in the case of increased salinity is the main cause of growth reduction. The toxicity of heavy metals, and nutrient deficiencies caused by interactions

between ions are outside the scope of this thesis.

Water is taken up by the roots and lost through transpiring leaves. A reduction of the transpiration rate may improve the water status of plants, and alleviate the negative effect of salinity. Figure 1.1 depicts the relationship between EC, transpiration and fruit fresh weight. EC and transpiration are the two factors that affect the plant water content, although their effects may differ in size and direction. EC determines water inflow through the roots, while transpiration controls water outflow. Therefore, salinity (osmotic potential) in the nutrient solution and potential transpiration in the shoot environment affect the water status of the plant. The effect of salinity and the effect of potential transpiration on the plant water content may interact. Although the potential crop productivity ultimately depends upon carbon fixation (photosynthesis) and dry matter production, the production of fresh marketable yield is of critical significance for horticultural crops. The complex route from photosynthetic assimilation to fresh fruit production offers many opportunities to influence crop yield and crop quality. In this respect, water relations are essential, because, as indicated before, the yield is largely governed by water accumulation.

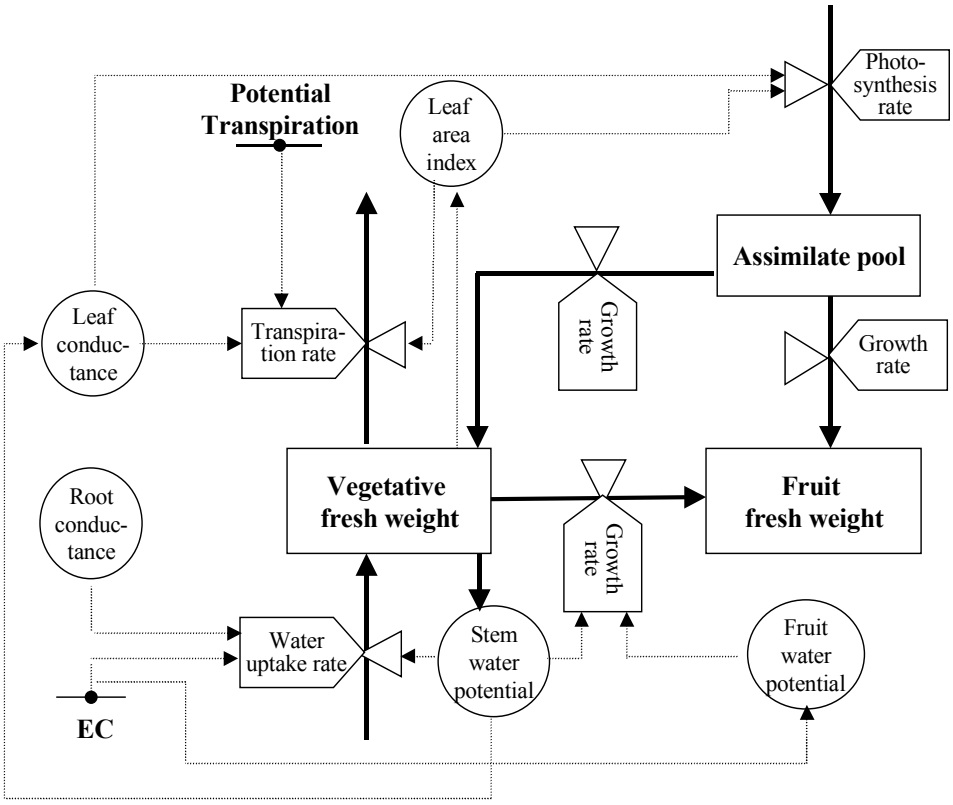

Figure 1.1 Schematic diagram of the influence of the EC and transpiration on fruit fresh weight.

Manipulation of transpiration in a greenhouse

Plant transpiration is governed by climate conditions, leaf area index and stomatal conductance. Transpiration in greenhouse cultivation differs from that in the open air, since the greenhouse cover prevents natural precipitation and seals the greenhouse interior from the ambient atmosphere. Thus the climate in a greenhouse can be controlled, and is normally more humid than in the open air. However, a high humidity may have some side effects and cause plant diseases (Grange and Hand, 1987; Hand, 1988). Adams and Holder (1992) found that dry matter accumulation by the leaves of tomato plants always decreased with increasing humidity (vapour pressure deficit from 0.1 to 0.8 kPa) during winter. After a prolonged period of high humidity, leaf expansion of tomato plants was restricted, smaller leaves were produced due to local calcium deficiency, which resulted in decreased fruit yield (Sonneveld and Welles, 1988; Bakker, 1990; Holder and Cockshull, 1990). In addition, fruits grown at high humidity generally have a shorter shelf life, since they soften more quickly (Janes and Welles, 1984). Therefore, manipulation of transpiration in greenhouses has to be incorporated in a strategy dealing with all aspects, not just salinity problems.

Solar radiation supplies energy to the canopy and is the cause of plant transpiration, which in turn lowers leaf water potential. A decrease of the leaf water potential increases the gradient of the water potential between the roots and the leaves, thus stimulating water uptake, water flow *via* the plant and transpiration into the atmosphere. Plant transpiration is a very important physiological process, which not only serves as the driving force for water uptake and water transport, but also affects the uptake and distribution of nutrients. Therefore, the interaction between transpiration and water uptake is also relevant for the nutrient balance. Cockshull (1988) suggested that direct manipulation of growth-related plant processes could improve the quality of produce and the efficiency of production. Stanghellini (1987) developed a model for the relation between the microclimate in a greenhouse and the transpiration rate of a greenhouse crop. With this model, the desired transpiration rate could successfully be achieved by controlling the humidity and temperature of a greenhouse under a given incoming global radiation (Stanghellini and Van Meurs, 1992). Jolliet and Bailey (1992) showed that among the different existing models, Stanghellini's model was reliable and gave a good prediction of the transpiration rate of tomato.

Research objective, delimitation and choices

To my knowledge, no research has been reported on the use of transpiration control to alleviate the salinity problem. Modern computer control systems and knowledge assembled in crop models, could be used to improve the plant internal water status by controlling transpiration in relation to the osmotic potential of the root environment. For a better understanding and optimal use of knowledge of climate control

in relation to salinity, a series of experiments was conducted with different salinity levels, under controlled potential transpiration. The **objective of the present study** is to develop the control of transpiration as a tool to reduce the negative effects of salinity, without decreasing produce quality. The **scientific aim of this work** is to explain the interaction between water inflow (root environment) and water outflow (shoot environment) in determining plant fresh weight accumulation. The approach adopted should help growers to achieve a combination of maximum fruit quality with minimum yield loss. The results of this thesis should be useful to optimise the management of water, nutrients and climate in a greenhouse.

The applied EC in the experiments was always below 10 dS m^{-1}, because at higher EC the salinity effects are more severe, and have little bearing to problems in practice. A decreased transpiration regime was implemented with the transpiration model of Stanghellini (1987). Since the present research aimed to provide information for the management of commercial greenhouses, the long-term cultivation and production of mature plants was studied. Tomato (*Lycopersicon esculentum* L.) was selected as the experimental crop. This choice was based on horticultural and botanical arguments. Tomato is a widely distributed annual horticultural crop. The indeterminate tomato continues developing fruits and leaves. The plant is easily trained with a single main stem and all lateral shoots can be removed. In this way, vegetative and generative development can be measured from the number of leaves or the number of fruit trusses. Nearly year-round growing of tomatoes provides an opportunity to observe the long-term response to salinity and transpiration. Tomatoes are classified as moderately tolerant to salinity (Maas and Hoffman, 1977), and much salinity research has been performed with tomato. The wealth of information about the response of this crop to salinity was a good starting and reference point for the present research.

Outline of the thesis

The most important characteristics of tomato for growers are fresh yield and fruit quality. In Chapter 2, crop performance in terms of fruit yield, fresh and dry yield, fruit number and unmarketable fraction is presented. To compare data from different experimental years, the efficiency of the total production and of the production of marketable fresh fruits (per MJ PAR, photosynthetically active radiation), are discussed and explained in relation to EC and transpiration. Leaves are the sites of transpiration and photosynthesis in a plant. Therefore, leaf growth was continuously investigated as an important parameter, especially in relation to water flow. In the range of 2 to 9.5 dS m^{-1}, the threshold EC-value for leaf expansion, and leaf area index (LAI) were investigated, and the light interception was estimated in relation to LAI (Chapter 3), to explain effects of salinity and transpiration on dry matter accumulation. The effect of sodium chloride in the nutrient solution on fruit yield and vegetative growth was also investigated. The final fruit size is a very im-

portant yield component and is the resultant of the (average) fruit growth rate and the fruit development period. The effect of salinity and potential transpiration on growth rate and development period is treated in Chapter 4. To understand the accumulation of dry matter in relation to the increase in fruit size, the diameter and the dry matter content of fruits were monitored during fruit development.

To test whether growth reduction is related to the flux of water, or to physiological changes, one experiment was designed in which the EC of the nutrient solution was lowered after a long-term exposure of plants to high salinity (Chapter 5). An analysis of the reversibility of plant growth, both of fruits and of leaves, after relieving salinity stress is given. In this experiment the progression of fruit cracking was also investigated. The latter data yielded valuable information about water flow into the fruits.

Differences in plant growth have a physiological basis. Water status of plants, and water flow through plants are related to the plant water potential. Transpiration affects the leaf water potential, and affects the gradient of water potentials between plant organs. Similarly, a high EC induces a low osmotic potential in the root zone and results in a low water potential in plants. The gradients of water potential together with the hydraulic resistance within a plant determine water flow. Therefore, water potentials in the stem, the leaves and the fruit were investigated in relation to the osmotic potential of the nutrient solution and the transpiration treatments (Chapter 6). The hypothesis that water flow into the fruits is affected both by the osmotic potential of the nutrient solution and by potential transpiration, through their effects on the stem water potential and the gradient of potentials between the stem and the fruits, is analysed.

In the general discussion (Chapter 7) an attempt is made to provide an overall picture of the interaction between transpiration and the effect of salinity. The function of transpiration to control and modify the effect of salinity on crop production, and to optimise the climate regime in horticultural practice is discussed.

Chapter 2

Effect of EC and transpiration on production of greenhouse tomato (*Lycopersicon esculentum* L.)

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Abstract

We investigated the hypothesis that manipulating water outflow of a plant through the shoot environment (potential transpiration, ET_0) in a glasshouse could modulate the effect of salinity/osmotic potential in the root environment upon yield of tomatoes. Contrasting root-zone salinity treatments were combined with two climate treatments—a reference (high transpiration, HET_0) and a "depressed" transpiration (low transpiration, LET_0). The salinity treatments, characterised by their electrical conductivity (EC) were 6.5, 8 and 9.5 dS m^{-1}, were always coupled with a reference treatment of EC 2 dS m^{-1}. In a fourth experiment, concentrated nutrients (Nutrient) and nutrients with sodium chloride (NaCl) at the same EC of 9 dS m^{-1} were compared.

Marketable fresh-yield production-efficiency decreased by 5.1% for each dS m^{-1} in excess of 2 dS m^{-1}. The number of harvested fruits was not affected; yield loss resulted from reduced fruit weight (3.8% per dS m^{-1}) and an increased fraction of unmarketable harvest. At the LET_0 treatments, yield loss was only 3.4% per dS m^{-1} in accordance with the reduction in fruit weight. Low transpiration did increase fruit fresh yield by 8% in both NaCl and Nutrient treatments at an EC 9 dS m^{-1}.

Neither EC nor ET_0 affected individual fruit dry weight. Accordingly, fruit dry matter content was significantly higher at high EC than in the reference (4% per each EC unit in excess of 2 dS m^{-1}) and responded to ET_0 to a minor extent.

Control of the shoot environment in a greenhouse to manipulate the fresh weight of the product may mitigate the effects of poor quality irrigation water without affecting product quality.

2.1 Introduction

In soilless cultivation, fertilisers are dissolved in the irrigation water (nutrient solution). The total concentration of solutes in the nutrient solution is characterised by the electrical conductivity (EC, dS m^{-1}). Usually EC in commercial tomato production is in the range of 2 to 5 dS m^{-1}. Too low a concentration causes mineral defi-

ciency and restricts plant growth (Winsor and Adams, 1987), whereas, there is no negative effect of an overabundant supply of nutrients, at least within a broad range. To avoid deficiencies and to control the quality of harvestable product, large amounts of nutrients are added to the irrigation water, with little attention to the actual uptake by the crop.

Re-use of drain water enables economic use of water and fertilisers combined with an ample water supply to the crop (Sonneveld and Welles, 1984). The Dutch government also stimulates re-use of drain water in order to reduce the emission of nutrients to the environment (Van Os, 1996). However, long-term re-circulation of drain water results in accumulation of the salts that may come with re-fill water and are not taken up and the fertilisers that may be injected in excess of actual needs.

It is known that salinity (high EC) reduces yield. Uptake of water into the fruits is reduced by a high osmotic pressure of the irrigation water and as a result the fruit size is smaller (Ehret and Ho, 1986a; Sonneveld and Wells, 1988; Van Ieperen, 1996), although the accumulation of dry matter per fruit is unaffected (Ehret and Ho 1986a). Increased salinity also increases the incidence of blossom-end rot (BER) (Adams, 1991; Sonneveld and Van der Burg 1991; Van Ieperen, 1996), a disorder that is associated with low calcium concentration in the fruit (Chiu and Bould, 1976) especially in the distal end (Ho and Adams, 1989). On the benefit side, mild saline irrigation water may improve the quality of horticultural products by increasing dry matter content and sugar concentration in the fruit (Sonneveld and Welles, 1988; Adams and Ho, 1989; Gough and Hobson, 1990; Willumsen *et al.*, 1996).

However, the salt concentration in the root environment is not the only factor that influences the water status of the plant. Normally, more than 90% of the water absorbed by the root is lost by transpiration. The water content of the plant is the resultant of the balance between inflow (water uptake) and outflow (transpiration). The water content (water potential) in turn affects plant growth and yield. Bruggink *et al.* (1987) proposed that it should be possible to enhance plant growth by adapting the salinity level to the rate of transpiration. Hoffman and Rawlins (1971) reported that high humidity (and thus low potential transpiration) significantly raised the salinity level at which the yield was reduced to 50% of the non-saline yield for onion and radish.

The aim of the present research was to investigate the hypothesis that manipulating water outflow of a plant through the shoot environment (potential transpiration, ET_0) in a glasshouse could modulate the effect of osmotic potential in the root environment upon yield of tomatoes. The practical implication of this study was to ascertain whether lowering potential transpiration could mitigate the negative effects caused by high EC in closed loop growing systems.

The approach was to combine different concentrations (EC) of the nutrient solution factorially with two climate treatments, “low” and “high” potential transpiration. The experiments were mainly focused on long-term effects and therefore con-

centrated on the production phase of the crops. For this reason we started the treatments after the plants were well developed.

2.2 Materials and methods

The experiments were performed in two compartments (300 m^2 each) of a multi-span Venlo glasshouse (IMAG, Wageningen, the Netherlands). The crop was in all cases tomato, *cv* Chaser, and the seedlings, growing in a rockwool cube (10×10×6.5 cm), were transplanted on rockwool slabs placed in a gutter, when the inflorescence of the first truss was visible. Crop density was 2.2 plants m^{-2}, in east-west oriented rows. The plants were trained in the high wire system (Van de Vooren *et al*., 1986), every other plant either to the north or to the south. Re-circulating nutrient solution was supplied (drain fraction in excess of 70%) with the aid of a trickle irrigation system. All axillary shoots were removed weekly and only the main stem was left. 3 to 5 leaves were pruned every fortnight, according to commercial practice, up to the fruit truss just before colouring. Bumblebees were used for pollination and pest control was mainly biological. Fungicide was sprayed whenever it seemed necessary.

2.2.1 Treatments

The experiments were performed in different seasons. Some relevant information about the experiments is provided in Table 2.1. Each experiment was carried out in two compartments with different climate treatments. In each compartment, two nutrition treatments were applied, fed by two commercial substrate-irrigation units, each feeding half of the rows in both compartments (Figure 2.1).

Table 2.1 Some basic information on the experiments: year, experiment number (Exp. No), period of experiment (from transplanting till last harvesting), electrical conductivity (EC, dS m^{-1}) of nutrition treatments, transpiration treatments (ET_0).

Year	**Exp. No**	**Plant growing period**		**EC**	**ET_0**
		From	*To*	*Low* *High*	*LET_0* *HET_0*
1996	1	Dec. 15 '95	Jul. 1	2 9.5	65% Normal
	2	Jul. 10	Oct. 28	2 8	65% Normal
1997	3	Dec. 16 '96	Jul. 3	9-NaCl 9-Nutrient	65% Normal
1998	4	Jan. 6	Sep. 28	2 6.5	Less ventilation and Limited to 0.15 l h^{-1} per plant Normal

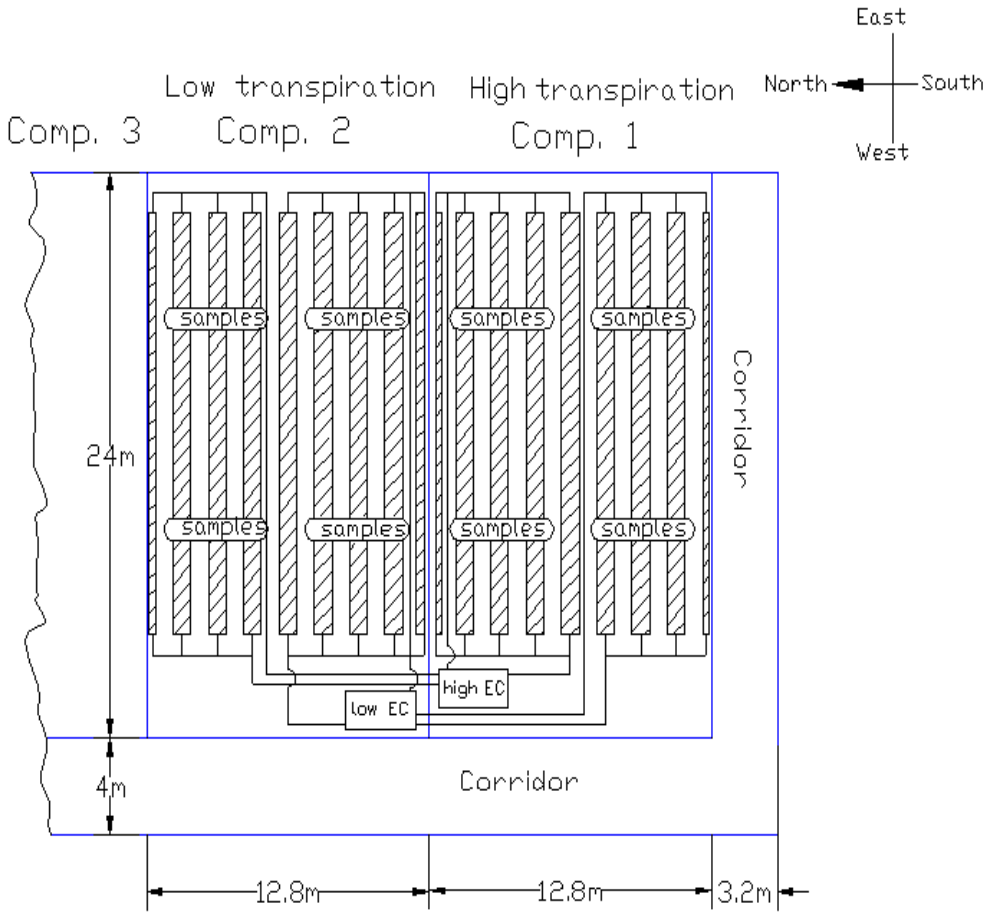

Figure 2.1 Design and arrangement of potential transpiration and salinity treatments in two glasshouse compartments. The 4-plants sample plots for yield monitoring were in the row marked "samples" (two each row).

Shoot environment treatment

In all experiments one compartment was controlled according to Dutch commercial practice, that is pre-fixed set-points of day- and night-temperature (20 and 18 °C) respectively, with an allowance for solar radiation and crop stage. Ambient humidity was controlled by setting minimum values (day- and night-time) for vapour pressure deficit (VPD). Roof windows would open whenever VPD fell below that minimum, regardless of the air temperature, which often meant the heating system had to be switched on, a practice known to contribute significantly to energy consumption in Dutch protected cultivation. A proportional controller regulated the opening angle of the windows. The transpiration rate that followed from this climate control was calculated on line, according to Stanghellini (1987) and served as the "reference", hereafter called high-transpiration treatment (HET_0). In the other compartment (low-transpiration treatment, LET_0) potential transpiration was reduced to 65% of HET_0, using an algorithm described by Stanghellini and Van Meurs (1992). Ambient humidity was controlled by a combination of venting and high-pressure misting. Only when humidity control alone was not sufficient to attain the required transpiration

reduction, was the set point of air temperature allowed to decline. In one experiment (experiment 4), transpiration was reduced by reducing VPD-ventilation (low than in the other compartment). In addition, the misting system was switched on whenever the transpiration calculated for the reference compartment exceeded 0.15 $l\ h^{-1}$ per plant that is 0.33 $mm\ h^{-1}$. In fact, the weather was so bad during that experiment, that the misting system had to work only for a total of 147 hours, and there were only 16 days during the nine months experiment when it worked at least three hours.

Pure carbon dioxide (CO_2) was injected in all cases up to a constant daytime concentration of about 400 vpm in both glasshouses.

Root environment treatments

In most experiments a "reference" nutrient solution (EC 2 $dS\ m^{-1}$) was compared with a treatment with a higher concentration (EC =6.5, 8 and 9.5 $dS\ m^{-1}$, respectively). In one experiment a high concentration of nutrients (Nutrient) was compared with sodium chloride (NaCl) (Table 2.1).

As common in re-circulating systems, drain water of each nutrition treatment was collected in a mixing tank whose level was kept constant by refilling with fresh water. At each irrigation event the system ensured that water drawn from the tank was brought (if necessary) to the required EC level by drawing from concentrated solution tanks. In the treatment with NaCl, the amount of sodium chloride equivalent to an EC of 7 $dS\ m^{-1}$ was put into the loop beforehand. Then the system would supply nutrients from the concentrated tanks till the required 9 $dS\ m^{-1}$. Each week the concentration of NaCl was manually controlled, and NaCl was added if necessary. In all cases, to ensure uniformity of concentration in the slabs, continuous re-circulation (without injection of nutrients) took place for about two hours each night.

The concentration of the nutrient solution in the root zone was manually controlled twice a week in blended random samples drawn from the slabs. Overabundance of supply ensured that the EC of the drained solution (that was monitored) seldom diverged significantly from the EC of the supply water (the one that was controlled). The elemental composition of extracts from the root environment was determined at intervals of 20 days up to one month. Results were used for preparing the concentrated solutions of each treatment. The average composition of the nutrient solution extracted from the root environment in each treatment and experiment is shown in Table 2.2.

In all experiments both climate and root-zone treatments started around the time that leaf 20 appeared (about one month after transplanting) to ensure similar crop and root development at the start of the experiment. The EC treatments were gradually achieved during a week, starting from a common value of 4 $dS\ m^{-1}$.

Table 2.2 Treatment EC (dS m^{-1}, irrigation EC) and mean EC of root extracts (root env. EC); mean pH and elemental composition (mmol l^{-1} for macro- and μmol l^{-1} for micro-elements) of root extracts, for the various experiments. Values are means of measurements at two weeks intervals, during the treatment period.

Exp. No	Irrigation EC	Root env. EC	pH	NH_4	K	Ca	Mg	NO_3	SO_4	H_2PO_4
1	2	2.1	5.9	0.1	4.7	4.5	1.9	9.5	3.6	0.7
	9.5	9.2	5.4	0.4	35.2	25.8	9.9	74.6	13.0	4.8
2	2	2.2	5.6	0.2	3.3	5.4	2.0	14.0	2.2	1.1
	8	8.3	4.9	0.2	31.7	19.1	7.3	59.6	9.6	4.7
3	9-NaCl	8.9	6.1	0.1	5.6	11.2	5.1	19.7	7.3	1.5
	9-Nutrient	9.1	5.6	0.2	21.4	23.8	11.8	56.4	13.6	4.4
4	2	2.3	6.1	0.1	2.0	6.4	2.3	12.0	3.8	0.4
	6.5	6.9	5.2	0.1	14.4	20.3	9.6	49.1	11.3	4.0
	Irrigation EC	Na	Cl	Fe	Mn	Zn	B	Cu	Mo	
1	2	2.8	1.9	20.0	4.8	7.9	43.6	3.3	1.0	
	9.5	5.2	2.9	63.2	25.0	22.8	125.1	4.0	2.9	
2	2	2.6	0.4	22.3	6.9	6.5	36.2	2.6	0.3	
	8	4.7	1.5	68.6	26.4	14.0	106.9	5.6	0.5	
3	9-NaCl	49.6	52.4	22.7	7.1	8.6	64.6	2.7	1.6	
	9-Nutrient	6.3	4.7	54.3	29.4	13.3	166.6	4.8	1.8	
4	2	4.6	2.3	20.5	3.7	7.9	30.0	4.8	0.6	
	6.5	5.8	2.4	51.8	15.4	13.9	134.5	5.1	1.2	

2.2.2 Measurements

Water uptake and climate

Actual water uptake of the crop in each treatment was determined from the balance of readings of irrigation and drain; re-fill of the tanks was also monitored to check for leaks. In experiments 1 and 2 only sunrise and sunset readings were available. Thereafter, all flow meters were logged at two-minute intervals; in addition, drain flow from an 8-plants section of a central row of each treatment was monitored, with the same frequency, by tipping buckets.

All the relevant climate data in each glasshouse, in particular temperature, vapor pressure deficit, CO_2 concentration, opening angle of ventilators and outside weather were recorded every 2 minutes.

Crop observations

Production was monitored on six 4-plant random samples from the central rows of each treatment (Figure 2.1). Ripe fruits were harvested twice a week. Total fruit

number and weight, marketable and unmarketable fraction were determined separately for each 4-plant sample. Marketable yield from each treatment was subsequently pooled and classified in four size grades, namely: A, B, C and CC (47-57 mm, >57 mm, 40-46mm, <40mm) (van de Vooren *et al*., 1986).

Thereafter, 50 ripe (red) class-A fruits were selected for each treatment and separated into five samples of 10 fruits each that were homogenised with a home-mixer. Dry matter was measured after 24 hours drying at 105 ^{0}C and ash content subsequently, after 4 hours at 550 ^{0}C. Acidity (pH) and EC of each mixed sample were determined. Refraction index (Brix index) of fruit sap was determined twice independently per sample, using juice clarified by centrifugation (4500-rpm, for 5 minutes). This was done for each harvest in experiments 1 to 3, and three times during experiment 4.

2.3 Results

2.3.1 Environment

Table 2.3 shows average values of VPD, day- and night-time temperature in each house and outside solar radiation for each experiment. In experiments 1, 2 and 3, daytime water uptake at LET_0 was indeed closely approaching the desired 65% ratio (Figure 2.2). The measurement with tipping buckets of 8 plants proved more ac-

Table 2.3 Mean vapour pressure deficit (VPD), temperature (T) during daytime (Day), night (Night) and 24 hour (24h), during the treatment periods of the various experiments. The last column is global radiation integral (GR) outside the house, averaged for the whole growing period.

	Treatment period						GR (MJ m^{-2}d^{-1})
	VPD (kPa)			T (^{0}C)			
	Day	Night	24h	Day	Night	24h	
Exp. 1							
HET_0	0.51	0.44	0.49	21.0	18.4	20.0	11.7
LET_0	0.29	0.29	0.30	19.5	17.1	18.5	
Exp. 2							
HET_0	0.47	0.38	0.43	21.6	18.7	20.2	11.7
LET_0	0.23	0.22	0.23	20.7	17.9	19.4	
Exp. 3							
HET_0	0.60	0.50	0.58	20.7	17.9	19.5	11.2
LET_0	0.35	0.34	0.36	19.9	16.5	18.5	
Exp. 4							
HET_0	0.68	0.45	0.60	20.5	17.9	19.5	11.4
LET_0	0.60	0.46	0.55	20.4	18.0	19.4	

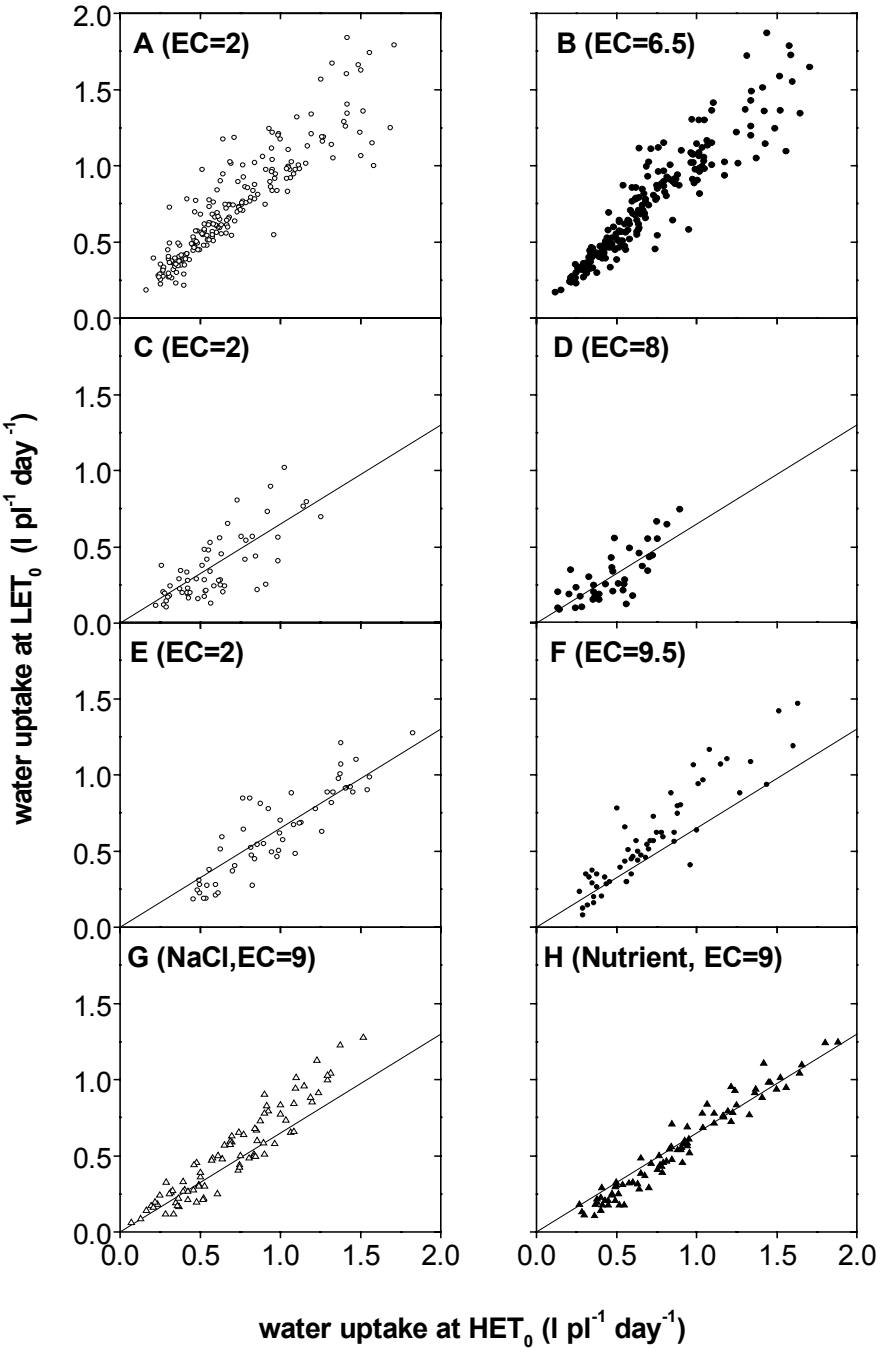

Figure 2.2 Daytime water uptake (litres per plant per day at the low potential transpiration treatment (LET_0) versus the one at the high potential transpiration treatment (HET_0). Plot A and B refer to the "low ventilation" treatment in experiment 4; C and D to experiment 2; E and F to experiment 1; G and H refer to the sodium chloride (NaCl) *vs* concentrated nutrients (Nutrient) in experiment 3. The slope of the lines (0.65) is the desired ratio. The number following "EC=" is the salinity treatment (dS m^{-1}). Values in plot A, B, G and H are from measurements on 8 plants with tipping buckets, otherwise from the balance of supply and drain.

curate than the measurements on the whole section. Figure 2.2 attests to the difficulty of controlling climate under high irradiation (large ET_0) which may be compounded by stomatal closure at the high EC treatments. The rather bland "ventilation treatment" of experiment 4, had a limited effect on water uptake (Figure 2.2, A and B).

2.3.2 Plant production

Fruit fresh yield

Marketable fresh yield of tomato fruit in all experiments was clearly influenced by salinity at HET_0 as well as at LET_0. High EC (6.5 to 9.5 dS m^{-1}) reduced fresh yield from 20 to 28 % compared to EC 2 dS m^{-1} at HET_0. LET_0 significantly reduced the negative effect of high EC (fresh yield was reduced only by 12 to 18 %), but did not affect yield at EC 2 dS m^{-1} (Table 2.4). The number of harvested fruits was not affected by any root or shoot treatment. Marketable fresh yield was 10% lower in NaCl than in concentrated Nutrient (Table 2.4), that is comparable to the difference in estimated osmotic pressure of the solutions. For comparing results of different experimental years and seasons, we calculated the efficiency of fresh production (η_F, g MJ_{PAR}^{-1}), according to Cockshull *et al.* (1992) *i.e.* plotting for each experiment the cumulated production *vs* the cumulated PAR (photosynthetically active radiation on top of the canopy). The slope of the best-fit linear regression (R^2>0.98 in all cases) is defined as the production efficiency. Figure 2.3 shows the relationship between η_F thus calculated and EC, for each shoot environment treatment. Fresh yield is negatively correlated to the EC in all cases. In particular, for total production efficiency:

$$\eta_{FT} = 33.03 - 1.26 * EC \qquad (R^2=0.94, \text{ at } HET_0) \qquad (2.1)$$

$$\eta_{FT} = 34.69 - 1.08 * EC \qquad (R^2=0.92, \text{ at } LET_0) \qquad (2.2)$$

and for marketable production efficiency:

$$\eta_{FM} = 33.39 - 1.54 * EC \qquad (R^2=0.93, \text{ at } HET_0) \qquad (2.3)$$

$$\eta_{FM} = 34.25 - 1.08 * EC \qquad (R^2=0.95, \text{ at } LET_0) \qquad (2.4)$$

where η_{FT} and η_{FM} is the efficiency of total and marketable fresh yield production in g per MJ_{PAR} at the top of the canopy, and EC is the prevailing electrical conductivity (dS m^{-1}) in the root environment.

The effect of EC on production efficiency was the same for total and marketable yield at LET_0 (Eqs (2.2) and (2.4) have the same slope), but not at HET_0. The difference in slopes between Eqs. (2.1) and (2.3) (that is, the difference in production efficiency of total fresh yield and marketable yield) is caused by the yield fraction

Table 2.4 Effects of EC and transpiration on marketable fresh yield (FM, kg per plant), marketable dry yield (DM, g per plant), average fruit dry weight (DW, g per fruit), total number of fruits per plant (No. per plant), and the number of unmarketable fruits as a percentage of total number of harvested tomatoes (unmark., %)[a]

	High transpiration		%[b]	Low transpiration		%[b]	LSD 5%[c]
Experiment 4							
EC	**2.3**	**6.8**		**2.4**	**7.0**		
FM	11.38	9.08	79.8	11.44	10.08	88.1	0.64
DW[d]	3.8	3.4		3.4	3.5		0.27
No.	158.8	158.0		156.6	162.5		6.88
Unmark.	3.1	8.1		3.2	9.2		2.55
Experiment 2							
EC	**2.3**	**8.3**		**2.2**	**8.1**		
FM	3.13	2.37	75.7	2.85	2.45	86.0	0.27
DM	144.3	128.6	89.1	134.8	133.3	98.8	14.77
DW	4.0	3.8		4.2	4.0		0.43
No.	36.4	34.7		31.6	33.4		3.58
Unmark.	0.3	4.3		0.3	1.5		1.50
Experiment 1							
EC	**2.2**	**9.3**		**2.2**	**9.0**		
FM	6.68	4.79	71.7	6.80	5.57	81.9	0.72
DM	335.9	260.0	77.4	354.2	349.0	98.5	38.83
DW	3.0	2.9		3.3	3.2		0.27
No.	107.3	114.3		100.9	106.6		6.26
Unmark.	0.2	21.5		0.6	2.3		3.15
Experiment 3							
EC	**9.1**	**9.0[e]**		**9.1**	**8.8[e]**		
FM	5.26	4.78	90.9[f]	5.70	5.14	90.1[f]	0.27
DM	327.8	317.4	96.8[f]	351.7	341.4	97.1[f]	15.06
DW	3.1	3.2		3.2	3.2		0.25
No.	106.6	99.5		106.8	101.2		3.80
Unmark.	2.3	1.3		1.0	1.4		1.30

a. Values are cumulative over the whole growing period. The EC (dS m^{-1}) given for each treatment is an average of root zone extracts drawn twice a week
b. Yield at high EC as a percentage of EC 2 dS m^{-1} in the same house.
c. Least significant difference at 5%
d. Values from 3 measurements.
e. NaCl treatment.
f. Yield in NaCl as a percentage of that in Nutrient.

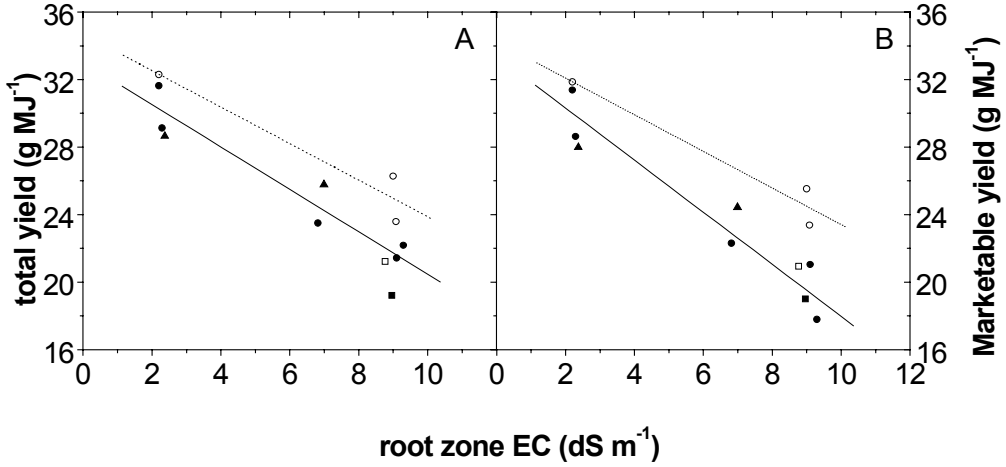

Figure 2.3 Total (A) and marketable (B) fresh yield production efficiency (g MJ_{PAR}^{-1}) *vs* mean EC in the root zone (●, HET_0; ○, LET_0; ▲, less ventilation; ■, NaCl-HET_0; □, NaCl-LET_0). Lines (solid, HET_0 and dotted, LET_0) show the best-fit linear relationship

that is lost because of BER. From Eqs. (2.3) and (2.4), it can be inferred that marketable fresh production was decreased by 5.1% and 3.4% per dS m^{-1} above 2 dS m^{-1} at HET_0 and LET_0, respectively. That is, a climate treatment (depressing transpiration) may reduce yield loss.

The yield reduction resulted from a decrease of fruit weight, as fruit number was largely unaffected by EC (except the loss caused by BER). Figure 2.4 shows the trend with EC of the mean weight of marketable fruits. The best-fit lines are:

$$\overline{f_w} = 108.5 - 3.8EC \qquad (R^2=0.99, \text{ at } HET_0) \qquad (2.5)$$

$$\overline{f_w} = 110.5 - 3.1EC \qquad (R^2=0.97, \text{ at } LET_0) \qquad (2.6)$$

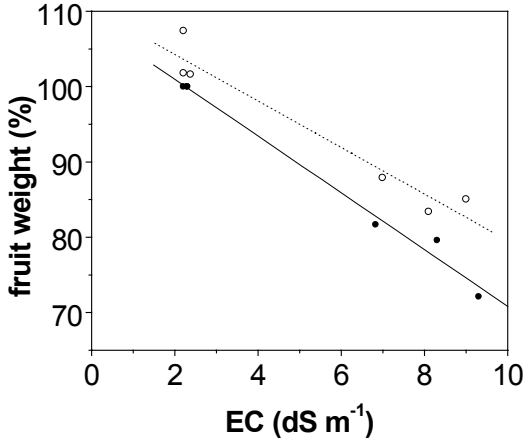

Figure 2.4 Fruit mean weight as a percentage of the reference treatment (EC 2 dS m^{-1} & HET_0) affected by EC and transpiration treatment (●, HET_0 and ○, LET_0, respectively) in different experimental years. Lines (solid, HET_0 and dotted, LET_0) show the best-fit linear relationship.

where $\overline{f_w}$ is the mean fruit weight of each treatment as a percentage of the mean fruit weight of the corresponding reference treatment (EC 2 dS m^{-1} & HET_0); and EC is the electrical conductivity (dS m^{-1}) in the root zone.

The decrease in mean weight caused by EC at LET_0 (3.2% per dS m^{-1}) corresponds to the decrease in production efficiency. Therefore reduced fruit weight accounts for the effect of EC on marketable yield. At HET_0 fruit weight was reduced by 3.8% per dS m^{-1}, whereas marketable yield was reduced by 5.1% per dS m^{-1}. The difference is caused by a significant effect on number of marketable fruits.

The decrease in fruit size caused by salinity was also expressed in the fruit class distribution (Figure 2.5). The fraction of fruit class A and B (large fruits) together was always higher at EC 2 dS m^{-1} than at high EC in the same experiment and higher at LET_0 than at HET_0, at high EC.

Fruit dry weight

Dry matter content (%) of marketable yield increased with EC (Figure 2.6). Although the "low transpiration" points were in most cases lower than the corresponding "high transpiration" points, the differences were not significant (they were certainly smaller than the effect of season or of the composition of the nutrient solution). Therefore the best-fit line was calculated through all points together:

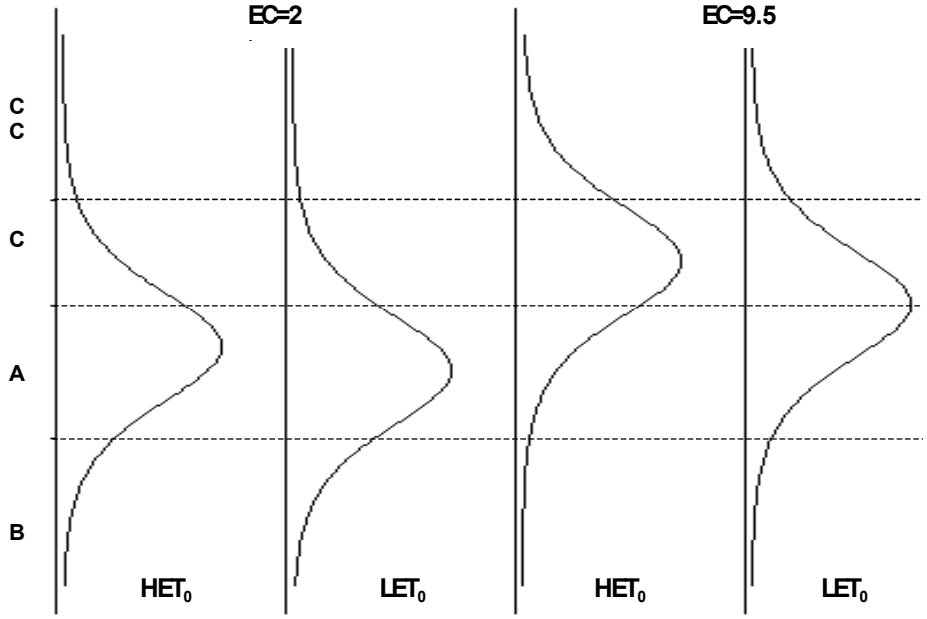

Figure 2.5 Frequency distribution with size of the number of marketable fruits. The dashed lines show cutpoints of size classes (from top to bottom: 40, 47 and 57 mm). The data was analysed with Genstat 5 Release 4.1(1997) by a proportional-oddS model (McCullagh and Nelder, 1989)

$$DM(\%) = 4.60 + 0.19 * EC \qquad (2.7)$$

where *DM*(%) indicates dry matter content (%) of marketable fruits, and EC is electrical conductivity (dS m^{-1}) in the root zone.

Dry matter content (%) increased by 4% per dS m^{-1} in excess of EC 2 dS m^{-1}. Average dry weight per fruit was neither affected by EC nor by ET_0 (Table 2.4). The decrease in total marketable dry weight by salinity was smaller (only 11 and 23% at EC 8 and 9.5 dS m^{-1}, respectively) than the decrease in fresh marketable weight at HET_0. At LET_0 the effect of EC on dry weight was nearly absent.

Fruit quality

The percentage of unmarketable fruit (mainly blossom-end rot) at high EC was higher than at EC 2 dS m^{-1}. The average percentage of unmarketable fruits in experiment 1, 2 and 4 at HET_0 was about 1.3% (by weight, or 1.5% by number) per dS m^{-1} increase. It fully accounted for the difference between marketable fresh yield and mean fruit weight.

Sugar content (Brix index) of fruits was always linearly correlated with the fruit dry matter content (%) (R^2=0.95). EC of fruit sap was obviously increasing with EC in the root zone. Low transpiration had some depressing effect on EC of fruit sap (Table 2.5) especially at high EC.

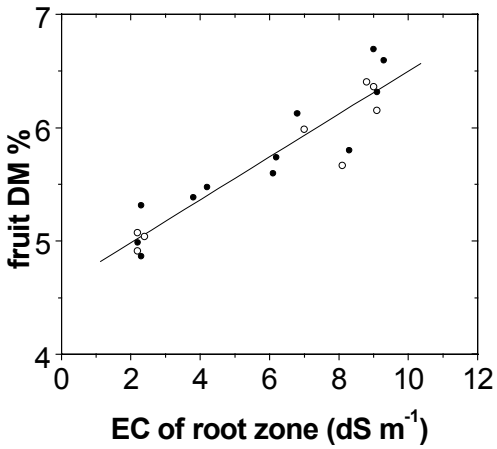

Figure 2.6 Dry matter content (%) of marketable fruits in relation to mean EC in the root zone. Closed symbols represent HET_0, open ones LET_0. Values of dry matter content at 4 and 6 dS m^{-1} are from a previous experiment (Stanghellini, 1997)

Table 2.5 Mean fruit quality parameters for each experiment and treatment: sugar content (%, Brix index); ash content (% of dry matter). Parameters were measured for each harvest, unless other indicated. The EC (dS m^{-1}) given for each treatment is average of root extracts drawn twice a week.

Exp. No.		High transpiration			Low transpiration			LSD 5%
4[a]	**EC**	**2.3**	**6.8**	**%**[b]	**2.4**	**7**	%[b]	
	Sugar %	4.55	5.20	14.3	4.40	5.16	17.3	0.122
Fruit	EC	4.97	5.61	12.9	4.90	5.39	10.0	0.154
sap	pH	4.19	4.19		4.18	4.21		0.034
	Ash %	8.88	9.01		8.93	8.50		0.291
2	**EC**	**2.3**	**8.3**		**2.2**	**8.1**		
	Sugar %	4.20	4.92	17.1	4.24	4.83	13.9	0.043
Fruit	EC	4.74	5.30	11.8	4.75	5.14	8.2	0.057
sap	pH	4.12	4.13		4.14	4.05		0.025
	Ash %	8.99	8.57		8.83	8.51		0.134
1	**EC**	**2.2**	**9.3**		**2.2**	**9.0**		
	Sugar %	4.32	5.67	31.3	4.33	5.30	22.4	0.045
Fruit	EC	5.54	6.19	11.7	5.62	6.04	7.5	0.038
sap	pH	4.21	4.19		4.23	4.16		0.015
	Ash %	10.40	9.48		10.46	9.69		0.132
3	**EC**	**9.1**	**9.0**[c]		**9.1**	**8.8**[c]		
	Sugar %	5.38	5.59	3.9[d]	5.14	5.32	3.5[d]	0.037
Fruit	EC	6.17	6.15		5.97	6.06		0.032
sap	pH	4.20	4.16		4.19	4.13		0.014
	Ash %	9.93	8.89		9.94	9.11		0.112

a. Parameters were measured only three times during the experiment.
b. Values at high EC as an increased percentage of EC 2 dS m^{-1} in the same house.
c. NaCl treatments.
d. Values in NaCl as an increased percentage of that in Nutrient.

2.4 Discussion

Tomato fresh yield decreased with salinity, in agreement with many studies (for instance, Sonneveld and Welles, 1988; Adams and Ho, 1989; Van Ieperen, 1996; Willumsen *et al.*, 1996). The general yield response curve to the root zone EC, first described by Maas and Hoffman (1977), assumes that crop yield depression is evident above a root-environment-EC threshold, beyond which yield decreases linearly. Sonneveld (1988) and Sonneveld and Welles (1988) put the threshold for tomato at 2.5 dS m^{-1}. The reduction rates they reported (also for other greenhouse crops) were usually less than values compiled by Maas and Hoffman (1977) for similar crops grown in the field. Sonneveld and Welles (1988) attributed the difference to a rather humid "sea" climate under glass, compared to a drier climate in the open. This con-

firms our hypothesis, since potential transpiration in a protected environment is always lower than under corresponding conditions outside. Our results are in line with this model: although we did not investigate EC around the supposed threshold, we did observe an approximately linear decrease in yield production efficiency with EC, and we did observe an effect of the shoot environment on the position of the line.

In our experiments fruit weight decreased with EC, which was attributed to reduced water transport to the fruits, since fruit dry weight was not affected (Table 2.4). This conclusion is supported by Ehret and Ho (1986a). High-EC fruits were larger at LET_0 than at HET_0. As average fruit dry weight was not affected by the transpiration treatments, the difference in fruit weight must be caused by a difference in water supply to the fruit. That is, the decrease of fruit weight at HET_0 had the same cause as at high EC. This confirms our working hypothesis that EC and transpiration to some extent have similar effects. From Eqs. (2.3) and (2.4) we could calculate that, with respect to marketable production, 1 dS m^{-1} increase at HET_0 was equivalent to a 1.4 dS m^{-1} increase at LET_0. Therefore we conclude that at LET_0 the same yield reduction will occur at a higher EC than at HET_0. Our result is consistent with the observation by Hoffman and Rawlins (1971) with root crops (onion and radish), that at high relative humidity the salinity level at which the yield was reduced to 50% of the non-saline yield was raised significantly. The marginal effect of potential transpiration on yield at low EC could be attributed to the threshold value for the EC effect.

The other well known EC effect is increased dry matter content in the fruit (Ehret and Ho, 1986a; Adams and Ho, 1989; Sonneveld and Van der Burg, 1991; Willumsen *et al.*, 1996) and this is also confirmed by our results. Salinity raised with NaCl seems to increase the effect at a given EC (about 10% less of fresh yield and a significantly higher dry matter content compared with Nutrients, Table 2.4 and 2.5). This is in line with Maas and Hoffman (1977). They attributed this to specific ion toxicity, although it could possibly be explained simply by a similarly small difference in the osmotic pressure of the solution.

From the discussion above, we can draw a few general conclusions about the mechanisms underlying the relationship between fruit production and EC and ET_0. Both EC and ET_0 affect the same plant state variable (the plant water content or water potential). In the design of our experiments, the effect of EC was dominant and ET_0 was a modulating factor. It seems logic, however, that to a certain extent EC and ET_0 could be mutually exchangeable. Reduction of yield through EC and/or ET_0 is mainly through plant water status (different fresh weight), and does not involve dry weight. Moreover, reduction of yield is only through reduction in fruit weight, not in number.

We did not observe an effect of humidity at low EC, whereas literatures report yield decreases at high humidity (for instance, Sonneveld and Welles, 1988; Bakker, 1990; Holder and Cockshull 1990). In most cases, localised calcium defi-

ciency, resulting in smaller leaf area was observed. After reviewing the relevant literature Grange and Hand (1987) concluded that humidity higher than 90% for a significant fraction of the growth period (of a fruit) may affect mineral balance and cause disorders of growth and development. Our climate control routine prevented relative humidity from exceeding 90%, and indeed we did not observe any calcium deficiency on tomato leaves at either high or low EC treatments.

This same limitation on relative humidity in our regime caused the temperature differences that sometimes had to be accepted to attain the desired potential transpiration ratio. This is unfortunate, since ambient temperature is known to affect plant growth (De Koning, 1994) and morphogenesis. The lack of any "greenhouse compartment" effect at EC 2 dS m^{-1} for the crop features discussed in this paper, demonstrates that the observed temperature differences could be ignored.

2.5 Conclusion

In good agreement with previous results, we have found that increasing the osmotic pressure (EC) in the root environment significantly decreases fresh yield of tomato, without affecting number of harvested fruits. Yield loss is the combined effect of smaller fruits and the fraction of fruits that is discarded. We have shown that a shoot environment treatment that depresses potential transpiration can modify the effect of the root zone salinity, both by reducing the fraction of fruits that is to be discarded and reducing the decrease in fresh weight of each fruit.

In addition, we have shown that dry yield is not affected by salinity in the root zone, so that dry matter content of the fruits increased with EC. So it is the smaller water content of fruits that mainly causes yield loss at high EC, aside from the fraction of unmarketable fruits. We have shown that manipulation of the shoot environment in a greenhouse, in order to depress potential transpiration, can mitigate the negative effect of root zone salinity.

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Chapter 3

Analysis of the effect of EC and potential transpiration on vegetative growth of tomato

Ya Ling Li and Cecilia Stanghellini. Scientia Horticulturae, Horti 1574, in press

Abstract

This paper analyses the response of vegetative growth of greenhouse tomato to both root-zone salinity and shoot-environment (potential transpiration), with the purpose of explaining the observed lack of effect on dry matter yield. A reference salinity (EC) of 2 dS m^{-1} was compared in three experiments with, respectively, 6.5, 8 and 9.5 dS m^{-1}. Another experiment investigated specific effects of sodium chloride, by comparing two high-EC treatments (both 9 dS m^{-1}), one with a high concentration of nutrients and one with addition of sodium chloride to a normal nutrient solution. The shoot environment was either a "normal" climate regime or a depressed potential transpiration regime, attained mainly by adaptation of the humidity set point. There was no detectable effect of the potential transpiration treatment, neither of the sodium chloride. Salinity effects on vegetative growth only showed up at EC exceeding 6.5 dS m^{-1}. The most evident EC effect was a reduction of leaf expansion: individual leaf area was reduced by 8% per dS m^{-1} exceeding 6.5. This was partly compensated by a slight increase (2% per unit EC) in the number of leaves, which explains why cumulative plant leaf area decreased by about 7% per unit EC in excess of 6.5 dS m^{-1}. Therefore, leaf area index (LAI) at the highest EC was reduced by some 20% compared to the LAI at an EC of 2 dS m^{-1}. It is estimated that this would cause a reduction of less than 8% in light interception, and thus in dry matter produced. Indeed, differences observed in dry weight between the EC treatments were never significant.

3.1 Introduction

Due to environmental regulations, re-use of drained irrigation water is becoming common practice for many greenhouse crops in the Netherlands. In these systems, both unused fertilisers and certain ions from the source water, for example, Na^+ and Cl^- tend to accumulate in the nutrient solution (Sonneveld, 2000). A high solute concentration in the root environment reduces yield (Ehret and Ho, 1986a; Sonneveld and Welles, 1988; Adams and Ho, 1989; Adams, 1991; Willumsen *et al.*, 1996; van Ieperen, 1996) and is related to some fruit disorders. However, high salinity

may also improve quality of fruits (Holder and Christensen, 1988; Adams and Ho, 1989; Gough and Hobson, 1990; Mitchell *et al.*, 1991). Weather/climate conditions during growth are believed to modulate all above-mentioned effects (Hoffman and Rawlins, 1971; Banuelos *et al.*, 1985; Adams and Holder, 1992; Cockshull, 1998; Stanghellini *et al.*, 1998).

Water uptake and transpiration are distinct plant physiological processes. The balance between these processes controls and is controlled by plant water potential, which, in turn, affects strongly the accumulation of water in growing tissue. At high salinity (low osmotic potential of the nutrient solution) the water potential of the plant will decrease. Likewise also high transpiration will cause a decrease of water potential of the whole plant. Because transpiration and salinity both affect plant water status (Van Ieperen, 1996) low transpiration may help to compensate negative effects of salinity (Hoffman and Rawlins, 1971). In other words, adapting climate conditions in relation to the root zone conditions could be a way to control the plant water status (water potential or relative water content) and related crop responses. Based on this assumption, experiments were conducted to investigate to what extent climatic manipulation may modulate the effect of salinity on plant growth and production.

In chapter 2 we reported that increasing the concentration of the nutrient solution significantly decreased fresh yield of tomato, mainly by reducing fruit size. We have shown that this was caused by a reduction of water import in the fruit, since individual fruit dry weight was not affected by solute concentration (electrical conductivity, EC) in the root environment. Reducing potential transpiration (that is the transpiration rate demanded by climate conditions) improved fruit fresh production at high EC, but had no significant effect on production of fruit dry weight.

Fruit production is determined by two fluxes (Ho *et al.*, 1987): water inflow and assimilate inflow. Vegetative growth, particularly leaf area, affects both fluxes. The surface of leaves is the site of both water loss (transpiration) and carbon intake (photosynthesis). Moreover, leaf enlargement in many species is said to be the most sensitive plant physiological process to water stress (Hsiao, 1973). Cells (and leaves) remain smaller during water stress, resulting in reduced area for photosynthesis. Therefore this paper analyzes the response of vegetative growth of greenhouse tomato to both EC and potential transpiration, with the purpose of explaining the observed lack of effect on dry matter yield.

3.2 Materials and methods

3.2.1 Treatments

Each of four experiments (Table 3.1), with tomato crop grown on rockwool, combined two solute concentrations in the root environment (characterised by their electrical conductivity, EC, dS m^{-1}) with two climate treatments (shoot environ-

ment). A standard concentration of nutrients (EC 2 dS m^{-1}) and a high concentration (EC 6.5, 8 or 9.5 dS m^{-1}) were subjected to a "high" and to a "low potential transpiration" climate. There was one experiment devoted to investigate specific effects of sodium chloride. Both root zone treatments had an EC of 9 dS m^{-1}, one of the two having the equivalent of 7 dS m^{-1} NaCl on top of the standard nutrient solution, the other simply a higher concentration increasing proportionally the concentration of all mineral nutrients. More details about all experiments have been given in chapter 2.

The climate treatments were effectuated in two identical glasshouse compartments (300 m^2 each). One compartment was controlled according to standard cultural practices in the Netherlands ("high" transpiration treatment, HET_0). The climate in the other compartment ("low" transpiration treatment, LET_0) was controlled so that potential transpiration was reduced by the desired amount, compared to the HET_0. The potential transpiration rate was calculated according to Stanghellini (1987) and the control algorithm has been described by Stanghellini and Van Meurs (1992). Ambient humidity was controlled by a combination of venting and high-pressure misting. When (and only in that case) this conflicted with a maximum relative humidity of 90%, ambient temperature in the LET_0 compartment was allowed to decline from the set point, in order to realise the desired reduction in potential transpiration. In three of the four experiments we maintained a constant

Table 3.1 Some basic information on the experiments: transpiration treatment (target transpiration at low transpiration treatment (LET_0) as % of high transpiration treatment (HET_0) and specific regime in experiment 4; electrical conductivity (EC, dS m^{-1}) in irrigation solution (Irrig. EC) and EC measured in extract from root environment (Extract EC); planting date, treatment periods and first harvesting date (all experiments with tomato, *cv.* Chaser).

LET_0 Treatment	*Irrig. EC*	*Extract EC*		*Planting date*	*Treatment Periods*	*First harvesting*
		HET_0	*LET_0*			
Experiment 1						
65%	2	2.2	2.2	Dec.15, 1995	Feb. 1 to Jul. 1	Feb. 29
	9.5	9.3	9.1			
Experiment 2						
65%	2	2.3	2.2	Jul. 10, 1996	Aug.7 to Oct.28	Sep. 9
	8	8.3	8.1			
Experiment 3						
65%	9-NaCl	9.1	8.8	Dec. 16, 1996	Jan.23 to Jul. 3	Mar. 13
	9-Nutrient	9.1	9.0			
Experiment 4						
Less ventilation; Misting for $ET_0 > 0.15$ l h^{-1}per plant	2	2.3	2.4	Jan. 6, 1998	Feb. 9 to Sep. 28	Mar. 26
	6.5	6.8	7.0			

ratio (2/3) between calculated potential transpiration in the two compartments. In one experiment (experiment 4), the low transpiration treatment was realised in a different way: the standard climate control was used, but vents opening in response to humidity was continuously 25% less than in the HET_0 house. In addition, a high-pressure misting system was switched on anytime the potential transpiration of the reference compartment exceeded 0.15 l h^{-1} per plant.

3.2.2 Measurements

The crop was managed according to commercial practice in the Netherlands; all side shoots were removed and all leaves under the ripe truss were picked. Leaf area of six randomly selected plants in the central rows of each treatment was monitored as follows. Every fortnight, starting before the treatments began, we measured length (from the base of leaf blade to the tip of leaf) and maximum width of each composite leaf (longer than 15 cm). Leaf area (A, m^2) was calculated from length (l, m) and width (w, m) according to a formula of Van der Varst and Postel (1972):

$$A = \frac{0.25lw}{1 - 1.48lw} \tag{3.1}$$

In experiment 4 we also determined fresh and dry weight of all pruned leaves from 24 plants per treatment, including the six of which leaf area was monitored. In the same experiment we made five destructive measurements, from the end of May till the end of June (3 plants per treatment) and at the end of the experiment (6 plants per treatment). Each time we determined stem length, dry and fresh weight of leaves, stems and fruits. All data were processed with the statistical analysis package Genstat5 (Release 4.1, 4th edition).

3.3 Results

There were hardly any differences between observations (at a given EC) in the two houses (Table 3.2). There was only a difference in number of leaves in one experiment. That, however, is fully explained (according to the model by De Koning, 1994) by the small difference in temperature between the two compartments in that experiment. Accordingly, we will further ignore the differences between the two houses that can be attributed to the temperature. Effects of climate treatment (other than temperature) were not detectable.

3.3.1 Vegetative development

The total number of leaves increased (not in all cases significantly) whereas leaf area (both individual and cumulative) decreased with increasing EC in all experiments (Table 3.2). Figure 3.1 shows total leaf number and average leaf dimension

Table 3.2 The effect of EC and transpiration on vegetative growth: total number of leaves (LNo., per plant), cumulative leaf area (LA, m^2 per plant, including harvested leaves) at the end of experiment, leaf area index (LAI) and number of leaves kept on the plant (Leaves) averaged for the whole growing period[a]

	High transpiration		**Low transpiration**		LSD 5%
Experiment 4					
EC	**2.3**	**6.8**	**2.4**	**7.0**	
LNo.	88.8	90.2	89.8	91.0	n.s.
LA	5.24ab	4.92a	5.44b	5.30ab	0.44
LAI	2.41a	2.36a	2.60b	2.63b	0.19
Leaves	20.4a	21.2ab	21.4ab	22.1b	n.s.
Experiment 2					
EC	**2.3**	**8.3**	**2.2**	**8.1**	
LNo.	43.4	44.6	42.6	44.0	n.s.
LA	2.50c	1.86a	2.21b	1.82a	0.24
LAI	2.40b	1.97a	2.27b	1.95a	0.22
Leaves	22.8	23.1	22.7	23.3	n.s.
Experiment 1					
EC	**2.2**	**9.3**	**2.2**	**9.0**	
LNo.	65.9ab	70.3c	63.0a	66.7b	3.29
LA	4.49c	3.85b	4.35c	3.57a	0.27
LAI	2.61b	2.18a	2.59b	2.15a	0.36
Leaves	21.3a	23.2b	21.0a	21.1a	1.25
Experiment 3					
EC	**9.1**	**9.0[b]**	**9.1**	**8.8[b]**	
LNo.	74.0	73.0	72.7	71.7	n.s.
LA	3.80b	3.69ab	3.65ab	3.54a	0.24
LAI	2.2	2.1	2.2	2.1	n.s.
Leaves	20.9	20.5	21.3	20.6	n.s.

a. Values are averages of measurements on 6 plants

b. NaCl treatment

at high EC as a percentage of the corresponding parameter observed in the reference EC (2 dS m^{-1}), in the same compartment. Points are averages over the six plants that were monitored for each treatment. The parameters of the best-fit lines of Figure 3.1 are presented in Table 3.3. Since the best-fit parameters of leaf length and width were not significantly different, only one line was fitted for both dimensions. Area of single leaves was much more sensitive to EC than number of leaves. The combined effect on average leaf area and leaf number resulted into a reduction of plant cumulative leaf area of some 7%, per unit EC exceeding 6.5 dS m^{-1}.

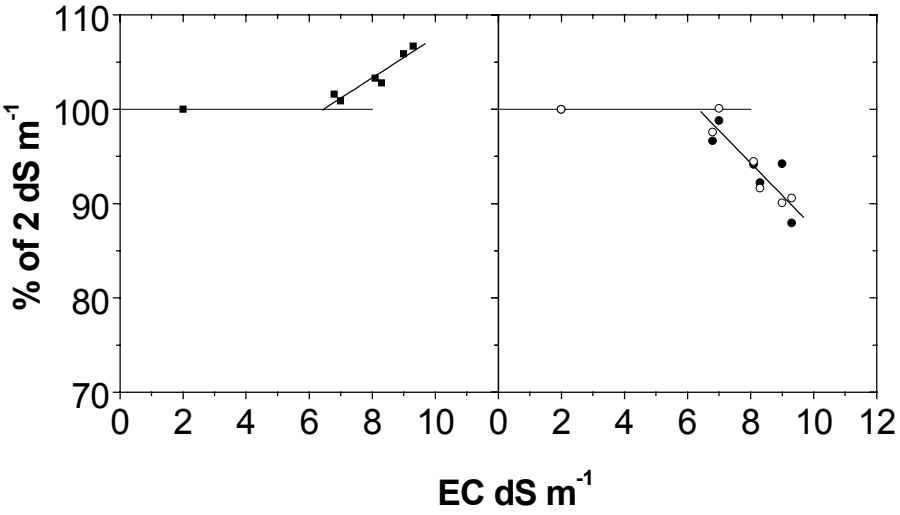

Figure 3.1 Number of leaves (left panel), average dimensions of individual leaves (right panel: ●, length and ○, width) for each experiment, as a percentage of the corresponding parameter at EC 2 dS m^{-1}, in the same compartment. Points are averages of observations on six plants per treatment. Lines are best fit. Parameters of the lines are in Table 3.3.

Table 3.3 Parameters of the lines describing the relative effect of EC compared to 2 dS m^{-1} (Figure 3.1). Zero-effect gives the EC where the estimated effect is nihil. Slope (value±standard error) is the sensitivity of the parameter. The other slope is the sensitivity if the relationship were forced to have no effect at 6.5 dS m^{-1}

	Zero-effect (dS m^{-1})	Slope (% per dS m^{-1})	Slope (zero-effect=6.5)
Number of leaves	6.46	2.15±0.36	2.20
Length and width	6.35	-3.43±0.54	-3.68
Individual leaf area	6.90	-9.94±2.57	-8.09
Cumulative leaf area	5.67	-5.55±2.77	-7.71

3.3.2 Leaf area index (LAI)

LAI is an overall result of plant density, leaf size, and number of leaves kept on the plant. Plant density was fixed in the experiments at 2.2 plants per square meter and only the main stem was left. Therefore, only the balance of leaf formation and leaf picking (together with leaf size) could affect LAI.

It appeared afterwards that in all our experiments slightly more leaves were kept on the plants at high EC (Table 3.2). The slightly shorter internode length (2%) at high EC may have caused the differences. Indeed, the depth of the leaf canopy (average number of leaves times average internode distance) was approximately the same in all experiments and treatments.

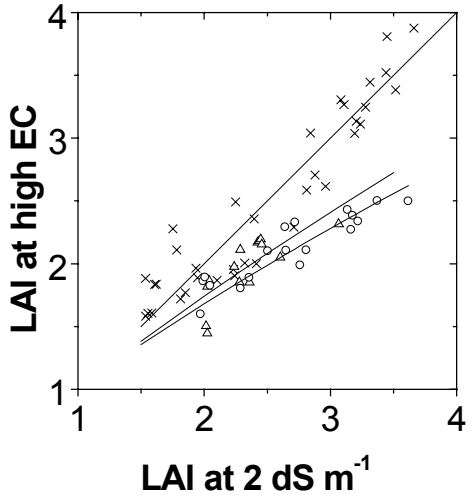

Figure 3.2 Leaf area Index (LAI, measured every fortnight) at high EC versus LAI measured at reference EC (2 dS m^{-1}) in the same house: ×, 6.5; Δ, 8 and ○, 9.5 dS m^{-1}. The line through the 6.5 dS m^{-1} points is the best-fit line and has slope 1. The other lines are drawn to help reading.

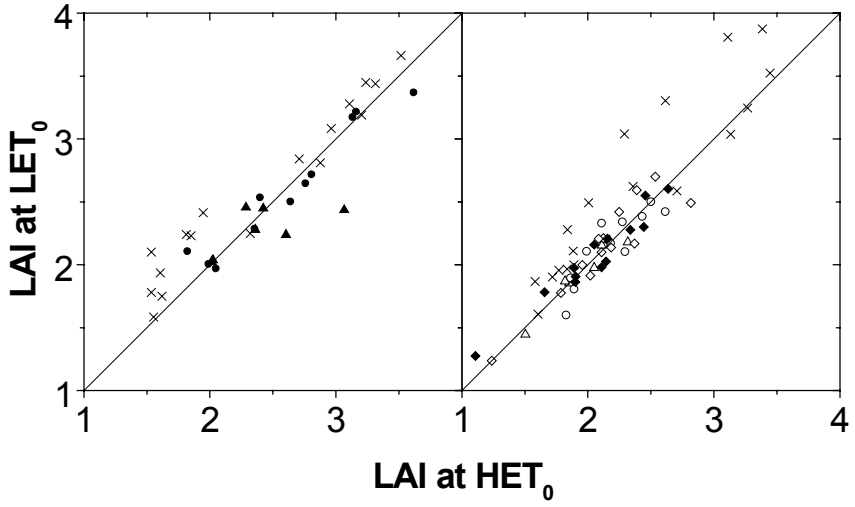

Figure 3.3 Leaf area index (LAI) at the low transpiration treatment (LET_0) *vs* LAI at the high transpiration treatment (HET_0), for the reference EC (2 dS m^{-1}) (left panel: ●, experiment 1; ▲, experiment 2; and ×, experiment 4) and high EC (right panel: ×, 6.5; Δ, 8 and ○, 9.5 dS m^{-1}; ♦ NaCl and ◊ Nutrient are EC 9 dS m^{-1} in experiment 3). Lines indicate the 1:1 relationship.

There were no significant differences at EC=9 dS m^{-1} between the two nutrition treatments, although leaves seemed to be slightly smaller at the NaCl treatment. Similarly, there was no effect at all on the number of leaves.

Figure 3.2 shows all measurements of LAI at high EC *vs* LAI at EC 2 dS m^{-1}. There was no effect at EC=6.5 dS m^{-1}, since the best-fit line has a slope of 1. The other points were fitted with curves to help reading. They are not straight because

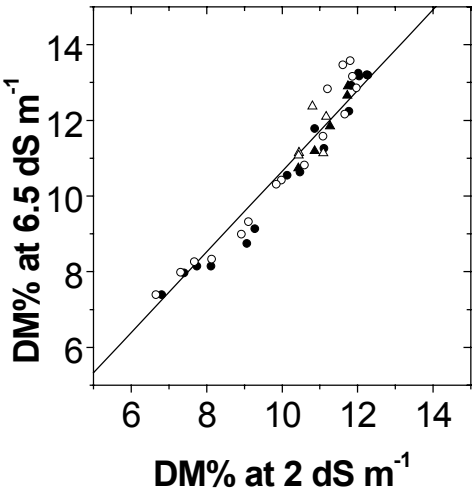

Figure 3.4 Dry matter content (DM%) of pruned leaves (●,○) and all leaves on the plant (▲, Δ, from the destructive measurements). Closed symbols represent values at HET_0, and open ones at LET_0. Slope (±standard error) of the best-fit line (shown) is 1.066±0.007 ($P< 0.0001$)

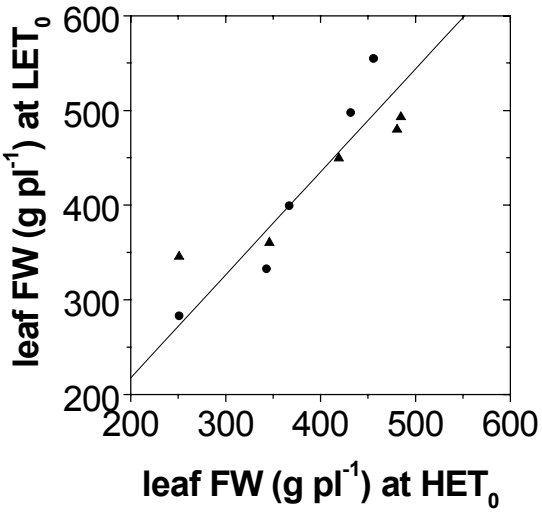

Figure 3.5 Fresh weight of leaves on the plant (FW) at low transpiration treatment (LET_0) against FW at high transpiration treatment (HET_0). Points represent five destructive measurements, each time of three plants per treatment. ▲, EC 2 and ●, 6.5 dS m^{-1}, respectively. Slope (±standard error) of the best fit line (shown) is 1.09±0.03 ($P< 0.001$).

at low LAI (first measurements) the effect of the treatments was not yet evident. The average slope of the line for EC=9.5 dS m^{-1} is 0.78. On the other hand, Figure 3.3 showed that the climate treatments did not have any effect upon LAI.

3.3.3 Weight

The variance among weight of leaves (dry and fresh) ensured that no effect of the

EC treatment (6.5 dS m^{-1}) could be detected, in pruned leaves as well as in the destructive samples. The effect of the EC treatment upon dry matter content, however, was highly significant (Figure 3.4). On the other hand, low transpiration significantly increased fresh weight of leaves (Figure 3.5), without modifying dry matter content.

Similarly, EC did not affect dry and fresh weights of the stem, contrary to transpiration that increased weight at high EC (Table 3.4). These limited results confirm our previous observation about yield, that at high EC less water is imported in organs, whereas the accumulation of dry matter is not affected.

Specific leaf area (SLA) of cumulated leaves, as well as in each pruning event, did not seem to be affected by any treatment, despite a trend of a lower SLA at high EC, as could be expected in relation to the difference in water content.

Table 3.4 Cumulated leaf fresh weight and dry weight (Leaf FW, DW; g per plant); stem fresh and dry weight (stem FW, DW; g per plant) at the end of experiment 4 and specific leaf area (SLA, calculated from cumulated leaf area and cumulated leaf dry weight, $cm^2\ g^{-1}$).

		HET_0		LET_0		LSD 5%
EC (dS m^{-1})		2.3	6.8	2.4	7.0	
Leaf	FW	1724	1675	1986	1896	137.6
	DW	180.2	183.0	203.9	207.3	17.56
Stem	FW	949	864	998	1017	131.6
	DW	133.7	126.9	133.6	150.1	21.27
SLA		292	269	268	256	26.2

3.4 Discussion

3.4.1 Vegetative development

Our results can be summarised as follows: vegetative development was not affected by our shoot treatment (other than temperature) and effects of root zone treatment showed up only at EC exceeding 6.5 dS m^{-1}. We have found that at high EC leaf formation rate increased slightly, a result we did not find in earlier reports. It may be that this (relatively small) effect is detectable only in long-term experiments. The observation is probably related to reports about generative development and precocity (early flowering) of tomato (van de Vooren *et al.*, 1986; and de Kreij, 1995). The EC effect upon leaf expansion is, however, well documented. We observed an 8% decrease of cumulative leaf area for each dS m^{-1} that EC exceeded 6.5. This is agreement with the observation of Van Ieperen (1996). He found a decrease of total leaf area in tomato crops of about 20-28% in young plants and of 25% (including harvested leaves) in a productive crop, at an EC of 9 dS m^{-1} com-

pared with an EC of 5 dS m^{-1}. Willumsen *et al.* (1996) observed that leaf length was reduced about 2-3% per dS m^{-1} on average with increasing salinity (from 5.2 to 8.1 dS m^{-1} compared to an EC of 3.6 and 3.8 dS m^{-1} in tomato "*Elin*" and "*Matador*"). Similar results have been reported for other crops (*e.g.* McCree, 1986; Awang *et al.*, 1993a). In his review paper, Hsiao (1973) stated that when water stress develops gradually in the plant, the first change is a slowing down of shoot and leaf growth brought about by reduced plant water potential.

We did not observe a response of leaf expansion to the climate treatment (essentially humidity), Figure 3.3. However, some authors found a significant reduction in leaf area at high humidity or low VPD (*e.g.* Burrage, 1988; Bakker, 1990; Holder and Cockshull, 1990), usually coupled to symptoms of calcium deficiency in the leaves. Other authors reported an increased leaf area of tomato plants at high humidity (Swalls and O'Leary, 1975; Banuelos *et al.*, 1985; Mortensen, 1986). Swalls and O'Leary (1975) observed that high humidity did not significantly reduce the amount of calcium delivered to leaves, whereas Banuelos *et al.* (1985) pointed out that increased leaf growth rate contributes to the development of Ca deficiency disorders in fruits. Therefore, the effect of transpiration or humidity on plant growth is mainly through mineral uptake and mineral balance. These effects mainly occur when humidity is high (less than 0.2 kPa VPD) for most of the growth period (Grange and Hand, 1987). In our case the relative humidity was restricted, which may fully explain the lack of negative effects of humidity.

3.4.2 LAI and dry matter production

We have shown that the effect of EC on leaf dimensions was evident only for EC exceeding 6.5 dS m^{-1}, and was independent of the transpiration treatment. We estimated a decrease of LAI by some 20% at the highest of our EC treatments. Even then, a model of the fraction of incoming light that is intercepted, validated by Heuvelink (1996, p77) for tomato, predicts that such a reduction in LAI would cause at most a decrease in light interception of about 8%. This gives an order of magnitude for the expected EC-effect upon dry matter production.

We could not detect any effect of EC on dry weight of leaves and stems. This limited result (one experiment), however, is consistent with our previous finding that there was no effect of EC upon dry matter accumulated into fruits, in all our experiments. Differences up to 8% in production that may have been caused by a change in light interception are very hard to measure (Cockshull *et al.*, 1992). In conclusion, we can say that our results are in line with the common observation from literature that dry weight is not, or only marginally, affected by EC (at least in this mild range) and that primarily fresh weight is affected. This view is supported by Hsiao (1993) who stated that, in a closed canopy, leaf growth may be inhibited, under mild water stress, with no significant inhibition of leaf photosynthesis and hence with little or no effect on biomass production rate.

3.5 Conclusion

We have shown that our observations on vegetative development support the statement that both EC and potential transpiration affect (almost) exclusively water content of organs.

More unexpectedly, we have shown that the EC effect upon vegetative growth of tomato shows up at higher EC than we have observed for fresh yield. Maas and Hoffman (1977) reported that storage-root yieldS might be decreased much more than shoot growth, with increasing salinity. They concluded that vegetative growth response to salinity might not be a reliable parameter for predicting fruit production loss. Our results support this observation.

Acknowledgements

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Chapter 4

Growth of tomato fruits at contrasting root-zone EC and potential transpiration

4.1 Introduction

In chapter 2, we have seen that increased electrical conductivity (EC, dS m^{-1}) in the nutrient solution reduced yield of greenhouse tomato, mainly by reducing water content of individual fruits. We have also seen that a climate management that reduced potential transpiration, significantly mitigated the negative effect of high EC. That is, weight of high-EC fruits was larger in a low-transpiration than in the reference environment, which is comparable to conditions in practice.

If fruit growth rate at time *t* is indicated by *FGR(t)* and the fruit development period is indicated by *FDP,* final fruit weight *W* is obviously:

$$W = \int_0^{FDP} FGR(t)dt \qquad (4.1)$$

Therefore, both a reduction in growth rate and a shorter FDP can lower final fruit size. Grange and Andrews (1993) showed that fruit growth rate (both diameter increase and weight increase) during the period of rapid growth is proportional to the final fruit size.

Reduced fruit size resulting from salinity in the root-environment is often related to a lower growth rate (for instance: Ehret and Ho, 1986b; Pearce *et al.* 1993b). There are few indications that FDP also is reduced, so the effect on growth rate is probably the most important effect. Ehret and Ho (1986b) observed a lower fruit growth rate at EC 17 dS m^{-1} than at 2 dS m^{-1} (particularly during daytime) and a consistently lower fruit weight. Pearce *et al.* (1993b) showed that fruit growth rate (measured by Linear Variable Displacement Transducers, LVDT) of young fruit was greatly influenced by EC of the nutrient solution as well as by high potential transpiration during mid-season (late May to August).

However, FDP could also be affected by growing environment, *e.g.* temperature (de Koning, 1994) or water stress (Hsiao, 1993). Although de Koning (1994) did not observe any salinity-effect upon fruit development period, within the EC range 3 to 9 dS m^{-1}, a relatively high EC (above 7 dS m^{-1}, van de Vooren *et al.*, 1986) after transplanting is advised in commercial greenhouse tomato production in order to

stimulate early flowering. Mizrahi (1982) observed earlier maturation of tomatoes subjected to a sodium chloride treatment. Nevertheless, if we assume that salinity stress is essentially water stress, it is relevant to notice that the latter does cause early maturation with tomato (Salter, 1958; Wolf and Rudich, 1988; Hsiao, 1993).

In order to understand the negative effect of salinity on fruit weight, and the interaction of salinity with potential transpiration, we investigated the fruit growth rate (FGR) and fruit development period (FDP) during some of the experiments described in the previous chapters.

4.2 Materials and methods

Diameter of individual fruits was measured manually between April 10 and June 5, 1996 (a total of 8 weekly measurements), when the EC treatments were 2 and 9.5 dS m^{-1}. In order to determine fruit age at the time of sampling, the flowering trusses were marked on April 10. Then, at each weekly measurement, the diameter of every second fruit from all trusses in each of three pre-selected plants was determined. The same fruits were gauged the week thereafter, and then picked to determine the dry matter content. Meanwhile, the same observations were started with three other plants from each treatment and the procedure continued. Fruit volume was calculated as 87% of the volume of a sphere of the same diameter, according to van de Sanden and Uittien (1995).

FDP was determined only for the experiment in 1998, when the EC treatments were 2 and 6.5 dS m^{-1}. FDP was defined as the difference between "flowering" and "harvesting" time. For estimating the flowering time we used the leaf measurements that have been described in chapter 3. While measuring, the position of all fruit trusses with respect to the leaves on the plant was recorded. Very few exceptions were observed (Li and Stanghellini, 1999) to the characteristic of tomato plant that there is a flower truss for every three leaves above the first inflorescence (Shishido and Hori, 1977).

Then, the number of the truss flowering (N_{Tf}, counting from the root) at any moment was estimated by relating it to the leaf observations as follows:

$$N_{Tf} = \frac{N_L - N_0}{3} \tag{4.2}$$

where N_L is the number of the youngest measured leaf; and N_0 is the number of leaves below the first source-sink unit (a truss together with the three leaves immediately below it, Tanaka and Fujita, 1974).

Of each truss of the 24 plants per treatment whose yield was monitored (see materials and methods in chapter 2) we recorded when both the first and the last fruit were picked (single ripe fruits were picked, not whole trusses). As stated earlier, fruits were harvested twice a week. A fairly linear trend in time was observed for

the number of the truss flowering, N_{Tf}, and both the numbers of the trusses at first and last harvest. Therefore, the dates of flowering and first harvesting of each truss were determined by linear interpolation, and all fruits of each truss were assigned the same FDP calculated as the difference between the two.

4.3 Results

4.3.1 Fruit size

The mean volume of the second fruit in each truss on a plant, during the whole measuring period is shown in Figure 4.1A. The EC treatment had by far the largest effect upon volume, as expected. The low transpiration treatment (LET_0) clearly increased size at high EC, whereas no definite influence could be detected at low EC. The EC effect was detectable already in the 4th truss (counted from truss 1 at anthesis), whereas the (smaller) climate effect appeared only in older fruits. Final volumes are consistent with mean weight of harvested fruits in the same period (Table 4.1), if we keep in mind that the second fruit is one of the largest on each truss. The relative effect of the EC treatment (3rd and 6th column in Table 4.1) is also consistent with the yield observations.

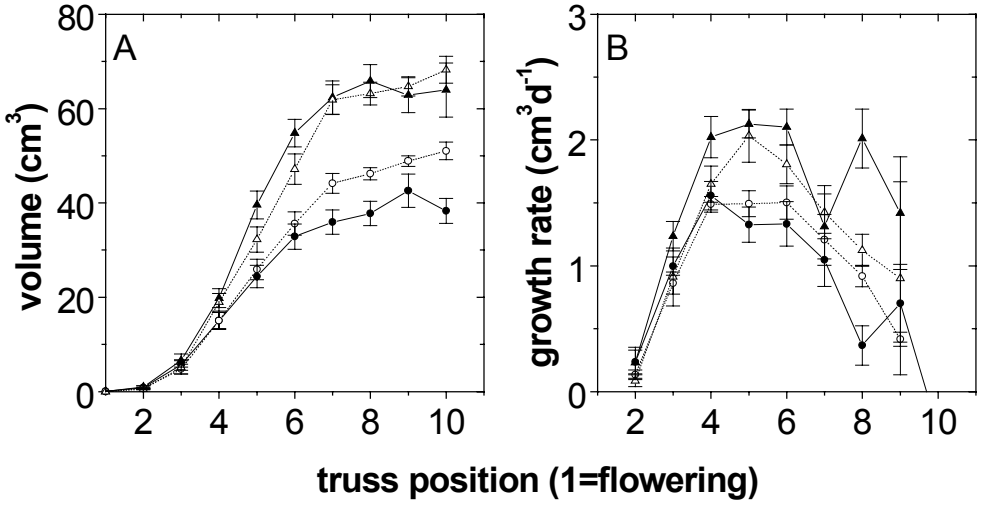

Figure 4.1 (A): Mean volume of the second fruit of each truss at EC 2 (▲, Δ) and 9.5 (●, ○) dS m^{-1}. Each point is the mean of 14 values, each being the average of 3 samples taken between April 10 and June 5, 1996. Closed and open symbols represent high and low transpiration treatment, respectively. Vertical bars are two times standard error (n=14); (B): Mean daily growth rate of the second fruit of each truss. Points are calculated from the difference between volume gaugings, one-week apart, and each point is the mean of 7 values, each being the average of 3 samples, between April 10 to June 5, 1996. Symbols as in (A).

Table 4.1 Fruit volume determined from the diameter of the second fruit in mature trusses (April 10 to June 5, 1996); mean weight (Mean W) of marketable fruits harvested during the same period; and average growth rate (FGR) of the second fruit of trusses 3 to 7. Values ± standard error (in time). The columns marked % show the values at 9.5 dS m^{-1}, as a percentage of the values at 2 dS m^{-1}, for each transpiration regime.

	HET_0			LET_0		
EC (dS m^{-1})	2	9.5	%	2	9.5	%
Volume (cm^3)	71.29±2.00	46.73±1.08	65.5	70.99±1.24	51.85±0.65	73.0
Mean W (g $fruit^{-1}$)	63.1±5.2	42.4±2.2	67.2	65.8±6.0	50.2±2.4	76.3
FGR (cm^3 d^{-1})	1.76±0.07	1.25±0.11	71.0	1.57±0.09	1.31±0.09	83.4

4.3.2 Fruit growth rate

Figure 4.1B shows the average daily growth rate of the 2nd fruit of each truss, calculated as the mean (in time) difference between the mean (of three) volumes, observed each time. As explained above, not always the same fruits were gauged, which may account for a few outliers. The highest daily growth rates were about 2 and 1.5 $cm^3 \cdot d^{-1}$ at EC 2 and 9.5 dS m^{-1} respectively, with a minor modulation caused by the transpiration treatment. As it can be gathered from Table 4.1, how

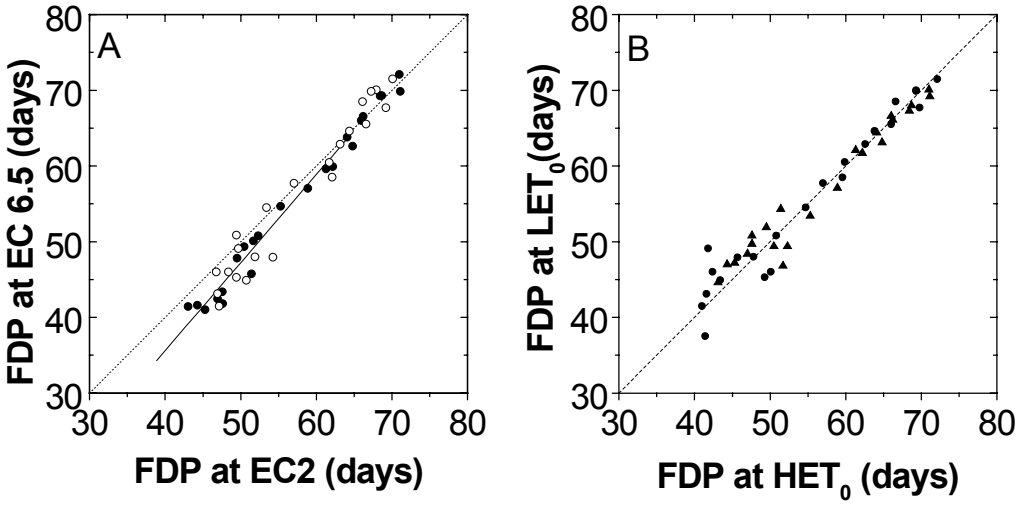

Figure 4.2 Fruit development period (FDP), days from flowering to harvest of the first ripe fruit of the truss. Each point is calculated from the mean of 6 plants per treatment (for flowering) and 24 plants (for date of first harvest). (A): 6.5 dS m^{-1} *vs* 2 dS m^{-1} at high transpiration treatment (HET_0, ●) and low transpiration treatment (LET_0, ○). Solid line is the best fit. (B): FDP at LET_0 *vs* HET_0 at EC 2 (▲) and 6.5 dS m^{-1} (●). Dotted line shows 1:1 ratio.

ever, the EC effect on fruit growth rate does not fully account for the reduction in final size, in either climate treatment.

4.3.3 Fruit development period (FDP)

The residual difference in fruit size might be accounted for by the observation that in all experiments fruits were ripe slightly earlier at high EC. Figure 4.2 shows separately the effect of both treatments upon FDP. Since FDP shortens as the mean temperature increases (de Koning, 1994), the first harvests for our spring-summer plants, are on the right hand side of both panels of Figure 4.2. Thereafter the FDP shortened gradually. Shortening of FDP at high EC became progressively evident (Figure 4.2A) reaching some 6 days (12%) at the end of the experiment. The mean difference (the two transpiration treatments pooled) was 5% (t-test paired two sample for mean, $p<0.0001$). The climate treatment did not affect FDP (Figure 4.2B): the slope of the best-fit lines is within 3‰ of unity ($P <0.0001$).

4.3.4 Dry matter accumulation into fruits

Dry matter accumulated by individual fruits was neither affected by EC nor by transpiration treatment (Figure 4.3A). Obviously, the dry matter percentage of fruits decreased with fruit growth (Figure 4.3B). As there was no effect of the treatments upon dry weight of fruits, but a large effect on fresh weight, the dry matter content of the high EC fruits is higher. Similarly, also the effect of the LET_0 on high EC is consistent with Figure 4.1A and Figure 4.3A.

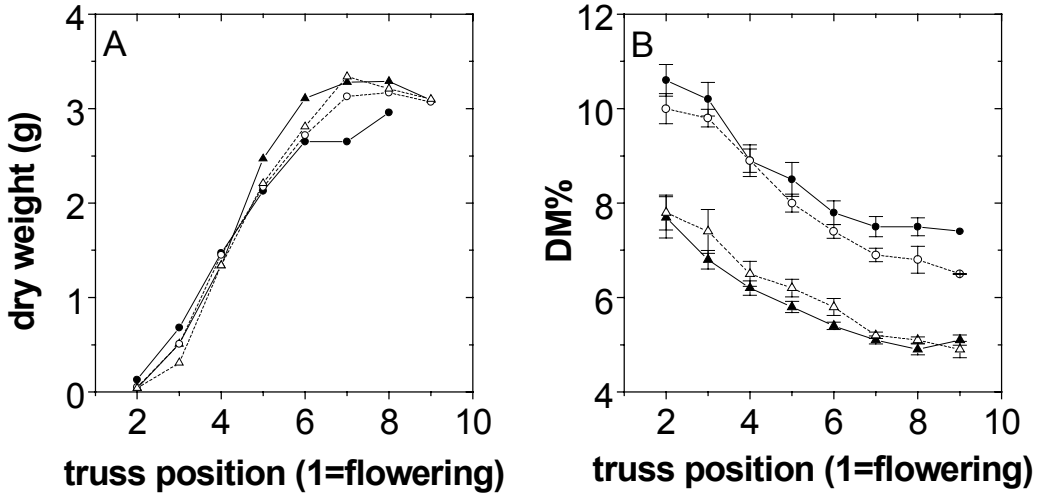

Figure 4.3 (A): dry weight of individual fruits in each truss; and (B): corresponding dry matter content. Points are means of six measurements during April 24 to June 5, 1996, each time three fruits were sampled per treatment. Symbols as in Figure 4.1. Vertical bars are plus and minus standard error (in time). Bars are not shown in the left panel for clarity: differences are non-significant.

4.4 Discussion

Growth of tomato fruits can be divided into three phases: slow growth in the first 2-3 weeks after anthesis (mainly cell division); rapid growth (cell expansion) when most weight is accumulated; and slow growth again for about 2 weeks before ripening (Ho and Hewitt, 1986). Fruit size below 10 cm^3 (largely the cell division phase) was not significantly affected by the salinity treatment (Figure 4.1). This may imply that fruit growth during the cell division phase is not sensitive to salinity stress. Because, the accuracy of the linear measurement (±0.05 mm) causes a relatively large error with such small fruits (±6% at 10 cm^3), this result needs further confirmation. Nevertheless, it is very possible that these tissues are less sensitive to water stress, because it is in the first place cell expansion that is affected. Alternatively, one might say that water demand of such small fruits might be easy to satisfy also under limited stress. Ho (1995) stated that differences in fruit size do not depend on the cell division rate after anthesis.

During the rapid growth phase, the increase in fruit size at high salinity slowed down (Figure 4.1). From our data we could only determine mean daily growth rate over one-week periods. Short-term observations, however, may be less straightforward to interpret. For instance Pearce *et al.* (1993b) could detect an effect of EC of the nutrient solution on the 24-h growth pattern only at daytime and in mid-season but not in the early (April) and late (September) season. Ehret and Ho (1986b) observed that the diurnal cycle of fruit growth rate was less explicit at EC 17 dS m^{-1} than at EC 2 dS m^{-1}. Also van Ieperen (1996) reported a significantly lower fruit weight when high EC was imposed on plants during daytime, rather than at nighttime. From this and our own data, we can conclude that high salinity decreases the mean growth rate, but that its effect does not need to be constant in time, and that it shows up particularly in conditions of high transpiration. Pearce *et al.* (1993b) concluded that plant water stress caused by a high transpiration demand during the day was responsible for the observed reduction in fruit expansion rate during the middle of the light period in mid-season plants.

An indirect confirmation of this conclusion is given by observing that the EC-effect (under HET_0) in Table 4.1 is larger than what would be calculated from the whole-season results of chapter 2 (33% *vs* 28.5%). The present results, in fact, have been obtained under particularly sunny conditions (the average global radiation integral outside during this measuring period was about 15 MJ $d^{-1}m^{-2}$). Similarly, Sonneveld and Welles (1988) concluded that the EC-effect on the yield was related to the production level (light intensity).

Our result that LET_0 could alleviate the salinity effect on growth rate is consistent with the finding by Leonardi *et al.* (2000). They showed that fruit growth rate during daylight hours was significantly decreased by a high vapour pressure deficit of the ambient. Ho *et al.* (1987) predicted that if a plant would be subjected to water stress, then carbon import into the fruits might not be accompanied by a propor-

tional increase in water accumulation and the resulting expansion might be less than expected. Transpiration reduction may help to improve plant water status. Maas and Hoffman (1977) already pointed out that many crops seem more salt-tolerant when grown under humid conditions than under arid ones. However, at low EC, LET_0 had little effect on fruit development and the final fruit size (Figure 4.1). Similarly, under sufficient water supply in the root zone, Stirzaker *et al.* (1997) also observed that misting of tomato plants during the hot period of the day did not affect fruit fresh weight. It may be concluded that the climate effect upon fruit growth only appears at high EC. Indeed, the present results about EC-effect on the final fruit weight under LET_0 (Table 4.1) are consistent with the whole-season results described in chapter 2.

Our observation that fruit development period was shortened by 5% at EC 6.5 dS m^{-1} compared with at EC 2 dS m^{-1} is consistent with Mizrahi (1982). He observed that salinity (6.6 dS m^{-1}, albeit raised with NaCl, compared with 1.5 dS m^{-1}) shortened duration of both fruit expansion and ripening of tomato, and resulted in decreased FDP by 4 to 15%, for various cultivars. Other researchers (for instance: Sharaf and Hobson, 1986; Alarcón *et al.,* 1994a) also noted that FDP of tomato was shortened by salinity. Shortened FDP in tomato was also observed under water stress conditions (*e.g.* Salter, 1958, Wolf and Rudich, 1988) and resulted in decreased fruit size (Salter, 1958). Hsiao (1993) concluded that mild to moderate water stress during the generative phase can be beneficial for tomato plants by promoting early partition of assimilates to fruits and, consequently, early maturity. However, the total fruit yield may be reduced because of restriction in canopy size. Earlier partitioning of assimilate to storage organs (thus probably earlier formation of tuber) was also observed in radish at EC 9 and 13 dS m^{-1} (Marcelis and Hooijdonk, 1999). This is probably an adaptation of a plant to stress condition (Mizrahi, 1982). It is not surprising that summer conditions may have an amplifying effect in this. With the increase of solar radiation, fruit surface temperature is often higher than ambient (Cockshull *et al.*, 1992) and a high temperature in fruits probably speeds up their metabolism (Walker and Ho, 1977; Pearce *et al.*, 1993a). It is well possible that earlier partitioning of assimilates interacts with speeding up of the metabolism.

The decline of the dry matter content of fruits during maturation and their dry weight growth pattern are consistent with common experience (for instance, Ehret and Ho, 1986a). An increased dry matter content at high EC, compared to the reference was obvious during fruit development (Figure 4.3B). The observation that there was no effect of EC nor transpiration on dry weight accumulation of individual fruits is in line with all our experiments (chapter 2).

4.5 Conclusion

The effects of decreased daily growth rate and a shortened fruit development period contributed to a smaller final fruit size at high EC, compared to the reference. The effect of salinity on fruit growth rate can be reduced through low-transpiration conditions, whereas there is no climate modulation upon the EC-caused shortening of the fruit development period.

Acknowledgements

I am greatly indebted to Dr L.F.M. Marcelis and J.J. Uittien (Plant Research International, Wageningen) for the data on fruit volume; and to A.M.R. Abdel-Mauwgoud (Horticulture Research Department, National Research Center, Egypt) and Arianna Cariglia (University of Milan, Italy) for help with the measurements that led to the determination of FDP.

Chapter 5

Response of tomato plants to a step-change in root-zone salinity under two different transpiration regimes

Ya Ling Li, Cecilia Stanghellini and Hugo Challa. Conditionally accepted by Scientia Horticulturae,

Abstract

The response of a tomato crop to a step-change in salinity was investigated under different potential transpiration conditions. A crop growing for 5 months under saline irrigation water (EC 9 dS m^{-1}) was given thereafter a standard nutrient solution with an EC of 2 dS m^{-1}. The previous effects of salinity were largely reversed, especially for fruits and leaves that had not yet reached the rapid growth phase. After a period of eight weeks, the final weight of fruits reached that of "normal" (EC 2 dS m^{-1}) fruits. There was a high incidence of fruit cracking, even greater in the low transpiration treatment than the high one. The peak incidence of cracking was in fruits that were harvested some 25 days after lowering the EC. The chance of cracking was positively affected by the increase in skin expansion rate due to a change in EC and further enhanced by reduced potential transpiration (high ambient humidity). New leaves formed after the EC was lowered were comparable in size with those grown at low EC, but leaves that were fully expanded at that moment did not respond to the change in EC.

5.1 Introduction

Most plants respond to salinity with reduced growth, whenever salt concentration in the root environment exceeds a threshold value, according to a model originally proposed by Maas and Hoffman (1977). In most subsequent publications on the subject (*e.g.* Delton and Poss 1990; Shannon and Grieve 1999; Sonneveld, 2000) threshold EC and yield decrease were established for various crops, under conditions of constant salinity in the root environment. In tomato, the salinity-induced yield reduction is mainly caused by a decreased inflow of water into fruits (Ehret and Ho, 1986a), combined with a shortening of the fruit growth period (Mizrahi, 1982). There is general agreement that other factors (most notably shoot environment), may modify yield response to salinity, as already pointed out by Maas and Hoffman (1977). We have shown that the "environment" effect can be quantified by potential evaporation, in particular, that reducing potential evaporation limits the

damage caused by salinity (chapter 2).

However, natural conditions are seldom constant: for instance, growers may have to use irrigation water of changing quality; or rainfall may wash out salts accumulated in the root environment. Not much is known about plant response to changing root-zone salinity. Alarcón *et al.* (1994b) showed that a decrease in relative growth rate and leaf area ratio in tomato plants in response to increasing osmotic pressure of the nutrient solution could be detected within an experimental period of 17 days. Van de Sanden and Uittien, (1995) showed that the fruit growth rate of tomato decreased and that the decrease of fruit size was related to relative exposure time at high salinity.

In the present study, the response of a tomato crop to a step change of root-zone salinity was observed in order to establish to what extent plants recover after a prolonged exposure to high salinity. Therefore the response to a step-change from a five-month-exposure to 9 dS m^{-1} root zone salinity (EC) to 2 dS m^{-1}, rather than the other way round, was determined in this experiment. In addition, the response under two levels of potential transpiration was determined to get some insight into the response dynamics and underlying mechanisms.

5.2 Material and methods

The general set-up of the series of experiments has been described in detail in chapter 2, and so only the points that are relevant to this paper will be summarised here. Tomato, *cv* Chaser, was grown in rockwool slabs and two potential-transpiration climate treatments were factorially combined with two (constant) salinity treatments (expressed by electrical conductivity, EC, dS m^{-1}). Experimental conditions were such that oversupply of the nutrient solution ensured the EC of the irrigation water was the same as the EC of the drain water and of water extracted from the root zone.

The two climate treatments were each given in one compartment (300 m^3) of a Venlo-type glasshouse. One compartment was controlled according to Dutch standard practice and served as the reference (high transpiration treatment, HET_0). Climate control in the other compartment (low transpiration treatment, LET_0) aimed at reducing potential transpiration by a third, by manipulating as far as possible only ambient humidity, by a combination of venting and misting. The model used for calculating the transpiration rate has been described by Stanghellini (1987) and the climate control algorithm by Stanghellini and Van Meurs (1992). Water supply and drain data from each treatment were used to check the effectiveness of the climate treatment (Figure 5.1). Misting caused slightly lower temperatures in the LET_0 compartment. Only at temperatures above 25 ^{0}C, however, did the difference between the two compartments steadily exceed 1 ^{0}C.

The crop had been subjected to two constant-salinity treatments, both 9 dS m^{-1}, between February and June 1997. In one treatment sodium chloride was added to a

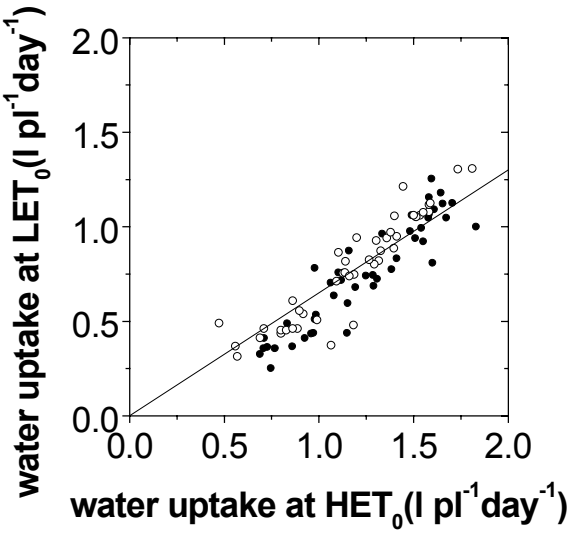

Figure 5.1 Daytime water uptake (litres per plant per day) at low potential transpiration (LET_0) *vs* the one at high potential transpiration (HET_0), between July 7 and August 20, 1997. ●: high EC (HEC) and ○: EC lowered (EC↓).

standard nutrient solution of 2 dS m^{-1}, whereas the other was a more concentrated version of the standard nutrient solution. At the start of the experiment, the solution containing NaCl was stepwise flushed out, and refreshed with a standard nutrient solution (EC=2 dS m^{-1}) over ten days (lowered EC treatment, EC↓). The other treatment, with high concentration throughout of nutrients in the solution (EC=9 dS m^{-1}, HEC) was used as reference for the subsequent eight weeks that the experiment lasted.

Growth and yield were monitored as follows: six random groups of four plants were marked in the central rows of each treatment. Vegetative growth was determined by monitoring one plant per group, of which the length and width of every leaf were measured non-destructively twice a month. Leaf area was determined by means of the Eq. (3.1).

Marketable and unmarketable yield (weight and number) were determined separately for each group, twice a week. In addition, the dates of the first and of the last harvesting from each truss were recorded. The date of formation of each truss was estimated by interpolation (a truss every three leaves) from the observations of number of leaves made every two weeks, one mean date for each treatment. Fruits of each truss were assigned a common development period (FDP) defined as the time elapsed between the estimated mean date of formation and the date the first fruit of that truss was harvested.

Although the two salinity treatments were not exactly comparable, the two crops were similar by the time the experiment started (Table 5.1). For comparison we also show the parameters for a similar crop (EC=9.5 dS m^{-1}) at the end of June the year before (Table 5.1), confirming that the reference crop was indeed sufficiently representative. Fruits in the NaCl treatment (the one that was to become EC↓) were

consistently smaller than the corresponding HEC fruits (Figure 5.2). This is probably due to the 10% difference in osmotic potential between the two solutions (chapter 6). This is unlikely, however, to have had any amplifying effect on the subsequent observations. In addition, the difference between weights at the time of starting this experiment (without accounting for previous history) was not significant (Table 5.1)

5.3 Results

After the EC was lowered, the mean weight of harvested fruits soon became larger

Table 5.1 Parameters of plant development at the beginning of the experiment. Fruit weight and other quality parameters are the average of harvests during the last two weeks before lowering the EC. The code 1996 indicates corresponding values (in the same period) from a similar crop grown at constant EC=9.5 dS m^{-1}, in an experiment the previous year (chapter 2). Figures are mean±standard deviation

	High transpiration			Low transpiration		
Code	EC↓	HEC	1996	EC↓	HEC	1996
EC root extract (dS m^{-1})	9.0	9.1	9.3	8.8	9.1	9.0
Leaf area (m^2 $plant^{-1}$)	0.96±0.07	0.92±0.15	0.85±0.12	0.90±0.07	0.87±0.10	0.86±0.18
Fruit trusses (pl^{-1})	6.9±0.4	7.0±0.7	-	7.7±0.8	7.5±0.4	-
Fruit weight (g)	58.9±1.9	56.8±1.8	55.0±4.6	58.3±3.4	59.4±2.6	59.2±3.0
Fruit DM (%)	6.72±0.15	6.52±0.33	6.58±0.15	6.42±0.14	6.31±0.20	6.78±0.18

Table 5.2 Mean weight of ripe fruit at EC↓ at the end of the experiment (Aug 18-28, 1997), compared with the mean weight of ripe fruits grown at a constant EC=2 dS m^{-1} the year thereafter (Aug. 17-27, 1998). Also given is the fruit development period (FDP) at the moment of lowering EC and at the end of the experiment. Figures are mean ± standard deviation.

Treatment	High transpiration			Low transpiration		
	EC↓ 1997	HEC 1997	EC 2 1998	EC↓ 1997	HEC 1997	EC 2 1998
Fruit weight (g)	74.2±4.3	45.6±5.7	71.9±1.9	76.6±4.0	51.4±2.9	75.9±6.3
FDP at the start	53	52	-	60	59	-
FD at the end	46	39	-	49	40	-

than that of the HEC fruits in the same greenhouse and the difference in weight kept increasing with time (Figure 5.2). At the end of the experiment average fruit weight of EC↓ was 63% and 49% higher than that of HEC in the high and the low transpiration houses, respectively (Table 5.2). As had been observed the year before, high EC fruits in the low transpiration house were larger than in the corresponding treatment in high transpiration (Figure 5.3). Lowering the EC caused fruit cracking, particularly in the low transpiration treatment. Over the whole period of the experiment, 44% at LET_0 compared with 12% at HET_0 (Figure 5.4). The first cracked fruits were harvested soon after lowering the EC. The highest proportion of

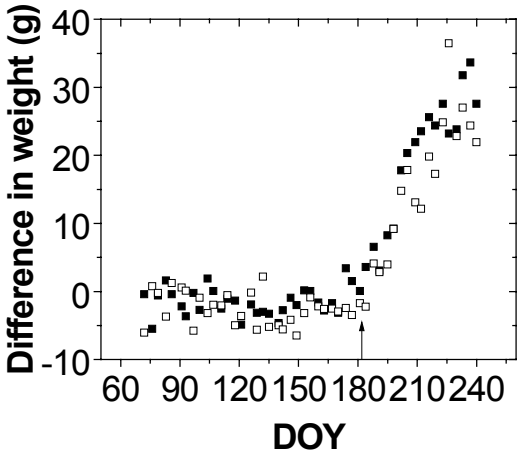

Figure 5.2 Difference (EC↓-HEC, g) between mean weight of fruits from the two nutrition treatments in the same greenhouse compartment. Symbols refer to the high (■) and low (□) transpiration greenhouse; the arrow indicates the time of lowering EC.

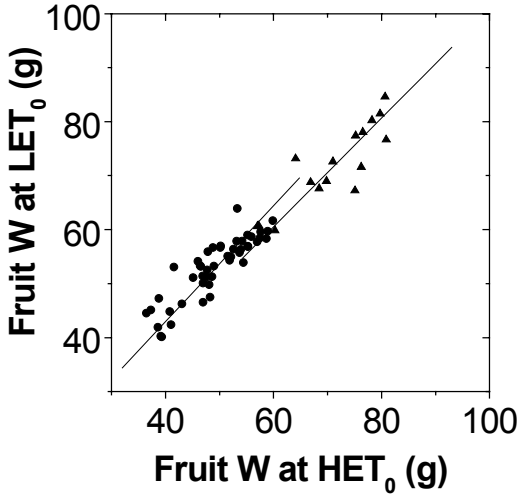

Figure 5.3 Mean fruit weight (g), in each harvest, from LET_0 *vs* corresponding weight at HET_0; at HEC (●) and EC↓ (▲). HEC points refer to the whole set of data, not just the period after EC was lowered. Solid lines show the best-fit relationships ($P<0.0001$): slope at HEC is 1.074 and at EC↓ is 1.009.

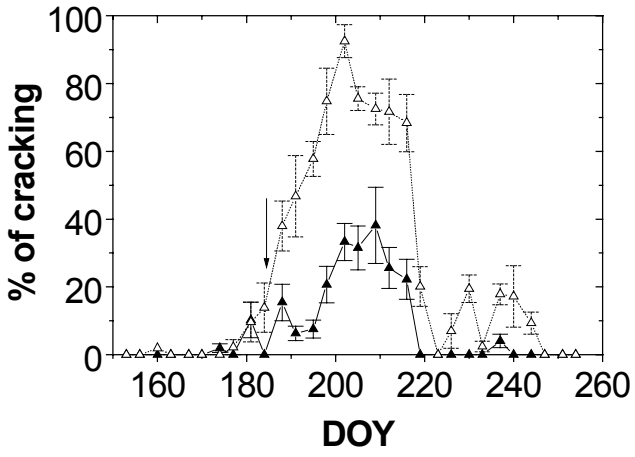

Figure 5.4 Percentage of cracked fruits of each harvest, for the treatment EC↓. Closed and open symbols indicate HET_0 and LET_0, respectively. The arrow shows the time of lowering EC. Vertical bars are plus and minus standard error (n=6).

cracked fruits was harvested some 25 days later, when it exceeded 90% at LET_0 and 30% at HET_0 (Figure 5.4).

A constant high EC slightly shortened fruit development period (chapter 4). In this experiment, FDP gradually extended at EC↓ to become 20% longer than in the HEC treatment, in both greenhouses (Figure 5.5). This result is comparable with the observations of Mizrahi (1982) that high salinity could shorten duration of fruit development by up to 15%.

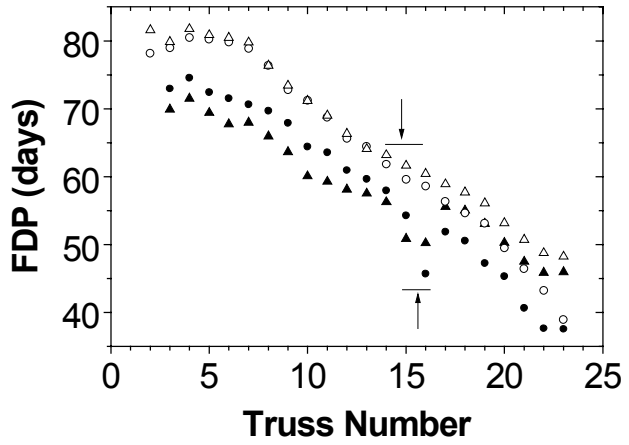

Figure 5.5 Fruit development period (FDP) plotted against truss number (referring to the position of the truss counting from the root) at EC↓ (▲, Δ) and HEC (●, ○). Closed and open symbols represent HET_0 and LET_0, respectively. The arrows together with lines indicate the trusses that were being harvested at the time of lowering the EC. Points show averages of each truss for 24 plants per treatment.

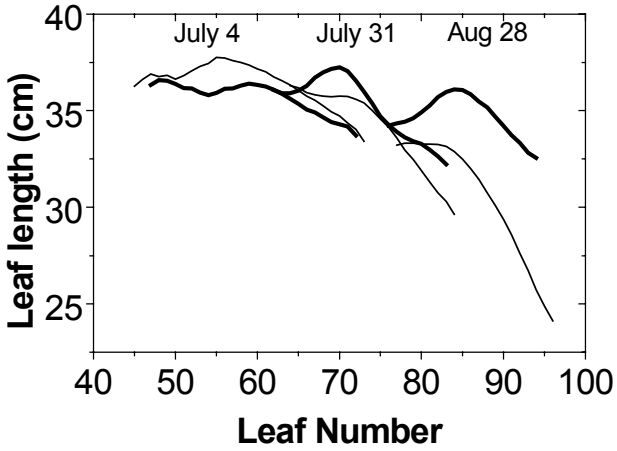

Figure 5.6 Profiles of leaf length during the experiment (at the start, after 4 weeks and after 8 weeks). The leaf number refers to the position of the leaves along the stem counting from the root. Lines show five-value running averages of mean profiles of 12 plants per treatment, at EC↓ (▬) and HEC (—). The data from the two transpiration treatments were pooled since there were no significant differences between them.

Figure 5.6 shows the profiles of leaf length measured at the start of the experiment, and 4 and 8 weeks thereafter. Since there was no leaf response to the transpiration treatment, data are pooled for each EC. Leaves that were fully expanded when the EC was lowered did not expand further, whereas after 4 weeks, higher leaves were some 2 cm longer at EC↓ than at HEC. After two months most leaves had been formed after the treatment started and the difference had increased to about 5 cm. Altogether, however, in the limited duration of this experiment, there was no significant difference between average leaf area index (LAI) at EC↓ and at HEC.

5.4 Discussion

5.4.1 Fruit growth

In chapters 2 and 4 it was shown that the main effect of high EC was a decrease of water inflow into the fruits. Consequently lowering the EC at the beginning of this experiment must have increased water inflow into fruits, *i.e.* fresh growth rate. Indeed, the weight of ripe fruits gradually increased with time (Figure 5.2) until fruits were harvested that had developed fully under the new EC. The experiment probably finished around the time that stage was reached, and so no plateau can be distinguished in Figure 5.2. In fact, the weight of EC↓ fruits harvested at the end of the experiment (*i.e.* 50 days after lowering the EC) was comparable to the weight of low-EC fruits, that were harvested during the corresponding period of the year

1998, in the same greenhouse compartment (Table 5.2).

5.4.2 Fruit cracking

The occurrence of fruit cracking after lowering the EC of the solution was to be expected. Indeed, it is well known that fruits may crack when there is a sudden increase in water availability, as a result of irrigation or rain after prolonged drought (*e.g.* Peet, 1992; Opara *et al.*, 1997), or a lowering of the conductivity of the fertiliser solution (Peet, 1992). Cracking is associated with decreased epidermis elasticity in mature-green or breaker stage (Kamimura *et al*., 1972; Bakker, 1988) that causes rupture under the stretching caused by increased water inflow.

The harvesting of cracked fruits continued for about five weeks and the peak incidence (of cracked fruits) was about 25 days after lowering the EC. In order to pinpoint the relationship between growth stage and susceptibility to cracking, it is possible to describe fruit growth in the two cases, since final fruit size and fruit development period before and after lowering the EC are known. The growth curves in Figure 5.7 (left panel) are based on the logistic function with the parameters given in Table 5.2. In all cases a ripening period equal to 20% of FDP has been taken into account (Ho and Hewitt, 1986; Bakker, 1991). For the sake of this analysis, fruit weight has been converted into surface area, assuming a spherical shape and unit density. Both the growth rate ($cm^2\ day^{-1}$) corresponding to the original (HEC) curve, and the difference between the "new" and the old growth rate are plotted in Figure 5.7 (right panel) *vs* the time remaining to harvest, to facilitate comparison with Figure 5.4. This may seem confusing, unless one realises that, since ripe fruits are represented in Figure 5.4, points to the right of any given day represent fruits that were still unripe at that moment. The right-hand panel of Figure 5.7 implies that fruits whose growth rate was maximal at the time EC was lowered would be harvested some 30 days thereafter, whereas fruits subjected to the largest "strain" (difference between "old" and "new" growth rate) would be some25 days from harvest. Low transpiration would stretch time-to-harvest in both cases by a few days. Comparison of this with Figure 5.4 implies that fruits were most susceptible to cracking when the difference between the growth rate in the new and old situation was maximal, rather than when the absolute growth rate was maximal. This analysis supports the hypothesis that the epidermis tends to cracks when the newly required expansion is much larger than the previous expansion rate (Kamimura *et al.* 1972). If the hypothesis of Peet (1992), that rapidly growing fruit might be especially predisposed to cracking, were true, the maximum occurrence of cracking would have taken place later (Figure 5.7).

The increased incidence of cracking of tomato fruits under low potential evaporation (high relative humidity, small vapour pressure deficit) is well documented (*e.g.* Peet, 1992, Maroto *et al.* 1995), most recently by Leonardi *et al.*, (2000). Peet (1992) inferred that high humidity effects on fruit cracking were related to gas and water pressure increases due to an increase in water supply or a temperature in

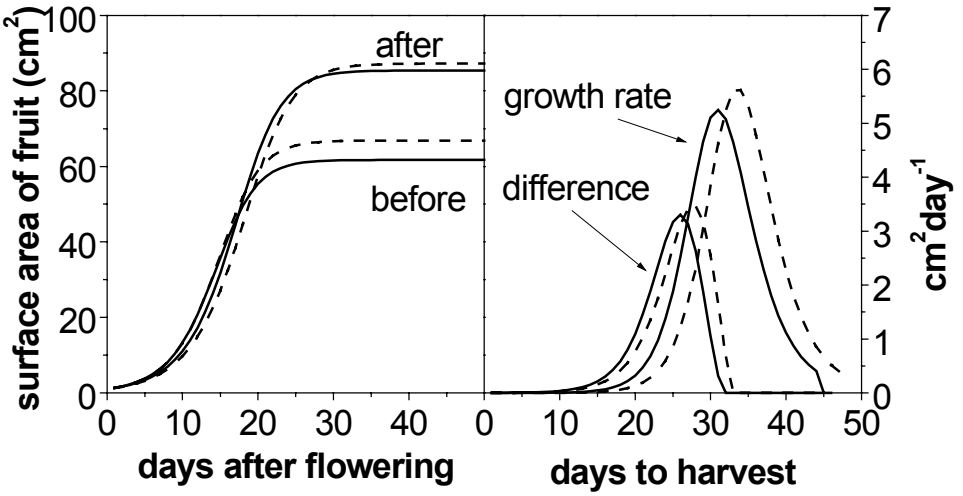

Figure 5.7 Left panel: Growth curve of the surface area (cm^2) of tomato fruits before and after lowering the EC. Right panel: The original growth rate (that is, the derivative of the curves in the left panel) and the difference between the new and the original growth rate in HET_0 (—) and LET_0 (---).

crease. The excess water supply (or water pressure increase) within the fruit, when fruit transpiration is small, such as in a humid environment (Ehert and Ho, 1986b; Leonardi *et al.,* 1999) can only be relieved by expansion of the epidermis. Indeed, our results seem compatible with the hypothesis that susceptibility to fruit cracking is proportional both to the difference in expansion rate between the new and the old situation and to the difference in water inflow and outflow to and from the fruits, which is determined by the potential evaporation.

5.4.3 Vegetative growth

The response of leaves and of fruits to a step change in osmotic pressure in the root zone is similar in one aspect. Organs formed and developed under the new situation are fully adapted to it, despite the prolonged exposure of the plant to high EC. Organs that are already formed can adapt only to a limited extent, as shown by Figure 5.2 and Figure 5.6. Munns *et al.* (1982) observed the same in a short-term experiment with barley plants. They concluded that leaf growth was limited at high salinity by water deficit in the elongating leaf tissue rather than by ion excess.

It can be concluded that the negative effect of high salinity on growth and yield is mainly related to the water balance of the plant, which can be restored even after quite a long exposure to high salinity. However, the time course for recovery is comparable to the duration of the organs' development.

Acknowledgements

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Chapter 6

Plant water relations as affected by EC of the nutrient solution and potential transpiration in tomato

Ya Ling Li, L.F.M.Marcelis, Cecilia Stanghellini, A.M.R. Abdel-Mawgoud and J. Uittien, (in preparation)

Abstract

The hypothesis that water flow into tomato fruits is affected similarly by osmotic potential of the nutrient solution and potential transpiration (shoot environment) was tested. For this, experiments were carried out in two glasshouses where climate was controlled to maintain a desired relationship between potential transpiration (normal and depressed, respectively). This climate treatment was combined with a root zone osmotic potential treatment, whereby in each experiment two values were compared. The three experiments entailed the following pairs: -0.07 and -0.4 MPa, -0.08 and -0.25 MPa, and twice -0.35 MPa but with different compositions (one largely with sodium chloride).

Water uptake per unit leaf area was not affected by osmotic potential of the nutrient solution. The hydraulic resistance within the plant, deduced from measurements of leaf and stem water potential, was independent of the transpiration flow and was not affected by the osmotic potential of the nutrient solution. Water import into fruits, determined by the stem-to fruit-potential difference was affected by both treatments. Results showed that fruit growth rate and the final fruit weight were correlated to the water potential gradient between the stem and the fruits. Since fruit osmotic potential was relatively constant at a given concentration of the nutrient solution, the stem water potential is a good indicator of fruit growth.

6.1 Introduction

The effects of increasing salinity of the nutrient solution on plant growth of tomato are well documented (*e.g.* Adams, 1991; Ehret and Ho, 1986a). It is well known that yields are significantly decreased when electrical conductivity (EC, dS m^{-1}) of irrigation water exceeds a crop-specific threshold (Maas and Hoffman, 1977). Salinity may lead to ion excess in the plant (Greenway and Munns, 1980) and can induce water stress caused by the increase of osmotic pressure of irrigation water. An accumulating body of evidence suggests that the predominant effect of high EC on fruit vegetables is water stress. For instance, Ehret and Ho (1986a), Adams and Ho

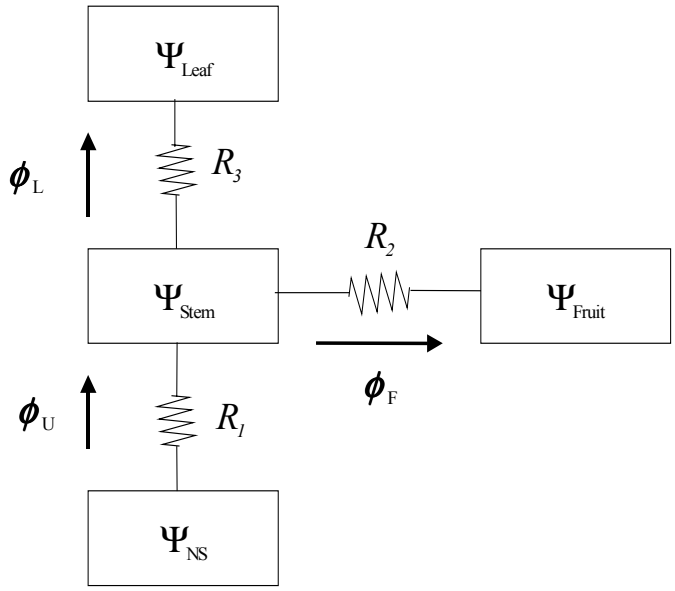

Figure 6.1. Schematic description of water movement in a plant. ϕ_U is the total water uptake of the plant; ϕ_L is the water flow to leaves (transpiration flow) and ϕ_F stands for the water flow to fruits. R_1 is the hydraulic resistance between the nutrient solution and the stem; R_2 is the hydraulic resistance on the water flow to fruits and R_3 is the resistance on the water flow to leaves. Ψ_{NS}, Ψ_{stem}, Ψ_{leaf} and Ψ_{fruit} represent, respectively, the water potential in the nutrient solution, in the stem, in the leaves and in the fruits.

(1989) and ourselves (chapter 2) observed that the salinity-caused reduction of yield in tomato is mainly due to less water accumulation into fruits, whereas dry weight of fruits seemed to be unaffected (within limits).

The water movement in a plant is driven by water potential difference (Van den Honert, 1948) and can be described by Ohm's law as in Figure 6.1. Water uptake is proportional to the difference in water potential between the nutrient solution and the stem, and inversely to the flow resistance between the two. Any decrease in water potential of the nutrient solution will lead to a decreased gradient in potential and hence to a smaller water uptake, unless the plant adapts by equally lowering its stem water potential or the flow resistance. Similarly, the water flow from stem to leaves or to growing fruits depends on the potential gradient and the flow resistance towards these organs. Things can be simplified further by regarding water flow to leaves as only transpiration and flow to fruits as only growth. That is, by neglecting fruit transpiration with respect to fruit growth and leaf growth with respect to leaf transpiration.

An increase in transpiration flow must be coupled to a larger potential gradient between root environment and leaves, unless one assumes that the flow resistance would decrease under high transpiration. In a root medium with plenty of liquid water available (such as nutrient film or a well-watered substrate) water potential in

the root environment, Ψ_{NS}, may be regarded as independent from plant water uptake. This means that an increase in the transpiration flow is coupled to a decrease in leaf water potential (Ψ_{leaf}), and that this drop is distributed along the continuum to the roots, so that it must lead to a decreased stem water potential (Ψ_{stem}). Therefore, the water import into fruits is expected to decrease at high transpiration, assuming no strong effect of potential transpiration on fruit water potential (Ψ_{fruit}) since fruit transpiration is relatively small (Johnson *et al*., 1992). From the above, we may expect a similar effect of EC of the nutrient solution and of potential transpiration on plant water status, whereby Ψ_{stem} is an important link between the EC and transpiration effects.

Water transport into tomato fruits is mainly (more than 90%) through the phloem (Ho *et al*., 1987; Lee, 1989). The driving force for phloem translocation is the turgor pressure gradient in the phloem sieve tubes rather than the apoplasmic water potential gradient. However, Johnson *et al*. (1992) discussed that, due to the hydraulic restriction in the xylem of the tomato pedicel and because most of the water enters the fruit through the phloem, the apoplasmic water potential gradient would be closely correlated with the phloem turgor pressure gradient. Indeed their data indicated a correlation between changes in fruit diameter and the water potential gradient from the stem to the fruits.

The aim of this paper is to investigate whether salinity and transpiration effects on plant water relations, using the above conceptual description of water flow in tomato plants, can explain the interactive effect of EC and potential transpiration on production. First we tested our hypothesis that Ψ_{stem} is the link between effects of EC and transpiration. Then we tested whether water uptake was proportional to the water potential gradient from the nutrient solution to the stem under a wide range of flow rates, and finally whether water flow into tomato fruits could be related to the gradient in water potential from the stem to the fruits.

6.2 Materials and methods

6.2.1 Experimental set-up and treatments

A series of experiments was conducted with tomato plants, *cv* Chaser, grown in greenhouse, in a re-circulating system with rockwool as a substrate in 1996, 1997 and 1998. All crops were transplanted around January 1st (when the first inflorescence was visible), and trained in the high-wire system. A high and a low potential transpiration climate were factorially combined with two solute concentrations in the root environment. Both nutrition and transpiration treatments started about one month after transplanting. The set-up of the series of experiments has been described in detail in chapter 2, and only the relevant items are briefly explained hereafter.

The potential transpiration treatments were provided in two identical glasshouse compartments (300 m^2 each). One compartment was controlled according to standard cultural practices in the Netherlands and served as reference (high transpiration treatment, HET_0). The transpiration rate was calculated on-line according to the model described by Stanghellini (1987). The transpiration in the other compartment was depressed (low transpiration treatment, LET_0) by calculating set point for ambient humidity, according to an algorithm described by Stanghellini and van Meurs (1992). Humidity was controlled by a combination of high-pressure misting and roof ventilator opening. In two experiments (1996 and 1997), potential transpiration at LET_0 was reduced by one third compared to HET_0; in the third experiment (1998) the low transpiration treatment was basically a "low ventilation treatment". Window opening in response to humidity was always 25% less than at HET_0, which resulted in about 10% lower vapour pressure deficit. In addition, the misting system was switched on anytime the potential transpiration of the reference compartment exceeded 0.15 l $(plant\ h)^{-1}$.

The nutrition treatments involved a "reference" and a "high" EC in the nutrient solution. High EC was created by increasing the concentration of all nutrients or by adding NaCl to the nutrient solution (one of two treatments in 1997). Water supply was abundant to avoid accumulation of salts. EC of supply and drain water were monitored and seldom diverged. The elemental composition of nutrient solution was analysed every fortnight from root zone extracts. The osmotic potential of the nutrient solution, Ψ_{NS} (MPa) was calculated by the relation (Slatyer, 1967, p26):

$$\psi_{NS} = -cRT \qquad (6.1)$$

with c the elemental concentration (mol cm^{-3}); R the universal gas constant (8.31 J K^{-1} mol^{-1}) and T the absolute temperature of the solution (here T=293 K).

The mean EC resulting from the treatments, for each experiment, and the corresponding osmotic potential are listed in Table 6.1. In this paper we will further refer only to the osmotic potential, calculated from the root extracts nearest in time to the observation we will be dealing with.

Table 6.1 Mean EC (dS m^{-1}) of the treatments and the corresponding osmotic potential in the nutrient solution (Ψ_{NS}, MPa) calculated according to the composition of extracts from rockwool, Eq. (6.1). As slightly different EC values were recorded sometimes between the two transpiration treatments, Ψ_{NS} values are given for both

Experiment (Year)		1996		1997		1998	
EC		2.1	9.5	9.0	9.0-NaCl	2.2	6.5
Ψ_{NS}	HET_0	-0.07	-0.40	-0.33	-0.36	-0.08	-0.25
	LET_0	-0.07	-0.40	-0.35	-0.36	-0.08	-0.26

6.2.2 Observation

Plant water uptake in each treatment was calculated from recordings of water supply and drain. With a few exceptions, the transpiration treatment indeed realised the desired difference in uptake (chapter 2).

During harvesting (twice a week), the number and the weight of total, marketable and unmarketable fruits were determined, separately, for each one of six random groups of four plants in the central rows of each treatment. Leaf area was determined twice a month for one of the four plants in each group, by non-destructive measurements of leaf length and width.

Fruit osmotic potential was determined on selected fruit samples, frozen immediately after harvesting. After thawing, the pericarp sap was mixed and centrifuged for 15 minutes (2500 rpm/min). Fruit osmotic potential was determined by vapour pressure osmometry (Wescor 5500). Since turgor potential of tomato fruits appears to be small (Shackel *et al*., 1991; Johnson *et al*., 1992) we assume hereafter that fruit osmotic potential is a good approximation of fruit water potential. Water potential of leaves was determined using a pressure chamber (Ritchie and Hinckley, 1975; Turner, 1988). Water potential of the stem was estimated by measuring the water potential of leaves that had been placed in polyethylene bags covered with aluminium foil 10-12 hours before the measurement, in order to prevent transpiration. The underlying assumption is that without water transport and after sufficient time to reach equilibrium, the water potential of stem and leaf should be equal (Jones, 1992).

Experiment 1996: The flowering trusses were marked on April 10, in order to determine fruit age at time of sampling. Measurements were conducted weekly, between April 17 and June 5. At each measurement three random plants in the midrow of each treatment were sampled. The diameter of the second fruit of all trusses was measured. Fruit growth rate was calculated from two such measurements, one week apart. After the second measurement all fruits were harvested (not later than 10:00), for determining fruit osmotic potential. Stem water potential was measured between 10:30 and 12:30, using leaves close to the truss that was at anthesis on April 10 (at a stem height of approximately 2.5m). Each measuring day we sampled two leaves per plant and three plants per treatment.

Experiment 1997: Water potential of the stem and osmotic potential of the fruit were measured weekly, between April 15 and June 25, at times of day comparable to the previous year. We did each measurement on one leaf per plant and three plants per treatment. Leaves to be measured were taken from the middle of the plant, around the fourth truss from the one that was flowering. Fruits (the second of each truss) were sampled from the truss closest to the sampled leaf.

Experiment 1998: Water potential of leaves and stems were measured in August and the beginning of September. One leaf per plant and three plants per treatment were sampled each time. Position of sampled leaves was similar to the year before. Measurements were done around 7:30, 13:00 and 19:00 each day, for five sunny

days and five cloudy days. Fruit osmotic potential was determined on fruits sampled, as the year before.

6.3 Results

Daytime water uptake per plant was up to 20% lower at the lowest Ψ_{NS} (the highest EC) with respect to the reference. However, as lower Ψ_{NS} (high EC) reduced leaf area (chapter 3), Ψ_{NS} did not affect water uptake per unit leaf area (Figure 6.2), which would imply that the stomatal resistance was not increased by lower Ψ_{NS} (high EC) (in the range that we have measured).

Fruit osmotic potential remained fairly constant with fruit development stage (referring to different trusses on a plant) and measuring date (Figure 6.3). However, Ψ_{fruit} was affected by Ψ_{NS} (Figure 6.4A) and slightly modified by the transpiration treatment. At HET_0 Ψ_{fruit} decreased with increasing radiation, whereas there was hardly any response to radiation at LET_0, Figure 6.4B.

The leaf and the stem water potential varied during a day, being more negative at noon and less negative in the morning and evening. The difference in water potential between stems and leaves increased with the flow (transpiration during the hour prior to the measurement) but did not change with Ψ_{NS} (Figure 6.5A). Given the spreading of the points, the relationship does not seem to deviate from a linear one, which would point to a resistance (R_3 in Figure 6.1) independent of the flow. Similarly, Figure 6.5B shows the difference in water potential between nutrient solution and stem; and Figure6.5C shows the difference between the stem water po-

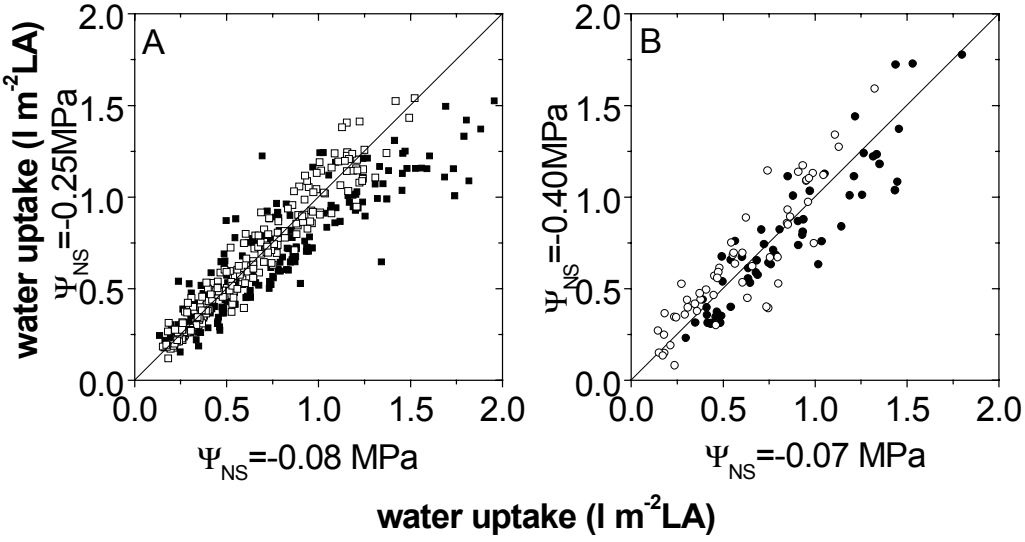

Figure 6.2 Daytime water uptake per unit leaf area at low Ψ_{NS} *vs* reference Ψ_{NS}. Each point is determined by the balance of metered supply and drains, from 6:00 to 18:00. Closed symbols refer to the high transpiration treatment, open ones to the low transpiration one.

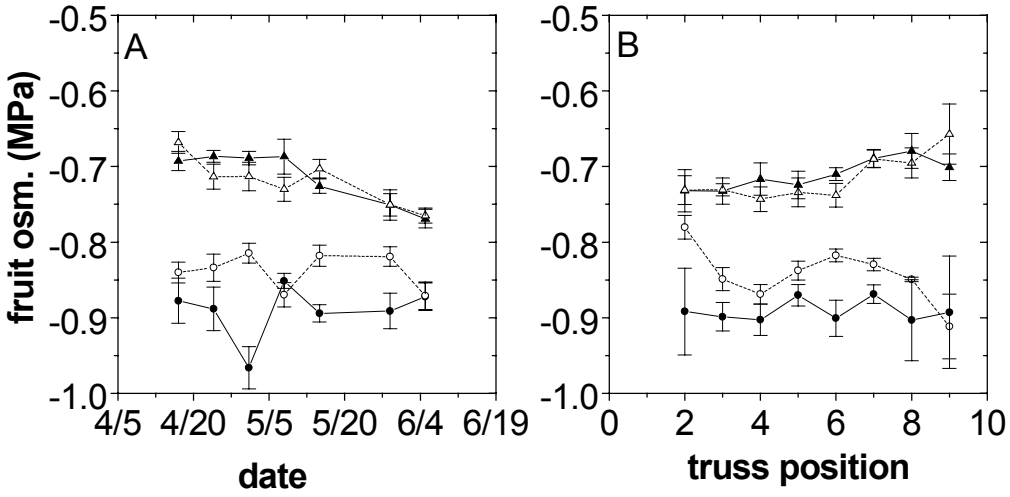

Figure 6.3 Fruit osmotic potential (A): against measuring date. Points are averages of data from all trusses in a measuring day; (B): against the truss position on the plants. Points are averages of 7 measurements (from April 15 to June 5, 1996), each is the mean of three plants on trusses at a given position. ▲, Δ: Ψ_{NS}=-0.07 MPa; ●, ○: Ψ_{NS}=-0.4 MPa. Open and closed symbols are the low and high transpiration treatment, respectively. Bars are twice standard error.

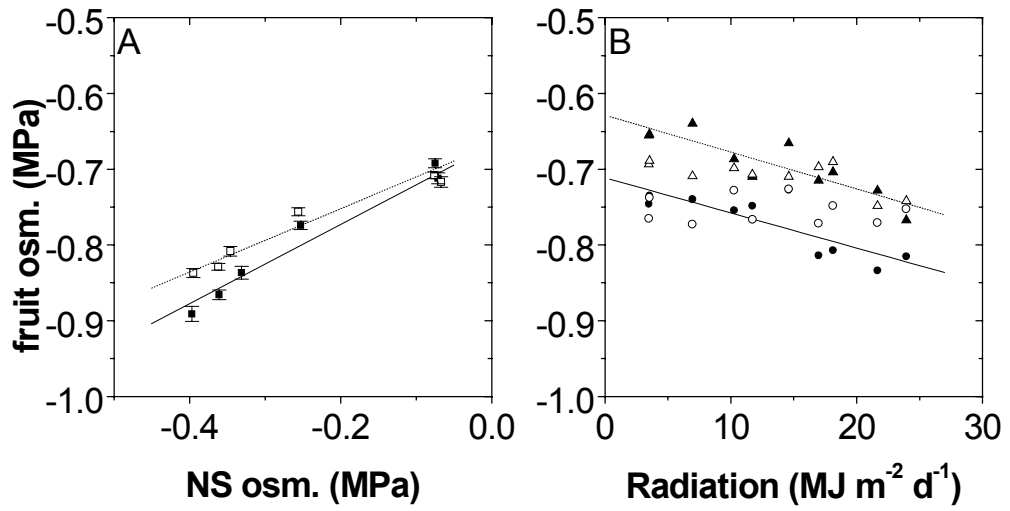

Figure 6.4 (A): Fruit osmotic potential (fruit osm.) *vs* the osmotic potential of nutrient solution (NS osm.) at high (■) and low (□) transpiration treatment. Each point is the average of all data in a given experiment and treatment and vertical bars are the standard error. Lines are the best-fit relationship at high (—) and low (·····) transpiration treatment. (B): Fruit osmotic potential *vs* daily solar radiation during the day that fruits were sampled. Each point is the average of measurements in the morning, noon and evening at Ψ_{NS}= -0.08 (▲, Δ) and Ψ_{NS}= -0.25 (●, ○) MPa. Closed and open symbols refer to the high and low transpiration treatment, respectively. Lines (·····, Ψ_{NS}= -0.08 Mpa; and —, Ψ_{NS}= -0.25 MPa) are the best-fit for HET_0.

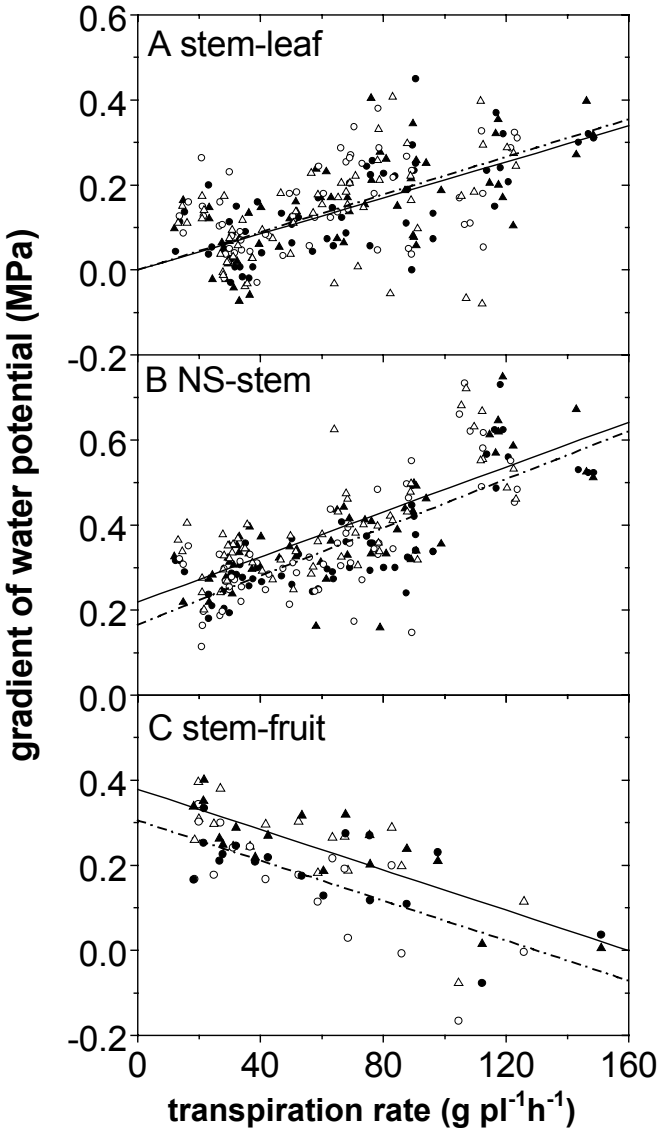

Figure 6.5 The gradient in water potential between the stem and the leaves (A), between the nutrient solution and the stem (B), and between the stem and the fruits (C) *vs* the transpiration rate the hour before the measurement. The transpiration rate was calculated, after checking that the model estimated correctly measured water uptake (on intervals of a few hours). ▲, Δ: Ψ_{NS}=-0.08 Mpa; ●, ○: Ψ_{NS}=-0.25 MPa. Closed symbols are for HET_0 and open ones for LET_0. Lines (—, Ψ_{NS}=-0.08 MPa and – - –, Ψ_{NS}=-0.25 Mpa) are the best-fit on pooled data of the transpiration treatments. The best-fit coefficients are listed in Table 6.2.

tential and fruit osmotic potential (measured simultaneously), both plotted against the transpiration rate. It is worth observing that in each figure the slopes of the linear best-fit for the two Ψ_{NS} treatments are [nearly] the same, which confirms (as far as the spreading of the points allows that) that none of the flow resistances was af-

Table 6.2 Coefficients of the best-fit linear correlation between the various gradients in potential (MPa) and the transpiration rate (g plant^{-1} h^{-1}) the hour prior to the measurements (value±standard error). Data of different transpiration treatments are pooled (refer to Figure 6.5). In all cases, the confidence of regression coefficient P<0.0001.

Ψ_{NS}	$\Delta\Psi_{NS\text{-}stem}$		$\Delta\Psi_{stem\text{-}fruit}$		$\Delta\Psi_{stem\text{-}leaf}$
	Slope	*Intercept*	*Slope*	*Intercept*	*Slope*
1996					
-0.07	0.0019±0.0003	0.1893±0.0258			
-0.40	0.0017±0.0003	0.0986±0.0227			
1998					
-0.08	0.0026±0.0002	0.2192±0.0162	-0.0024±0.0003	0.3791±0.0228	0.0021±0.0001
-0.25	0.0028±0.0002	0.1665±0.0163	-0.0024±0.0004	0.3055±0.0281	0.0022±0.0001

fected by the Ψ_{NS} treatments. The parameters of the best-fit lines are shown in Table 6.2, also for the year 1996, as far as allowed by the data that were collected.

The growth rate of individual fruits increased with increasing gradient in water potential from the stem to the fruit (Figure 6.6). When comparing the different treatments, the mean final weight of ripe fruits also showed a positive correlation with the mean stem-fruit gradient in water potential (Table 6.3).

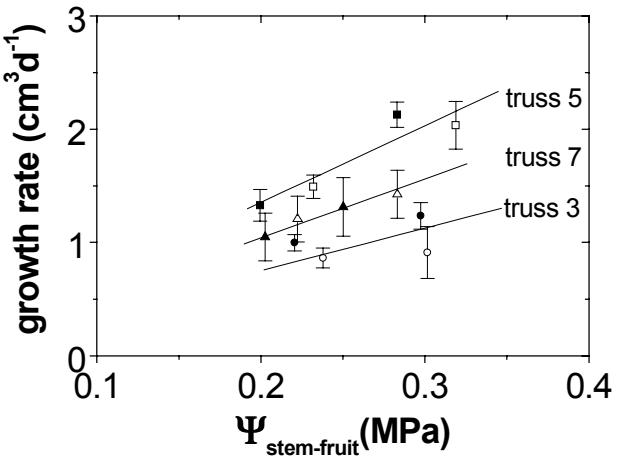

Figure 6.6 Growth rate of the second fruit of the 3rd (●, ○), 5th (■, □) and 7th (▲, Δ) truss from the one flowering (truss 1) *vs* water potential difference between the stem and the fruits. Closed symbols HET_0 and open ones LET_0. Each point is the average of 7 samples of three fruits from different plants, between April 15 and June 5, 1996. Each sample was determined from diameter measurements one week apart, on three marked plants. Bars are twice standard error of the mean. Fruits were harvested after the second diameter measurement, for determining osmotic potential. Water potential of the stem was determined at the same time, on the same plants.

Table 6.3 Final fruit mean weight (W, g) and daytime difference in water potential between the stem and the fruits (ΔΨ, MPa), affected by the osmotic potential in the nutrient solution (Ψ_{NS}, MPa) and by the transpiration treatment: ET_0, H(igh) and L(ow). Fruit weight was the mean of the fruits harvested during the period when the water potential was measured.

1998				1996				1997			
Ψ_{NS}	ET_0	$\Delta\Psi$	W	Ψ_{NS}	ET_0	$\Delta\Psi$	W	Ψ_{NS}	ET_0	$\Delta\Psi$	W
-0.08	H	0.229	75.8	-0.07	H	0.273	63.1	-0.34	H	0.265	47.9
	L	0.235	82.3		L	0.305	65.8		L	0.292	52.2
-0.25	H	0.178	61.2	-0.40	H	0.221	42.4	-0.36	H	0.270	45.4
	L	0.147	69.4		L	0.232	50.2		L	0.319	49.1
LSD 5%		0.063	4.75			0.101	4.73			0.146	2.22

6.4 Discussion

6.4.1 Hydraulic resistance and plant water uptake

As we pointed out above (Figure 6.5), linear relationships between the transpiration rate and the water potential gradients (from the nutrient solution to the stem and from the stem to the leaves) would imply that the hydraulic resistance within a plant is independent of the transpiration water flow. The literature is not unanimous on this matter, nor does the spreading of points in Figure 6.5 prove this statement beyond doubt. For instance, Janes (1970) observed in sweet pepper the slope of the relationship to increase with decreasing light. However, when ambient humidity was used to control the transpiration flow, the relationship was linear, at each light level, over a wide range of transpiration rates (*cf.* Figure 6.4B). Also for tomato and sunflower, Shalhevet *et al.*, (1976) proved the relationship to be linear when the transpiration flow was controlled by changing humidity. More recently, Zwieniecki and Boersma (1997) similarly observed the resistance of tomato plant to be independent of the flow with both well-watered and stressed plants. There is along the pathway at least one resistance (stomatal) that is known to be modified by light level. A possible light-induced modification might account for some of our own spreading, as well as the different slopes that we observed in 1996 (a sunny year) and 1998 (a cloudy one), Table 6.2. However, an apparent decrease of root hydraulic resistance as flow rate increase has been observed, for instance by Slatyer (1967) and Kramer (1969). Barrs (1973) demonstrated that this is a stress-induced plant response. Fiscus (1975) provided a theoretical explanation why water uptake increases more than proportionally with increasing water potential gradient at low flow rates. It is clear that the transpiration ranges of our experiments do not allow extrapolation of our results to stress (even incipient stress) conditions.

Similarly, the fact that the slopes of the above-mentioned relationships are hardly changed by the root zone treatment implies that the hydraulic resistance is not

modified by prolonged exposure to [mild] salinity. This is consistent with our observation that water uptake per unit leaf area was not modified by the salinity treatment and that salinity effects were immediately reversible (chapter 5). Shalhevet *et al*. (1976), also showed the root hydraulic resistance of tomato and sunflower was not affected by salinity within the range –0.04 MPa to –0.4 MPa. However, the root hydraulic resistance has been found to increase by prolonged exposure to water stress in some species, also in tomato (Cruz *et al*., 1992; Nobel and North, 1993; Zwieniecki and Boersma, 1997). The conclusion must be here as well, that our results may not hold in conditions more extreme than the ones we have applied.

The non-zero intercept in the relationship $\Psi_{NS\text{-}stem}$ *vs* transpiration flow (Figure 6.5B) implies a residual gradient of water potential that may be related to root pressure developed during night. Furthermore the residual gradient was different between two EC treatments, with lower gradient at high EC. This is consistent with Ehret and Ho (1986c) that high salinity reduced root pressure that is related to xylem water movement during night. This potential gradient accounts for the water uptake necessary for growth. For instance, cumulated fresh weight (leaves, stem and fruits) of the treatment –0.25 MPa at the end of September 1998 was 86% of the weight of the treatment –0.08 MPa (average of the two transpiration treatments). From Table 6.2 it may be calculated, that the ratio of the residual potentials was 76%. We are satisfied that the two values are consistent with each other, given the awkwardness of comparing instantaneous and integrated observations.

6.4.2 Fruit water potential and fruit growth

There is sufficient evidence to suggest that water transport into tomato fruits mainly (90%) depends on phloem transport which is governed by pressure gradients in the sieve tubes (Ho *et al*., 1987; Lee, 1989). Nevertheless, we have shown a clear correlation between the apoplasmic fruit-stem water potential gradient and fruit growth rate (Figure 6.6) and fruit weight (Table 6.3), which is supported by observations of Johnson *et al*. (1992) and Van de Sanden and Uittien (1995). Therefore, our data indicate a strong correlation between apoplasmic water potential gradient and turgor pressure gradient from stem to fruit in tomato. This is in agreement with Lang and Thorpe (1986), Johnson *et al*. (1992) and others in concluding that water potential gradients within the plant can have a direct effect on phloem translocation.

Since the fruit osmotic potential remained fairly constant, we propose that variations in stem water potential might be a good indicator of fruit growth. Stem water potential as well as the difference between stem water potential and fruit osmotic potential showed a stronger diurnal variation on sunny than on cloudy days, as it is also implicitly shown by Figure 6.5. Similarly, Ehret and Ho (1986b) found the diurnal variation in fruit expansion was stronger on sunny rather than cloudy days, corroborating the statement that variations in stem water potential may indicate

variations in fruit growth. Decrease of fruit growth rate during mid-day when transpiration was higher has been reported often (*e.g.* Lee *et al*., 1989; Pearce, *et al*., 1993b; Johnson *et al*., 1992; Leonardi *et al*., 2000). Also in apple plants, Naro (1997) reported that decreased daily fruit growth rate, the reduction in yield and average fruit size were all associated with midday decreased stem water potential.

Throughout this paper, we have used fruit fresh weight as an indicator of water import into the tomato fruits, which ignores fruit transpiration. Fruit transpiration estimated by Johnson *et al*. (1992) was only 10.5% of daily fruit growth or water imported into fruit. Ehret and Ho (1986b) observed transpiration from fruit of 10-40 g was about 12 mg water per day per gram fresh weight. Similarly, Leonardi *et al*. (1999) measured a transpiration rate between 3.6 and 16.8 mg d^{-1} per gram fruit fresh weight, on a fruit weight range between 10 and 150g.

6.5 Conclusion

The hydraulic resistance along the water pathway from the nutrient solution to leaves was independent both from the flow and from the osmotic potential of the nutrient solution (Ψ_{NS}), at least in the ranges that were explored here. As water outflow from the leaves is dictated by the climate (potential evaporation), a drop in water potential of the nutrient solution was transferred, in this case, along the pathway, and the water potential of the stem dropped similarly. Since the water potential of the fruits was found to react weakly to variations in Ψ_{NS}, the water transport from stem to fruits was decreased. Our data indicate a strong correlation between apoplasmic water potential gradient and phloem turgor pressure gradient from stem to fruit in tomato.

The other way round, when water outflow (transpiration) from the leaves was increased, the absence of reaction in the hydraulic resistances implies that stem water potential became smaller, in order to accommodate the enlarged flow. That reduced import of water into the fruits. We have shown that the hypothesis that potential evaporation and root-zone water potential have similar effect on plant water relations and fresh weight accumulation is borne out by our experiments.

Acknowledgements

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Chapter 7

General discussion

The scientific objective of this research (Chapter 1) was to analyse the relationship between yield of tomato and high salinity in the root environment, under two transpiration regimes. The basic hypothesis was that, since fresh yield is closely related to the water balance of the crop, factors that modify uptake of water (such as osmotic potential in the root zone) and water loss (such as evaporative demand, *i.e.* potential transpiration) should have a similar effect upon yield. The practical aim of this work was to determine the potential of the control of climate (potential transpiration) as a tool to reduce the adverse effects of salinity on crop production. In this chapter, the effect of salinity on fruit yield and on vegetative growth, mediated by potential transpiration, is discussed and integrated by using the theoretical framework of Figure 1.1. Furthermore, some considerations about the feasibility of transpiration control in practice, with respect to the criterion of the control of the stem water potential, are given. Finally, the implication, limitation and disadvantage of limiting transpiration in greenhouse management, to counteract the adverse effect of salinity, are evaluated.

Integration of the results

The results of this study, summarized as the effect of high *vs* low salinity (EC) and low *vs* high potential transpiration (ET_0) (Table 7.1), show a combined effect of EC and ET_0 on total fruit yield and fresh weight per fruit.

The mean weight of marketable fruits decreased at high EC, while fruit dry weight was the same as at low EC. A similar absence of effect upon mean fruit dry weight by rising EC from 2 to 17 dS m^{-1} was observed, for the second fruit of each truss, by Ehret and Ho (1986a). However, van Ieperen (1996), based on observations on all fruits, reported that the dry weight of individual fruits decreased with increasing EC. Similar results were obtained by Gough and Hobson (1990) for cherry tomato and by Petersen *et al.* (1998) for round tomato. These findings contrast with our results. Nevertheless, the same dry weight per marketable fruit (Chapter 2) from plants grown at different EC values, is consistent with the estimated marginal effect of leaf area index (LAI) on light interception, in spite of a decrease of LAI up to 20% at EC 9.5 dS m^{-1} compared with 2 dS m^{-1} (Chapter 3). Identical rates of water uptake per unit of leaf area (Chapter 6) suggest that stomatal conductance was not affected by EC. Therefore, the data presented in this thesis seem consistent with the observation of Ehret and Ho (1986a) and support the interpretation that the reduction of fruit fresh weight is due to reduced water content in the fruit, rather than to a decrease of the dry weight per fruit. The decrease of

Table 7.1 Effect of salt concentration (EC) and potential evaporation (ET_0) upon fruit yield and vegetative growth of tomato plants. The first block shows the effect of salinity under two transpiration regimes, the second block shows the effect of depressed transpiration, under two salt concentration conditions.

	High EC *vs* Low EC		Low ET_0 *vs* High ET_0	
	High ET_0	Low ET_0	Low EC	High EC
Fruit yield				
Total fresh yield	-	-*	0	+
Mean weight per fruit[a]	-	-*	0	+
Number of fruits[b]	0	0	0	0
Dry weight per fruit[a]	0	0	0	0
Dry matter content[a]	+	+	0	-*
Incidence of BER[c]	+	+*	0	-
Vegetative growth				
Number of leaves	+	+	0	0
Leaf area	-	-	0	0
Leaf area index	-	-	0	0

a. Marketable fruits;
b. Total number of harvested fruits;
c. Blossom-end-rot

+ = more or higher; - = less or lower; 0 = no effect;
+* = reduced + effect, -* = reduced – effect

crease of fruit fresh weight caused at high EC is mainly caused by the reduction of the fruit growth rate, and partly by a decreased fruit development period (Chapter 4), especially during summer.

The mean weight of fruits, and thus the fruit fresh yield, at high EC increased when the transpiration was decreased (Table 7.1). The dry weight of fruits was not affected by the transpiration treatment. The fact that transpiration did not affect the leaf area (Chapter 3, Table 7.1) explains this finding. The water status within a plant grown at high salinity is improved by decreasing the transpiration, which was also observed by Hoffman and Rawlins (1971) and by O'Leary (1975). However, decreased transpiration may cause some nutrient deficiency, due to reduced water uptake. Growing tomato at an EC of 3.0 dS m^{-1}, Bakker (1990) found that fruit fresh weight was decreased by high humidity (Vapour Pressure Deficit, VPD, below 1.0 kPa). Sonneveld and Welles (1988) reported similar results at an EC 3.5 dS m^{-1}. In both cases, a significant calcium deficiency in leaves was found. Bakker (1990) suggested that if no calcium deficiency would occur, higher air humidity would improve fruit growth. In the present study, there was neither a difference in the fresh weight and dry weight per fruit, between high and low transpiration

treatments at EC 2 dS m^{-1}, nor a difference in LAI (Table 7.1). Also, no symptoms of calcium deficiency were observed. Stizaker *et al.* (1997) also observed a similar absence of effect of misting the tomato canopy during hot time in midday, when the water supply in the root zone was sufficient. It may be concluded that, in absence of deficiencies, decreased transpiration only improved the fruit fresh weight at a high EC, and had no effect at a normal EC (2 dS m^{-1}). The increase of fruit fresh weight by a low transpiration regime was due to alleviation of the salinity-effect on fruit growth rate (Chapter 4). Based on 24-hour measurement of fruit growth by linear variable displacement transducers (LVDT), Leonardi *et al.* (2000) also observed increased fruit growth rate when transpiration was reduced.

The same amount of yield reduction at high EC as under high transpiration treatment was found at a higher EC under the low transpiration regime (Chapter 2). This finding is consistent with studies by Hoffman and Rawlins (1970; 1971), who concluded that high humidity (85 and 90%) significantly increased the EC value, at which 50% yield reduction occurred in bean, radish and onion. Salim (1989) reported that 90% relative air humidity (RH) is beneficial for salinity-affected crops, compared with 30% RH. Plants grown at high RH seem more salt tolerant than those grown at low RH, which indicates that water stress is the primary factor that limits growth at high salinity. In the present experiments, the slope of the yield-response-to-EC curve (yield-EC curve) was less at the low transpiration regime (Chapter 2, Figure 2.3). Since there are no observation between EC 2 and 6.5 dS m^{-1}, it cannot be said whether a decrease in transpiration reduced the slope of the linear part of the curve or raised the threshold EC value for salt damage, or both. In general, both the threshold EC value and the slope of the yield-EC curve are related to salt tolerance (Maas and Hoffman, 1977). By assuming a constant threshold EC, however, the focus is usually on the slope of yield-EC curve. This is because experiments to determine accurately the threshold EC value are not easy to carry out. In fact, (a) it is not easy to keep the EC really constant during long-term experiments; (b) plants can adapt to small changes in the EC-value, and may not show any response; (c) a response may be too small to be noticed; (d) the threshold EC value is more related to the cultivar than to the climate, as shown in the literature. Sonneveld (2000) found the threshold EC value of some crops grown in greenhouses, comparable to the values reported by Maas and Hoffman (1977) for field conditions. However, the slope of the yield-EC curve was less for greenhouse crops. Basically, plant response to salinity is a reaction to the osmotic potential of the nutrient solution. Therefore, the slope of the yield-EC curve may regulate the yield response to salinity in relation to climatic conditions. Indirect evidence comes from the present experiments in which decreased transpiration did not increase the maximum fruit growth rate at high EC (Chapter 4).

Most salinity studies (*e.g.* Mitchell *et al.*, 1991; Gough and Hobson, 1990; Petersen *et al.*, 1998) agree that the fruit quality is improved at high EC, especially the dry matter content and sugar content of the fruit (Chapter 2). A low transpiration

regime, as adopted in the present experiments, had a slightly negative effect on fruit dry matter content (increased water content). However, the effect of decreased transpiration was smaller than the effect of an increased EC. Decreased transpiration, obviously, did not completely reverse the negative effect of an increased EC on the fruit's water content. Moreover, decreased transpiration significantly decreased the incidence of blossom-end rot (BER) (Chapter 2), presumably due to an increased accumulation of calcium in the fruits (Adams and Holder, 1992). Therefore, it is concluded that by controlling the transpiration, fruit quality is largely maintained, while the yield loss due to salinity is reduced.

Analysis of the results

All known forms of life depend upon water, and there is no substitute for water (Naylor, 1993). The water content of a plant is usually at least 70 to 80%. Leaves and other plant organs enlarge (grow) in a co-ordinated fashion by absorbing water. Thus, water must enter all cells to enable cells, tissues and organs to grow (Molz and Boyer, 1978). Therefore, any change in water status may influence plant growth.

The assumption that the cause of yield decrease by increased salinity is water stress, was confirmed in this thesis. The effect of ion excess or ion toxicity was tested by comparing sodium chloride (NaCl) and a concentrated nutrient solution of identical EC (9 dS m^{-1}), whereby ionic effects could be excluded. The slightly more negative effect (*ca* 10% lower fruit fresh weight) of NaCl (Chapter 2) could be explained by the difference in osmotic potential of the nutrient solution (Chapter 6), as pointed out by Sonneveld (2000). The reduction of the incidence of BER, which is caused by calcium deficiency, in the low transpiration regime (Chapter 2) indicates that a mineral imbalance is not involved in the EC-range explored in the present experiments. In addition, the incidence of fruit cracking and increased fruit weight after salinity stress was released (Chapter 5) suggest that it is water stress that restricts fruit growth under salinity.

The number of fruits per plant was not affected by our treatments (Table 7.1). Therefore, the change of the weight per fruit was the main cause of the change of the fresh yield of fruits (Chapter 2). The fruit weight is determined by the flows of water and of assimilates, as postulated in Figure 1.1. Changes in both flows could reduce fruit weight.

Assimilate flow: Photosynthesis is related to leaf conductance (or leaf resistance) and to leaf area index. Any treatment that decreases the plant's water content or water potential may affect leaf conductance and thus the rate of photosynthesis. A decreased water content, or water potential, may decrease leaf expansion and thus the leaf area index. At an EC of 4.5 dS m^{-1}, Xu *et al*. (1994) found that the photosynthesis of tomato plants was decreased due to a decreased stomatal conductance,

caused by decreased water potential. McCree (1986) stated that water stress, due to salinity, reduced photosynthesis by reducing both the leaf area and the photosynthetic rate per unit of leaf area in sorghum. At high air humidity, Bakker (1990) found that the fruit weight of tomato was decreased, because the leaf area was decreased by calcium deficiency, although stomatal conductance was increased. However, in the present experiments, there was a marginal effect of the treatments on light interception (potential for assimilation) and no effect on conductance (transpiration rate per unit leaf area). Thus assimilate flow towards the fruits was not affected by EC nor by transpiration regime.

Water flow: The fresh weight of fruits was significantly affected by both treatments. Water flow within a plant is governed by the gradient in water potential built up by transpiration. The osmotic potential of the nutrient solution also affects this gradient, and thus water uptake (Chapter 6). It was suggested in Chapter 6 that the gradient of the water potential between the stem and the fruit was strongly related to the fresh weight of the fruits. In short-term experiments, the gradient of the water potential between the stem and the fruits was lower at high EC compared to EC 2 dS m^{-1}, and the gradient was higher at a low transpiration regime compared to high transpiration. Since the gradient is the driving force for water flow, these results are consistent with the lower water content of fruits at high EC and, inversely, higher water content at a low transpiration regime. The results show that small differences in water potential may cause large differences in fruit weight. One should keep in mind that the measurements of water potentials are instantaneous, whereas fruit weight is determined by long-term water accumulation. A relation between the gradient of the water potential and the growth rate was established by Lang and Thorpe (1986) and Johnson *et al.* (1992); and is supported by the data in the present experiments (Chapter 6). This relation emerges also from data on fruit cracking and the gradual increase of fruit fresh weight after lowering the EC (Chapter 5). In the high-EC period, a low water potential in the stem and a relatively small gradient in water potential between the stem and the fruits occurred, which restricted water inflow into fruits. A rapid increase of the water potential in the stem and a slow response in the water potential of the fruits as observed by Lee *et al.* (1989) after rewatering, probably occurred similarly after lowering the EC in the present experiment. Thus the gradient of the water potential between the stem and the fruits was increased, which resulted in increased water flow into the fruits and, consequently, increased fruit growth. However, the relationship between the gradient of the water potential and fruit weight was not strong at EC 2 dS m^{-1}. Probably, a short period of water stress during the middle of the day has little effect at a low EC without water stress in the root zone (*cf.* Stirzaker *et al*., 1997).

In addition, a higher threshold EC values for the response of tomato to salinity was found for vegetative growth (Chapter 3) than the 2 dS m^{-1} commonly assumed

for fruit weight (Chapter 2). An explanation for this could be different mechanisms of osmotic adjustment in the different plant organs. Accumulation of sugar prevails in fruits (Mitchell *et al*., 1991; Rudich and Luchinsky, 1986) and accumulation of salt prevails in leaves (Alarcón *et al*., 1994b). In our experiments the degree of change of the water potential in the leaves and the stems are the same, suggesting that water flow to the leaves may have a higher priority than to the fruits. Therefore, a higher threshold EC value may be found for leaf expansion than for fruit growth.

Practical implementation of the control of transpiration

Transpiration can interact with salinity through its effect on the plant water status. The water potential of the stem will respond to the EC in the nutrient solution and the transpiration regime, and this, in turn, will affect the water potential and the growth of tomato fruits (Chapter 6). Under steady conditions, the stem water potential stabilises at a value that is dictated by transpiration and the osmotic potential in the nutrient solution. The internal water potential of a plant thus reflects its prevailing environment. The consistently lower water potentials at high EC and, inversely, the relatively high water potentials at a lower EC corroborate this conclusion. Similarly, Bruggink *et al.* (1987) found that the plant water potential could be controlled by the EC-level in the root environment. The response of the water potential to the EC, in turn, determines the gradient of the potential between the stem and the fruits. In the short-term, the stem water potential responds to the transpiration demand and hence fluctuates with the diurnal pattern of transpiration (Chapter 6). The long-term response is the modification of the gradient between the stem and the fruit, which affects the flow of water towards the fruits. From Figure 6.5C and Table 6.2, we calculated that a decrease of potential transpiration of about 30 g h^{-1} per plant was needed to keep the gradient between the stem and the fruit at EC 6.5 at the same level as at EC 2 dS m^{-1}. Because the fruit water potential is relatively constant at a given EC, the water potential in the stem may be used as a criterion for transpiration control in tomato production.

The diurnal pattern of radiation creates a diurnal pattern of plant transpiration. At high evaporation demand during daytime, water flow within a plant is mainly towards the leaves to meet the requirement of transpiration. Inversely, water flow is mainly towards the fruits during the night, to sustain fruit growth (Lee *et al*., 1989; Johnson *et al.*, 1992). Both processes support the uptake and transport of minerals. Calcium can only be transported and distributed by the xylem. The long term impact of the fluctuations in water flow need some attention, since the mineral balance in the various organs of the plant may be affected.

An increased transpiration, *e.g.* at lower air humidity, may cause calcium deficiency in the fruits due to a decrease of the water transport to the fruits through the xylem (Ho *et al*., 1993). Calcium deficiency results in a high incidence of BER

(Ehret and Ho, 1986b). On the other hand, high humidity has often been used, in practice as in experimental studies as a means to decrease transpiration. It has often been observed that high air humidity may cause calcium deficiency in the leaves of tomato (Holder and Cockshull, 1990; Bakker, 1990; Adams and Holder, 1992) due to decreased water uptake. Moreover, high humidity may also stimulate some plant diseases (Hand, 1988), and fruit cracking (Peet, 1992; Moreshet *et al*. 1999), especially when the EC in the substrate is lowered (Chapter 5).

The control principle adopted in the present experiments is to control transpiration, rather than air humidity. Obviously, this type of control results in a modification of ambient humidity to an extent dictated by concurrent values of other variables, such as temperature and solar radiation. That means that a relatively high humidity was required more at daytime (when it is not harmful) than at night-time. In particular, we achieved the desired manipulation of transpiration (Figure 2.2) in spite of a ceiling of 90% to relative humidity, in view of the above-mentioned drawbacks. As shown in this thesis, decreased transpiration had no negative effect on plant growth, but allowed an increased growth at high EC.

In view of the fact that most growers do not have a "transpiration control module", one experiment was designed attempting to limit transpiration by means of a commonly available method: a proportional reduction in humidity-driven ventilation and misting above a pre-set ceiling. In that experiment fruit fresh weight at high EC was clearly increased by this climate treatment. The length of the experiment (8 months) lends reliability to this result.

A high transpiration rate decreases plant water potential. Therefore, control of the maximum transpiration rate (pre-set ceiling) leads to control of the minimum stem water potential, which seems a good way to manipulate water status and fruit growth. Rudich *et al*. (1981) and Rudich and Luchinsky (1986) suggested that water stress in tomato would occur when the leaf water potential falls below –0.6 MPa. In the present experiments, transpiration control at EC 2 dS m^{-1} had little effect. At this EC, the lowest stem water potential (at midday) was -0.5 to -0.6 MPa. The transpiration model of Stanghellini (1987) may be used to regulate the threshold value of the maximum transpiration rate, by taking the stem water potential at different EC levels into account. That is, that EC and potential transpiration (ET_0) concur in controlling the stem water potential. When the stem water potential falls below the threshold value, controlling transpiration is needed if one maintains the same EC in the nutrient solution. Because of the technical difficulty to measure the stem water potential continuously and at short time intervals, a detailed examination of the relationship between plant transpiration and stem water potential was not feasible. Further experiments are needed at a higher EC (*e.g.* 6.5 to 10 dS m^{-1}) to determine the threshold value of the stem water potential in order to accurately control plant transpiration with respect to root-zone salinity. The stem water potential and the transpiration regime should be fitted into future climate control system.

Conclusions

As a result of poor quality of re-fill water and of accumulation of unused nutrients, a high EC of the nutrient solution in closed systems has become normal in commercial practice. The consequence of growing crops at high EC is a significant yield loss. Our study confirms that this yield loss is mainly caused by water stress.

In the present experiments transpiration, rather than humidity, was controlled. Transpiration-control experiments proved that the shoot environment did interact with the root environment, and could improve the plant water status at high EC.

A reduction of transpiration of a tomato crop by one-third yielded good results. The yield loss was reduced and there was no effect on vegetative development and leaf growth. A strict regime of transpiration control is probably not suitable in commercial practice, because transpiration would have to be calculated on line. In addition, frequent misting requires good quality water and costs energy. Moreover, reduction of transpiration may not be necessary during periods of low transpiration. By applying a climate control strategy, that is easy to implement in practice (reduced humidity-ventilation and misting above a given potential evaporation rate), we obtained similar results. This proves that control of shoot environment in view of root-zone conditions can also be achieved by means that are available in commercial greenhouse production. The principle of transpiration control developed here, gives a blueprint for climate control when dealing with high EC in the nutrient solution.

Transpiration control did not have any negative effect on vegetative and generative growth in tomato, and fruit quality, when EC in the nutrient solution was 2 dS m^{-1}. Lowering EC by flushing closed systems is commonly done when EC reaches too high values. This should be done carefully with fruiting plants. In particular, during high humidity or low transpiration periods, such as a cloudy one, significant fruit cracking would be the results. In this case, stimulating transpiration by climate manipulation would be a good choice.

There are some limitations to transpiration control. Transpiration is primarily dependent on the radiation. For instance, a cut-down by one-third is the maximum reduction that could be reliably maintained without limiting radiation.

It is concluded that depressed transpiration, especially in periods of high radiation, could be a good tool for controlling greenhouse climate in response to high EC in the root environment, in order to limit yield loss.

References

Adams, P., 1991. Effect of increasing the salinity of the nutrient solution with major nutrients or sodium chloride on the yield, quality and composition of tomatoes grown in rockwool. *Journal of Horticultural Science,* 66(2): 201-207

Adams, P. and Ho, L.C., 1989. Effect of constant and fluctuating salinity on the yield, quality and calcium status of tomatoes. *Journal of Horticultural Science,* 64(6): 725-732

Adams, P. and Holder, R., 1992. Effects of humidity, Ca and salinity on the accumulation of dry matter and Ca by the leaves and fruit of tomato (*Lycopersicon esculentum*). *Journal of Horticultural Science,* 67(1): 137-142

Alarcón, J.J., Bolarín, M.C., Sánchez-Blanco, M.J. and Torrecillas, A., 1994a. Growth, yield and water relations of normal fruited and cherry tomato cultivars irrigated with saline water. *Journal of Horticultural Science,* 69(2): 283-288

Alarcón, J.J., Sánchez-Blanco, M.J., Bloarín, M.C. and Torrecillas, A., 1994b. Growth and osmotic adjustment of two tomato cultivars during and after saline stress. *Plant and Soil,* 166: 75-82

Awang, Y.B., Atherton, J.G. and Taylor, A.J., 1993a. Salinity effects on strawberry plants grown in rockwool. I. Growth and leaf water relations. *Journal of Horticultural Science,* 68(5): 783-790

Awang, Y.B., Atherton, J.G. and Taylor, A.J., 1993b. Salinity effects on strawberry plants grown in rockwool. II. Fruit quality. *Journal of Horticultural Science,* 68(5): 791-795

Bakker, J.C., 1988. Russeting (cuticle cracking) in glasshouse tomatoes in relation to fruit growth. *Journal of Horticultural Science,* 63(3): 459-463

Bakker, J.C., 1990. Effect of day and night humidity on yield and fruit quality of glasshouse tomatoes (*Lycopersicon esculentum* Mill.). *Journal of Horticultural Science,* 65(3): 323-331

Bakker, J.C., 1991. Analysis of humidity effects on growth and production of glasshouse fruit vegetables. *PhD dissertation, Wageningen Agricultural University, Wageningen,* 155 pp.

Banuelos, G.S., Offermann, G.P., and Seim, E.C., 1985. High relative humidity promotes blossom-end Rot on growing tomato fruit. *HortScience,* 20(5): 894-895

Barrs, H.D., 1973. Controlled environment studies of the effect of variable atmospheric water stress on photosynthesis, transpiration and water status of *Zea mays* L. and other species. In: *Plant response to Climate Factors*. Proc. Uppsala Symp. UNESCO, 249-258

Bernstein, L., 1975. Effects of salinity and sodicity on plant growth. *Annual review of phytopathology,* 13: 295-312

Blum, A., 1986. Salinity resistance. In: Blum, A. (Ed.), *Plant Breeding for stress environments,* CRC Press, Boca Raton, Florida, USA, 163-169

Bruggink, G.T., Schouwink, H.E. and Coolen, E.A.J.M., 1987. Effects of different day and night osmotic pressure of the nutrient solution on growth, water potentials and osmotic potentials of young tomato plants in soilless culture. *Soilless Culture*, 3(2): 8-19

Buras, N., 1992. Efficient irrigation, environmental effects, and its long term sustainability. *ICID 3rd Pan American Regional Conference,* Mazatlan, Mexico, Vol. 2, 7 pp.

Burrage, S.W., 1988. Growth and ion uptake in tomatoes grown in high and low humidities. In: Cockshull, K.E. (Ed.), *The Effects of High Humidity on Plant Growth in Energy Saving Greenhouse,* Report EUR 11261, Office for Official Publications of the European Communities, Luxembourg, 9-18

Chiu, T. and Bould, C., 1976. Effect of shortage of calcium and other cation on ^{45}Ca mobility, growth and nutritional disorders of tomato plants (*Lycopersicon esculentum*). *J. Sci. Fd. Agric*., 27: 969-977

Cockshull, K.E., 1988. Integration of plant physiology and physical aspects of the greenhouse climate. *Acta Horticulturae,* 229: 113-123

Cockshull, K.E., 1998. Plant responses and adaptation to water issues in the greenhouse environment. *Acta Horticulturae,* 458: 201-206

Cockshull, K.E., Graves, C.J. and Cave, C.R.J., 1992. The influence of shading on yield of glasshouse tomatoes. *Journal of Horticultural Science,* 67(1): 11-24

Cruz, R.T., Jordan, W.R. and Drew, M.C., 1992. Structural changes and associated reduction of hydraulic conductance in roots of *Sorghum biocolor* L. following exposure to water deficit. *Plant Physiology,* 99: 203-212

Cuartero, J. and Fernández-Muñoz, R., 1999. Tomato and salinity. *Scientia Horticulturae,* 78: 83-125

Dalton, F.N. and Poss, J.A., 1990. Water transport and salt loading: A unified concept of plant response to salinity. *Acta Horticulturae,* 278: 187-293

Ehret, D.L. and Ho, L.C., 1986a. The effect of salinity on dry matter partitioning and fruit growth in tomatoes grown in nutrient film culture. *Journal of Horticultural Science,* 61(3): 361-367

Ehret, D.L. and Ho, L.C., 1986b. Effect of osmotic potential in nutrient solution on diurnal growth of tomato fruit. *Journal of Experimental Botany,* 37(182): 1294-1302

Ehret, D.L. and Ho, L.C., 1986c. Translocation of calcium in relation to tomato fruit growth. *Annals of Botany,* 58: 679-688

Fiscus, E.L., 1975. The interaction between osmotic- and pressure-induced water flow in plant roots. *Plan Physiology,* 55: 917-922

Flower, T.J., 1999. Salinisation and horticultural production. *Scientia Horticulturae*, 78: 1-4

Garfield, E., 1987. Citation classics in plant science and their impact on research. *Current contents*, 40: 3

Gough, C. and Hobson, G.E., 1990. A comparison of the productivity, quality, shelf-life characteristics and consumer reaction to the crop from cherry tomato plants grown at different levels of salinity. *Journal of Horticultural Science,* 65(4): 431-439

Grange, R.I and Hand, D.W., 1987. Review Article—A review of the effects of atmospheric humidity on the growth of horticultural crops. *Journal of Horticultural Science,* 62(2): 125-134

Grange, R.I. and Andrews, J., 1993. Growth rate of glasshouse tomato fruit in relation to final size. *Journal of Horticultural Science,* 68(5): 747-754

Greenway, H. and Munns, R., 1980. Mechanisms of salt tolerance in nonhalophytes. *Annual Review of Plant Physiology,* 31: 149-190

Hand, D., 1988. Effect of atmospheric humidity on greenhouse crops, *Acta Horticulturae,* 229: 143-158

Heuvelink, E., 1996. Tomato growth and yield: quantitative analysis and synthesis. *PhD dissertation*, *Wageningen Agricultural University, Wageningen*, 326 pp.

Ho, L.C., 1995. Carbon partitioning and metabolism in relation to plant growth and fruit production in tomato. *Acta Horticulturae*, 412: 396-409

Ho, L.C. and Adams, P., 1989. Effect of diurnal change in the salinity of the nutrient solution on the accumulation of calcium by tomato fruit. *Annals of Botany,* 64: 373-382

Ho, L.C. and Hewitt, J.D., 1986. Fruit development. In: Thereon J.G. and Rudich, J. (Eds), *The Tomato Crop: A scientific basis for improvement*. Chapman and Hall, London, 201-239

Ho, L.C., Belda, R., Brown, M., Andrews, J. and Adams, P., 1993. Uptake and transport of calcium and the possible cause of blossom-end rot in tomato. *Journal of Experimental Botany,* 44(259): 509-518

Ho, L.C., Grange, R.I. and Picken, A.J., 1987. An analysis of the accumulation of water and dry matter in tomato fruit. *Plant, Cell and Environment,* 10: 157-162

Hoffman, G.J. and Rawlins, S.L., 1970. Design and performance of sunlit climate chambers. *Trans. Amer. Soc. Agr. Eng.*, 13: 656-660

Hoffman, G.J. and Rawlins, S.L., 1971. Growth and water potential of root crops as influenced by salinity and relative Humidity. *Agronomy Journal,* 63: 877-880

Hoffman, G.J., Shalhevet, J. and Meiri, A., 1980. The leaf age and salinity influence water relation of pepper leaves. *Physiol. Plant*, 48: 463-469

Holder, R. and Christensen, M.H., 1988. The effect of electrical conductivity on the growth, yield and composition of Cherry tomatoes grown on rockwool. *Seventh International Congress on Soilless Culture Proceeding,* 213-228

Holder, R. and Cockshull, K.E., 1990, Effect of humidity on the growth and yield of glasshouse tomatoes. *Journal of Horticultural Science,* 65(1): 31-39

Honert, T.H. van den, 1948. Water transport in plants as a catenary process. *Discussion Faraday Society,* 3: 146-153

Hsiao, T.C., 1973. Plant responses to water stress. *Annual Review of Plant Physiology*, 24: 519-570

Hsiao, T.C., 1993. Growth and productivity of crops in relation to water status. *Acta Horticulturae,* 335: 137-148

Ieperen, W. van, 1996. Consequences of diurnal variation in salinity on water relations and yield of tomato. *PhD dissertation*, *Wageningen Agricultural University, Wageningen*, 176 pp

Janes, B.E., 1970. Effect of CO_2, osmotic pressure of nutrient solution and light intensity on transpiration and resistance to flow of water in pepper plants. *Plant Physiology,* 45: 95-103

Janes, J. and Welles, G.W.H., 1984. Effects of energy saving measures on keeping quality of tomato and cucumber fruits. *Acta Horticulturae,* 163: 261-269

Johnson, R.W., Dixon, M.A, and Lee, D.R., 1992. Water relation of the tomato during fruit growth. *Plant, Cell and Environment,* 15: 947-953

Jolliet, O. and Bailey, B.J., 1992. The effect of climate on tomato transpiration in greenhouse: measurements and models comparison. *Agricultural and Forest Meteorology,* 58(1-2): 43-62

Jones, H.G., 1992. *Plants and microclimate*: *a quantitative approach to environmental plant physiology*. Second Edition. Cambridge University Press, Cambridge, London, 428pp

Kamimura, S., Yoshikawa, H. and Ito, K., 1972. Studies on fruit cracking in tomatoes. *Bulletin Horticultural Research Station Morioka*, Iwate Japan, 7: 73-138

Koning, A.N.M. de, 1994. Development and dry matter distribution in glasshouse tomato: a quantitative approach. *PhD dissertation, Wageningen Agricultural University, Wageningen*, 240 pp.

Kramer, P.J., 1969. *Plant and Soil Water Relationships: a Modern Synthesis*. McGraw-Hill Book Co., New York, 482pp

Kreij, C. de, 1995. Latest insight into water and nutrient control in soilless cultivation. *Acta Horticulturae,* 408: 47-61

Lang, A. and Thorpe, M.R., 1986. Water potential, translocation and assimilate partitioning. *Journal of Experimental Botany,* 37(177): 495-503

Lee, D.R., 1989. Vasculature of the abscission zone of tomato fruit: implications for transport. *Canadian Journal of Botany,* 67: 1898-1902

Lee, D.R., Dixon, M.A. and Johnson R.W., 1989. Simultaneous measurements of tomato fruit and stem water potential using in situ stem hygrometers. *Canadian Journal of Botany*. 67: 2352-2355

Leonardi, C., Baille, A. and Guichard, S., 1999. Effects of fruit characteristics and climatic conditions on tomato transpiration in a greenhouse. *Journal of Horticultural Science & Biotechnology*, 74(6): 748-756

Leonardi, C., Guichard, S. and Bertin, N., 2000. High vapour pressure deficit influence growth, transpiration and quality of tomato fruits. *Scientia Horticulturae,* 84: 258-296

Li, Ya Ling and Cecilia Stanghellini, 1999. The leaf characteristics of a tomato plant in rockwool during long season growing (in Chinese). *Journal of Shanxi Agricultural University,* 19(3): 214-217

Maas, E.V., 1986. Salt tolerance of plants. *Applied Agricultural Research*, 1: 12-26

Maas, E.V. and Hoffman, G.J., 1977. Crop salt tolerance-Current assessment. *Journal of the Irrigation and Drainage Division, Proceedings of the American Society of Civil Engineers,* 103(IR2): 115-134

Marcelis, L.F.M. and Hooijdonk, J. van, 1999. Effect of salinity on growth, water use and nutrient use in radish (*Raphanus sativus* L.). *Plant and Soil,* 215: 57-64

Maroto, J.V., Bardisi, A., López, S., Pascual, B. and Alagarda, J., 1995. Influence of relative humidity in the appearance of cracking in tomato (*Lycopersicon esculentum* Mill.) fruit. *Acta Horticulturae,* 412: 306-312

McCree, K. J., 1986. Whole plant carbon balance during osmotic adjustment to drought and salinity stress. *Australian Journal of plant physiology*, 13: 33-43

McCullagh, P. and Nelder, J.A., 1989. *Generalized linear models*, Second Edition, Chapman and Hall, London, 511pp

Mitchell, J.P., Shennan, C. and Grattan, S.R., 1991. Developmental changes in tomato fruit composition in response to water deficit and salinity. *Physiologia Plantarum*, 83: 177-185

Mizrahi, Y., 1982. Effect of salinity on tomato fruit ripening. *Plant Physiology,* 69: 966-970

Molz, F.J. and Boyer, J.S., 1978. Growth-induced water potential in plant cell and tissues. *Plant Physiology*, 62: 423-429

Moreshet, S., Yao, C., Aloni, B., Karni, L., Fuchs, M. and Stanghellini, C., 1999. Environmental factors affecting the cracking of greenhouse-grown bell pepper fruit. *Journal of Horticultural Science*, 74(1): 6-12

Mortensen, L.M., 1986. Effect of relative humidity on growth and flowering of some greenhouse plants. *Scientia Horticulturae,* 29: 301-307

Munns, R., 1988. Why measure osmotic adjustment? *Australian Journal of plant Physiology*, 15: 717-726

Munns, R., Greenway, H., Delane, R. and Gibbs, J., 1982. Ion concentration and carbohydrate states of the elongating leaf tissue of *Hordeum vulgare* growing at high external NaCl. II. Cause of the growth reduction. *Journal of Experimental Botany*, 33: 574-583

Naro, A., Klein, I., Doron, I., Gal, Y., Ben-David, Z. and Bravdo, B., 1997. The effect of irrigation and crop load on stem water potential and apple fruit size. *Journal of Horticultural Science,* 72(5): 765-771

Naylor, A.W., 1993. Environmental signals, receptors, physiological and genetic regulation in plants. In: Hashimoto, Y., Bot, G.P.A., Day, W., Tantau, H.J. and Nonami, H. (Eds), *The computerized Greenhouse,* 243-265

Nieman, R.H. and Poulsen, L.L., 1967. Interactive effects of salinity and atmospheric humidity on the growth of bean and cotton plants. *Gazette,* 128: 69-73

Nobel, P.S. and North, G.B., 1993. Rectifier-like behaviour of root-soil system: new insights from desert succulents. In: Smith, J.A.C., Griffiths, H. (Eds.), *Water Deficit: plant response from cell to community.* Oxford: BIOS Scientific Publishers Limited, 163-176

O'Leary, J.W., 1975. High humidity overcomes lethal levels of salinity in hydroponically grown salt-sensitive plants. *Plant and Soil,* 42: 717-721

Opara, L.U., Studman, C.J. and Banks, N.H., 1997. Fruit skin splitting and cracking. *Horticultural Reviews,* 19: 217-262

Pearce, B.D., Grange, R.I. and Hardwick, K., 1993a. The growth of young tomato fruit. I. Effect of temperature and irradiation on fruit grown in controlled environments. *Journal of Horticultural Science,* 68(1): 1-11.

Pearce, B.D., Grange, R.I. and Hardwick, K., 1993b. The growth of young tomato fruit. II. Environmental influences on glasshouse crops grown in rockwool or nutrient film. *Journal of Horticultural Science,* 68(1): 13-23.

Peet, M.M., 1992. Fruit cracking in tomato. *HortTechnology,* Apr./June 2(2): 216-223

Petersen, K.K., Willumsen J. and Kaack K., 1998. Composition and taste of tomatoes as affected by increased salinity and different salinity sources. *Journal of Horticultural Science,* 73(2): 205-215

Qiao, Y.L., 1995. An application of aerial remote-sensing to monitor salinization at Xinding Basin. *Space Research,* 18: 133-139

Ritchie, G.A. and Hinckley, T.M., 1975. The pressure chamber as an instrument for ecological research. In: Macfadyan, A. (Ed.), *Advances in Ecological Research,* Academic Press, London, Vol. 9: 165-254

Rudich, J. and Luchinsky, U., 1986. Water economy. In: Thereon J.G. and Rudich, J. (Eds), *The Tomato Crop: A scientific basis for improvement*. Chapman and Hall, London, 335-367

Rudich, J., Rendon-Poblete, E., Stevens, M.A. and Ambri, A.I., 1981. Use of leaf water potential to determine water stress in field grown tomato plant. *Journal of American Society for Horticultural Science,* 106: 732-736

Salim, M., 1989. Effects of salinity and relative humidity on growth and ionic relations of plants. *New Phytol.,* 113: 13-20

Salter, P.J., 1958. The effect of difference water-regimes on the growth of plants under glass. IV. vegetative growth and fruit development in the tomato. *Journal of Horticultural Science,* 33: 1-12

Sanden, P.A.C.M. van de and Uittien, J.J., 1995. Root environment water potential and tomato fruit growth. *Acta Horticulturae,* 401: 531-536

Savvas, D. and Lenz, F., 2000. Effect of NaCl or nutrient-induced salinity on growth, yield and composition of eggplants grown in rockwool. *Scientia Horticulturae,* 84: 37-47

Schulze, E.D., 1991. Water and nutrient interactions with plant water stress. In: Mooney, H.A., Winner, W.E. and Pell, E.J. (Eds*.), Responses of plant to multiple stresses,* Press, London, 89-101

Shackel, K.A., Greve, C., Labavitch, J.M. and Ahmadi, H., 1991. Cell turgor changes associated with ripening in tomato pericarp tissue. *Plant Physiology,* 97: 814-816

Shalhevet, J., Mass, E.V., Hoffman, G.J. and Ogata, G., 1976. Salinity and the hydraulic conductance of roots. *Physiol. Plant,* 38: 224-232

Shannon, M.C. and Grieve, C.M., 1999. Tolerance of vegetable crops to salinity. *Sciential Horticulturae,* 78: 5-38

Sharaf, A.R. and Hobson, G.E., 1986. Effect of salinity on the yield and quality of normal and non-ripening mutant tomatoes. *Acta Horticulturae,* 190: 175-181

Shishido, Y. and Hori, Y., 1977. Studies on translocation and distribution of photosynthetic assimilate in tomato plants. II. Distribution pattern as affected by phyllotaxis. *Tohoku Journal of Agricultural Res*., 28(2): 82-95

Slatyer, R.O., 1967. *Plant-water relationships*. Academic Press, London, 366pp

Sonneveld, C., 1988. The salt tolerance of greenhouse crops. *Netherlands Journal of Agricultural Science,* 36: 63-73

Sonneveld, C., 2000. Effects of salinity on substrate grown vegetables and ornamentals in greenhouse horticulture. *PhD dissertation*, *Wageningen University, Wageningen*, 151pp.

Sonneveld, C. and Van Der Burg, A.M.M., 1991. Sodium chloride salinity in fruit vegetable crops in soilless culture. *Netherlands Journal of Agricultural Science,* 39: 115-122

Sonneveld, C. and Welles, W.H., 1984. Growing vegetables in substrates in the Nehterlands. *Proc. 6th ISOSC Int. Cong. Soilless culture,* 613-632

Sonneveld, C. and Welles, W.H., 1988. Yield and quality of rockwool-grown tomatoes as affected by variations in EC-value and climatic conditions. *Plant and soil,* 111: 37-42

Stanghellini, C., 1987. Transpiration of greenhouse crops: an aid to climate management. *PhD dissertation*, *Wageningen Agricultural University, Wageningen*, 150 pp

Stanghellini, C., 1997. Ottimizzazione del drenato nelle coltivazioni protette. Rivista di Irrigazione e Drenaggio, 44(4): 30-34.

Stanghellini, C. and Van Meurs W.Th.M., 1992. Environmental control of greenhouse crop transpiration. *Journal of Agricultural Engineering Research,* 51: 297-311

Stanghellini, C., Van Meurs, W.Th.M., Corver, F., Van Dullemen, E. and Simonse, L., 1998. Combined effect of climate and concentration of the nutrient solution on a greenhouse tomato crop. II. yield quantity and quality. *Acta Horticulturae*, 458: 231-237

Steiner, A.A., 1984. The Universal nutrient solution. In: *Proc. Sixth Int. Congress on Soiless Culture,* Lunteren 1984, Int. Soc. Soiless culture, Pudoc, Wageningen, pp633-649.

Stirzaker, R.J., Hayman, P.T. and Sutton, B.G., 1997. Misting of tomato plants improves leaf water status but not leaf growth. *Australia Journal of Plant Physiology*, 24: 9-16

Swalls, A.A. and O'Leary, J.W., 1975. The effect of relative humidity on growth, water consumption, and calcium uptake in tomato plants. *Journal of the Arizona Academy of Science,* 10: 87-89

Tanaka, A. and Fujita, K., 1974. Nutrio-physiological studies on the tomato plant. IV. Source-sink relationship and structure of the source-sink unit. *Soil Science and Plant Nutrient,* 20: 57-68

Turner, N.C., 1988. Measurement of plant water status by the pressure-chamber technique. *Irrigation Science,* 9: 289-308

Van der Varst, P.G.I. and Postel, J.D.G., 1972. Bepaling bladoppervlak van tomatenplanten. ITT, Wageningen, report 46, 36pp

Van Os, E.A., 1995. Engineering and environmental aspects of soilless growing systems. *Acta Horticulture,* 396: 25-32

Van Os, E.A., 1996. Closed soilless growing system in the Netherlands: the finishing touch. *Acta Horticulture,* 458: 279-291

Vooren, J. van de, Welles, G.W.H. and Hayman, G., 1986. Glasshouse crop production. In: Thereon J.G. and Rudich, J. (Eds), *The Tomato Crop: A scientific basis for improvement*. Chapman and Hall, London, 581-623

Walker, A.J. and Ho, L.C., 1977. Carbon translocation in the tomato: carbon import and fruit growth. *Annals of Botany,* 41: 813-823

Willumsen, J., Petersen K.K. and Kaack, K., 1996. Yield and blossom-end rot of tomato as affected by salinity and cation activity ratios in the root zone. *Journal of Horticultural Science,* 71(1): 81-98

Winsor, G. and Adams, P., 1987. Diagnosis of mineral disorders in plants. In: Robinson, J.B.D. (Ed.), Vol. 3, *Glasshouse crops.* Crown, London, UK, 166pp

Wolf, S. and Rudich, J, 1988. The growth rates of fruits on different parts of the tomato plant and the effect of water stress on dry weight accumulation. *Scientia Horticulturae,* 34: 1-11

Xu, H.L., Gauthier, L. and Gosselin, A., 1994. Photosynthetic responses of greenhouse tomato plants to high solution electrical conductivity and low soil water content. *Journal of Horticultural Science,* 69(5): 821-832

Yeo, A.R., 1983. Salinity resistance: physiologies and prices. *Physiol. Plant,* 58: 214-222

Yeo, A., 1999. Predicting the interaction between the effects of salinity and climate change on crop plants. *Scientia Horticulturae*, 78: 159-174

Zwieniecki, M.A. and Boersma, L., 1997. A technique to measure root tip hydraulic conductivity and root water potential simultaneously. *Journal Experimental Botany,* 48(307): 333-336

Summary

Intensive greenhouses cultivation may give rise to year-round production of horticultural crops with high yield. Furthermore, soilless cultivation contributes to allowing sufficient and uniform water and nutrient supply, and good aeration, and a suitable temperature of the root zone. Re-circulated (closed) growing systems are increasingly adopted, saving water and fertilisers, and hence reducing pollution of soil and surface water. Plants normally do not take up nutrients in the ratio that is present in the nutrient solution; thus certain ions will accumulate after a certain period. In addition, water used to make and re-fill the nutrient solution may contain ions (Na^+ and Cl^-, in most cases) that are not easily absorbed by the crop, and thus will accumulate in the solution. Therefore, an increasing concentration of salts in the nutrient solution in such growing systems is inevitable.

It is known that high salinity can significantly decrease fruit yield, by reducing fruit size and inducing some fruit disorders, such as blossom-end rot, although moderate salinity may increase fruit quality. From the literature, it is known that effects of salinity and water stress are often similar, and that yield response to salinity is modulated by environmental conditions. In particular, there is an interaction between salinity in the root zone and humidity in the shoot environment.

The hypothesis at the basis of this work is that modern greenhouse management offers an opportunity to optimise environmental conditions in relation to root zone salinity. In particular, by "controlling" the evaporative demand of the ambient, it is possible to manipulate plant water status in order to restore the balance distorted by a high salinity (osmotic pressure) in the root environment. The scientific aim of this work is to explain the interaction between water inflow (root environment) and water outflow (shoot environment) in determining crop fresh yield. The practical aim of this study is to provide a blue-print for greenhouse climate management in relation to salinity problems.

This work is based on a series of long-term experiments with commercially-grown greenhouse tomato. Thereby two contrasting "potential transpiration treatments" (ET_0) were combined with two salinity treatments. In particular, in four experiments a constant ratio (2/3) was maintained between potential transpiration of the two "shoot" treatments, whereas in the last experiment a "low transpiration" treatment was attained by means more commonly available to growers. For the "root zone" treatments, each time a concentrated solution [respectively: electrical conductivity (EC) 6.5, 8, 9.5 dS m^{-1}] was compared with a reference of EC 2 dS m^{-1}. One experiment was aimed at investigating ion-specific effects, by combining two different compositions (one with a large fraction of sodium chloride) of nutrient solutions at the same (high) EC level (9 dS m^{-1}). Finally, in order to test

whether salinity-induced growth reduction is flux-related (decreasing flux equals to decreased growth) or whether there are physiological changes that play a role, one experiment was designed to investigate the response to a step change of the EC in the nutrient solution.

After a general introduction to the problem, in chapter 2 the interaction between shoot and root treatments in determining fresh yield of tomato plants is discussed. Neither EC nor ET_0 had effect on the number of harvested fruits or on dry weight of individual fruits. However, dry matter content (%) of fruits increased with increasing EC with a slope of 4% per dS m^{-1}, with non-significant effects of ET_0. That is, neither treatment had an effect on dry matter production, whereas EC affected water content of fruits. Marketable fresh-yield production-efficiency (η_F) was determined (for each experiment and treatment) as the slope of the cumulated production *vs* cumulated photosynthetically active radiation (PAR) on top of the canopy. η_F decreased linearly with increasing EC of the nutrient solution. In particular, η_F decreased by 5.1% for each dS m^{-1} in excess of 2, a fraction that resulted from a reduced weight of individual fruits (3.8 % per dS m^{-1}) and an increased fraction of unmarketable fruits (mainly caused by blossom-end rot). For the low transpiration treatment, however, yield loss was only 3.4 % per dS m^{-1} fully accounted for by the reduction in fruit weight. That is, at high EC, depressing potential transpiration can reduce the loss in fruit weight and reduce the incidence of blossom-end rot.

Leaf area, a very important parameter both for controlling water outflow and carbon inflow, is analysed in chapter 3. There was no detectable effect of the present climate treatments upon leaf area or the number of leaves on a plant. Response of leaf area to EC was different from that observed in fruits: a higher threshold and a larger slope were observed. In particular, the individual leaf area was reduced (8% per dS m^{-1}) only at EC exceeding 6.5 dS m^{-1}. The number of leaves produced by each plant, however, was slightly increased by EC (2% per dS m^{-1}), a somewhat unexpected result. Leaf area index was reduced about 20% at the highest EC (9.5 dS m^{-1}), but even then the reduction of light interception was estimated to only 8%. This relatively small effect is consistent with the above-mentioned observation that dry matter accumulated into fruits was not significantly reduced by EC.

As the main effect of our treatments seems to be on fresh weight of individual fruits (a parameter that is very important for economic yield) fruit growth is the subject of chapter 4. The factors that may affect fruit size, *i.e.* fruit growth rate (FGR) and fruit development period (FDP, time lapse between the appearance of a flower truss and the first harvest of the truss) were investigated. The decrease of the final fruit size at high EC was mainly caused by the smaller fruit growth rate, especially during the cell-expansion phase. The highest FGR was 1.5 $cm^3 day^{-1}$ at 9.5

dS m^{-1}, whereas FGR exceeded 2 $cm^3 day^{-1}$ at 2 dS m^{-1}. High EC shortened the fruit development period, especially during the summer season. There was no effect of transpiration on fruit growth rate at 2 dS m^{-1}, but a significant effect at high EC. The dry matter accumulation and dry matter content during fruit growth are in line with the statement that the root and the shoot environment treatments never affected dry weight of individual fruits, and that the main effect they created was on the rate of accumulation of water into fruits.

Chapter 5 concentrates on the nature of the EC-effect by analysing the dynamic response of a tomato crop to a step-change in root-zone EC. The EC of the nutrient solution was lowered (to 2 dS m^{-1}) after a long-term (5 months) high-salinity treatment (9 dS m^{-1}). The size of harvested fruits increased gradually after the EC was lowered, until fruits were harvested that had developed fully under the new EC condition (8 weeks), with a final weight comparable to the normal volume at 2 dS m^{-1}. Similarly, leaves formed at the new EC expanded accordingly, but the leaves that were already expanded at the moment of lowering EC did not respond to the change in EC. Sudden expansion of fruits may be the cause of the high incidence of cracked fruits that peaked some 25 days after lowering EC. Incidence of cracking was much reduced in the high transpiration environment. It is concluded that the negative effect of high salinity on growth and yield is mainly related to the water balance of the plant, which can be restored even after a long time exposure at high salinity.

Therefore, uptake and movement of water within a plant, is the subject of chapter 6. The hypothesis was tested that potential evaporation and water potential of the root-zone have similar effects on plant water relations and hence fresh weight accumulation. Ohm's law was applied to the transfer of water along the various segments of the pathway from nutrient solution to leaves, in order to determine the hydraulic resistance from measurements of water potential. The hydraulic resistance within the plant, deduced from measurements of the leaf and the stem water potential, was independent of the transpiration flow and was not affected by the osmotic potential of the nutrient solution, at least in the ranges explored here. Further, it was shown that water outflow from the leaves is primarily dictated by the climate (potential evaporation), since water uptake per unit leaf area was not affected by osmotic potential of the nutrient solution. Therefore, a decrease of water potential of the nutrient solution, for instance, must cause a decrease of the water potential of the stem. The other way round, when water outflow (transpiration) from the leaves is increased, a constant hydraulic resistance implies that the stem water potential must become smaller, in order to accommodate the enlarged flow. Since the water potential of the fruits responded weakly to variations in both root and shoot environment, the gradient in water potential between the stem and the fruit (the water transport into fruits) decreased. Therefore, the stem water potential appears to be an

important link between effects of EC and ET_0, and the gradient between the stem and the fruits is an indicator of fruit growth. Water import into the fruits, related to fruit growth rate and fruit weight, was affected by both treatments and was correlated to the water potential gradient between the stem and the fruits.

Water is taken up by the roots and lost through transpiring leaves. Therefore, both the effect of salinity in the nutrient solution and the effect of potential transpiration/humidity in the shoot environment on plant growth are mediated by the same variable—plant water status. EC plays a role in determining water inflow through root water uptake, while transpiration controls water outflow. Therefore, depressed transpiration proved an efficient way to mitigate the negative effect of high EC. In the last chapter (7), the overall effects of EC and ET_0 are discussed. Water stress (caused by reduced water potential in the root zone) was considered the main factor that restricts plant growth at high EC. It is further shown that other aspects of high salt concentration (*e.g.* ion toxicity and mineral imbalance) do not play an important role with respect to the results presented in this work. Special attention has been paid to transpiration control as a tool for manipulating fruit growth, using stem water potential as a criterion. The results show that it is useful to reduce transpiration and avoid high transpiration rates, when growing tomato with saline water. This can also be done by means available in commercial greenhouses. However, for accurate control of the greenhouse environment, with respect to root zone salinity, further experiments are needed for determining the "climate" effect upon the yield-response-to-salinity curve. Finally, shortcomings, limitations and possible extensions of the "transpiration control" idea are discussed.

Samenvatting

De intensieve productiewijze in kassen leidt tot een hoge productie van tuinbouwgewassen gedurende het gehele jaar. Het gebruik van substraatteelten draagt bij aan verdere productieverbetering, dankzij een voortdurend adequate en uniforme voorziening met water en nutriënten, goede aëratie van het wortelmilieu en een juiste temperatuur. In toenemende mate wordt gebruik gemaakt van recirculerende teeltsystemen, die besparing op water en meststoffen paren aan een verminderde vervuiling van de bodem en van het oppervlaktewater. Planten nemen nutriënten meestal niet op in de verhouding waarin zij in de voedingsoplossing voorhanden zijn, daarom accumuleren bepaalde ionen meestal na een zekere periode van recirculatie. Bovendien kan het water waarmee de voedingsoplossing wordt aangelengd ionen bevatten (veelal Na^+ en Cl^-), die niet worden opgenomen en dus accumuleren. Daarom is een in de tijd toenemende ionenconcentratie in dergelijke teeltsystemen niet te voorkomen.

Het is bekend dat sterke verzilting de productie in belangrijke mate kan doen dalen door afname van de vruchtgrootte en het teweeg brengen van fysiogene afwijkingen, zoals neusrot, hoewel de kwaliteit ook in positieve zin kan worden beïnvloed. Uit de literatuur is bekend dat effecten van verzilting en van waterstress veel gelijkenis vertonen en voorts dat de reactie op verzilting wordt beïnvloed door de klimaatomstandigheden. Meer in het bijzonder is het bekend dat er een interactie bestaat tussen verzilting in de wortelzone en de luchtvochtigheid.

De aanname die ten grondslag ligt aan het onderhavige onderzoek is dat de huidige kasteelt mogelijkheden biedt om de omgevingsfactoren te optimaliseren met betrekking tot verzilting van de wortelzone. Speciaal door het sturen van de drogende kracht van de lucht is het mogelijk om de wateropname van de plant te beïnvloeden, teneinde de, door de verzilting van de wortelzone (osmotische druk) verstoorde, waterbalans te herstellen. Het wetenschappelijke doel van dit onderzoek is de interactie tussen wateropname en verdamping te doorgronden in relatie tot de groei in versgewicht van de plant. De praktische doelstelling van deze studie is om een richtsnoer voor de klimaatbesturing te verschaffen voor de teelt bij verhoogde zoutconcentraties in het wortelmedium.

Het onderzoek is gebaseerd op een aantal langlopende proeven met op commerciële wijze geteelde tomaat. Daarbij werden twee “potentiële verdamping” niveaus (ET_0) gecombineerd met twee zoutniveaus. In vier experimenten werd een constante verhouding van 2:3 gehandhaafd tussen de potentiële verdampingsniveaus, terwijl in een vijfde experiment een laag verdampingsregime werd gerealiseerd met behulp van de mogelijkheden die een tuinder thans reeds ten dienste staan. De wortelzone behandelingen betroffen steeds een geconcentreerde

oplossing [resp. geleidbaarheid (EC) van 6.5, 8.0, 9.5 dS m^{-1}], gecombineerd met een referentiebehandeling van EC 2 dS m^{-1}. Eén experiment was gericht op ion-specifieke effecten, door twee verschillende samenstellingen van de voedingsoplossing (één met een hoog NaCl aandeel) met een zelfde hoge EC (9 dS m^{-1}) te vergelijken. Tenslotte, teneinde te testen of de zout geïnduceerde groeireductie kan worden toegeschreven aan de waterstroom naar de vrucht (lage flux leidt tot vermindering van groei), of dat er sprake is van fysiologische veranderingen, was een experiment opgezet, waarin de reactie werd onderzocht op stapsgewijze veranderingen in de EC van de voedingsoplossing.

Na het probleem algemeen te hebben ingeleid, wordt in hoofdstuk 2 de interactie tussen spruit- en wortelbehandelingen besproken. Noch EC, noch ET_0 hadden effect op het aantal of op het gewicht van de geoogste vruchten. Het droge stof gehalte (%) van de vruchten nam echter toe met de EC met 0.04 % per dS m^{-1}, terwijl er geen significant effect van ET_0 werd waargenomen. Geen van de behandelingen had effect op de droge stof productie, maar het watergehalte van de vruchten werd door de EC beïnvloed. De productie-efficiëntie van de verkoopbare verse productie (η_F) werd bepaald (voor elk experiment en behandeling) als de helling van cumulatieve productie versus fotosynthetisch actieve stralingssom boven het gewas. η_F nam lineair af met toenemende EC van de voedingsoplossing. Om precies te zijn, de efficiency nam af met 5.1% per dS m^{-1}extra ten opzichte van een EC van 2, een afname die kon worden toegeschreven aan een afname van het gemiddelde vruchtgewicht (3.8% per dS m^{-1}) en een toegenomen fractie onverkoopbare vruchten (vooral als gevolg van neusrot). Bij de lage-transpiratie behandeling bedroeg het productieverlies echter slechts 3.4% per dS m^{-1}, dat volledig kon worden toegeschreven aan de afname van het gemiddelde vruchtgewicht. Met andere woorden, bij een hoge EC kan reductie van de potentiële verdamping leiden tot een vermindering van het verlies in vruchtgewicht en vermindering van het optreden van neusrot.

Het bladoppervlak, een zeer belangrijke parameter in verband met de waterstroom uit het gewas en de koolstof stroom in het gewas, wordt geanalyseerd in hoofdstuk 3. Er was geen aantoonbaar effect van de klimaatbehandelingen op bladgrootte of aantal bladeren per plant. De respons van bladgrootte op EC was anders dan die van de vruchten: de drempelwaarde en de helling waren beide groter. Om precies te zijn: het oppervlak per blad nam af met 8% per dS m^{-1} bij een EC boven de 6.5 dS m^{-1}. Het aantal bladeren per plant nam echter iets toe met de EC (2% per dS m^{-1}), een onbekend effect. De Leaf area index (LAI) werd met 20% gereduceerd bij de hoogste EC (9.5 dS m^{-1}), maar zelfs in dat geval was de geschatte lichtonderscheppingsvermindering slechts 8%. Dit relatief kleine effect is in overeenstemming met de eerder genoemde waarneming dat het drooggewicht van de vruchten niet werd beïnvloed door EC.

Aangezien het belangrijkste effect van de behandelingen optrad in het gemiddelde vrucht vers gewicht (een belangrijke opbrengstparameter), is de groei van vruchten het onderwerp van hoofdstuk 4. De factoren die de vruchtgrootte kunnen beïnvloeden werden onderzocht: De vruchtgroeisnelheid (FGR) en de vruchtgroeiduur (FDP, de periode tussen het moment van verschijnen van de tros tot aan het moment van de eerste oogst). De afname van de uiteindelijke vruchtgrootte bij hoge EC werd vooral veroorzaakt door de geringere vruchtgroeisnelheid, in het bijzonder tijdens de celstrekkingsfase. De maximale FGR was 1.5 cm^3 dag^{-1} bij 9.5 dS m^{-1}, terwijl deze meer dan 2 cm^3 dag^{-1} bedroeg bij 2 dS m^{-1}. De vruchtgroeiduur werd door een verhoogde EC verkort, speciaal tijdens de zomerperiode. Er was geen effect van verdamping op de vruchtgroeisnelheid bij 2 dS m^{-1}, maar er was een significant effect bij hogere EC. De effecten op drogestof toename en drogestofgehalte zijn in overeenstemming met de waarneming dat het drooggewicht van de vruchten door geen van de spruit- of wortelbehandelingen werd beïnvloed en dat het voornaamste effect werd bewerkstelligd via de waterstroom naar de vruchten.

In hoofdstuk 5 wordt het EC-effect onderzocht door de dynamiek van de respons op een stapsgewijze verandering van de EC in de wortelzone van een tomatengewas te bestuderen. De EC van de voedingsoplossing werd verlaagd (tot 2 dS m^{-1}) na langdurige (5 maanden) blootstelling van het gewas aan een hoog zoutgehalte (9 dS m^{-1}). De grootte van de geoogste vruchten nam daarna geleidelijk toe, totdat vruchten werden geoogst die volledig bij de nieuwe EC waren gegroeid (8 weken) en die een grootte bereikten die ook zou worden verwacht bij een EC van 2 dS m^{-1}. Ook de bladeren die bij de nieuwe EC werden gevormd groeiden als balderen bij een EC van 2 dS m^{-1}, maar bladeren die reeds volledig waren uitgegroeid reageerden niet meer op de verandering in EC. Geconcludeerd wordt dat het negatieve effect van zout op groei en productie voornamelijk is terug te voeren op de waterbalans van de plant, die kan worden hersteld, zelfs na langere blootstelling aan een hoog zoutgehalte.

Opname en transport van water in de plant zijn daarom het onderwerp van hoofdstuk 6. Hierin wordt een aantal experimenten beschreven, die waren opgezet om de hypothese te onderzoeken dat potentiële verdamping en waterpotentiaal van de wortelomgeving een vergelijkbaar effect hebben op de waterbalans en de versgewichtstoename. De overdrachtsvergelijking voor water langs de route van voedingsoplossing naar bladeren werd gebruikt om de hydraulische weerstand af te leiden uit waterpotentiaalmetingen. De hydraulische weerstand binnen de plant, berekend uit metingen van de waterpotentiaal van bladeren en stengel was onafhankelijk van de transpiratiestroom en van de osmotische potentiaal van de voedingsoplossing, althans binnen het gebied dat in het onderzoek werd bestreken. Verder werd aangetoond dat de waterstroom uit de bladeren voornamelijk wordt

bepaald door de klimaatomstandigheden (potentiële verdamping), aangezien de wateropname per eenheid bladoppervlak niet door de osmotische potentiaal van de voedingsoplossing werd beïnvloed. Derhalve moet bijvoorbeeld een daling van de potentiaal van de voedingsoplossing een daling veroorzaken van de waterpotentiaal van de stengel. Omgekeerd, als de waterstroom uit de bladeren toeneemt moet, aangezien er geen effect is op de hydraulische weerstand, de waterpotentiaal in de stengel lager worden, teneinde de grotere stroom mogelijk te maken. De waterpotentiaal van de vruchten reageerde daardoor slechts zwak op veranderingen in de omgeving van de wortel en de spruit. Daardoor wordt de waterpotentiaalgradiënt van stengel naar vrucht (verantwoordelijk voor watertransport naar de vruchten) in dat geval kleiner. Daarom is de waterpotentiaal van de stengel een belangrijke schakel, die effecten van EC en ET_0 verbindt en is de potentiaalgradiënt tussen stengel en vruchten een belangrijke indicator voor vruchtgroei. De waterimport in de vrucht, die nauw is gerelateerd met de vruchtgroeisnelheid en met het uiteindelijk vruchtgewicht, werd beïnvloed door beide behandelingen en was gecorreleerd met de apoplastische waterpotentiaalgradiënt tussen stengel en vrucht, ondanks de evidentie dat water de vruchten hoofdzakelijk binnentreedt via het floeem.

Water wordt opgenomen door de wortels en verlaat de plant via de transpiratiestroom door de bladeren. Daarom worden de effecten van de zoutconcentratie in de wortelzone en van de potentiële verdamping beide tot stand gebracht via dezelfde toestandsgrootheid, de waterstatus van de plant. EC speelt vooral een rol bij de wateropname, terwijl transpiratie bepalend is voor het waterverlies van de plant. Daarom is transpiratie een effectief instrument om negatieve effecten van een hoge EC te verkleinen. In het laatste hoofdstuk worden de overall effecten van EC en ET_0 besproken. Waterstress (veroorzaakt door een lage waterpotentiaal in de wortelzone) wordt beschouwd als de voornaamste factor die de groei van de plant belemmert bij een hoge EC. Verder wordt aangetoond dat andere mogelijke effecten van een hoge zoutconcentratie (b.v. ion toxiciteit en verstoring van de minerale balans) geen belangrijke rol spelen in verband met de verklaring van de resultaten van dit onderzoek. Speciale aandacht werd besteed aan de beïnvloeding van vruchtgroei middels besturing van de verdamping, gebruikmakend van de stengelpotentiaal als stuurcriterium. Het blijkt dat het nuttig is om verdamping te beperken en hoge verdamping te vermijden bij het telen van tomaten op een zoute voedingsoplossing. We hebben aangetoond dat dit doel ook kan worden bereikt met middelen die in de praktijk voorhanden zijn. Voor een nauwkeurige besturing van het kasklimaat in relatie tot verzilting is verder onderzoek nodig om het klimaateffect op de opbrengst in relatie tot EC vast te kunnen stellen. Voorts worden tekortkomingen, beperkingen en mogelijke uitbreidingen op het principe van de transpiratiebesturing bediscussieerd.

Curriculum Vitae

Ya Ling Li was born on October 3, 1962, in Lingshi County, Shanxi Province, People's Republic of China. She obtained her BSc degree in 1983, majoring in Vegetable Cultivation and Breeding, at Shanxi Agricultural University. In the same university, she defended her thesis entitled "Study of Water Physiological Index of Tomato Seedling" and obtained her MSc degree in the summer of 1986. From 1986 till present, she has taught at the Department of Horticulture at Shanxi Agricultural University as assistant lecturer, lecturer and associate professor. As a researcher, she participated in projects as "Greenhouse Vegetable Growing with Geothermal Water" and "Study and Popularization of an Energy-Saving Greenhouse in Shanxi Province", from the Science Committee of Shanxi Province. In the projects of "Vegetable Growing with Perforated Plastic Film" and "Raising Vegetable Seedlings in Industrialised Form", she was a main researcher and won prizes from the Government of Shanxi Province. At the beginning of 1997, she received a grant from the Government of Shanxi Province and worked as a guest scholar at the Institute of Agricultural and Environmental Engineering (IMAG), Wageningen, the Netherlands. The World Laboratory (ICSC, Geneva, Switzerland) later extended the grant till 2000. During this time she worked as a PhD student at IMAG, which resulted in this thesis.

CONTENT