NUTRIENT AND WATER USE OF TOMATO (*SOLANUM LYCOPERSICUM*) IN SOILLESS PRODUCTION SYSTEMS

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DECLARATION

By submitting this dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

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Summary

(Limited to 500 words)

Soilless production of crops relies on the addition of high concentrations of nutrients with the irrigation water. The drained nutrient solution should be re-used to reduce the risk of pollution and to increase the water- and nutrient use efficiency of the system. Besides the risk of pathogen build-up, one of the main impediments of a wider application of this method is the frequent analysis required to maintain optimum nutrient concentrations and ratios in the rootzone. Yield reductions may be caused by an unbalanced nutrient solution.

Alternatively the addition level of nutrients can be calculated through the use of nutrient uptake models that simulate the change in the re-circulated nutrient solution. To simulate crop water and nutrient demand necessary for model based regulation it was necessary to quantify the key factors affecting nutrient uptake by plants.

The nutrient solution concentration and ratios between the macro-nutrients affected the uptake of water and nutrients. The total nutrient uptake per root dry weight increased and more specifically the nitrate (NO_3^-), phosphate ($H_2PO_4^-$), potassium (K^+) and sulphate (SO_4^{2-}) uptake increased with an increase in nutrient solution electrical conductivity (EC) from 0.8 to 4.0 mS cm^{-1} while water uptake decreased. Except for Ca^{2+} uptake there was no correlation between nutrient and water uptake. Nutrient uptake can thus not be calculated based on water uptake. Instead a mechanistic high-affinity Michaelis-Menten based model can be used to estimate macro-nutrient uptake (U_n, mg m^{-2} hr^{-1}).

Water and nutrient uptake was also affected by the solar radiation levels. Since nutrient uptake is related to the growth rate, solar radiation levels can be expected to influence nutrient uptake. The uptake of all ions increased with an increase in the solar radiation levels and for NO_3^-, K^+ and $H_2PO_4^-$ the uptake rate was higher at higher nutrient solution concentrations. The Michaelis-Menten based model was adjusted to incorporate the effect of solar radiation levels on nutrient uptake. Water uptake (Wu, L m^{-2} day^{-1}) was simulated as a function of crop transpiration and crop leaf area using a linear regression model, but since leaf area development was affected by solar radiation levels this was additionally incorporated into the estimation of the leaf area index (LAI).

The composition of the nutrient solution also affected the biomass allocation of the crop which can again affect nutrient use as well as the fruit yield. There was also a direct effect of nutrient solution

composition on fruit yield and quality with higher EC's resulting in smaller fruit but an increase in fruit dry matter %, total soluble solids (TSS), titratable acidity (TA) and lycopene content.

The results in this thesis make a valuable contribution to our understanding of the effect of nutrient availability (concentration and ratios) and nutrient requirement for growth (solar radiation levels) on nutrient uptake. Incorporating these into nutrient uptake models resulted in the development of a handy tool to simulate changes in composition of re-circulating nutrient solutions ultimately resulting in an improvement of the water and nutrient use efficiency of soilless systems.

Opsomming

Die grondlose verbouing van gewasse is afhanklik van toediening van voedingselemente teen hoë peile in die besproeiingswater. Die voedingsoplossing wat dreineer moet hergebruik word om die risiko van besoedeling te verminder en ook om die water en nutriënt verbruik doeltreffendheid van die sisteem te verbeter. ՚n Ongebalanseerde voedingsoplossing kan ՚n verlaging in opbrengste veroorsaak. Benewens die risiko van patogene wat opbou, is die gereelde analises nodig word vir die handhawing van optimale nutriënt konsentrasies en verhouding tussen elemente in die wortelsone een van die hoof faktore wat ՚n meer algemene gebruik van die metode verhoed.

Alternatiewelik kan die nutriënt toedieningspeile bereken word deur voedingstof opname modelle en simulasie van die verandering in water en nutriente wat dreineer. Om ՚n model gebaseerde reguleringsmetode daar te stel was dit nodig om die belangrikste faktore wat nutriënt opname beïnvloed te kwantifiseer.

Beide die konsentrasie van die voedingsoplossing en die verhouding tussen elemente het ‘n effek gehad op die opname van water en nutriënte. Die totale nutriënt opname per wortel droë massa het toegeneem. Terwyl water opname afgeneem het met ‘n toename in die elektriese geleding (EG) van die voedingsoplossing vanaf 0.8 tot 4.0 mS cm^{-1} het die nitraat (NO_3^-), fosfaat ($H_2PO_4^-$), kalium (K^+) en sulfaat (SO_4^{2-}) opname verhoog. Behalwe vir Ca^{2+} opname was daar geen korrelasie tussen water en nutriënt opname nie. Nutriënt opname kan dus nie bepaal word gebaseer op wateropname nie. Alternatiewelik is die gebruik van ՚n meganistiese hoë-affiniteit Michaelis-Menten-gebaseerde model voorgestel om die opname van makro-nutriente (Un, mg m^{-2} hr^{-1}) te bepaal.

Water- en voedingstofopname is beinvloed deur die ligintensiteit vlakke. Voedingsopname word bepaal deur die groei van die plant, daarom is dit verwag dat ligintensiteit vlakke die opname van voedingstowwe sal beïnvloed. Die opname van al die ione het toegeneem met 'n toename in die ligintensiteit vlakke en die tempo van NO_3^-, K^+ en $H_2PO_4^-$ opname was hoër by 'n hoër voedingsoplossing konsentrasie. Die Michaelis-Menten gebaseerde model is aangepas om die effek van ligintensiteit vlakke op nutriënt opname te inkorporeer. Opname van water (Wu, L m^{-2} dag^{-1}) is gesimuleer as 'n funksie van transpirasie en blaaroppervlakte met behulp van 'n lineêre regressiemodel en aangesien die blaaroppervlak ontwikkeling ook deur ligintensiteit vlakke beïnvloed word, is dit opgeneem in die skatting van die blaaroppervlakte-indeks (LAI).

Die samestelling van die voedingsoplossing het die biomassa verspreiding beïnvloed. Dit kan nutriënt gebruik en vrug opbrengs beïnvloed. Die voedingsoplossing samestelling het vrug opbrengs en -kwaliteit beinvloed met kleiner vrugte, maar 'n toename in droëmateriaal %, totale oplosbare vastestowwe (TOVS), titreerbare suur (TA) en likopeen inhoud by ’n hoër EG.

Die resultate in hierdie tesis lewer 'n waardevolle bydrae tot ons begrip van die effek van nutriënt beskikbaarheid (konsentrasie en verhoudings) en voedingstof behoefte vir groei (ligintensiteit vlakke) op voedingsopname. Deur die inligting te inkorporeer in voedingsopname modelle het gelei tot die ontwikkeling van 'n handige instrument om die veranderinge in die samestelling van hersirkulerende voedingsoplossings te simuleer. Dit lei gevolglik tot die verbetering van die water en voedingstof gebruik doeltreffendheid van grondlose stelsels.

Chapter 1

NUTRIENT AND WATER USE IN SOILLESS SYSTEMS: A REVIEW

Introduction

In commercial agriculture the application of fertilizers is essential to obtain economically sustainable yields. In a thorough review of data from 362 cropping seasons Stewart et al. (2005) concluded that at least 30 to 50% of crop yields can be attributed to fertilizer nutrient inputs. All fertilizer applied do however not relate to increased crop yields and often fertilizers are applied in excess to a crops need. This was evident in the study by Elia and Conversa (2012) where farmers apply 350-400 kg of Nitrogen (N) ha^{-1} although the recommendation for the specific area is 200 kg of N ha^{-1}. A large percentage of nutrients applied is therefore lost and leached to the environment. According to Le Bot et al. (2001) an average of 10-30 kg of N ha^{-1} per year is lost in intensive open field production. Nitrate and phospate runoff may cause environmental damage such as eutrophication, and nitrate can cause drinking water to be unsafe. It is therefore understandable that there are concerns regarding the possible environmental side effects caused by fertilizer leaching and the urgent calls for better management of fertilizer application to reduce losses to the environment. A major agricultural challenge is to increase yields to be able to feed the growing world population while reducing inputs to minimize the pressure on land use and resources. To maintain a steady food supply it is not realistic to severely reduce or eliminate the use of chemical fertilizers but rather it necessitates the improvement of crop production systems in terms of the nutrient use efficiency (NUE) (Lea and Azevedo 2006) and water use efficiency (WUE) (White et al. 2004). Moreover, due to the impact of global climate change on agricultural production and the strong demand the world population is starting to exert on the availability of fresh water, less high quality water will be available for crop production in future.

An intensive production system that is still gaining ground is soilless crop production in a protected environment such as a greenhouse (Massa et al. 2011). This makes it possible to produce food and ornamental crops year-round, even out of season and in areas where it would otherwise not be possible. It helps to ensure food security and economic opportunities for the local populations, also in peri-urban areas where traditional agricultural production is not possible. Growing plants in soilless culture, also referred to as hydroponics, is a method of cultivating crops in any growing medium different than soil or in a pure water culture where all the nutrients are added to the irrigation water (Raviv and Lieth 2008). A wide variety of crops can be grown in soilless systems including vegetables such as tomatoes, lettuce and cucumbers and flowers including roses, tulips and potted plants such as cyclamens (Van Os et al. 2008). Crops grown hydroponically are grown with particularly high nutrient levels in order to maintain optimal concentrations of nutrients in the rootzone at all times.

Unfortunately only 30 to 80 % of the nutrients supplied to crops in an open hydroponic system is used by crops (Rácz 2007) and up to 1000 kg N ha^{-1} per year can be lost in traditional drain to waste soilless production systems (van Noordwijk 1990). Using this system where the drained nutrient solution is not re-used result in nutrient rich water running to waste where it can contribute to the pollution of groundwater and rivers. Nitrate (NO_3^-) concentrations of 400-1000 mgL^{-1} in water drained from soilless production systems can potentially contaminate underlying water aquifers (Thompson et al. 2007) and this requires the implementation of crop management practices to reduce NO_3^- contamination of aquifers in vulnerable areas (Gallardo et al. 2009). In South Africa potable water should contain less than 40 mg NO_3^--N per liter of water (Tredoux et al. 2009).

Soilless production can however be an environmentally friendly technology with a high water use efficiency (WUE) and nutrient use efficiency (NUE) when the application of water and nutrients is better managed to match the plants need and to re-use the drained fertigation water as is practiced in the so-called closed system (Sonneveld and Voogt 2009; Zebarth et al. 2009). Although conversion to a closed or semi-closed system can result in considerable fertilizer savings (Raviv and Lieth 2008), conversion is often hindered by the high cost and availability of expertise in the setup and maintenance of such a system. Besides the increased risk of disease contamination which will require the installation of equipment to disinfect the nutrient solution before re-use, the nutrient levels in the drained nutrient solution needs to be monitored and adjusted regularly to avoid yield losses. According to Le Bot et al. (1998) a dual approach to fertigation monitoring is currently practiced namely an inductive approach versus a deductive approach. The inductive approach consists of providing the crop with a pre-set nutrient solution and altering the concentration should the EC of the drainage water differ from the supplied, reference nutrient solution. One method involves mixing the drainage water and fresh water in such a ratio as to maintain a pre-set electrical conductivity (EC) in the outgoing mixture (Savvas 2002). The amount of fertilizers injected is therefore adjusted routinely. With this method it is possible to maintain a constant EC in the nutrient solution supplied to the crop. Alternatively fertilisers are mixed into water at pre-set doses and then mixed with the effluents before being used to fertigate the plants (Savvas 2002). With both these methods real-time measurement of EC and automatic re-adjustment is needed. This is a relatively low cost method to control the nutrient solution concentration and indirectly quantifies the total amount of dissolved ions in the solution. The biggest limitation of this approach is that the ratios between the individual nutrients cannot be measured and adjusted in real time and in many areas there can be a considerable time lag between nutrient solution sampling, analysis and reporting from a laboratory and solution adjustments. Alternatively, the nutrient solution concentration can be monitored and adjusted in real-time by measuring nutrients separately with the use of ion-specific sensors (Neto et al. 2014). There are however still some practical difficulties related to these sensors that need to be resolved before they will be implemented in commercial systems, including the high cost, life expectancy and availability of these sensors (Gieling et al. 2005).

The alternative method for regulating fertigation is the deductive approach where plant physiological functions and climatic parameters are incorporated in crop models that can be used to simulate plant growth, the water and nutrient requirements as well as the nutrient concentration in the root zone of a soilless system (Le Bot et al. 1998). This approach aimed at predicting plant nutritional needs, has the potential to accurately control fertigation and should reduce the producers' dependence on lengthy and expensive analysis of the nutrient concentrations. Before this approach can however be effectively applied as a tool in decision support systems, knowledge of all relevant parameters need to be incorporated into these mathematical models and these models need to be vigorously validated, under different growing conditions.

Nutrient uptake and transport in the plant

According to Marschner (1995) ion uptake is characterized by selectivity, accumulation and genotype. Selectivity refers to the fact that some nutrients are taken up to a larger extent than others while the accumulation points to concentration of nutrients in the cell sap that can be considerably higher than that of the external solution. There are also considerable differences in ion uptake between different plant species and also between cultivars (Sharifi and Zebarth 2006) but it can also be affected by environmental conditions (Wheeler et al. 1998).

Crop nutrient needs depend on the nutrient requirements for the production of biomass and also the rate of biomass production. Mineral nutrient uptake by roots has a significant effect on the vegetative and reproductive development of the shoots and nutrient uptake is to a large extent regulated by demand from the shoots (Wang et al. 2006). When fertilizers are applied at the correct time to meet a crops needs at that time, production will be more productive, profitable and environmentally friendly.

Plants accumulate nutrients from the rootzone solution and nutrients must therefore be dissolved to be mobile in the soil. Nutrient transport towards roots and contact between roots and nutrients occur primarily as a result of two processes: mass flow and ion diffusion (Barber 1962). Mass flow is driven by the absorption of water by the roots whereas diffusion is a result of ion concentration gradients between the soil and the root. Water is essential for both of these processes and changes in plant water use can therefore significantly alter nutrient uptake (Marschner 1995). As the plant transpires, nutrients in solution are transported convectively towards the root surface. The volume of water transpired as well as the concentration of the soil solution will determine the contribution mass flow will make to a plants nutrient acquisition (Barber 1995; Chen and Gabelman 2000; Havlin et al. 2005). The transpiration rate will directly affect the mass flow of water to the root surface, and also the mechanism of ion transport and nutrient uptake. For nutrients at a low solution-phase concentration, mass flow alone will not deliver sufficient quantities to the root surface. As the root volume increases, concentrations of these nutrients in the in the rootzone will be depleted. Movement by diffusion is a function of the water content of the growing medium, and the concentration gradient created through root uptake (Barber 1995).

Root morphology and nutrient uptake

The primary function of roots is to acquire nutrients and water and be able to do this under varying conditions. Root growth rate, root morphology and architecture including root surface area, root length and dry weight are important factors regulating nutrient uptake (Silberbush and Barber 1983; Yamauchi 2001).

Physical and chemical factors can influence root development. The concentration and distribution of nutrients in the rootzone influence root development with more lateral roots developing in areas with high concentrations of nutrients (Wang et al. 2006). Shoots also exert some control over root development. High N concentrations in the rootzone have been linked to fewer resources being allocated from the shoots to the roots (Ericsson 1995) and root branching is often closely related with the supply of photosynthates from the shoot (Ogawa et al. 2005). Low phosphate availability has also been shown to increase plants sensitivity to auxin, a plant hormone responsible for lateral root development (Lopez-Bucio et al. 2002).

Root morphology can influence nutrient uptake and finer roots is associated with a larger nutrient uptake, especially nitrate, per unit root mass as the root surface area is increased (Wang et al. 2006). Root morphology and some physiological characteristics often differ between soil- and solution-grown plants. For example root exudation of organic solutes is higher in the presence of soil where there is mechanical root impedance (Marschner 1995).

Besides the moisture content in the root zone, temperature will also determine the uptake of nutrients primarily through changes in root growth and morphology (Marschner 1995). Increasing the root zone temperatures from 15 to 30^{o}C increased the root surface area and availability and uptake of potassium (K) by maize seedlings at both high and low K application rates (Ching and Barber 1979). For maize it was shown that an increase in rootzone temperature (19 to 25^{o}C) increases the root surface area and phosphorus (P) accumulation at both low and high application rates (Mackay and Barber 1985). They also reported a strong, linear relationship (R^2=0.96) between P uptake and root surface area in different soils and at different moisture levels. Root zone temperatures affect the uptake of minerals in different ways with the uptake of P being the most sensitive to low temperatures (Marschner 1995). In cucumbers which is chilling sensitive it was found that the uptake rate of nitrate (NO_3) was reduced to a larger extent than that of ammonium (NH_4) at low rootzone temperatures (Tachibana 1987).

Uptake mechanisms of specific nutrients

Although the movement of ions from the nutrient solution into the cells is a passive process, the cell walls can assist or restrict movement to the plasma membrane for further uptake (Marschner 1995). Cations can accumulate in the apoplasm where carboxylic groups act as cation exchangers and plant species differ in the number of these exchange sites in the cell walls (Marschner 1995). The result is that the concentration of cations increases in the vicinity of the active uptake sites in the plasma membrane. Depending on the concentration of ions, transport across the plasma membrane can be passive or active. At low concentrations the active ion transport across the plasma membrane requires energy as well as a specific binding site. During vegetative growth up to 36% of the total respiratory energy is used for ion uptake (Marschner 1995).

Generally most cations are transported along the electrical potential gradient across the plasma membrane in a uniport whereas most anions are transported via proton-anion co-transport using the electrical and chemical gradient as driving force (Marschner 1995). The specific nutrient absorption mechanisms do however differ resulting in variable nutrient uptake efficiencies for the different ions (Sonneveld and Voogt 1985; Wild et al. 1987; Sonneveld 2000). Transport of ions across the root membranes is so important that about 12% of the total genome encode for the transporter proteins responsible for the uptake of the sixteen nutrients plants need (Marschner 1995; Tanner and Caspari 1996). This also points to the fact that plants can adapt to fluctuating conditions in the rootzone probably through the use of different transport mechanisms to obtain each of these nutrients. Uptake of nutrients can be divided into high affinity transport systems (HATS) and low affinity transport systems (LATS). While the low affinity system is constantly active, the high affinity systems typically responding to nutrient deprivation through increased activity (Reid 1999). For the purpose of this review only the macro-nutrients will be discussed.

Nitrogen

Nitrate (NO_3^-) is usually the main source of nitrogen for plants (Barker and Pilbeam 2007). In various species it was found that the presence, not the absence of NO_3^- in the external solution will induce the high affinity uptake system for this ion (Reid 1999). Nitrate (NO_3^-) is mobile in plants and can be stored in vacuoles but will be reduced to ammonium (NH_4^+) before it can be used for the synthesis of proteins (Barker and Pilbeam 2007). According to the “N demand” theory, the N status of the shoot will determine the NO_3^- uptake by the roots. In some plants the NO_3^- uptake will decrease when amino acids accumulates in plants but the mechanism of how these changes in plant N status affect N uptake is not yet clear (Sonneveld 2000; Wang et al. 2006). In rice plants a large percentage of the root-sourced N is transported to the shoots and root growth is dependent on the N transported via the phloem to the roots (Tatsumi and Kono 1980). There is therefore often a co-operation between the root-sourced xylem and leaf-sourced phloem to supply all growing organs with sufficient N (Yoneyama et al. 2003).

Nitrogen can also be taken up as a monovalent cation namely NH_4^+. Ammonium (NH_4^+) can however be toxic even at low concentrations in the cell and need to be metabolized into an organic molecule for detoxification. This can result in a rapid depletion of carbon reserves when plants are supplied with more NH_4^+ compared to NO_3^- (Barker and Pilbeam 2007). Competition for binding sites on the plasma membrane takes place for ions with similar physiochemical properties and NH_4^+ effectively competes with K^+ although high K^+ concentrations will not inhibit the uptake of NH_4^+ (Marschner 1995). Ammonium (NH_4^+) can result in toxicity symptoms in many plants when it is supplied as the only nitrogen source (Britto and Kronzucker 2002). Crops differ in their sensitivity to ammonium toxicity and this is attributed to differences in sugar concentrations in the roots where ammonium is metabolized (Kafkaffi 1990). Ammonium (NH_4^+) will also inhibit the uptake of NO_3^-, whereas the external concentration of NO_3^- generally has no effect on the NH_4^+ uptake (Breteler and Siegerist 1984). High Cl^- levels can also reduce the uptake of NO_3^- by plant roots (Marschner 1995). Spinach plants often take up excessive amounts of NO_3^- to use as osmoticum but this can reduce the nutritional quality of this crop. By increasing the Cl^- content in the nutrient solution, this NO_3^- content of the plants can therefore be reduced (Marschner 1995).

Potassium

Potassium (K^+) is the most abundant essential cation in plant cells (Wang and Wu 2013). Many fruiting crops, tomatoes included have a very high K^+ requirement and plants have evolved mechanisms to acquire sufficient K^+ even at low root zone K^+ concentrations (Chen and Gabelman 2000). Plant membranes are fairly permeable to K^+ as a result of various K^+ channels in the plasma membrane (Barker and Pilbeam 2007). A dual affinity K^+ uptake system operates in higher plants depending on the availability of K^+ (Epstein et al. 1963; Barker and Pilbeam 2007). The low affinity K^+ uptake system absorbs K^+ when it is present at sufficient levels and is passive via the electrochemical gradient for this ion. High affinity K^+ uptake is coupled to H^+ transport and consists of electrochemical potential-driven type transporters (Maathuis and Sanders 1996; Wang and Wu 2013). Plants are able to sense the availability of K^+ in roots and K^+ uptake is also regulated by its concentration in the phloem (Wang et al. 2006; Wang and Wu, 2013). Other ions can affect the uptake of K^+ and the presence of Cl^- in the rootzone has been associated with an increase in the influx of K^+ in corn roots (Kochian et al. 1985). Sodium (Na^+) has been shown to induce K^+ deficiency (Kronzucker et al. 2008).

Phosphorus

Phosphorus is mostly taken up by plant roots as inorganic phosphate (Pi) and plants require specialized transporters to extract the Pi from the rootzone solution (Bieleski 1973). Pi is absorbed by plant roots as either $H_2PO_4^-$ or HPO_4^{2-} depending on the pH in the rootzone (Barker and Pilbeam 2007) but Pi uptake rates are highest between pH 5.0 and 6.0 where most Pi will be present as the monovalent $H_2PO_4^-$ species (Furihata et al. 1992).

A large percentage of Pi in the rootzone becomes immobile and unavailable for plant uptake because of adsorption, precipitation, or conversion to an organic form and because Pi is moved in the rootzone mainly through diffusion (Holford 1997). A zone that is depleted of Pi around the root is often formed because of its slow diffusion rate (10^{-12} to 10^{-15} m^2s^{-1}). Plant root morphology is very important in maximizing Pi uptake. When the supply of Pi is limited, root growth will increase and the rate of uptake by roots will increase (Schachtman et al. 1998). In phosphate-starved Arabidopsis plants the decrease in the number of lateral roots has been linked to changes in auxin distribution and sensitivity (Al-Ghazi et al. 2003).

Pi enters the root through co-transport with positively charged ions and the cytoplasmic acidification associated with Pi uptake suggests that the cation is H^+ (Schachtman et al. 1998). Results from kinetic studies also suggest that two Pi uptake systems exist with different affinities for Pi. The high affinity system is characterized by transporters with an affinity (Km) range from 3 to 7 µm. Evidence suggests that the high-affinity system is repressed by high concentrations of Pi (Schachtman et al. 1998). Except under severe Pi deficiency in the rootzone, the Pi in the cytoplasm is maintained at a constant concentration. However the vacuolar Pi concentrations can vary widely depending on the external Pi concentration (Mimura 1995; Schachtman et al. 1998). Pi absorbed by the roots is transported in the xylem to the younger leaves and retranslocation of Pi in the phloem from the shoots to the roots and from older leaves to the younger leaves also takes place, especially when Pi supply to the roots become limiting. Under these circumstances the vacuolar stores of Pi will be used (Schachtman et al. 1998). Interestingly, about half of the Pi translocated via the phloem from the shoots to the roots is again transferred to the xylem and recycled back to the shoots (Jeschke et al. 1997). When plants are supplied with sufficient Pi and the rate of absorption exceeds demand, there are certain processes that will prevent Pi toxicity. These processes include the conversion of Pi into organic storage compounds like phytic acid and a reduction in the Pi uptake rate (Lee et al. 1990).

Calcium

Calcium (Ca^{2+}) moves either via the symplast represented by the cytoplasm of cells linked by plasmodesmata or through the apoplast represented by the spaces between cells. The current theory is that initially Ca^{2+} enters the roots through the cell walls into the intercellular spaces, the apoplast until it reaches the Casparian band of the endodermis. The Casparian band of the endodermis however acts as a barrier to the movement of Ca^{2+} from the apoplast into the xylem. Movement through the apoplast takes therefore primarily place in the young root tip where the Casparian band and suberized endodermal cells are not yet well developed (state I endodermis) (White 2003; Wang et al. 2006). In the older parts of the root the endodermis has suberized lamellae covering the entire cell wall (state II endodermis) and although other cations such as K^+ can pass through state II endodermis Ca^{2+} cannot (Barker and Pilbeam 2007). There are a number of Ca^{2+} specific ion channels in the membranes of root cells which facilitates the further movement of Ca^{2+} into the cytoplasm, thus in the symplast. (Barker and Pilbeam 2007).

Inside cells Ca^{2+} is actively transported against its electrochemical gradient through Ca^{2+} specific transporters from the cytosol to either the apoplast or vacuoles and other intracellular organelles (Hirschi 2001; Barker and Pilbeam 2007).

Calcium (Ca^{2+}) movement in the plant takes place almost exclusively via the xylem, therefore from the roots to the shoots (Marschner 1995; Barker and Pillbeam 2007). Once the Ca^{2+} entered the xylem it is transported via the transpiration stream and the rate and selectivity of Ca^{2+} transport to the shoot is therefore predominantly controlled via the symplastic pathway (White 2001; Wang et al. 2006; Barker and Pilbeam 2007). As Ca^{2+} is not phloem mobile it will not be re-translocated from old shoots to younger plant tissue (Kirby and Pilbeam 1984; Marschner 1995; Barker and Pillbeam 2007). Plant organs with low transpiration rates, such as tomato fruit can therefore often have a low Ca^{2+} content that can result in a physiological disorder such as blossom end rot (Marschner 1995).

High temperature and transpiration levels enhance water uptake, and therefore the uptake and translocation of Ca^{2+} via the xylem to the leaves will increase at the expense of transport of water to fruits (Taylor et al. 2004). When transpiration is limited due to a too high relative humidity in the greenhouses a Ca^{2+} deficiency in the leaves of tomato can also be induced, resulting in reduced yield and fruit quality (Hamer 2003). According to Barker and Pilbeam (2007) the link between Ca^{2+} uptake and transpiration can be purely incidental. The reason for this is that the movement of Ca^{2+} in the symplasm of the endodermis is required for xylem loading. New cation exchange sites are made available in new tissue as the crop grows and Ca^{2+} uptake is therefore proportional to crop growth and transpiration will increases in bigger plants.

Sulphate

Sulfate (SO_4^{2-}) uptake from the soil is an energy-independent mechanism performed via proton/ SO_4^{2-} co-transporters (Droux 2004). Both high and low affinity SO_4^{2-} transporters exist which operate at SO_4^{2-} concentrations of < 0.1mM and > 0.1mM respectively. A decrease in the SO_4^{2-} availability in the external solution will result in an increase in the activity of the high affinity transport system (HATS) (Reid 1999). Sulphate (SO_4^{2-}) is transported in plants across the plasma membrane, intracellular from the root to the shoot, and then redistributed via the phloem. Uptake of SO_4^{2-} is then regulated by its concentration in the phloem (Wang et al. 2006). The majority of SO_4^{2-} taken up by the plant roots is reduced to sulphide before being incorporated into cysteine (Barker and Pilbeam 2007). In the plastids the SO_4^{2-} is then reduced and stored in the vacuole before assimilation (Wang et al. 2006). In the shoots reduction of SO_4^{2-} takes place predominantly in the chloroplasts (Barker and Pilbeam 2007).

Magnesium

In contrast to other cations (K^+, Ca^{2+} and NH_4^+), Mg^{2+} is comparatively mobile in the rootzone. Since Mg^{2+} is not as strongly bound to soil charges, higher Mg^{2+} concentrations in the soil solution compared to that of the other cations can often be observed (Shaul 2002).

Mass flow plays an important role in the Mg^{2+} nutrition of crops but under adverse conditions, including poor irrigation management where the rootzone dries out too much, the transport of Mg^{2+} to the roots can be severely impaired (Gransee and Führs 2013). Mg^{2+} is also subject to considerable leaching from the rootzone especially when the water balance is high (Gransee and Führs 2013). The binding strength of Mg^{2+} at the exchange sites on cell walls and the plasma membrane is quite low and other cations, including K^+, Ca^{2+}, Mn^{2+} and NH_4^+ will compete strongly with Mg^{2+} for uptake by the roots (Marschner 1995). Magnesium (Mg^{2+}) uptake rates in wheat seedlings were found to be significantly higher when plants were supplied with only NO_3^- compared to plants only supplied with NH_4^+ (Huang and Grunes 1992).

An increase in the nutrient solution Ca^{2+} concentration will however result in antagonism between the Ca^{2+} and Mg^{2+} resulting in the reduction of Mg^{2+} uptake (Barker and Pilbeam 2007).

Measuring nutrient uptake

The first method of measuring nutrient uptake consists of measuring the nutrient content of the plant tissues. With this method nutrient uptake and also its allocation to different plant parts can be determined. Measuring the nutrient content of healthy, high yielding plants throughout the cultivation period can help to generate nutrient absorption curves that can be used to formulate nutrient solutions. The disadvantage of this technique is that it is a destructive technique. The critical nutrient value of plant tissue is the minimum tissue nutrient concentration (normally from youngest fully expanded leaves) required for 90% of optimum growth or yield, although this critical nutrient ‘‘value’’ should rather be thought of as a range of values (Mattson and van Iersel 2011).

The second method consists of quantifying plant nutrient uptake through determining the nutrient depletion in the root zone. The concentrations of the different ions are usually measured at different times and the difference will give an indication of the nutrients taken up. The following equation from Cabrera et al. (1995) can be used to determine the nutrient uptake rate:

$$\text{Nutrient uptake rate} = (V1 \times C1) - (V2 \times C2) \quad (1)$$

Where V1 and V2 are the nutrient solution volume (L) at time 1 and 2, and C1 and C2 are the nutrient concentrations (mmol L^{-1}) on time 1 and 2. Results of nutrient uptake over time obtained using this method can be very accurate but can also be affected by several factors including rootzone and climatic conditions (Sanchez 2009). It is however important to take into account when using this method that some elements may form a sediment on the substrate or roots. Care should also be taken when collecting the nutrient solution samples. When using a growing medium the concentration of nutrients in the growing medium and that in the rootzone may differ considerably and therefore the specific location where the nutrient solution is obtained can have an impact on the measured concentration of the ions. Excessive evaporation can also result in loss of accuracy of the measurements and should therefore be determined or better yet avoided through the type of growing system used. According to Le Bot et al. (1998) this method is also not as accurate when using nutrient solutions with a high EC.

Nutrient needs of crops can also be determined by using growing medium analysis. The EC of the growing medium is often used as an indication of nutrient availability but is only really accurate when the irrigation water and growing medium have a low EC (Mattson and van Iersel 2011). Simply measuring the root zone EC is not a good indicator of plant demand. A low growing medium EC does not necessarily indicate a deficiency; it can simply indicate that the plant is absorbing nutrients effectively. A complete analysis can indicate whether fertilizer inputs are required and at what rate and it can indicate the amount of nutrients available for crop uptake. Growing medium analysis will provide an index of nutrient availability in the rootzone and not an absolute amount that will be taken up by plants since the effectiveness of laboratory nutrient extraction methods differs from the efficiency of nutrient uptake by plants. Analysis results may also differ between laboratories since extraction methods also differ. This is very important to take into account when compiling or comparing fertilizer recommendations (Mattson and van Iersel 2011).

Uptake concentrations are also used to determine nutrient uptake. The nutrient uptake concentration (Cu) is defined as the ratio between the ions and the water taken up by the plants in the same time interval (Gallardo et al. 2009; Massa et al. 2011). Cu has no physiological basis but is deemed useful as a guide in formulating nutrient solutions (Sonneveld 2000). Ions dissolved in the nutrient solution at a concentration higher than Cu will accumulate in the root zone. Pardossi et al. (2005) found that nutrient uptake is linearly related to the water uptake and the uptake rates of different nutrients were closely inter-correlated. However in other studies it was found that nutrient uptake is not directly related to water uptake. Delhon and his co-workers (1995) found NO_3^- uptake to be independent of variations in transpiration.

Using the mass balance approach, the required nutrient solution concentration is often calculated from:

Required nutrient concentration in solution (mg L^{-1}) = tissue nutrient concentration (mg g^{-1}) X water use efficiency (g L^{-1}).

The water use efficiency (WUE) of a plant can also be determined as the ratio of plant yield to water use [(kg ha^{-1} mm^{-2}].

Instead of monitoring the changes in all nutrient concentrations when a nutrient solution is recycled changes in the EC alone can be monitored and could possibly be linked to changes in certain ions such as Na and K (Carmassi et al. 2002; Pardossi et al. 2005) which could then be used as guide ions.

Mixing nutrient solutions

One of the theories used to explain the uptake of nutrients by plants is that plant nutrient uptake is proportional to nutrient supply and therefore the solution concentration should reflect the amount of nutrients found in plant tissues. Another theory is that nutrient uptake is regulated by the plant according to its needs, implying that the nutrient solution should match the plants demand (Marschner 1995; Sonneveld 2000). The composition of nutrient solutions is more a reflection of the chemical composition of plant shoots than of soil solutions. One of the first complete nutrient solutions for soilless crop production was developed by Arnon and Hoagland (1940). Then Steiner (1968) proposed his “universal nutrient solution” with the ideal cation (K:Ca:Mg) ratio (measured in meq L^{-1})to be 35:45:20 and the ideal anion (NO_3:H_2PO_4:SO_4) ratio as 60:5:35. He also described safe areas for these ratios and set out the upper limits above which deficiencies or toxicities may develop. The nutrient solutions used today are mostly variations of these nutrient solutions although research in this regard is still continuing. The ‘ready mixes’ available from many fertilizer companies also use the guidelines set out by Steiner in compiling their mixes (Combrink and Kempen 2011). Although these ready mixes are convenient to use it can only be used when good quality feeding water is available in a drain to waste system. The quality of the feeding water used to compile a nutrient solution is determined by the EC as well as the concentration of specific ions in the water (Combrink and Kempen 2011).

High levels of ferric iron Fe^{3+} and manganic $Mn^{4+}O_2$ can precipitate as insoluble salts in irrigation water resulting in blocked drippers (Combrink and Kempen 2011). These ions should therefore be precipitated out of the feeding water, through increasing the pH and then aerating the water in a separate tank before mixing the nutrient solution. Certain fertilizers may also contain some Cl^- which is not a problem when the Cl^- concentration in the feeding water is low or when the crops are not chloride-sensitive. Feeding water often also contain high levels of Mg^{2+} and the Mg^{2+} applied in the nutrient solution should take this into account or else the optimum Mg^{2+} level as prescribed by Steiner can easily be exceeded and Mg^{2+} at this higher level may suppress the uptake of Ca^{2+} and K^+. When present at excessive levels, which will depend on the specific crop, Na^+ and Cl^- ions as well as other ions such as Mg^{2+}, Cu, Zn and B should be removed through reversed osmosis.

Adjustments to the pH should not be made purely according to the pH of the feeding water but the total alkalinity of the feeding water should be taken into account. The total alkalinity of feeding water or the nutrient solution is the total concentration of bases including carbonates, bicarbonates and hydroxides. Alkalinity is usually expressed as HCO_3, but sometimes as $CaCO_3$. The alkalinity can be neutralized by adding an acid (H^+) such as HNO_3. Addition of an acid to alkaline feeding water, results in the release of carbon dioxide gas as well as water. The HCO_3^- is replaced with NO_3^-, $H_2PO_4^-$ or SO_4^{2-} by using either nitric acid (HNO_3), phosphoric acid (H_3PO_4), or sulphuric acid (H_2SO_4). Fertilizers such as potassium sulphate (K_2SO_4) and mono potassium phosphate (MKP) may however contain some acid residues which is responsible for the release of H^+. This can be neutralized by adjusting the feeding water's total alkalinity to between 0.2 and 1.0 meq L^{-1} using soluble alkaline such as KOH before adding the fertilizers to between 0.2 and 1.0 meq L^{-1} (Combrink 2005). Organic substrates release HCO_3^- during decomposition and the alkalinity of feeding water should therefore be lowered to 0.2 to 0.4 while the alkalinity is set at 0.5 to 1.0 meq L^{-1} for inert substrates (Benoit 2003). When the nutrient solution contains ammonium, a decrease in the alkalinity and pH can be expected in the root zone. It will therefore be necessary to adjust the feeding water to a higher alkalinity before adding the fertilizers (Combrink 2005).

Nutrient solutions are not as well buffered as soil solutions normally are and should therefore special care should be taken to keep the pH in the optimal range between 5.3 and 6.3. Adding fertilizers may result in a decrease in the pH of the nutrient solution. The feeding water should therefore be slightly alkaline before addition of the fertilizer salts (Combrink and Kempen 2011). In saline feeding water, the alkalinity level is usually high, due to the high OH^{1-}, HCO^{1-} and even CO_3^{2-} levels. By adding nitric- or phosphoric acid to lower the alkalinity these ions are replaced by nitrate or phosphate. Phosphoric acid shoud not be added to high alkalinity saline water since Ca-phospate may precipitate. The total alkalinity should then be lowered with nitric acid first. The composition of the nutrient solution can also affect the rootzone pH since the uptake of ions is linked to secretion of either OH^- or H^+ ions. In soil-less production systems NH_4^+ can also be used as pH regulator, decreasing the pH in the rootzone.

Factors influencing water and macro nutrient uptake in a hydroponic growth system

Detailed guidelines for nutrient solutions for different greenhouse crops based on Dutch and Belgian information was published by Combrink (2005) although he emphasized that local research is needed to improve these guidelines. In closed systems it is even more important to synchronize the supply of nutrients to the crops demand since even a slight imbalance between the supply and uptake of nutrients can result in major shifts in the rootzone nutrient concentration. It is therefore necessary to understand all the factors that may influence the uptake of nutrients in soilless production systems.

Nutrient solution pH

The pH of the nutrient solution can affect the availability of nutrients for uptake by affecting their solubility and is therefore maintained at between 5.8 and 6.5. Nutrients may precipitate and form insoluble salts, such as phosphates at a low root zone pH and many micronutrients, especially Fe and Zn may precipitate at a high pH (Havlin et al. 2005). The phosphate dissociation curve (Steiner 1961) indicates that at a pH lower than 6 more than 96% of P is present in the soluble form of $H_2PO_4^-$.

Cation absorption will be inhibited by low pH while anion absorption is either not affected or enhanced at a low pH (Marschner 1995). At a too high pH level in the root zone, iron deficiency is frequently noticed in soilless grown crops (Passam et al. 2007).

The variation in uptake between cations and anions can also have a large effect on the pH in the rootzone and that of the drained nutrient solution. If more anions than cations are taken up it will result in an increase in the efflux of OH^- protons (H^+) in the root zone leading to an increase in the pH whereas if more cations than anions are taken up the pH will decrease. During the vegetative phase of crops the uptake of nitrate is especially high and the rootzone and drained nutrient solution therefore tend to become alkaline, which can result in certain elements like P becoming unavailable for uptake by the plant roots (Adams 2002). Lozano et al. (2007) found this to be especially true for crops with a short life cycle, such as cucumbers and greenbeans in Spain. In contrast during fruit development a situation can develop where the plants' demand for K is so high that cation uptake exceeds anion uptake and the rootzone and drained nutrient solutions therefore acidifies. Lozano et al. (2007) mentions that in Granada, Spain this is often found with melons during harvest time and that this is often associated with very high P concentrations in the drained nutrient solutions.

Nitrogen is the only nutrient that can be taken up by plants either as an anion (NO_3^-) or a cation (NH_4^+) (Forde and Clarkson 1999) and the fraction of each in the nutrient solution can have a significant effect on the rootzone pH. This is due to both nitrification and a preferential NH_4^+ uptake, which will be accompanied by the release of H^+ by the roots (Kafkafi et al. 1971; Savvas and Gizas 2002). The pH can also affect the uptake of the different N forms with a decrease in pH resulting in an increase in NO_3^- uptake (McLure 1990). Using high concentrations of NH_4^+ in hydroponic tomato production systems will reduce crop growth and fruit yield and the extent of this inhibition will depend on the impact on the rhizosphere pH, which is also affected by environmental factors (Chaignon et al. 2002 and Siddiqi et al. (2002). Savvas and Gizas (2002) found a decrease in the Mn and P tissue concentrations of roses grown in a re-circulating nutrient solution compared to plants in a drain to waste system and ascribed this to the increase in pH of the nutrient solutions. To prevent this they suggest a controlled increase of the NH_4^+:total-N injection ratio to levels higher than those in open systems.

Nutrient solution composition

Nutrient solution concentration

Most nutrient solutions are more concentrated than soil solutions and not as well buffered by ion-exchange, adsorption-desorption, and dissolution-precipitation reactions (Parker and Norvell 1999). The N, P, K, Ca, and Mg concentrations are mostly higher in nutrient solutions compared to soil while for S it is often lower. Elemental toxicities can however occur at these high nutrient concentrations in solution culture. Several studies have shown the toxicity of P even at very low concentrations compared to that added in a conventional Hoagland-type solution (Parker and Norvell 1999). In soilless culture, the occurrence of phosphorus toxicity can occur due to the fact that excess P is not immobilized in insoluble forms (Passam et al. 2007). When the irrigation water contains ions, such as Na^+ and Cl^-, at concentrations higher than what the plant can take up, salt accumulation occurs in the root zone (Sonneveld 2000; Carmassi et al. 2005). Tomato plants can tolerate Na^+ toxicity through active exclusion and retention of Na^+ by the xylem parenchyma of the roots, stems and petioles of older leaves and thereby keeping the Na^+ levels in the younger, photosynthetically active leaves low (Shannon et al. 1987).

In a semi-closed hydroponic system, the nutrient solution is usually recirculated until its total salt content (indicated by the electrical conductivity (EC)) and/or the concentration of certain ions reach a threshold value, above which crop yield will be negatively affected (Carmassi et al. 2007). If the EC is allowed to become very high it can have an osmotic effect, reducing the ability of a plant to take up water, leading to a reduction in growth, yield, nutrient uptake, and photosynthetic activity (Munns 2002).

Referring to several studies Mankin and Fynn (1996) point out that maximal plant growth can be sustained under considerably lower concentrations and uptake remains independent of concentration over a wider range of nutrient concentrations than was found in earlier studies. According to Zheng et al. (2005) and Rouphael et al. (2008) nutrient solution concentrations can be reduced by up to 50% without a negative effect on biomass production and product quality for geraniums and gerberas. They conclude thus that the nutrient demand seems more important than the supply and plant nutrient uptake will be determined by demand. The mineral demand of a crop will vary according to species, developmental stage and environmental conditions (Le Bot et al. 1998).

In a study with apple trees an increase in the N concentration in the nutrient solution applied to the plants resulted in an increase in the rate of N uptake while the rate of water uptake was not affected (Bar-Tal 1990). Ho et al. (1995) found that the linear correlation between water uptake and Ca^{2+} uptake was the same at two different nutrient solution concentrations for five tomato cultivars over a growing period of 83 days.

Nutrient ratios

Plants do not take water and ions up at the same ratios as they are present in the nutrient solution. The ion composition in the drained nutrient solution will therefore deviate from that of the starting solution. If this solution is re-used the divergence will increase and certain ions will start accumulating while others will be depleted as the time period of recirculation increases. This can result in deviations from the specific target values in the rootzone (Voogt 1993).

An imbalance in concentrations of specific ions (especially potassium, calcium, and magnesium) can also negatively affect plant growth, yield and quality of vegetables (Roorda van Eysinga and Smilde 1981). Increasing the K^+ concentration in the nutrient solution from 3.4 meq L^{-1} to 14.2 meq L^{-1} increased the fruit dry matter, total soluble solids content and the lycopene concentration of tomatoes (Fanasca et al. 2006).

The continuous reuse of the drained nutrient solution can result in yield and quality reductions of crops. Savvas and Gizas (2002) found that the total number of flowers per plant and the flower stem length and flower head diameter was reduced for when the nutrient solution was re-used without adjusting the nutrient ratios. Under saline conditions the addition of NH_4^+ to the total N in the nutrient solution has also been found to positively influence fruit yield (Ben-Oliel et al. 2004). In a closed or semi-closed hydroponic system the nutrient solution will be leached whenever a crop specific Na^+ concentration is reached (usually between 3 and 8 mol m^{-3}). For tomatoes, a salt-tolerant crop, this value is usually 8 mol m^{-3} (Baas and Berg 1999; Stanghellini et al. 2007). In areas where the quality of the irrigation water is not very good, the potential to re-use the water is therefore reduced. According to Grattan and Grieve (1999) increasing the ratio of Ca^{2+} to other macro-elements in the rootzone can ameliorate the deleterious effects of salinity on tomato biomass production. Increasing the ratio of NH_4^+ to total N in the nutrient solution can also mitigate salinity stress (Ben-Oliel et al. 2004).

The uptake and translocation of sufficient calcium to the tomato fruit is crucial to prevent blossom end rot (BER), a physiological disorder often associated with greenhouse tomatoes. The incidence of BER is linked to damaged permeability of cell membranes and cell wall structure due to a localized Ca^{2+} deficiency in the distal part of the fruit which results in a collapse of tissue structure in that area (Adams 2002). One of the main factors resulting in BER is antagonism between the cations in the nutrient solution (Dong et al. 2004). The number of fruit with blossom end rot (BER) is also significantly higher when a larger percentage of the total applied N is in the form of NH_4^+. This is a result of an inhibiting effect high NH_4^+ levels will have on Ca^{2+} uptake (Siddiqi et al. 2002). The flavour of the fruits might however be enhanced if the NH_4^+ levels make up 10% of the total N (Siddiqi et al. 2002). The incidence of BER also increase with an increase in salinity and according to Willumsen et al. (1996) this is due to an increase in the K^+ and Mg^+ uptake which will restrict the uptake and distribution of Ca^{2+}.

Increasing the NH_4^+ in the nutrient solution can improve fruit quality by increasing the sugar and organic acids content of the fruit (Flores et al. 2003). A high NH_4^+: total N ratio can application to crops can also affect water uptake and the transpiration rate of crops. In alfalfa and tomato plants the transpiration rate was increased when NH_4^+ was applied (Khan et al. 1994; Lugert et al. 2001) while water uptake was reduced for muskmelon and sugar beet crops (Raab and Terry 1994; Adler et al. 1996).

The K:N ratio of the nutrient solution can be used to control tomato crop growth and production (Papadopoulos and Khosla 1993). The nutrient uptake ratio of K to N for tomato ranges between 1:1 and 2.5:1 calculated for ion concentrations in meq L^{-1} (Tapia and Gutierrez 1997). A high supply of K can also influence the Ca and Mg uptake of plants. When rose plants were deprived of N, P, or K for up to 20 days, the absorption of that specific nutrient increased when these nutrients were re-introduced relative to control plants where all nutrients were supplied in adequate quantities (Mattson and Lieth 2008). A synergistic effect exists between N, P, and K on tomato growth and when P and K are applied in the correct ratio the utilization of N will be enhanced (Gunes et al. 1998). Liu et al. (2012) found that K application rates significantly affected the plant N utilization and that fruit had a higher N content when at a lower K application rate (200 kg K_2O ha^{-1} compared to 600 kg K_2O ha^{-1}).

Climate

The productivity of greenhouse crops is strongly related to the climatic conditions. Carbohydrates are required for respiration to produce the energy needed for ion uptake by the roots (Marschner 1995). A limited supply of assimilates from the shoots to the roots can therefore affect nutrient uptake and any environmental factors that will limit the production of assimilates, such as low light intensities can therefore have a negative effect on nutrient uptake. Likewise, environmental factors that alter transpiration will affect nutrient uptake since it will impact mass flow of water and nutrients to the root surface. Light intensity and the transpiration rate are considered as being two of the most important factors determining crop water and nutrient uptake (Voogt 1993). Light intensity or the photosynthetic photon flux (PPF) influences crop growth and also the water use efficiency (WUE) of the crop. The PPF influences crop transpiration rates by providing energy for the transfer of water from the leaf surface to the atmosphere and therefore affects water uptake of crops. The WUE of crops generally increase with an increase in PPF (Nemali and van Iersel 2004). The WUE of crops differs significantly between species and it can also be influenced by conditions that will affect transpiration of which the relative humidity (RH) is vital. Partial closure of stomata at a very low RH for instance will result in a great reduction of water loss but only a minimal reduction in CO_2 uptake therefore increasing dry matter accumulation per unit of water transpired. Crop growth and yield of tomato under saline conditions can also be increased through increasing the air humidity during hot weather (An et al. 2005).

A co-ordination between the photosynthetic activity of the shoot and ion uptake in the root exists (Forde 2002). The uptake rates of many ions are dependent on the light intensity and are significantly lower at night (Clément et al. 1978; Le Bot and Kirby 1992). Martinez et al. (2004), found a correlation between the cumulated solar radiation and the NO_3^- uptake rate as well as a correlation between the NO_3^- uptake rate and water uptake and nutrient solution temperature. More precisely, it is the availability of sugars, transported from photosynthesizing leaves, that has been linked to the control of NO_3^- uptake (Delhon et al. 1996). Evidence also exists for the relationship between K^+ uptake by roots and the light intensity, rate of photosynthesis and sugars in the shoot of Arabidopsis (Deeken et al., 2000). Fruit yield is also directly proportional to the accumulated solar radiation. Cockshull et al. (1992) found that during the first 14 weeks of harvest 2.01 kg fresh weight of fruit was harvested for every 100 MJ of solar radiation incident on the crop and for the remainder of the growing period 2.65 kg fruit fresh weight per 100 MJ was obtained. Under poor light conditions in winter and autumn high EC levels did not affect tomato yield but a high EC when the light intensity is high can be detrimental to yields (Sonneveld and Welles 1988).

Ion uptake will also be affected by temperature since chemical reactions are temperature dependant (Marschner 1995). The risk of ammonium toxicity increases at high root zone temperatures (Kafkaffi 2000). A high rootzone temperature in combination with a high supply of NH_4^+ can result in a low concentration of assimilates in the roots necessary for respiration and consequently a reduction in ion uptake and crop growth (Kafkaffi 1990).

Growing mediums

Most greenhouse crops are grown hydroponically are planted and fertigated in a growing medium instead of soil. The most important advantages of these growing media include improved control over water and nutrient availability, aeration and disease management. The nutrient status in the growing medium should be kept optimal for the specific crop under the existing growing conditions (Sonneveld and Straver 1994).

Nutrient ions are often unevenly distributed in the root environment and this can affect the osmotic potential in the rootzone and the uptake of nutrients. Similar to the unequal distribution of salts observed with field grown crops in arid areas where trickle irrigation is used, salt concentrations in a growing medium in the greenhouse can differ significantly in the different layers, both horizontally and vertically of the growing medium (Sonneveld and Voogt 2001). This is especially noticeable in sub-irrigated systems such as an ebb and flood system (De Kreij and Straver 1988). Plants often respond to an uneven distribution of nutrients in the rootzone through an increase in lateral roots development within the nutrient-rich zones (Huang and Eissenstat 2000).

When leaching from the growing media is restricted and crop water use and evaporation from the soil surface is high salts will accumulate in the rootzone. Under saline conditions tomato crop growth and yield can be increased through good oxygen supply to the roots (Bhattarai et al. 2006). Crops with a restricted root system as is found in greenhouses where crops are grown in in bags with growing media, cannot escape areas with high nutrient concentrations as easily as crops in soil with an extended root system. To escape increasing salt concentration the plant must adjust its root system which can be time consuming and therefore the length of the growing period is also important. Nutrient uptake efficiency will be determined by whether a nutrient ion in the growing medium is in a form that is available for uptake. This is influenced by the chemical properties of the growing medium as well as the distance the ion must travel to reach the root surface (Jungk 2002).

In soilless crop production it is common practice to try to maintain the nutrient levels at a set amount in the applied nutrient solution. Since evapotranspiration and nutrient absorption does not remain stable, the nutrient concentrations in the substrate will not stay as constant (Kang and van Iersel 2009). Gertsson (1995) found that the K^+ uptake rate was higher in a nutrient film hydroponic system compared to crops grown in rockwool as a growing medium. An increase in the EC of the growing medium generally points to an accumulation of ions. These are often ions that are taken up at a lower rate than what they are supplied as or ions present in the irrigation water and not readily taken up by plants such as Na^+ and Cl^- (Massa et al. 2008).

During the decomposition of organic growing mediums, bicarbonates are released. This results in an increase in the alkalinity of the growing medium. The addition of ammonium to the nutrient solution can be used to stabilize the pH in the rootzone under these conditions (Combrink and Kempen 2011).

Root and container size and fertigation strategies

Compared to soil-grown crops, crops in a growing medium, grown hydroponically have a restricted root volume and a high shoot:root ratio, limited nutrient reserves and a restricted buffering capacity for water and nutrients (Sonneveld 1981). The physiological capacity of the root system may become a limiting factor for the uptake of water and nutrients by the plant, ultimately affecting dry matter production (Bar-Tal 1999). In small containers the nutrient uptake can be reduced as a result of a reduction in root growth and a reduction in the quantity of water and nutrients available in the rootzone (Bar-Tal 1999). However Bar-Tal (1999) cites several studies where nutrient uptake was not affected or even increased when the root volume was reduced through pruning of the roots. Bar-Tal et al. (1990) showed that pepper seedlings increased their uptake of N and P when the container size was increased while the nutrient concentrations were kept constant. They concluded that the most likely mechanism by which the container size affected the uptake of nutrients was by affecting the nutrient concentration at the rootzone and in a follow-up trial showed that the availability of nutrients can be increased by increasing the fertigation frequency (Bar-Tal et al. 1993). Although plant growth and nutrient uptake increased when tomato plants were grown in 20 L instead of 10 L containers, the ratio of transpiration to dry matter production remained constant (Bar-Tal 1990). The N, P, K, Mg and Ca concentration in the plant tissue was not affected by the size of the container. The uptake rates per plant were however higher in the larger containers and this correlated with larger root systems and higher uptake rates per unit root area in these containers (Bar-Tal 1990). In another study dry matter production and the uptake of P and K was shown to increase with an increase in the size of the container (Bar-Yosef et al. 1997). This increase in P and K uptake was linked to an increase in the P and K uptake rates per unit root area and the plants with the restricted roots where in effect more efficient in taking up nutrients. When the nutrient solution concentration was increased by 50% it compensated for the decrease in container size from 40 L to 20 L, although the same was not true when the container size was decreased from 20 L to 10 L. In most of these studies the size of the container affected the dry matter production and N uptake but not the N content of the leaves.

The rate of diffusion of an ion in the growing medium increases with an increase in temperature and also depends on the moisture content of the rootzone since the diffusion pathway becomes longer when the moisture content of the growing medium is low (Barber 1995). Moisture stress will reduce root surface area, nutrient availability and uptake and ion diffusivity (Mackay and Barber 1985).

The irrigation frequency is primarily controlled to ensure that the crops water demand is met. Approximately 90% of water taken up by the plant is lost again through transpiration (Li et al. 2001) and irrigation is therefore often controlled through measurements of transpiration rates. Less mobile elements such as P and K can become unavailable for plant uptake through adsorption and precipitation. Increasing the irrigation frequency have however been shown to maintain higher dissolved P and K concentrations in the substrate solution and can therefore increase their uptake (Silber and Bar Tal 2008).

Tilling et al. (2007) showed that a tomato crops' response to fertilizer N is strongly affected by the water supply and Santos (2009) showed that with sufficient irrigation the N application rates can be reduced from 336 to 224 kg N ha^{-1} without a significant drop in yields. This is the result of an increase in the availability of N when there is adequate soil moisture (Kim et al. 2008). Liu et al. (2012) found that the N uptake of tomato plants increased when drip irrigation was used.

In drain to waste the leaching fraction (LF, percentage of supplied nutrient solution that is drained) can be between 20 and 30% and in semi-closed systems it is usually up to 50% (Carmassi et al. 2007). When using the mass balance approach to determine the amount of nutrients to apply it is assumed that all applied nutrients are available to the crop. When over-irrigating however nutrients will be leached to below the root zone (Sonneveld 2000; Massa et al. 2011). Over-irrigation also assists in balancing the variation in transpiration and nutrient demands between plants in the system.

Since the uptake of ions is energy dependant and this energy is dependent on respiration, low oxygen levels in the rootzone can affect nutrient uptake. Hopkins et al. (1950) showed this in a classic experiment with barley where the decrease in the percentage from 20% to 0.5% resulted in 63 % decrease in K uptake and a 70% decrease in P uptake. Low rootzone oxygen conditions often occurs when over-irrigation occurs and the growing medium becomes waterlogged.

Developmental stage of crop

Genotypic variation related to nutrient uptake and utilization also exists for certain species (Brown and Byrd, 1997). As tomato plants increase in age from twenty three to forty two days after planting the flux of water per unit mass decreased from 53 to 11 ml/g/day (Bar-Tal 1990). To understand the nutrient requirements of a crop it is necessary to have knowledge of the pattern of biomass production of crops throughout the growing season (Setiyono et al. 2010). Understanding the nutrient requirements of a crop also implies knowledge of how crop nutrient requirements depend on its developmental stage (Malagoli et al. 2005). Nutrient requirements differ for vegetative and reproductive organs and changes in nutrient requirements depending on the crops growth stage are especially important in crops with a distinct transition from vegetative to reproductive growth (Mattson and van Iersel 2011).

An adjustment of the nutrient solution added to the growing system is necessary during crop development and the total nutrient use can be reduced when nutrients are applied according to their need at a specific growth stage. The nitrogen to potassium uptake ratio changes from the vegetative to reproductive life stage of tomato plants (Voogt 1993). As an example, the K:Ca ratios of fruits are much higher than those of leaves and for tomato and other fruit vegetables the change from the vegetative to the reproductive phase coincides with an increase in the K:Ca uptake ratio (Voogt 1993; Voogt 2002).

The guidelines given by Voogt (1993) for adjusting the nutrient application for greenhouse grown tomatoes during the different developmental stages was based on several long-term trials and remains one of the best studies in this regard. Moreno et al. (2003) found that the P concentration in the leaves of tomato plants significantly increased during fruit development and ripening while that of N, K, Na, Ca, Mg and S decreased. High N levels in the nutrient solution during fruit development can however interact negatively with Ca uptake (De Kreij 1996).

Nutrient solution composition and tomato fruit quality

Adjusting the EC of the nutrient solution allows greenhouse growers to modify the water availability to the plant and therefore also the rate of fruit expansion (Johnson et al. 1992). Increasing the EC in the root environment to levels higher than the optimal range for tomatoes (between 2.5 and 2.9 mS cm^{-1}), will affect yield, mainly as a result of a decrease in average fruit size and number of fruit per truss (Ehret and Ho 1986; Adams 1991; Li et al. 2001; Olympios et al. 2003; Passam 2007). This negative effect of high EC on tomato fruit size is due to a restriction of water transport into the fruit and an enhanced rate of dry matter accumulation (Plaut et al. 2004). The vegetative growth of tomato plants seems to be less sensitive to high root zone EC than during fruit development and plants are more sensitive during early development compared to a later growing stage (Olympios et al. 2003). Under high ECs tomato fruit do however have a lower susceptibility to fruit cracking (Hao et al. 2000). Estergaard et al. (2001) recommends a range value of 3.90 and 4.35 mS cm^{-1} for the nutrient solution to minimise greenhouse tomato fruit cracking. Increasing the nutrient solution's EC from 2 mS cm^{-1} to 4 mS cm^{-1} in an attempt to improve the sugar content of 'Daniela', one of the first "long shelf life" tomato cultivars grown in South Africa, resulted in an increase in the fruit's total soluble solids (°Brix). The higher sugar content was however the result of less water being absorbed and not due to an increase in sugar production and was accompanied by a 30% reduction in yield and fruit size (Combrink 1998).

Abrupt changes to the EC in the growing medium due to climatic variations are also known to negatively affect the plant water status and therefore tomato fruit quality (Dorais et al. 2001). Plants grown at a low EC during the day and a high EC during the night also tended to have larger fruit and less blossom-end rot (Van Ieperen 1996). However, no difference in tomato fruit cracking was observed for plants fed with a nutrient solution varying in EC (1.5 - 2.7 mS cm^{-1} during midday and 3.0 - 4.0 mS cm^{-1} for the remaining of the day) and plants fed with a solution at a constant EC (1.8 to 3.5 mS cm^{-1} according to the solar radiation) (Dorais et al. 2001).

A small degree of osmotic stress caused by increasing the nutrient solution EC may be however improving the organoleptic quality and anti-oxidant content of fruit (De Pascale et al., 2001). By increasing the root zone EC to 9.0 mS cm^{-1} by adding macronutrients and NaCl Petersen et al. (1998) found plants had reduced water content but an increase in the carotene content of the tomato fruit. De Pascale et al. (2001) and Fanasca et al. (2007) found a decrease in the lycopene content of tomato fruit grown at a high rootzone EC.

Although optimum yields can be reached at relatively low K^+ concentrations, relatively high K^+ concentrations, at least 400 mg.L^{-1}, are needed in the rootzone to enhance fruit quality (Adams and Grimmett 1986). The titratible acidity will be increased, ripening disorders will be reduced and the fruit colour will be improved (Adams and Grimmett 1986; Passam et al. 2007). If the K:N ratio in the nutrient solution is decreased, fruit quality can be negatively affected primarily through a decrease in reducing sugar content (Passam et al. 2007). The proportion of hollow tomato fruit also tended to decrease as the K^+ concentration in the nutrient solution increased (Adams and Grimmitt 1986) although they could not find a correlation between fruit firmness and K^+ application level.

One of the major tomato quality problems is fruit cuticle cracking and mineral nutrients applied during fruit development, especially calcium and boron are essential in prevention of this physiological disorder (Dorais et al. 2004).

Linking crop growth to nutrient uptake

Crop growth models

Crop growth models can be classified as descriptive/empirical or explanatory/ mechanistic and are primarily used to describe and understand systems and to relate different circumstances. Crop growth models are often used for greenhouse climate control and production planning (Lentz 1998). Descriptive models are also known as statistical, regression, empirical or black-box models. Descriptive models do not reflect give insight into the mechanisms causing a specific action. Nevertheless, descriptive models have a better practical value and often consist of submodels and reflect physiological structures to a large extent, describing mechanisms and processes (Marcelis et al. 1998). The predictive value of descriptive models can be high and they generally contain few variables but extrapolation is often impossible (Marcelis et al. 1998). Descriptive models are often used to relate yield, crop growth or development rate to environmental factors for example the model of Wurr et al (1989) predicting the time from transplanting to maturity of iceberg lettuce based on radiation sum and the model of Lieth et al. (1991) predicting the increase in petunia shoot dry weight based on light intensity and average daily temperature. Developmental stages (e.g. germination, vegetative- and floral development) are often distinguished in descriptive models. To assist with production planning, several simple descriptive models considering crop developmental processes such as germination, and flower and fruit development have been developed (Marcelis et al. 1998). Examples of these types of models include models based on heat sums which imply that temperature is the main factor (Karlsson et al. 1991; De Koning 1996). However, when these models are extended to include other factors, such as light intensity (Wurr et al. 1988) the accuracy of the model can be increased. All mechanistic models eventually make use of empirical data. By selecting models containing both descriptive and mechanistic components often gives the best results since knowledge of the physiology will influence the choice of variables (Pardossi et al. 2005). For example, the variables expected to influence crop nutrient uptake, such as environmental conditions and water uptake, can be regarded as mechanistic assumptions in descriptive models for nutrient uptake (Pardossi et al. 2005). Descriptive models of photosynthesis and transpiration was used by Klaring and Cierpinski (1998) to calculate the nitrate uptake of sweet pepper plants grown in rockwool and to develop an algorithm to adjust the nitrate concentrations in the nutrient solution based on the basis of light intensity.

TOMGRO is a physiological model of tomato crop development and yield that uses a source-sink approach for partitioning carbohydrate into growth of different organs (Jones et al. 1991). Crop yield is determined by dry matter (DM) production and distribution and DM production is primarily driven by photosynthesis. Photosynthesis is primarily dependant on the total leaf area and the percentage of light being intercepted while leaf growth is a function of the total DM production (Lentz 1998). Crop models still need to be calibrated with measured data and validated in independent experiments.

Nutrient uptake models

When re-using drained nutrient solutions for fertigating crops, several different techniques can be used to manage the nutrient application. Two of the most widely used techniques are to either automatically adjusting the electrical conductivity (EC) of the nutrient solution to a set value or by adding the set nutrient solution to the drain water (De Kreij et al. 1999). Both of these methods can be done in real-time and is used widely in greenhouse agriculture. The disadvantage however is that only the EC of the outgoing nutrient solution can be controlled, but not the individual nutrients. The in situ determination of individual nutrients is not done on a commercial scale yet. In Belgium the drained nutrient solution in closed systems are analysed weekly or once every two weeks. According to the EC and content of the specific nutrients in the drained water an adjusted nutrient solution is calculated for the grower. This system works well because the needed infrastructure and expertise exists to do these analyses regularly and give prompt feedback to the producers on recommended changes.

Another method of calculating the injection rate of nutrients when re-using drained nutrient solution is based on using nutrient uptake models. Nutrient uptake models can be used in decision support systems to manage nutrient solutions and thereby reducing growers' dependence on frequent analysis of the recirculated irrigation water. The traditional nutrient uptake models used for field grown crops are not adequate to describe nutrient uptake in a soilless system which is characterized by a limited root volume and high nutrient concentrations (Sonneveld 1991). Recently various modeling tools intended to describe and/or predicting the processes related to plant nutrition has been developed (Le Bot 1998). Most models use a mechanistic approach including Michaelis-Menten kinetics and the concepts of relative addition and plant nutrient demand combined with empirical relationships (Mathieu et al 1999). When modeling nutrient uptake it is important that nutrient concentrations in the rootzone are not limiting. Epstein et al. (1966) noted that the relationship between ion uptake and its concentration conform to a rectangular hyperbola when plotted, similar to Michaelis-Menten enzyme kinetics. According to Silberbush et al. (2005), if it is assumed that the uptake of nutrients is directly correlated to their concentration in the nutrient solution Michaelis Menton kinetics can be used to determine nutrient uptake. This approach has been proved and has been used by several authors to develop nutrient uptake models (Cardenas-Navarro et al. 1999; Silberbush and Lieth 2004; Mattson and Lieth 2007; Massa et al. 2009). Michaelis-Menten kinetics relates the concentration of a specific nutrient to its uptake using the following equation:

$$U = \frac{U_{max}(C - C_{min})}{K_m + (C - C_{min})}$$

Where U is the rate of nutrient uptake, U_{max} is the maximum rate of nutrient uptake; C is the concentration of the nutrient in the solution, C_{min} the concentration at which influx equals efflux and K_m a constant. U_{max} was found to vary with the relative growth rate and the root to shoot ratio of the crop but not with the shoot N concentration while U_{max} and C_{min} is also affected by the plant age (Steingrobe and Schenk 1994). When efflux of a specific ion becomes significant compared to its influx, Michaelis-Menten kinetics does not seem to describe the relationship between influx and ion concentration accurately requiring the inclusion of C_{min} in the equation to overcome this problem when developing mechanistic models, although it remains a highly variable parameter (Reid 1999). Two mechanisms for Michaelis-Menten kinetics are distinguished: mechanism I for low nutrient solution concentrations and mechanism II for situations where the nutrient solution concentration is high (Le Bot et al. 1998).

According to Gallardo et al (2009) models that simulate dry matter (DM) production can easily be adapted to simulate crop N uptake. Models for nutrient uptake based on global radiation inside the greenhouse have been proposed for peppers (Klaring and Cierpinksi 1998), rose (Brun & Moriset 1996) and chrysanthemum (Zerche 2001). Global radiation is used in these models based on the assumption that the relationship between net photosynthetic rate (Pn, g $m^{-2}.hr^{-1}$) and growth is linear since the relative growth rate is directly related to the uptake rate of nutrients and that nutrient uptake is equal to the demand (Mankinn and Fynn 1996). Besides the importance of light intensity to predict nutrient uptake, other researchers have also shown that factors such as solution temperatures (Martinez et al. 2004), canopy CO_2 level and even spectral quality (Mankin & Fynn 1996) also need to be taken into account when developing models to predict nutrient uptake.

Pardossi et al. (2004) found that in melon plants the nutrient uptake linearly related to the water uptake for different nutrient solutions and that the uptake rates of different nutrients were closely inter-correlated and suggested therefore that testing for a single guide-ion could be used to predict nutrient demand. This may however not hold true for tomatoes, as the uptake ratios may change through successive growth stages.

Carmassi et al. (2003) introduced a simple model for the changes in ion concentration in a recirculating nutrient solution where the variation in EC could be strongly related to changes in Na concentration, to a lesser extent to K concentration but not related to Ca and Mg concentrations. Van Straten et al. (2006) described their 3Bigs model as a dynamic model that defines the mineral content, fruit dry matter content, and biomass of greenhouse tomato to be used in a trial looking at controlling the fertigation for optimal production cost, fruit yield and quality. The model can relate dry matter content to the ion concentration in the growing medium and describes how nutrient deficiencies affect crop growth. The number of states in the model was kept to a minimum and they got good fits for total biomass and K, N, and Ca contents of the fruits.

Model based on the concept of uptake ratios

The volume of drained nutrient solution that can be re-used after mixing with the standard nutrient solution is usually calculated based on the EC of the drained nutrient solution. Alternatively fixed uptake ratios can be used as a basis for replenishing nutrients in the solution to be re-used (Savvas 2002). The solution mixed with the recycled nutrient solution will therefore contain different absolute nutrient concentrations but the macronutrient concentrations will remain constant at each application. As starting point target ratios of the macronutrients to be applied, corresponding to the expected uptake ratios are given as input data.

The models proposed by Savvas (2002) where the drained nutrient solution is mixed with fresh water and then reused, assume that if the irrigation solution supplied to the crop has a specific composition the nutrient concentrations in the root zone can be maintained close to the target levels. The concentration of the supplied nutrient solution, the pH and volume of the drainage solution to be recycled are variables. The target concentration in the rootzone is also of importance and still has to be determined for different crops (De Kreij et al. 1999; Savvas 2002). The variables are measured on-line when the irrigation solution is automatically prepared. These models can supply nutrients at the optimum ratios, if the concentrations of Ca^{2+}, Mg^{2+}, and SO_4^{2-} in the fresh water are not disproportionate.

Combining growth models that simulate leaf area development with models simulating water consumption throughout the crops growth cycle can be used for irrigation scheduling in greenhouses. Neto et al. (2014) developed a control system based on transpiration estimates for the real time preparation and application of nutrient solutions for soilless tomato production. This system effectively adjusted the frequency of fertigation cycles according to plant transpiration estimates, and maintaining the EC of the drained nutrient solution below the upper preset limits (Neto et al. 2014).

Objectives of the thesis

Management of the nutrient composition in re-circulating systems is still mainly based on frequent and extensive laboratory analysis and timely adjustments. In some areas this is not feasible due to a lack of appropriate facilities or a long delay between submission of samples and obtaining results and interpretations. Not being able to make the necessary adjustments to the nutrient application rates at the appropriate time is therefore one of the most important factors that hinder the more widespread adoption of nutrient solution re-cycling.

In order to develop an alternative method to help manage the nutrient concentrations in re-circulating systems the overall objective of this thesis is to develop original models and calibrate existing models to simulate water and nutrient uptake by tomato (*Solanum lycopersicum*) plants in a closed hydroponic system with coir as a growing medium. This will ultimately enable growers to adjust the application rate of nutrients pre-emptavily, reducing the complete reliance on laboratory analysis.

To accomplish this water and nutrient uptake by tomato plants needs to be quantified and related to crop demand and the factors affecting. This will be systematically deliberated through determining:

- The effect of the nutrient solution composition both in terms of concentration (EC, mS cm^{-1}) and ratio between macro-nutrients on the uptake of water and nutrients. This will be done in a system where water and nutrient uptake is not limited by any other factors (such as the chemical and physical properties of a growing medium). Trials will therefore be conducted in a pure water culture since the uptake rate of water and nutrients can be assumed to be closely related to the demand from the crops (Le Bot et al. 1998).
- How changes in nutrient solution composition will affect the biomass partitioning as well as fruit yield and quality parameters of tomato plants in a pure water culture.
- The uptake rate of water and nutrients by tomato plants both over the short term (hours) and long term (days and season) under differing levels of solar radiation and nutrient solution composition. Again a pure water culture was chosen since to exclude the effect of any other rootzone conditions on the availability and uptake of nutrients by the plant roots.
- How changes in solar radiation level using different nutrient solutions will affect the biomass partitioning as well as fruit yield and quality parameters of tomato plants in this pure water culture.
- To translate the results from the first trials to a commercial growing system an assessment was be done on the availability and uptake of water and nutrients in a coir growing medium.

In the first trials nutrient uptake was not limited by the availability in the rootzone, similar to when a high irrigation frequency is applied in a growing medium. Therefore the effect of irrigation frequency on the rate of nutrient and water uptake was assessed. Additionally crop growth, fruit yield and quality was also assessed using different irrigation frequencies.

- The data from all these trials, data was analysed through multiple regression (MR) analysis and then linear equations were generated that was used in either adjusting existing models for or developing original models for simulating water and nutrient uptake of tomato plants.
- In the last chapter these models for water and nutrient uptake was calibrated and validated with 3 separate greenhouse trials. Additionally in these trials different fertigation methods were applied; no re-circulation (FM1), re-circulation where topping up the re-circulation water with a full strength nutrient solution (FM2) was done or re-circulation where topping up to a desired EC level (FM3) was done. This was performed to evaluate the accuracy of these uptake models under different fertigation management scenarios.

This thesis will be presented in 5 Chapters. Chapter 1 was a review of the water and nutrient use in soilless systems. Chapter 2 will focus on the effect of the composition of the nutrient solution on nutrient uptake as well as the biomass partitioning and fruit quality of hydroponically grown tomatoes. This is presented in two separate articles, the first, article 1 dealing with water and nutrient uptake and the second, article 2, dealing with the effect on growth and fruit quality. Chapter 3 focus on the influence of solar radiation levels on the water and nutrient uptake, biomass production and partitioning of hydroponically grown tomatoes. Again this is presented in two separate articles.

- The reason for presenting these two chapters in 2 separate articles each is that presenting a thesis in a form with articles ready for publication / already published is required within our department. This not only to teach students to write in the required style but also to increase publication output from students research. Since journals place a limitation on the length of articles it was inevitable that the work in this study had to be subdivided in this way. The author is therefore aware of some repetition in the introduction and methods and materials of article 1 and 2 and article 3 and 4 but this was unavoidable.

Chapter 4 then deals with the growth, biomass partitioning and water and nutrient uptake of soilless grown tomato plants in relation to solar radiation levels and nutrient solution concentration. Lastly chapter 5 uses the data sets generated in all these trials in modelling water and nutrient uptake of soilless grown tomatoes grown in coir. Chapter 6 provides a general conclusion and discussion of all the results.

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Chapter 2

The composition of the nutrient solution affects the nutrient uptake as well as the biomass partitioning and fruit quality of hydroponically grown tomatoes.

Article 1

Variations in macro-nutrient uptake in soilless culture as affected by the nutrient solution composition.

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Abstract

To determine crop nutrient demand the effect of different nutrient solution compositions on the uptake of nutrients by tomato plants was investigated. Plants were grown in a water culture where both the concentration (EC, mS cm^{-1}) and ion ratios were varied and nutrient uptake determined through solution and tissue analysis. The nitrate (NO_3^-), phosphate ($H_2PO_4^-$), potassium (K^+) and sulphate (SO_4^{2-}) uptake increased with an increase in nutrient solution EC. The nutrient uptake concentrations (UC, mmol L^{-1}) defined as the ratio between nutrient ions (mmol) and water (L) taken up by plants during the same time interval was significantly different at an EC of 0.8 and 4.0 mS cm^{-1}. In the residual nutrient solution the specific cation and anion ratios deviated from the optimum even after adjustments to correct this in the applied nutrient solution. These results indicate that the nutrient solution composition alone cannot be used to predict nutrient uptake of plants as there are several other factors playing a role.

Keywords: electrical conductivity (EC), nutrient solution, nutrient uptake, soilless production, uptake concentrations (UC).

Introduction

In order to obtain high yields and optimal quality, high concentrations of nutrients are supplied to plants in soilless production systems. A large percentage of the supplied nutrients are however drained to waste in open systems. In semi-closed systems the nutrient solution can be re-used as long as the concentration and composition of the nutrient solution will sustain crop nutrient demands and product quality. Plants however do not necessarily take up nutrients at the same quantity or ratio as that supplied (Voogt 1993), resulting in an increase or depletion relative to other elements in the nutrient solution to be re-used (Giufridda et al. 2003). This necessitates frequent analysis and adjustment of the drained nutrient solution. An alternative approach is to simulate the nutrient uptake of crops and thereby the composition of the solution to be re-used (Le Bot et al. 1998). One of the major factors affecting the nutrient uptake of crops that needs to be quantified in order to simulate nutrient uptake is the concentration and composition of the supplied nutrient solution.

Although the composition of nutrient solutions is often based on earlier studies where the nutrient composition of plant tissue was determined (Voogt 1993) a wide variation exists for the recommended nutrient solution concentrations even for a model crop such as tomatoes. In a review of the literature Dorais et al. (2001) concluded that the electrical conductivity (EC, mS cm^{-1}) should be between 1.6 and 5.0 mS cm^{-1} for optimal growth. Generally higher ECs are believed to enhance yield and especially fruit quality but research has shown that yield and fruit quality are not necessarily affected by a reduction of the macronutrient concentrations in the nutrient solution (Siddiqi et al. 1998; Giuffrida and Leonardi 2012). It is however not possible from these studies to find a direct correlation between nutrient solution composition and nutrient uptake and studies looking at the effect of nutrient solution composition on nutrient uptake often use only very narrow concentration ranges (Siddiqi et al. 1998; Weerakkody et al. 2011).

A close relationship between nutrient and water uptake has been reported and it has been suggested that this relationship can be used as a method of determining daily nutrient supply (Sonneveld 2000, Pardossi et al. 2004; Thompson et al. 2013). The uptake concentration (UC, mmol L^{-1}) of different nutrients has been determined for several crops and can be used in the equation given by Sonneveld (2000) to determine the concentration of nutrients in the drainage water. Since both water and nutrient uptake is driven by radiation the variation in UC was found to be less than the absolute values of nutrient uptake (kg ha^{-1}) (Sonneveld 2000). Using this method the variation in optimum EC will mainly be linked to the variation in water use. There is however a large difference in UC between crops and also growing conditions and although this can be attributed to the variation in water use (Sonneveld

2000), the rate of nutrient uptake itself will also be affected by other factors including cultivars, environmental conditions, developmental stage and cultural practices which includes the concentration and composition of the supplied nutrient solution (Le Bot et al. 1998; Dorais et al. 2001).

The concentration and composition of the nutrient solution can directly affect the uptake of ions. From the literature the effect of EC on the uptake of specific ions is described inconsistently. Nitrogen (total-N) and phosphorus ($H_2PO_4^-$) uptake tend to either increase (Giuffrida and Leonardi 2012) or decrease (Magán et al. 2005) with an increase in EC while that of Magnesium (Mg^{2+}) is not affected. Calcium (Ca^{2+}) uptake can be either not affected (Seo et al. 2009) or reduced by an increase in EC (Sonneveld and Welles 2005). Potassium (K^+) uptake is either not affected by the nutrient solution concentration (Seo et al. 2009) or can increase with an increase in nutrient solution EC (Giuffrida and Leonardi 2012). This inconsistency may indicate that it is also the concentration and ratio of specific ions and not purely the EC in the nutrient solution that can have either synergetic or antagonistic effects on their or other ions uptake. Increasing either the $H_2PO_4^-$ or Mg^{2+} concentration in a nutrient solution can increase these ions' uptake while increasing the sulphate (SO_4^{2-}) level in the nutrient solution can reduce the uptake of Ca^{2+} and Mg^{2+} (Seo et al. 2009).

In order to ultimately simulate crop nutrient demand necessary for model based regulation of water and fertilizer application to crops it was necessary to determine the effect of the nutrient solution composition on the uptake of macro nutrients in a soilless system using tomato as a model crop. The aim of this article was therefore to determine the uptake of water and macro-nutrients under varying concentrations and ratios of macro-nutrients in a water culture where the uptake of nutrients can be assumed to be equal to demand from the crop (Le Bot et al, 1998). Additionally the effect of nutrient uptake from the solution on the composition of the residual nutrient solution was evaluated as this solution needs to be re-used in a closed growing system.

Material and methods

Plant material and growth conditions

Six week old tomato (*Lycopersicon esculentum* Mill. cvs. MFH 9343 and FA593, Sakata, South Africa) seedlings, germinated in a mix containing vermiculite, perlite and coco-peat were transplanted to 5L closed plastic containers filled with nutrient solution. The nutrient solution was aerated continuously. The cultivars differed in their salt tolerance; FA593 is tolerant to high salinity while MFH 9343 is sensitive to high salinity (Personal communication, J Stronkhorst, Sakata Seed, South Africa, 2009). Trials were done in a temperature controlled glasshouse in Stellenbosch, from May 2009 to December 2010. The glasshouse temperature was set to 20 / 28^{O}C (night / day temperature). Temperature (^{O}C), relative humidity (RH), light intensity (µmol m^{-2} s^{-1},PAR) and CO_2 concentration was logged throughout the trial. Midday photosynthetic photon flux density (PAR) ranged from 300 to 1500 µmol.m^{-2}.s^{-1} and the humidity remained between 60 and 85%. Plants were pruned to a single stem with side shoots removed once a week. All trusses were pruned to six fruit per truss as soon as fruit set was complete.

Treatments

For the first trial five different nutrient solutions were used. They differed in terms of the concentration of macro nutrients but the ratio between nutrients was kept constant. The pH of the nutrient solution was 5.8 and the EC's were 0.8, 1.6, 2.4, 3.2 and 4.00 mS cm^{-1} at 25^{O}C (Table 1). In the second trial three EC treatments (EC 0.8, 2.4 and 4.0 mS cm^{-1} at 25^{O}C) were combined with three macro nutrient ratio combinations (Standard, Re-use A and re-use B) (Table 1), based on the change in the concentration of nutrients in leached nutrient solutions as a result of the selective nutrient uptake by the crops (unpublished data of earlier research). A constant concentration of micronutrients were applied: 40.6 µmol L^{-1} Fe^{3+}; 35.0 µmol L^{-1} $H_2BO_3^-$, 4.6 µmol L^{-1} Zn^{2+}; 3.6 µmol L^{-1} Cu^{2+}; 10.9 µmol L^{-1} Mn^{2+}. Since this trial was terminated at 71 days after planting and only fruit from the first two trusses were matured, the nutrient solution was kept at the formulation recommended for vegetative growth and not adjusted to a formulation suggested during fruit development (Voogt 1993).

Growth and development parameters

The leaf area was determined at 35 days after planting (DAP) and again at the last destructive harvest, 71 DAP. To determine assimilate partitioning the fresh and dry weight of the leaves stems and roots were determined at the last destructive harvest, 71 DAP after drying in an oven for 72 hours at 80^{O}C. The leaf area and shoot dry weight of the side shoots were determined with every pruning. The leaf area was measured and the specific leaf area (SLA, m^2 kg^{-1}) determined as the total leaf area per leaf dry weight.

Water and nutrient uptake

Water uptake (Wu) was determined by measuring daily the volume of nutrient solution decline in the container as there was no leaching and evaporation from the sealed containers was negligible. The residual nutrient solution was then topped up with the reference nutrient solution at the specific concentration used per treatment daily when the water uptake was determined. Changes in EC and pH were also recorded daily. After a five day period the nutrient solutions in each container was replaced with a fresh nutrient solution. Prior to replacement of the solution, and macro-nutrient uptake was calculated by determining the depletion of nutrients in the residual nutrient solution as well as through quantitative dry matter analysis.

Table 1. Macro-nutrient composition (meq L^{-1}) of the municipal water and the final nutrient solutions at different ECs used to determine the nutrient and water uptake of tomato plants.

Trial 1

	NH_4^+	K^+	Ca^{2+}	Mg^{2+}	NO_3^-	$H_2PO_4^-$	SO_4^{2-}
				Municipal water			
	0.05	0.01	0.17	0.03	0.01	0.01	0.04
EC ($mS\ cm^{-1}$)				**Nutrient solutions**			
0.8	0.4	2.8	3.4	1.4	5.0	0.6	2.4
1.6	0.8	5.6	6.8	2.8	10.0	1.2	4.8
2.4	1.2	8.4	10.2	4.2	15.0	1.8	7.2
3.2	1.6	11.2	13.6	5.6	20.0	2.4	9.6
4.0	2.0	14.0	17.0	7.0	25.0	3.0	12.0

Trial 2

EC ($mS\ cm^{-1}$)	**Nutrient ratio**	NH_4^+	K^+	Ca^{2+}	Mg^{2+}	NO_3^-	$H_2PO_4^-$	SO_4^{2-}
0.8	Standard	0.4	2.8	3.4	1.4	5.0	0.6	2.4
	Re-use A	0.6	3.1	2.9	1.4	6.0	0.5	1.5
	Re-use B	0.8	3.4	2.4	1.4	7.0	0.4	0.6
2.4	Standard	1.2	8.4	10.2	4.2	15.0	1.8	7.2
	Re-use A	1.8	9.3	8.7	4.2	18.0	1.5	4.5
	Re-use B	2.4	10.2	7.2	4.2	21.0	1.2	1.8
4.0	Standard	2.0	14.0	17.0	7.0	25.0	3.0	12.0
	Re-use A	3.6	15.5	14.5	7.0	30.0	2.5	7.5
	Re-use B	4.0	17.0	12.0	7.0	35.0	2.0	3.0

The rate of ion uptake (U, mg $plant^{-1}\ d^{-1}$) was determined for a five day period based on the concentration at the beginning and end of the period. From this the uptake ratios (UC) of the nutrients calculated as the amount of nutrient absorbed per volume of water absorbed could also be calculated. On 71 DAP all plant material were oven dried at 80 ^{O}C to constant weight and ground to determine the dry weight and the elemental concentration of the plants.

The K^+, Ca^{2+}, Mg^{2+} and $H_2PO_4^-$ of dried leaf and fruit samples were determined after HCl extraction from the plant material and ash drying at 550 ^{O}C for 5 hours. The total-N in the leaf samples was determined using the Kjeldahl method and the concentrations of K^+, Ca^{2+}, Mg^{2+} was determined by atomic absorption spectrophotometry. The $H_2PO_4^-$ SO_4^{2-} and NH_4^+ concentrations were determined colorimetrically using a spectrophotometer at 460nm for $H_2PO_4^-$ and for SO_4^{2-} and NH_4^+ at 640nm. The nutrient content was determined as the tissue concentration (%) * dry weight (g).

Statistical analysis and experimental design

Each treatment combination was repeated four times in a completely randomized block design. Analysis of variance (ANOVA) was used for evaluating data (STATISTICA 11.0, Statsoft (SA) Inc., Tulsa, Oklahoma, USA). Differences among the mean values were determined using using Fischer's LSD ($P<0.05$) equations.

Results and discussion

Water uptake

Statistical analysis of the data revealed that the water uptake (Wu) during the first trial was reduced for plants from both cultivars when grown at higher nutrient solution concentrations (Table 2). For FA593, the salinity tolerant cultivar, the reduction in water use at an EC of 4.0 mS cm^{-1} was 17% compared to plants grown at an EC of 1.6 mS.cm^{-1} while the cultivar that is not tolerant to saline conditions, MFH9343 had a 32% reduction in water use per plant at and EC of 4.0 mS cm^{-1}. This was most likely an osmotic effect created by a high rootzone EC, which is known to result in a limited water and nutrient uptake by plants (Marschner 1995). Part of the reduction in water uptake at the higher nutrient solution concentrations can be attributed to morphological adaptations plants make when grown at a higher external salt concentration. At the lower EC levels (0.8, 1.6 and 2.4 mS cm^{-1}) the water uptake per m^2 leaf area remained constant (Figure 1). Although the total water uptake was reduced at higher ECs, the water uptake per leaf area increased for both cultivars at higher EC levels (3.2 and 4.0 mS cm^{-1}). This trend was the same for both cultivars although the water uptake per leaf area was higher for the salt sensitive variety (MFH 9343). This indicates that the high EC of the nutrient solution had a greater effect on the morphology of the plant, the leaf area, than on the water use of the plant.

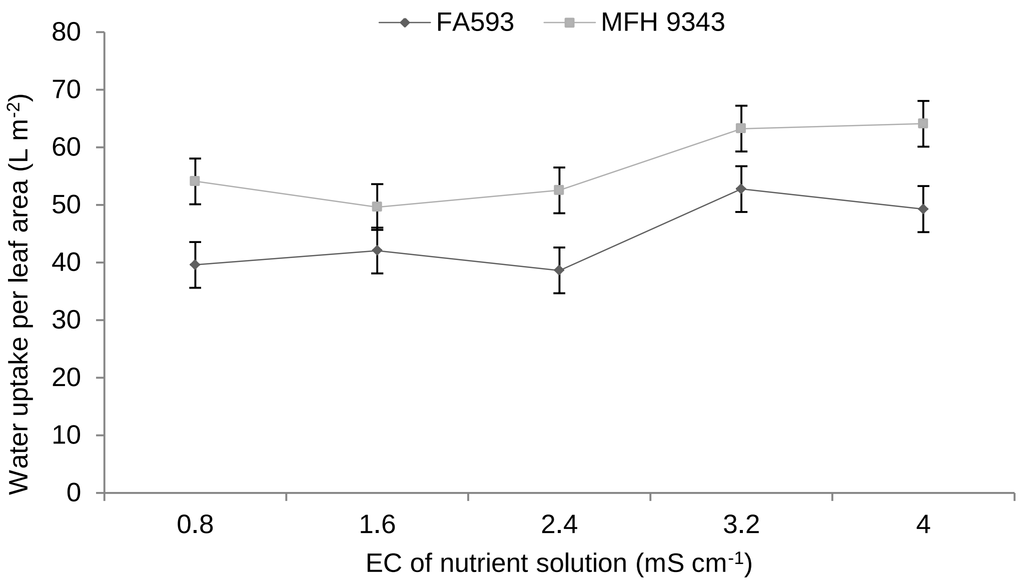

Figure 1. The water uptake per leaf area (L m^{-2}) per plant at 71 DAP for two tomato cultivars at different nutrient solution concentrations (EC, mS cm^{-1}). (Error bars indicate the LSD value at $p \leq 0.05$).

Nutrient uptake

For both cultivars the total-N, $H_2PO_4^-$ and SO_4^{2-} uptake increased with an increase in nutrient solution concentration from 0.8 to 4.0 mS cm^{-1} (Table 2). The Ca^{2+} uptake remained constant as the EC increased for FA593 while for MFH 9343 it decreased slightly as the EC increased to 4.0 mS cm^{-1}. Although there was no significant difference in the K^+ uptake at different EC levels for MFH9343 it increased with an increase in nutrient solution EC for FA593. This increase in K^+ uptake at an increasing EC for the salinity tolerant cultivar, FA593, may be linked to the plants need for osmotic regulation at higher nutrient solution concentrations (Sonneveld and Voogt 2009).The high tissue $H_2PO_4^-$concentrations indicate that luxury uptake of $H_2PO_4^-$ took place that can be attributed to the increased availability in $H_2PO_4^-$ in water culture. Although toxic levels were not reached during this trial, $H_2PO_4^-$ toxicity has been reported for substrate grown cucumbers (Sonneveld 2000) and is something to monitor when growing plants hydroponically.

Table 2. Water and nutrient uptake of two tomato cultivars grown in a water culture at different nutrient solution concentrations for 71 days.

		[a] **Water Uptake**	[b] **Nutrient uptake (Nu, g plant^{-1})**					
		(Wu, L plant^{-1})	**N**	**P**	**K**	**Ca**	**Mg**	**S**
Cultivar	**EC (mS cm^{-1})**							
FA593	0.8	60.59ab	6.74de	2.07f	11.13c	4.89ab	1.15a	1.58e
	1.6	63.58a	7.45bcd	2.21ef	12.39abc	5.02a	1.19a	1.63de
	2.4	57.53bc	8.12ab	2.49c	13.17ab	4.87ab	1.15a	1.85bc
	3.2	58.62ab	8.95a	2.93ab	13.85a	4.65ab	1.24a	1.99abc
	4.0	52.32cd	8.85a	3.02a	14.02a	4.48bc	1.23a	2.18a
MFH 9343	0.8	63.31a	6.44e	2.08f	11.05c	4.47bc	1.14a	1.54e
	1.6	52.13cd	6.52e	2.11ef	11.17c	4.25bcd	1.12a	1.59e
	2.4	50.17d	7.13cde	2.27de	11.54bc	3.90d	1.13a	1.82cd
	3.2	46.65de	7.84bc	2.45cd	12.23abc	3.70de	1.18a	1.89bc
	4.0	43.32e	8.23ab	2.53bc	12.45abc	3.32e	1.12a	2.03ab
LSD ($p<0.05$)		5.70	0.89	0.18	1.82	0.52	0.13	0.19

Significant differences between cultivars for means are indicated by different letters in superscript.

[a] *Water uptake is the cumulative value obtained at the end of the season, 64 DAP.*

[b] *Nutrient uptake is the combined nutrient content of all plant parts, including pruned side shoots*

The tissue analysis at 71 DAP in the first trial indicated that nutrient uptake was sufficient at all the different EC treatments since the tissue concentrations were within the ranges given by Raviv and Lieth (2008). It is well known that plants are able to take up sufficient quantities of nutrients even when present at relatively low concentrations in the rootzone, but in soilless systems the availability of nutrients is limited by the small root volume and higher nutrient concentrations are therefore needed to sustain optimal yields (Sonneveld and Voogt 2009).

A linear correlation between nutrient solution EC and tissue ion concentration could however only be shown for S (r^2 = 0.94). The Mg^{2+} uptake was not affected by the nutrient solution EC for either of the cultivars and the Ca^{2+} uptake tended to decrease as the nutrient solution EC was increased, although this was only significant for cultivar MFH9343 at an EC of 4.0 mS cm^{-1}. In their study Sonneveld and Welles (2005) found that the most significant effects of an increased rootzone EC were the increased K^+ and the reduced Ca^{2+} uptake.

Results showed no correlation between cation and water uptake but a significant difference in the nutrient uptake concentrations (UC, mmol L^{-1}) were noticed (Table 3). The UC defined as the ratio between nutrient ions and water taken up by plants during the same time interval has no physiological basis but is often used as a guide to nutrient use and to assist in formulating nutrient solutions (Sonneveld 2000; Gallardo et al. 2009; Massa et al. 2011; Thompson et al. 2013).

Table 3. Uptake concentrations (UC) of macronutrients for two tomato cultivars grown in a water culture at different nutrient solution concentrations for 71 days.

		UC (mmol L^{-1})					
Cultivar	**EC**	**N**	**P**	**K**	**Ca**	**Mg**	**S**
	0.8	7.95f	1.10f	4.71e	2.02ab	0.79f	0.81fg
	1.6	8.37def	1.12f	5.00de	1.97bc	0.78f	0.80g
FA593	2.4	10.08d	1.40e	5.87c	2.12ab	0.83ef	1.00de
	3.2	10.91cd	1.61cd	6.06bc	1.98ab	0.88de	1.06de
	4.0	12.08b	1.86ab	6.87a	2.14a	0.98bc	1.30b
	0.8	7.27f	1.06f	4.48e	1.77c	0.90.75f	0.76g
	1.6	8.93e	1.31e	5.49cd	2.04ab	0.90cde	0.95ef
MFH 9343	2.4	10.15d	1.46de	5.90c	1.94abc	0.94cd	1.13cd
	3.2	12.00bc	1.69bc	6.72ab	1.98ab	1.05ab	1.27bc
	4.0	13.57a	1.88a	7.37a	1.92bc	1.08a	1.46a
LSD (p<0.05)		1.10	0.17	0.75	0.21	0.09	0.15

Significant differences between cultivars for means are indicated by different letters in superscript.

The uptake-concentration of potassium UC^K, uptake-concentration of nitrogen UC^N, uptake-concentration of phosphorus, UC^P and uptake-concentration of sulfate UC^S was affected by the EC of the nutrient solution and differences were also noticeable between the cultivars used during this trial. Although the uptake-concentration of calcium UC^{Ca} and the uptake-concentration of magnesium UC^{Mg} remained more constant in the range of nutrient solution concentrations used during this trial, there were also differences. In several studies it is reported that the UC of most of the macro-nutrients is reported to remain consistent over a range of conditions (De Kreij et al. 1996; Sonnelveld 2000). Sonneveld and Voogt (2008) found that for Kohlrabi and lettuce the UC was lower at a relatively low EC (1.3 mS cm^{-1}) but remained stable as the nutrient solution EC was increased further. However, results from this study indicate that nutrient uptake is not linearly related to the water uptake and the EC affects water and nutrient uptake, but not necessarily to the same degree. Using UC to determine nutrient uptake of crops and making recommendations regarding adjustments to the input concentrations of ions does not seem to be the most accurate method. It is however possible that the UC remains more stable when plants are grown in a medium instead of water culture and this should be tested. As a percentage of the total plant dry matter the only significant differences were however found at an EC of 4.0 mS cm^{-1} where the plant tissue concentrations of all the macro nutrients except for Ca^{2+} were significantly higher (data not shown) indicating luxury consumption without a simultaneous increase in plant growth. These results support the statement made by Mankin and Fynn (1996) that nutrient uptake will be determined more by plant demand than supply and will remain relatively independent of concentration over a range of ECs.

Composition of residual nutrient solution

The concentration of most of the nutrients in the residual nutrient solution was affected by the EC of the applied nutrient solution, similarly for both cultivars used in these trials. The ratio between the anions and between the cations was also affected. The concentration of all the anions when measured five days after replacement of the nutrient solution decreased and this decrease was more pronounced at lower ECs, especially at an EC of 0.8 mS cm^{-1}. Although the concentration of all the cations decreased, the decrease for NO_3^- and $H_2PO_4^-$ was much larger than that of SO_4^{2-} in the residual nutrient solution at all the EC levels evaluated (Figure 2). This resulted in an imbalance between the anions, which can be expected to increase the longer the solution is being used without replacement. In order to re-use drained nutrient solution, the composition needs to be either similar to that deemed optimal for crop growth or need to be adjusted before it can be re-used to prevent imbalances from occurring that can result negative effects on crop growth, yield and fruit quality (Roorda van Eysinga and Smilde 1981). At an EC of of 0.8 mS cm^{-1} NO_3^- contributed only 31% of the total anions in the residual nutrient solution five days after the nutrient solution was replaced, compared to 63% in the starting solution. For most crops 80 to 90% of the total anion uptake can consist of NO_3^- uptake and a large decrease in the NO_3^- concentration in the residual nutrient solution can therefore be expected (Sonneveld and Voogt 2009). However, at a higher EC (4.0 mS cm^{-1}), the difference was much smaller with NO_3^- making up 59% of the total anions in the residual nutrient solution. In the original nutrient solution, 30% of the anions consist of SO_4^{2-} but in the residual nutrient solution it made up between 68% (EC of 0.8 mS cm^{-1}) and 35% (EC of 4.0mS cm^{-1}) of the total anions. The uptake of SO_4^{2-} is much lower than that of NO_3^-, resulting in the accumulation of SO_4^{2-} ions in the nutrient solution and imbalances if the nutrient solution is not adjusted correctly before re-use. This is in agreement with findings from Giuffrida and Leonardi (2012) who found an accumulation of sulphate when using a reduced strength nutrient solution. At higher EC levels the anion ratio will therefore remain stable for longer if the nutrient solution is re-used.

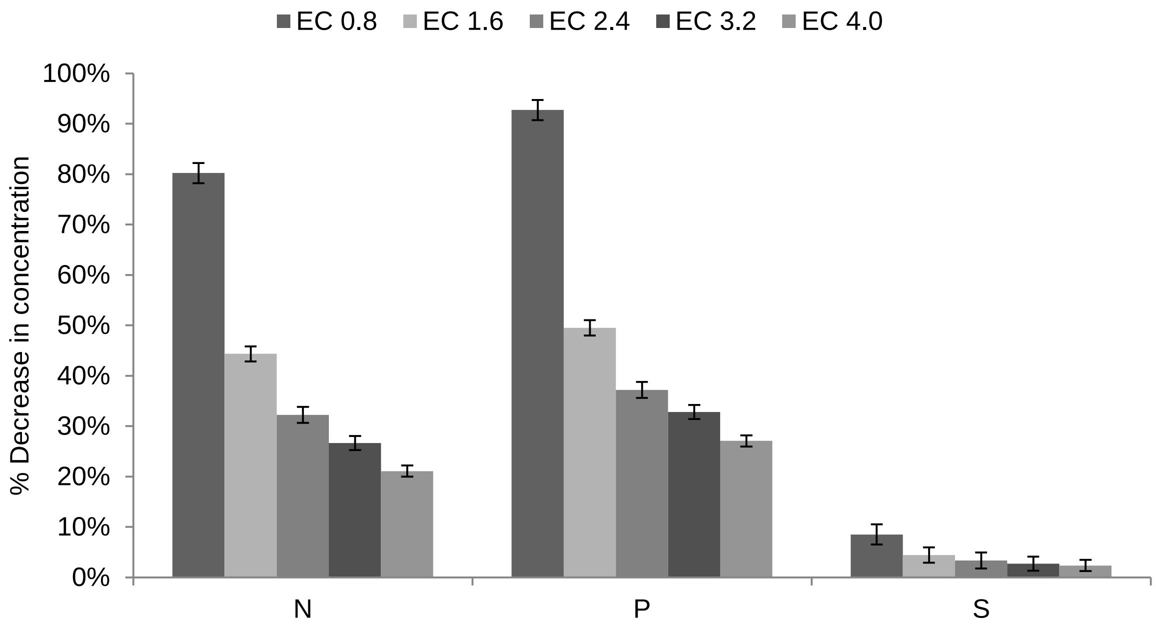

Figure 2. Change in the composition of the anions in the nutrient solution five days after replacement with a fresh nutrient solution as indicated by the decrease in their concentration in the residual nutrient solution. Values are the mean for the two cultivars at different nutrient solution EC values (0.8, 1.6, 2.4, 3.2 and 4.0 mS cm^{-1}). (Error bars indicate the LSD value at $p \leq 0.05$).

The same trend was evident with the cations with a decrease in the concentration of all the cations although percentage wise it was much larger for K^+ and this effect was again more pronounced as the EC of the nutrient solution decreased (Figure 3).

This resulted in a change in the K^+:Ca^{2+} and K^+:Mg^{2+} ratio in the residual nutrient solution. At a higher EC the decrease in the Ca^{2+} concentration was only 3%. When recirculating a nutrient solution containing 5mmol L^{-1} Ca^{2+}, Lozano et al. (2007) found the Ca^{2+} concentration in the drainage solution to be even greater than in the applied nutrient solutions. The mutual ratios of nutrients in the root environment are considered even more important in determining nutrient uptake than their concentrations (Sonneveld and Voogt 2009). Interactions between nutrients with regard to their absorption and utilization are more likely to occur when one nutrient occurs at excessive concentrations in the rootzone (Fageria 1997). The ratio between K^+ and Ca^{2+} should be monitored as it can have substantial effects on the fruit quality of tomatoes (Adams and Ho 1993).

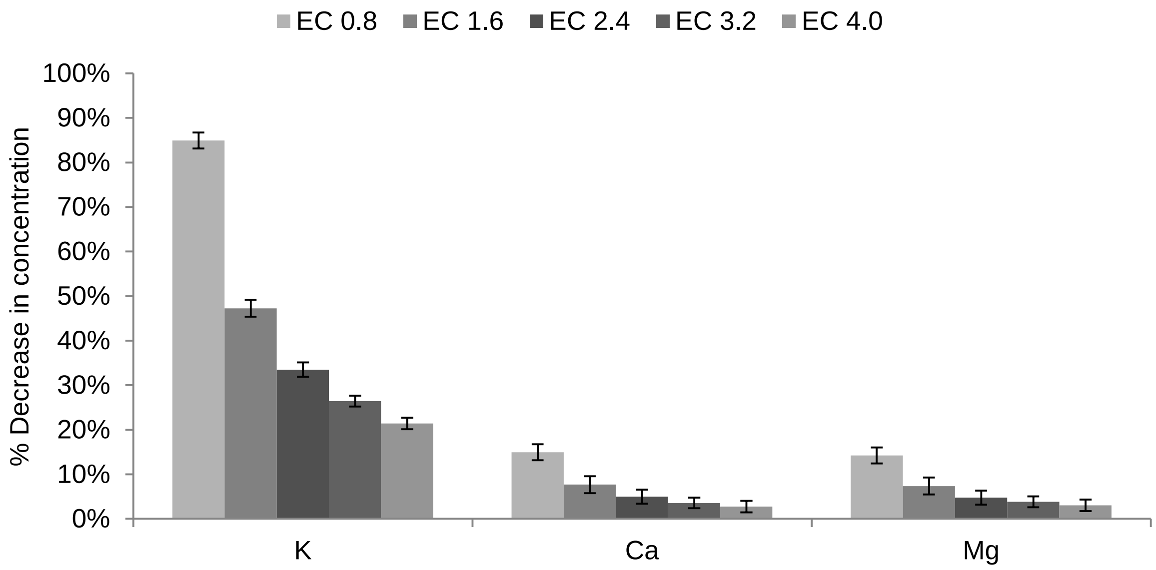

Figure 3. Change in the composition of the cations in the nutrient solution five days after replacement with a fresh nutrient solution as indicated by the decrease in their concentration in the residual nutrient solution. Values are the mean for the two cultivars at different nutrient solution EC values (0.8, 1.6, 2.4, 3.2 and 4.0 mS cm^{-1}). (Error bars indicate the LSD value at $p \leq 0.05$).

The recommended K^+: Ca^{2+}: Mg^{2+} meq rootzone ratio for many crops is 1:2:1 (Sonneveld and Welles 2005) and an increase in the concentration of K^+ and/or Mg^{2+} in the rootzone can result in a reduction of Ca^{2+} uptake through antagonism, which can result in physiological disorders such as blossom end rot in tomatoes (Omar 1966; Sonneveld and Voogt 1985). This is the main reason for the relatively high Ca^{2+} concentration in relation to its uptake in most recommended nutrient solutions.

From these results it is apparent that deviations in both the cation and anion ratios will become apparent relatively quickly at a low EC, necessitating better monitoring and adjustment of the nutrient solution composition to maintain availability of all nutrients. Fopr a producer to prolong the re-use period of a nutrient solution it will therefore be necessary to maintain the ratios in the residual solution closer to that in the original nutrient solution in the root-medium by increasing the concentrations of fast depleting ions while at the same time decreasing the concentrations of ions that tend to accumulate. This should be done without affecting optimum nutrient uptake.

In the second experiment, the K^+: Ca^{2+}: Mg^{2+} ratio of the two alternative nutrient solutions (re-use A and re-use B) varied from 1:2.4:1 in the original solution to 1.1:2.1:1 in solution A and 1.2:1.7:1.0 in solution B. Although still within the optimum range recommended for tomatoes, this variation in K^+: Ca^{2+}: Mg^{2+} ratios resulted in differences in the tissue Ca^{2+} content of the plants when grown at an EC of 2.4 and 4.0 mS cm^{-1} (Figure 4). The decrease in tissue Ca^{2+} concentration can be a direct result of the reduction in Ca^{2+} application in both the re-use solutions A and B but it can also be a result of the increase in NH_4^+ in these two nutrient solutions (Table 1). Fageria (2001) found that Ca^{2+} uptake is higher when a larger percentage of the total-N is applied as NO_3^- instead of NH_4^+. If anions (specifically NO_3^-) are taken up in greater quantities than cations it can result in an increase in the pH of the drained nutrient solution. To compensate for this a percentage of the total nitrogen in the nutrient solution is often added as NH_4^+. Ammonium (NH_4^+) however not only reduces the root zone pH but can directly compete for uptake with Ca^{2+}, Mg^{2+} and K^+. Low $H_2PO_4^-$ concentrations and high SO_4^{2-} can also reduce the uptake of Ca^{2+} and result in $CaSO_4$ sediment (De Kreij 1996; Voogt and Sonneveld 2004).

Effect of altered nutrient solution composition

The plant tissue macro-nutrient concentration was affected by the EC of the nutrient solution as well as the ratio between the nutrients (Table 4). Whereas the tissue Ca concentration increased at an EC of 4.0 mS cm^{-1} for cultivar MFH 9343 in all three nutrient solutions, it was significantly lower for cultivar FA 9343 at an EC of 4.0 mS cm^{-1} in solutions Re-use A and Re-use B. The same trend was visible at an EC of 2.4 mS cm^{-1} although the effect was not statistically significant. At the lowest EC, 0.8 mS cm^{-1} cultivar FA 9343 had a higher tissue Ca concentration than cultivar MFH 9343. The tissue K concentration was significantly higher for both cultivars at an EC of 4.0 mS cm^{-1} in all three nutrient solutions (Table 4). At the low EC (0.8 mS cm^{-1}) cultivar FA 593 had a higher tissue K concentration whereas cultivar MFH 9343 had a higher tissue K concentration at the higher EC (4.0 mS cm^{-1}), although this was not significantly different in solution Re-use B. Adams and Grimmit (1996) found that the K content of tomato leaves increased linearly with an increase in nutrient solution K concentration between 10 and 800 mg L^{-1}. For cultivar FA 593, the tissue Mg concentration was not affected by the composition or concentration of the nutrient solution (Table 4) but for cultivar MFH 9343 the tissue Mg concentration was significantly higher in solution Re-use A and Re-use B at an EC of 4. mS cm^{-1}).

Besides the variation in tissue cation concentration, the levels of Ca, Mg and K remained above the minimum recommended level for tomatoes during vegetative growth (Peet 2005).

The tissue N concentration was not affected by the composition of the nutrient solution but at the high EC (4.0 mS cm^{-1}) it was significantly higher for both cultivars (Table 4). An interesting trend was also noticed where cultivar MFH 9343 tended to have a lower tissue N concentration compared to cultivar FA 593 at low nutrient solution EC whereas the reverse was observed at a high nutrient solution EC.

Table 4. Plant tissue macro-nutrient concentrations (% Dry weight) for two tomato cultivars grown in a water culture for 71 days in nutrient solutions of which the composition and concentration was varied.

Cultivar	**Nutrient solution**	**Plant tissue concentration (% Dry weight)**					
		Ca	**K**	**Mg**	**N**	**P**	**S**
MFH 9343	EC 0.8 Standard	1.82def	4.51gh	0.47c	2.63g	0.85efg	0.63hi
	EC 0.8 Re-use A	1.76efg	4.43h	0.43cd	2.64g	0.7gh	0.58i
	EC 0.8 Re-use B	1.71efgh	4.41h	0.38d	2.78fg	0.68hi	0.58i
	EC 2.4 Standard	1.86def	4.79fgh	0.47c	2.95fg	1.01d	0.88def
	EC 2.4 Re-use A	1.84def	4.88fg	0.44cd	3.02efg	1.00de	0.84defg
	EC 2.4 Re-use B	1.68fgh	4.97ef	0.49bc	3.07efg	0.98def	0.78efgh
	EC 4.0 Standard	2.24a	7.73a	0.56b	5.08ab	1.68a	1.37a
	EC 4.0 Re-use A	2.14ab	7.74a	0.68a	5.11a	1.62ab	1.27ab
	EC 4.0 Re-use B	2.01bcd	7.55ab	0.68a	4.99abc	1.53abc	1.23ab
FA 593	EC 0.8 Standard	2.15ab	5.33de	0.39d	3.22ef	0.83fgh	0.75fghi
	EC 0.8 Re-use A	2.09abc	5.35de	0.38d	3.23ef	0.69hi	0.6ghi
	EC 0.8 Re-use B	2.13abc	5.60d	0.39d	3.44e	0.60i	0.68ghi
	EC 2.4 Standard	1.92cde	5.16ef	0.39d	3.18ef	0.96def	0.73fghi
	EC 2.4 Re-use A	1.74efgh	4.83fgh	0.38d	2.98efg	0.86defg	0.63hi
	EC 2.4 Re-use B	1.60gh	5.14ef	0.38d	3.17ef	0.90defg	0.64hi
	EC 4.0 Standard	2.01bcd	7.19bc	0.39d	4.54cd	1.50bc	1.11bc
	EC 4.0 Re-use A	1.52hi	7.09c	0.44cd	4.50d	1.43c	1.00cd
	EC 4.0 Re-use B	1.35i	7.23bc	0.44cd	4.62bcd	1.39c	0.95cde
LSD (P<0.05)		0.21	0.43	0.07	0.47	0.15	0.17

Significant differences between cultivars for means are indicated by different letters in superscript.

In agreement with results from the first trial, the tissue P concentration decreased with a decrease in the EC of the nutrient solutions (Table 4). It was also significantly lower in solution Re-use B at an EC of 0.8 mS cm^{-1} compared to the standard and re-use A solutions. The tissue S concentration was again significantly higher at an EC of 4.0 $mS.cm^{-1}$ for both cultivars (Table 4). When using solutions Re-use A and Re-use B at a high EC (4.0 $mS.cm^{-1}$) cultivar MFH 9343 had a higher tissue S concentration compared to FA 593. For all the treatments the nutrient anion tissue concentrations also remained well above the lower threshold for deficiency (Peet 2005).

To prolong the re-use period of a nutrient solution it is necessary to maintain the ratios in the residual solution closer to that in the original applied nutrient solution. The adjustments made in the two alternative nutrient solutions, Re-use solution A and Re-use solution B resulted in a reduction in the severe depletion of K^+ and NO_3^- that was apparent in the standard nutrient solution (Figure 4 and 5). The depletion was more prominent, for both K^+ and NO_3^- at the lowest nutrient solution concentration (EC 0.8 mS cm^{-1}).

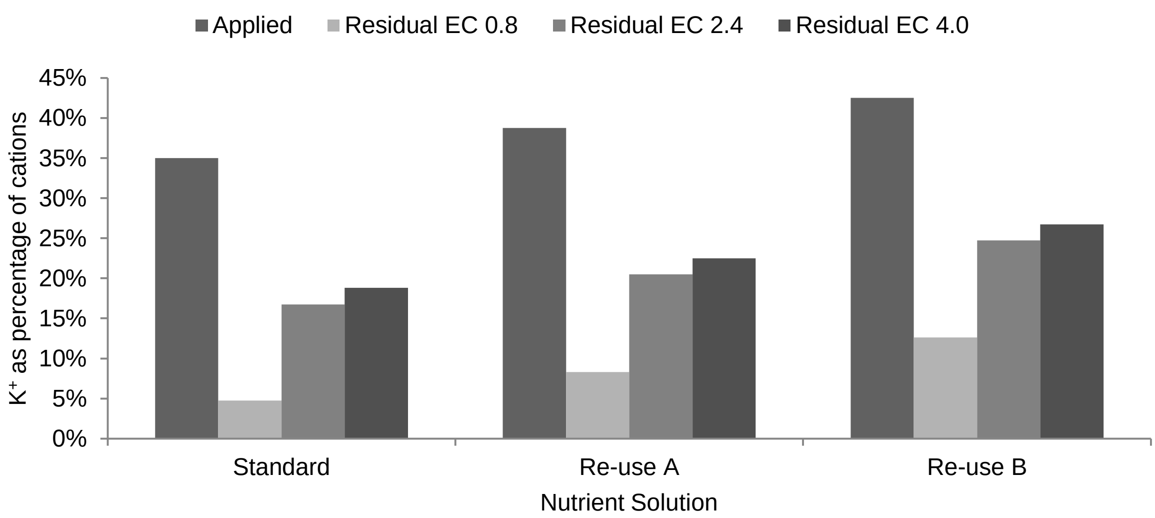

Figure 4. Concentration of potassium (K^+) as a percentage of either the total cations or anions in the applied and residual nutrient solutions of the standard and re-use solutions A and B at three different nutrient solution concentrations (EC, mS cm^{-1}).

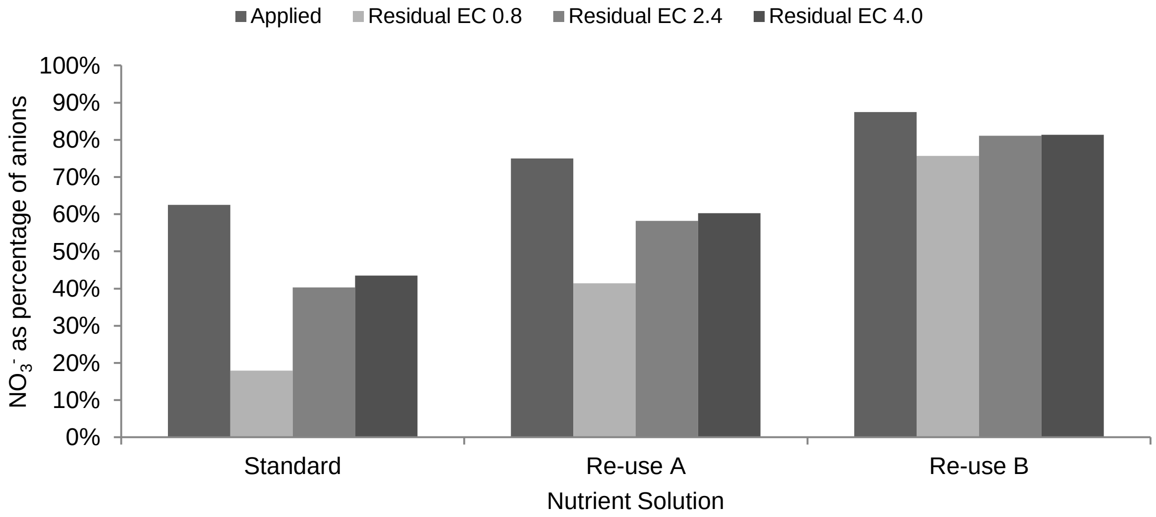

Figure 5. Concentration of NO_3 as a percentage of either the total cations or anions in the applied and residual nutrient solutions of the standard and re-use solutions A and B at three different nutrient solution concentrations (EC, mS cm^{-1}).

A similar trend was noticed in the residual solution for SO_4 that tended to accumulate in the original nutrient solution (Figure 6). At an EC of 2.4 and 4.0 the rate of accumulation was much less in both of the re-use nutrient solutions compared to the standard nutrient solution. The K:Ca ratio in the applied nutrient solution was 1:1.2 in the standard, 1:1.0 in re-use solution A and 1.4:1 in re-use solution B. This variation in the applied nutrient solution should not have a significant effect on the fruit quality. In the residual nutrient solution these ratios changed significantly at an EC of 0.8 mS.cm^{-1} for all three nutrient solutions (1:14, 1:3.5 and 1:3 respectively for the standard, re-use solution A and re-use solution B). At a nutrient solution EC of 2.4 the ratios remained lower in the two re-use solutions at 1:2.5 and 1:2.2 in re-use solution A and B respectively compared to 1:7 in the standard nutrient solution. The K:Ca ratio remained even more constant in the two re-use solutions at an EC of 4.0 mS.cm^{-1} at 1:1.8 and 1:1.7 compared to 1:4 in the standard nutrient solution.

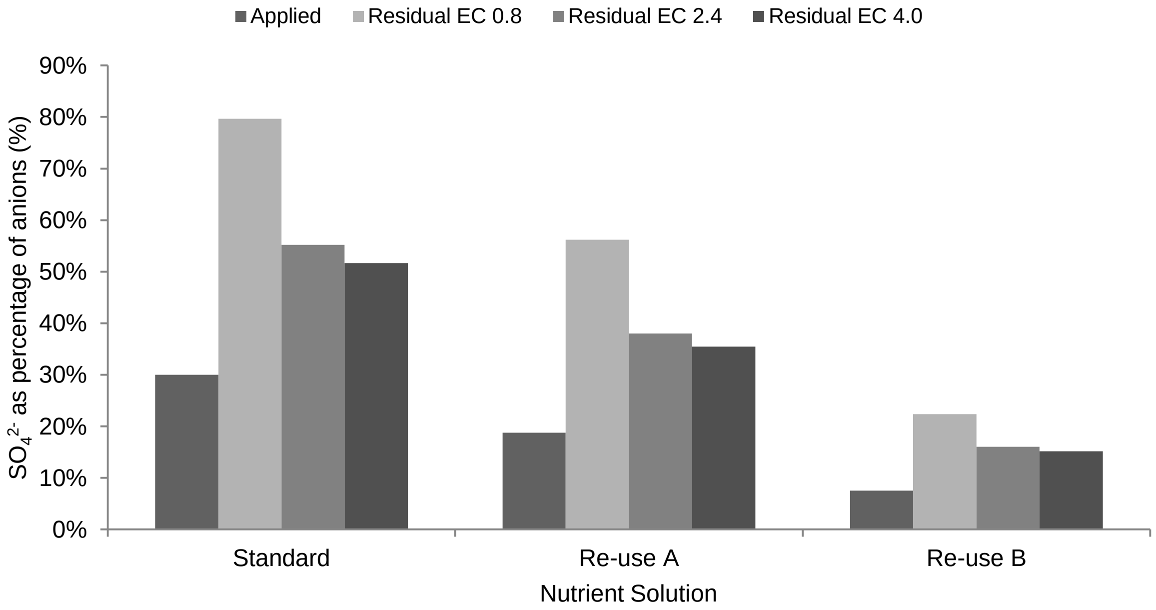

Figure 6. Concentration of sulphate (SO_4^{2-}) as a percentage of the total anions in the applied and residual nutrient solutions of the standard and re-use solutions A and B at three different nutrient solution concentrations (EC, mS cm^{-1}).

The anions were reduced at a greater extent than the cations in all the nutrient solutions used in these trials which will result in an increase in the nutrient solution pH over time if not adjusted frequently. An unequal uptake of cations and anions can have a significant effect on the pH of the nutrient solution, which in turn can affect the availability of elements such as P and Ca^{2+} (Marschner 1995). Although NH_4^+ was included in the two re-use solutions to counteract the unequal uptake between cations and anions, the concentrations used, 7% and 10% of the total N application, had no effect on the cation:anion ratio in the residual nutrient solutions. According to Steiner (1980), the ratio of anions and cations taken up remains the same, regardless of the anion and cation ratios in the nutrient solution since plants have the ability to select ions in a ratio favorable for their growth and development.

Conclusion

Although the composition of the nutrient solution, both the EC and ratios between elements, can influence the plant tissue concentrations, no clear trend was shown, indicating that uptake is not purely dependent on the external concentration of ions. The tissue concentrations remained within acceptable limits or slightly elevated in the case of P, and would not be expected to have a significant effect on growth, yield and fruit quality. The relationship between nutrient and water uptake was affected by the EC of the nutrient solution and this should be considered when attempting to use pre-determined uptake concentrations (UC) to recommend adjustments to nutrient solutions. Due to plants selectivity in nutrient uptake, the composition of the residual nutrient solution will be significantly different from that in the supplied nutrient solution and this can only be overcome to a certain extent through changing the composition of the applied solution. The use of UC can be useful in determining the concentration of ions in the residual nutrient solutions although it is affected by the composition of the nutrient solution and will have limited usefulness in modelling nutrient uptake. Although more complicated, the use of mechanistic models should be investigated further as a means of predicting nutrient uptake of plants in soilless growing systems.

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Article 2

Biomass partitioning and fruit quality of tomatoes in a soilless growing system as affected by the macro-nutrient composition

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Abstract

In soilless production systems where the nutrient solution is continually being re-circulated the concentrations and ratios between ions will start to deviate from the target values resulting in negative effects on crop growth and yield. Making use of a nutrient solution where these ratios are pre-emptively adjusted can possibly simplify management in these systems. Tomato plant growth, biomass partitioning and fruit quality were assessed by cultivating tomato plants from two cultivars for 71 days in 5L containers with nutrient solutions differing in total concentration and macro-nutrient ratios. A relatively high rootzone EC (3.2 mS cm^{-1} and 4.0 mS cm^{-1}) can potentially limit leaf area development and the relative growth rate (RGR) of tomato plants, resulting in smaller fruit but an increase in fruit dry matter %, total soluble solids (TSS), titratable acidity (TA) and lycopene content. Increasing the total-N and K^+ concentrations in the nutrient solution resulted in a reduction in biomass allocation to the fruit but an increase in the fruit quality parameters, especially at an EC of 4.0 mS cm^{-1}. Adjustments to the standard nutrient solutions to reduce fluctuations during re-cycling should be carefully considered since both yield and fruit quality can be affected.

Keywords: electrical conductivity (EC), nutrient solution, nutrient uptake, soilless production, uptake concentrations (UC).

Introduction

Growing crops in soilless systems in a protected environment is a complex production system associated with a high degree of control on inputs and outputs. This production system can be an environmentally friendly technology with a high use efficiency of both water and nutrients if a closed system is used where the drained nutrient rich water is re-used for fertigation (Sonneveld and Voogt 2009). Nutrient uptake, yield and quality of crops is strongly related (Sonneveld 2000). Total yield will also be determined by assimilate partitioning and for tomatoes the sink strength is normally higher than the source strength. Whereas the sink strength of developing tomato fruit is influenced by temperature and determined by the sucrose import rate, assimilate partitioning is regulated by the relationship between the activity of different plant parts which can be affected not only by environmental conditions but also the nutrient uptake rate (Heuvenlink 2005).

A large variation however exists in the prescribed nutrient application rates for optimum yield and quality of soilless grown crops. In a review of the relevant literature Dorais et al. (2001) concluded that for tomatoes (*Solanum lycopersicum*), a much studied crop as a model system for plant physiology, the electrical conductivity (EC, mS cm^{-1}) of the applied nutrient solution, should be between 2.3 – 5.1 mS cm^{-1} for optimal fruit yields whereas the fruit quality will be improved at EC values between 3.5 and 9.0 mS cm^{-1}. The osmotic effect of high EC can result in a reduction in the water flow to the fruit and reduce the rate of fruit expansion, resulting in significantly smaller fruit. Although it is generally believed that higher ECs are needed for optimum yield and quality a reduction of the macronutrient concentrations in the nutrient solution of up to 25% had no detrimental effect on tomato yield or fruit quality (Siddiqi et al. 1998) and a 40% reduction in nutrient solution concentration enhanced marketable production of peppers (Giuffrida and Leonardi 2012). Only when the nutrient solution concentration was reduced to 10% of what is recommended was a 30% yield reduction noted.

The ratio of nutrients (especially the cations potassium (K^+), calcium (Ca^{2+}), and magnesium (Mg^{2+})) in the nutrient solution is also known to affect crop growth, yield and fruit quality (Roorda van Eysinga and Smilde 1981). The K:N ratio of the nutrient solution can be used to control tomato crop growth and production (Papadopoulos and Khosla 1992). The nutrient uptake ratio of K to N for tomato ranges between 1:1 and 2.5:1 (Tapia and Gutierrez 1997) and increasing the K^+ in the nutrient solution can improve fruit quality through increasing the sugar and organic acids content of the fruit (Flores et al. 2003). A high NH_4^+: total N ratio can however also inhibit K^+ uptake by plants (Allen and Raven 1987). The number of fruit with blossom end rot (BER), a physiological disorder often associated with greenhouse tomatoes is also significantly higher when a larger percentage of the total applied N is in the form of NH_4^+.The uptake and translocation of sufficient calcium to the tomato fruit is crucial to prevent blossom end rot (BER) and one of the main factors resulting in BER is antagonism between the cations in the nutrient solution (Dong et al. 2004). However, under saline conditions the addition of NH_4^+ in the nutrient solution has been found to positively influence fruit yield (Ben-Oliel et al. 2004) and the flavour of the fruits might be enhanced if the NH_4^+ levels make up 10% of the total applied N.

When re-using drained nutrient solution the absolute concentration (EC) as well as the balance between the ions will start deviating from the specific target values due to the selectivity in uptake of ions by plant roots (Voogt 1993). As the time period of recirculation increases, the imbalance will intensify (Carmassi et al. 2002) resulting in osmotic effects and antagonism between ions, reducing the ability of a plant to take up water and nutrients. Ultimately this will result in a reduction in growth, yield and photosynthetic activity (Roorda van Eysinga and Smilde 1981; Munns 2002; Carmassi et al. 2007). To maintain the composition of the nutrient solution in a closed system closer to target values, frequent monitoring and adjustment is needed (Combrink and Kempen 2011). In addition it may be possible to anticipate deviations from the target values based on nutrient uptake data and to use this information to adjust the composition of the nutrient solution.

Although tomato is one of the most studied crops in terms of growth and development, most research on biomass production and partitioning has been done under temperate conditions (Heuvenlink 2005). The aim of this study was therefore to determine the effect of nutrient solutions differing in concentration and ion balance, that may occur when drained nutrient solution is re-used, on crop growth, assimilate partitioning and fruit quality of two tomato cultivars differing in their tolerance to salinity. This will enable the identification of upper and lower levels of EC and nutrient concentrations for nutrient solutions in re-circulating systems with coir grown tomatoes.

Methods and materials

Plant material and growth conditions

Six weeks after germination tomato (*Solanum lycopersicon* Mill. cvs. MFH 9343 and FA593, Sakata, South Africa) seedlings were transplanted to 5L plastic containers filled with nutrient solution. The cultivars differed in their salt tolerance; FA593 has a high salinity tolerance while MFH 9343 is sensitive to high salinity (Personal communication, J Stronkhorst, Sakata Seed, South Africa, 2009). The containers were closed to prevent evaporation and the nutrient solution was aerated continuously.

Trials were done in a temperature controlled glasshouse in Stellenbosch, from May 2009 to December 2010. The glasshouse temperature was set to 20 / 28^{O}C (night / day temperature). Temperature (^{O}C), relative humidity (RH), light intensity (µmol m^{-2} s^{-1}, PAR) and CO_2 concentration was logged throughout the trial. Midday photosynthetic photon flux density (PAR) ranged from 300 to 1500 µmol m^{-2} s^{-1} and the humidity remained between 60 and 85%. Plants were pruned to a single stem with side shoots removed once a week. All trusses were pruned to six fruit per truss as soon as fruit set was complete.

Treatments

Two separate trials each with a set of treatments were assessed. In the first trial, five nutrient solutions was used where the ratio between nutrients was kept constant but the concentration i.e. the EC (electrical conductivity, mS cm^{-1} (25 °C)) was the altered. The EC's of the nutrient solutions were 0.8, 1.6, 2.4, 3.2 and 4.00 mS cm^{-1} (Table 1). In the second part, three EC treatments (EC 0.8, 2.4 and 4.0 mS cm^{-1}) were combined with three macro nutrient ratio combinations (Standard, Re-use A and re-use B) (Table 1), based on the change in the concentration of nutrients in leached nutrient solutions observed in previous trials (unpublished data).

Growth and development parameters

For each of the two trials at 35 days after planting (DAP) and again at 71 DAP, 3 plants per treatment combination was harvested, the leaf area, stem and leaf fresh and dry weights as well as the chemical composition of leaves 3-5 from the apex determined. Leaf samples consisted of both petioles and leaflets. To determine assimilate partitioning the fresh and dry weight of the leaves, stems and roots were determined at the last destructive harvest, 71 DAP after drying in an oven for 72 hours at 80^{O}C. The leaf area and shoot dry weight of the side shoots were determined with every pruning. The leaf area was measured and the specific leaf area (SLA, m^2 kg^{-1}) determined as the total leaf area per leaf dry weight.

To assess plant growth the relative growth rate (RGR, mg g^{-1} d^{-1}) was determined as:

$$RGR = 1000 * [\ln W(tx) - \ln W(tx^{-1})] / [tx - tx^{-1}]$$

where W is the dry mass (g), and tx and tx^{-1} refer to the sampling days (0, 35 and 71 DAP).

Table 1. Macro-nutrient composition (meq L^{-1}) of the feeding water (municipal water) and the final nutrient solutions of two sets of nutrient solutions used to determine the nutrient and water uptake of tomato plants. In trial 1 different ECs were used whereas in trial 2 the macro-nutrient ratios were varied.

Trial 1

	NH_4^+	K^+	Ca^{2+}	Mg^{2+}	NO_3^-	$H_2PO_4^-$	SO_4^{2-}
				Municipal water			
	0.05	0.01	0.17	0.03	0.01	0.01	0.04
EC (mS cm^{-1})				**Nutrient solutions**			
0.8	0.4	2.8	3.4	1.4	5.0	0.6	2.4
1.6	0.8	5.6	6.8	2.8	10.0	1.2	4.8
2.4	1.2	8.4	10.2	4.2	15.0	1.8	7.2
3.2	1.6	11.2	13.6	5.6	20.0	2.4	9.6
4.0	2.0	14.0	17.0	7.0	25.0	3.0	12.0

Trial 2

EC (mS cm^{-1})	**Nutrient ratio**	NH_4^+	K^+	Ca^{2+}	Mg^{2+}	NO_3^-	$H_2PO_4^-$	SO_4^{2-}
0.8	Standard	0.4	2.8	3.4	1.4	5.0	0.6	2.4
	Re-use A	0.6	3.1	2.9	1.4	6.0	0.5	1.5
	Re-use B	0.8	3.4	2.4	1.4	7.0	0.4	0.6
2.4	Standard	1.2	8.4	10.2	4.2	15.0	1.8	7.2
	Re-use A	1.8	9.3	8.7	4.2	18.0	1.5	4.5
	Re-use B	2.4	10.2	7.2	4.2	21.00	1.2	1.8
4.0	Standard	2.0	14.0	17.0	7.0	25.0	3.0	12.0
	Re-use A	3.6	15.5	14.5	7.0	30.0	2.5	7.5
	Re-use B	4.0	17.0	12.0	7.0	35.0	2.0	3.0

Micronutrients were applied at a constant concentration of 40.6 µmol L^{-1} Fe^{3+}; 35.0 µmol L^{-1} $H_2BO_3^-$, 4.6 µmol L^{-1} Zn^{2+}; 3.6 µmol L^{-1} Cu^{2+}; 10.9 µmol L^{-1} Mn^{2+}. Since this trial was terminated at 71 days after planting and only fruit from the first two trusses were matured, the nutrient solution was kept at the formulation recommended for vegetative and early fruit growth (Voogt 1993).

Fruit quality parameters

Red ripe fruit from the first two trusses were harvested twice weekly, graded as marketable or unmarketable fruit based on size and presence of physiological disorders and the number and weight of fruits with blossom end rot determined. The taste-related quality attributes were also determined. The total soluble solid (TSS, ^{O}Brix) content was determined using a refractometer (Atago, Japan) and on 71 DAP fruit were oven dried at 70^{O}C for 72 hours to determine the dry weight and the elemental concentration. Titratable acidity (TA) was determined as citric acid in fresh juice by titration of tomato juice with 0.1M sodium hydroxide using a 862 compact titrosampler (Metrohm 862, Herisau, Switzerland) (Cliff et al. 2012). The lycopene content was determined spectrophotometrically at 474nm (Helios Omega UV-Vis Thermo Scientific, USA) after extraction with n-hexane: acetone (3:2 v v^{-1}), (Sharma and Le Mageur 1996).

Statistical analysis and experimental design

Each treatment combination was repeated six times in completely randomized trial. Analysis of variance (ANOVA) was used for evaluating data (STATISTICA 11.0, Statsoft (SA) Inc., Tulsa, Oklahoma, USA). Differences among the mean values were determined using using Fischer's LSD ($P<0.05$) equations. Statistical analysis was carried out using a general linear model for plant growth parameters. Plant growth parameters measured repeatedly throughout the trial were first transformed to their logarithm to avoid heteroscedacity before analysis.

Results and discussion

Plant growth and development

The nutrient solution EC had a significant effect on the growth and development of both cultivars. At 71 DAP the higher EC levels resulted in a reduction in total leaf area (leaf area from main stem and removed side shoots) for both cultivars. The total leaf area of the salt tolerant cultivar (FA593) was significantly higher than that of the salt sensitive cultivar (MFH 9343) at the lower ECs (0.8, 1.6 and 2.4 mS cm^{-1}) but not at an EC of 3.2 or 4.0 mS cm^{-1} (Figure 1). This was likely due to the decrease in side shoot development for FA593 compared to MFH9343 at an EC of 3.2 and 4.0 mS cm^{-1}. The leaf area index (LAI, m^2 leaf area m^2 ground area) of FA593 remained above 3 at all EC treatments while that of MFH9343 decreased to 2.2 and 2.0 at an EC of 3.2 and 4.0 mS cm^{-1} respectively. At a LAI of 3, 90% of the incident light will be absorbed. A LAI below 2 can negatively affect crop photosynthesis but at the same time a LAI of more than 4 will not have a beneficial effect on crop biomass accumulation (Heuvelink 2005). These results indicate that, depending on the specific cultivar a nutrient solution with an EC of 3.2 mS cm^{-1} and above can therefore potentially negatively affect growth through limiting the leaf area development.

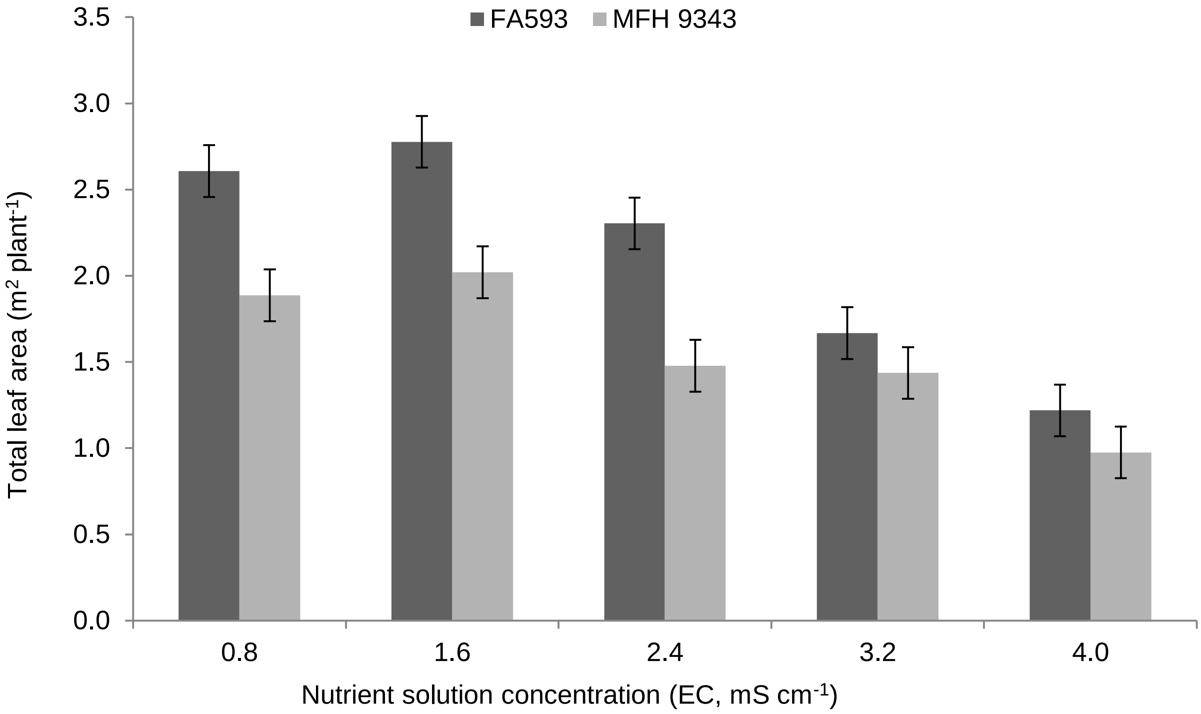

Figure 1. Total leaf area (m^2 $plant^{-1}$) at 71 days after planting (DAP) for two tomato cultivars (FA593 the salt tolerant cultivar and MFH 9343, the salt sensitive cultivar) grown hydroponically at different nutrient solution ECs. (Error bars indicate the LSD value at $p \leq 0.05$).

In this study the nutrient solution concentration had a significant effect on the RGR during early plant development. At 35 DAP the RGR for the salt sensitive cultivar (MFH9343) was significantly decreased as the EC was increased to 3.2 and 4.0 mS cm^{-1} while the RGR remained constant at all EC levels for the salinity tolerant cultivar (FA593) (Figure 2). The relative growth rate (RGR, mg g^{-1} d^{-1}) gives valuable information regarding crop growth especially during early plant development when growth is mainly vegetative. The decrease in leaf area and RGR of the salt sensitive cultivar (MFH 9343) at high nutrient solution ECs can delay the initiation of the first inflorescence as the rate of assimilate production will be reduced since the amount of assimilates available to the apex has to reach a certain amount before flower initiation can take place (Heuvenlink 2005).

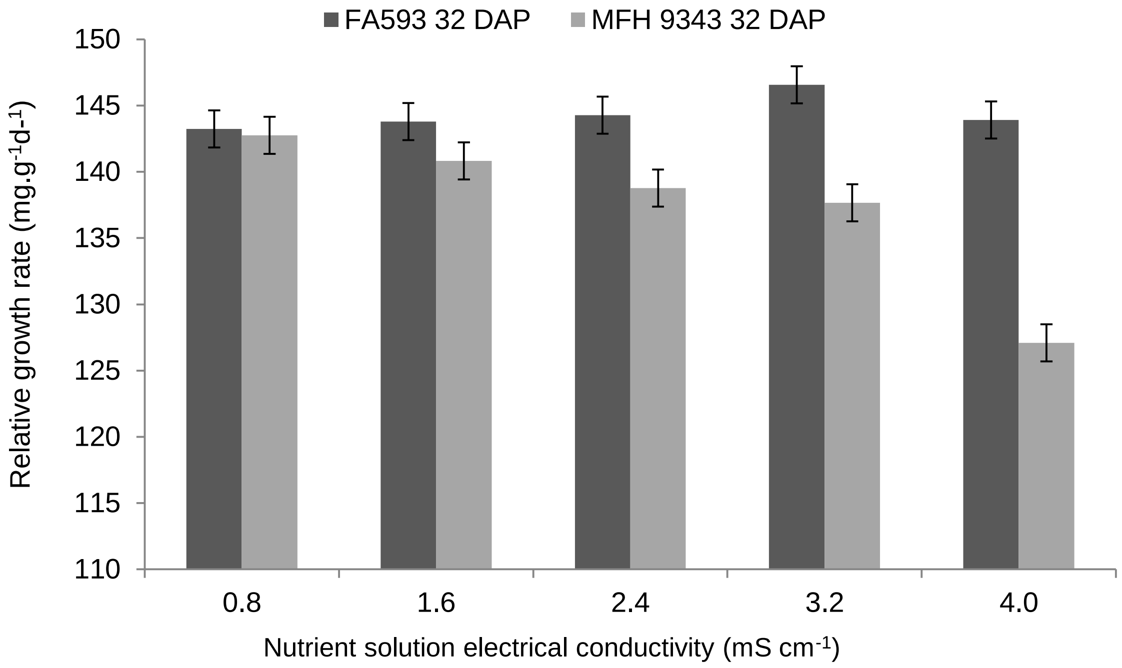

Figure 2. Relative growth rate (mg g^{-1} d^{-1}) at 35 days of growing two tomato cultivars in five nutrient solutions differing in EC (mS cm^{-1}). (Error bars indicate the LSD value at $p \leq 0.05$).

Biomass partitioning

A decrease in the root:shoot ratio and a changing pattern of biomass partitioning for the two cultivars evaluated was observed (Table 2). The salt tolerant cultivar (FA593) tended to allocate a smaller percentage of its biomass to the roots compared to the salt sensitive cultivar (MFH 9343). FA 593 had a reduction in biomass partitioning to the roots at the highest EC treatment (4.0 mS cm^{-1}) while the biomass allocation to the roots increased at the high EC treatment for MFH9343. At low nutrient availability, especially nitrogen, the dry matter partitioning to plant roots generally increase (de Groot et al. 2002). According Ehret and Ho (1986) a decrease in yield as a result of high salinity is directly related to the decrease in plant growth since the dry matter partitioning is not affected by salinity. In contrast these trials found significant differences at 71 DAP in growth and biomass partitioning between the cultivars as affected by the nutrient solution EC. The relationship between shoot weight and root weight is normally linear during early vegetative growth and as plants become more reproductive, the shoot growth rate increases faster compared to the root growth rate (Russel 1977; Heuvenlink 2005). Since there was no noticeable increase in biomass partitioning to the roots at the low EC treatment it can be concluded that under these conditions nutrient uptake did not become limiting at the EC of 0.8 mS cm^{-1}.

Biomass partitioning to the leaves was also reduced at higher ECs (Table 2). For cultivar MFH 9343 the biomass partitioning to the leaves was reduced at a EC of 2.4 mS cm^{-1} and higher, whereas biomass partitioning to the leaves only started decreasing at an EC of 3.2 mS cm^{-1} and higher for cultivar FA593. Partitioning between shoot and root is regulated by an equilibrium between root activity (water and nutrient absorption) and shoot activity (photosynthesis). The shoot:root ratio tend to be higher for plants grown with improved nutrition Heuvenlink 2005).

The stems of cultivar MFH 9343 was significantly thicker at an EC of 4.0mS cm^{-1} indicated by the high percentage of biomass allocated to this treatment combination (Table 2). For cultivar MFH9343 biomass partitioning to the fruit was reduced by the high EC treatment (4.0 mS cm^{-1}) while the biomass partitioning to the fruit increased at an EC of 3.2 and 4.0 mS cm^{-1} for cultivar FA593 (Table 2). This was primarily the result of both an increase in the average size of fruit for this cultivar with an increase in EC while the high EC (4.0mS cm^{-1}) resulted in a significant reduction in average fruit size for the saline sensitive cultivar (Figure 3). According to Heuvenlink (2005), salinity stress tends to favour generative development in tomato and young plants are often stressed to stimulate fruit development. These results are in agreement with this statement since on average 2.4 fewer leaves developed before the first inflorescence for both cultivars. The effect`t of high EC on fruit size will however result in a reduction in total yield

Table 2. Biomass partitioning ratio as affected by the nutrient solution electrical conductivity for two tomato cultivars (FA 593 and MFH 9343) at 71 DAP.

Cultivar	**EC (mS cm^{-1})**	**Root**	**Stem**	**Leaves**	**Fruit**
FA593	0.8	0.135d	0.157b	0.314bc	0.394cd
	1.6	0.126d	0.162ab	0.306bc	0.406cd
	2.4	0.144cd	0.146bcd	0.280c	0.431c
	3.2	0.127d	0.145bcd	0.237d	0.490b
	4.0	0.074e	0.147bcd	0.187e	0.592a
MFH 9343	0.8	0.183ab	0.129d	0.370a	0.318fg
	1.6	0.151cd	0.134cd	0.381a	0.334ef
	2.4	0.177ab	0.130d	0.319b	0.375de
	3.2	0.161bc	0.152bc	0.305bc	0.383cde
	4.0	0.202a	0.212a	0.321b	0.265g
LSD ($p \leq 0.05$)		0.025	0.021	0.034	0.054

Significant differences between cultivars for means are indicated by different letters in superscript.

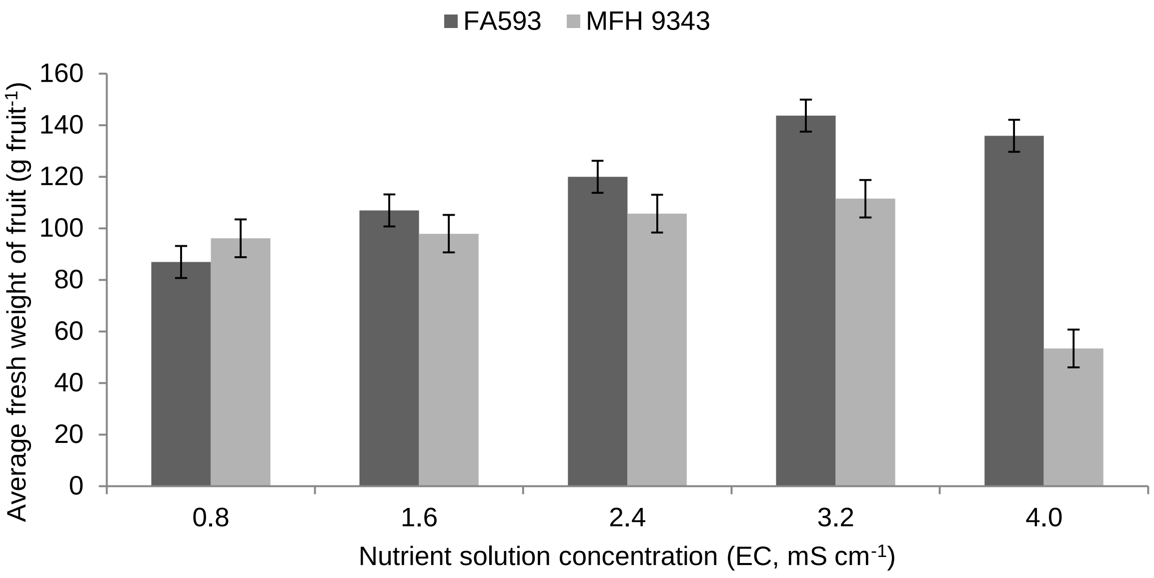

Figure 3. The average fresh weight of tomato fruit harvested from plants of two cultivars grown at five nutrient solution concentrations. (Error bars indicate the LSD value at $p \leq 0.05$).

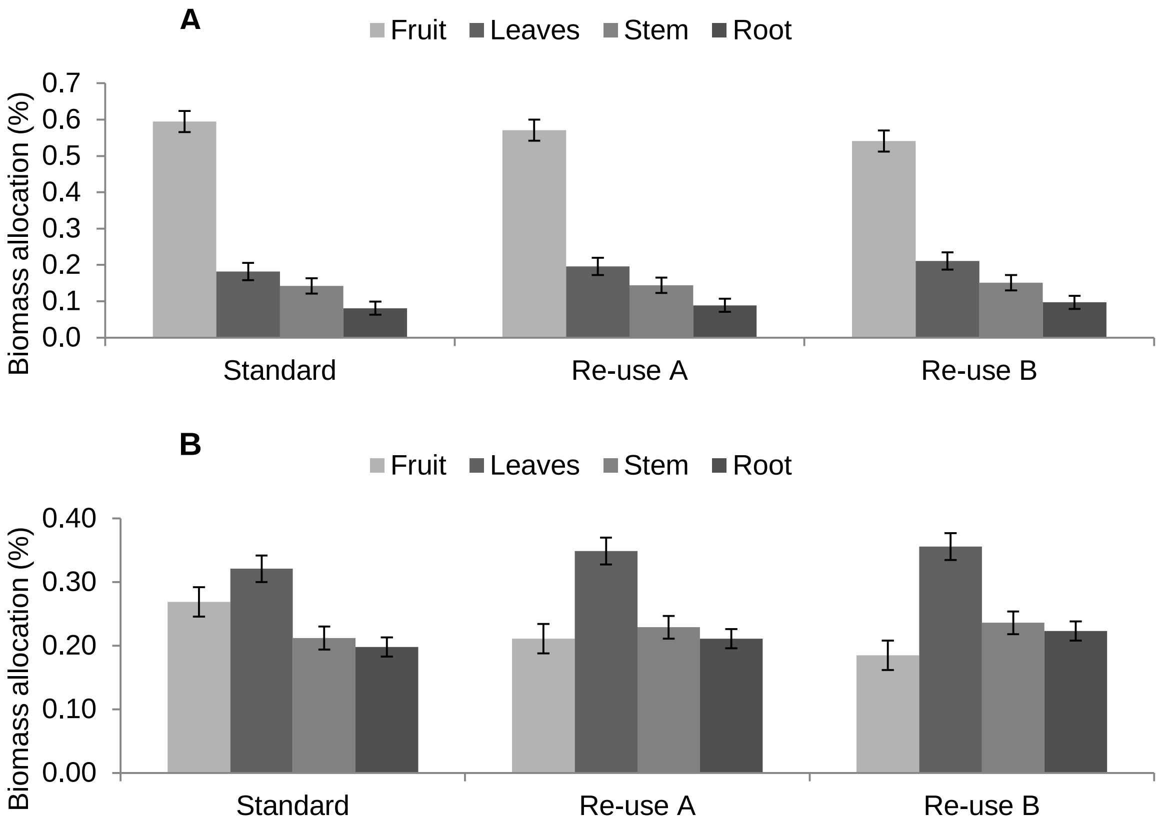

Figure 4. Biomass partitioning between the different plant organs when adjusting the macro-nutrient ratios in the nutrient solution in which tomato plants of two tomato cultivars were grown for 71 days. (Error bars indicate the LSD value at $p \leq 0.05$). A: Cultivar FA593; B: Cultivar MFH 9343.

When changing the ratios of the macro-nutrients in the second set of treatments (Table 1) a difference in biomass allocation was observed in favour of vegetative growth for both cultivars (Figure 4). This is probably due to the increase in both the NH_4^+ and the NO_3^{2-} concentration in both solutions Re-use A and Re-use B. Ammonium (NH_4^+) is often found to decline severely in the drained nutrient solution which can result in an increase in the pH if the solution is re-used without a pH adjustment (Savvas and Gizas 2002). The increase in nutrient solution pH can result in deficiencies of other nutrients, primarily Fe, Mn and P necessitating either a pH correction of the feeding water through application of an acid such as HNO_3 or an increase in the NH_4^+ concentration when re-circulating. Gent (2002) found that while supplemental NH_4NO_3 decreased tomato plant yield and fruit size, supplemental $Mg(NO_3)_2$ had no detrimental effect on yield and fruit size, and concluded that as long as the NH_4^+ concentration in the nutrient solution is not increased, an excess supply of N and K had little effect on tomato yield and quality. Although a shift towards vegetative growth was noticed, the suitability of these solutions in a re-circulating hydroponic system will have to be evaluated over a full growing season to determine the overall effect on yield and fruit quality.

The average fruit size decreased (Figure 3) while the dry matter content (%) and total soluble solids (TSS) (°Brix) increased for fruit from both cultivars with an increase in the nutrient solution EC (Table 3). Increasing the nutrient solution EC restricts the water transport to fruits and thus increases the TSS, as was also reported by Adams (1991). Increasing the nutrient solution's EC from 2 mS cm^{-1} to 4 mS cm^{-1} in an attempt to improve the sugar content of 'Daniela', one of the first "long shelf life" tomato cultivars grown in South Africa, resulted in an increase in the fruit's total soluble solids. The higher sugar content was however the result of less water being absorbed and not due to an increase in sugar production and was accompanied by a 30% reduction in yield and fruit size (Combrink 1998). The osmotic effect resulting from a high nutrient solution EC can reduce the ability of a plant to take up water, leading to a reduction in growth, yield, nutrient uptake, and photosynthetic activity (Munns 2002). Increasing the root zone salinity can also decrease the rate of fruit expansion (Johnson et al. 1992) and an increase in the fruit dry matter content of fruit, not as a result of an increase in fruit sink strength, but due to an increase in the starch concentration caused by enhanced sucrose unloading to the developing fruits (Heuvenlink 2005). A high EC is therefore often associated with a decrease in average fruit size, number of fruit per truss but also an increase in tomato fruit quality (Ehret and Ho

1986; Adams 1991; Dorais et al 2001; Olympios et al. 2003; Passam 2007). Although only the red-ripe fruit from the first two trusses were analysed results from this trial is in agreement with these reports. An increase in the titratible acidity (TA) of fruit was also observed with an increase in the nutrient solution EC for both cultivars (Table 3). The TA of the fruit is also an important contributor to the tomato taste and flavour and while organic acids only constitute 0.4% of the fresh fruit, variation in acid content has a greater impact on flavour than the sugar content (Heuvenlink 2005). The lycopene content of the fruit was significantly affected by the EC of the nutrient solution. For both cultivars the fruit lycopene content increased with an increase in the EC of the nutrient solution (Table 3). It is not clear if the increase in lycopene content is a result of a limitation in water uptake or as a result of altered metabolism in the fruit.

Table 3. Fruit quality parameters for fruit from two tomato cultivars as affected by the nutrient solution electrical conductivity for two tomato cultivars at 71 DAP.

Cultivar	**EC ($mS\ cm^{-1}$)**	**Dry matter content (%)**	**Total soluble solids ($^{O}Brix$)**	**Titratable acidity (TA) ($mmol.L^{-1}$)**	**Total lycopene content ($mg.kg^{-1}$)**
FA 593	0.8	6.12c	4.83e	14.12cd	71.23d
	1.6	6.95bc	5.12de	14.25cd	73.67cd
	2.4	8.03b	5.27de	15.29bc	76.98abc
	3.2	9.85a	5.97bcd	15.94ab	77.12abc
	4.0	10.76a	6.86ab	16.78a	79.13ab
MFH9343	0.8	6.34c	4.99de	13.81d	69.34d
	1.6	7.12bc	5.35cde	14.32cd	70.22d
	2.4	7.95b	5.67cde	14.96bcd	72.64cd
	3.2	10.13a	6.19abc	15.74ab	76.32bc
	4.0	10.89a	7.03a	16.12ab	81.34a
LSD ($p\leq0.05$)		1.51	0.91	1.34	4.51

Significant differences between cultivars for means are indicated by different letters in superscript.

The ratios of macro nutrients in the solutions tested also had a significant effect on tomato fruit quality. The dry matter %, TSS, TA and lycopene content tended to increase in both the re-use solutions for both cultivars although the differences were not in all cases statistically significant (Table 4). The dry matter % was only significantly higher for fruit from solution Re-use B compared to the standard solution at the higher EC level of 4.0mS cm^{-1} for cultivar FA593. The TSS was significantly higher for fruit from both cultivars in solution Re-use B at an EC of 4.0 mS cm^{-1} while the TA seems to be primarily affected by the total concentration of the nutrient solution since the only significantly difference was between the EC 2.4mS cm^{-1} and 4.0mS cm^{-1} treatments for both cultivars.

At an EC of 2.4 mS cm^{-1} and 4.0 mS cm^{-1} the lycopene content of the fruit from both cultivars was higher for plants using solution Re-use B compared to the standard solution and solution Re-use A (Table 4).

Table 4. Fruit quality parameters for fruit from two tomato cultivars as affected by the nutrient solution cation and anion ratios for two tomato cultivars at 71 DAP.

Cultivar	**EC (mS cm^{-1})**	**Nutrient ratio**	**Dry matter content (%)**	**Total soluble solids (^{O}Brix)**	**Titratable acidity (TA) (mmol L^{-1})**	**Total lycopene content ($mg.kg^{-1}$)**
	0.8	Standard	6.19f	4.83e	14.02fg	71.19gh
		Re-use A	6.14f	4.85e	14.09fg	71.26gh
		Re-use B	6.09f	4.91e	14.49efg	76.9ef
FA 593	**2.4**	Standard	8.1e	5.19de	15.18def	76.83ef
		Re-use A	8.5de	5.25de	15.27def	79.38e
		Re-use B	8.7de	5.32de	15.91bcd	88.21bc
	4.0	Standard	9.5cd	6.79c	16.73ab	79.18e
		Re-use A	10.8abc	7.34abc	17.19ab	84.96cd
		Re-use B	11.9a	7.82a	17.73a	97.41a
	0.8	Standard	6.26f	4.91e	13.74g	69.23gh
		Re-use A	6.3f	4.84e	13.69g	67.32h
		Re-use B	6.29f	4.95e	13.81g	71.34gh
MFH 343	**2.4**	Standard	7.84e	5.71d	14.92defg	72.54fg
		Re-use A	7.89e	5.75d	15.11def	77.9e
		Re-use B	7.9e	5.85d	15.39cde	89.91b
	4.0	Standard	10.45bc	6.99b	16.16bcd	81.41de
		Re-use A	10.56abc	7.59ab	16.63abc	89.43bc
		Re-use B	10.98ab	7.91a	17.05ab	98.31a
LSD ($p \leq 0.05$)			1.35	0.72	1.28	4.78

Significant differences between cultivars for means are indicated by different letters in superscript.

The K^{+} application level in solution Re-use B was substantially higher compared to the other two nutrient solutions used (Table 1). Potassium plays an essential role in the plants osmotic regulation and water uptake and its uptake is linked to fruit development and fruit load (Marschner 1995). These results are in agreement with other studies that indicated that increasing the K^+ concentration in the nutrient solution from 3.4 meq L^{-1} to 14.2 meq L^{-1} increased the fruit dry matter % , TSS and the lycopene and carotenoid content and and a decrease in uneven ripening of the tomato fruit. (Dorais 2001; Fanasca et al. 2006). A high supply of total N in the nutrient solutions has also been linked to a decline in the tomato fruit quality in terms of a reduction in the sugar content, pH, soluble solids, glucose and fructose content, as well as the ratio of reducing sugars to total solids (Parisi et al. 2006.) Since these negative effects was not noticed in this trial when increasing both NH_4^+ and NO_3^- concentration in solutions Re-use A and Re-use B, it can be concluded that the levels used are still below the threshold level where fruit quality will be negatively affected for these two cultivars. Also including part of the total nitrogen in the form of NH_4^+ may again improve fruit quality through an increase in the content of sugars and organic acids (Flores et al. 2003) possibly explaining the observed increase in fruit quality when using solutions Re-use A and Re-use B. The titratible acidity of tomato fruit is also affected by the K^+ concentration in the nutrient solution (Claussen et al. 2006). Very high K^+ applications have however also been associated with an increase in the number of fruit with BER, associated with reduction in the Ca^{2+} content of tomato fruit (Bar-Tal et al. 1996).

The lower Ca^{2+} concentration in the re-use solutions (Table 1) did not appear to negatively affect the fruit quality. Marín et al. (2009) also found that the Ca^{2+} concentration in the nutrient solution did not affect the dry weight or TSS content of pepper fruit. The uptake and translocation of sufficient Ca^{2+} to the tomato fruit is however crucial to prevent blossom end rot (BER), a physiological disorder often associated with greenhouse tomatoes. A high EC or K^+ concentration can influence the Ca^{2+} uptake of plants (Bar-Tal and Pressman 1996; Adams 2002) but since no BER was noted on any of the harvested fruit it can be concluded that the EC as well as the K^+ concentrations evaluated did not result in a noticeable Ca^{2+} deficiency in the fruit.

Conclusion

When re-using the nutrient solution in a closed soilless production system the concentration and the composition will start to deviate from the original solution based on target values for a specific crop. Adjusting the concentration and composition of the nutrient solution might limit these deviations but it should still allow for optimal growth, yield and tomato fruit quality. These results showed that a high rootzone EC (3.2 mS cm^{-1} and 4.0mS cm^{-1}) can potentially limit leaf area development and the RGR of tomato plants and therefore their ability to produce assimilates especially cultivars in that are not tolerant to salinity. This can even result in a delay in the formation of the first inflorescence. Increasing the total-N and K^+ concentration and reducing the SO_4^{2-} concentration in the nutrient solution resulted in more vegetative plants and at the same time increased the fruit quality. This effect was more pronounced at a higher nutrient solution EC. In a re-circulating system both solution Re-use A or Re-use B can be used for growing tomatoes although care should be taken at high ECs as total yield can be negatively affected. Ultimately this information will assist in simulating crop nutrient demand necessary for model based regulation of water and fertilizer application to crops to optimize yield and fruit quality.

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Chapter 3

The influence of solar radiation levels on the water and nutrient uptake, biomass production and partitioning of hydroponically grown tomatoes.

Article 3

Relating solar radiation to crop water and macro-nutrient uptake.

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Abstract

In a closed soilless production system the continual recycling of the nutrient solution will results in nutrient imbalances that need to be adjusted to prevent losses in crop growth and yield. Since nutrient uptake is not constant but is related to the growth rate, climatic factors such as radiation input which is one of the most important driving factors are expected to influence the uptake of nutrients. Although water uptake is linked to solar radiation level, different physiological processes are involved in water and nutrient uptake. In this study, tomato plants were grown in a water culture during two seasons and modified solar radiation levels by the use of shade netting and by using 5 different nutrient solution concentrations. The short-term (3 hour) water and macro-nutrient uptake was determined. The uptake of all the ions increased with an increase in the solar radiation levels and for NO_3^-, K^+ and $H_2PO_4^-$ the uptake rate was higher at higher nutrient solution concentrations. The only macro-nutrient showing a good correlation with water uptake was Ca^{2+} at all nutrient solution concentrations and over the range of solar radiation levels tested. Under low solar radiation levels a good correlation between the uptake of macro-nutrients was observed but under high solar radiation levels this pattern was not present. Incorporating daily solar radiation levels in models used to predict nutrient changes will result in a more accurate method to control nutrient application should therefore lead to a more integrated greenhouse management system, in harmony with the regulation of water and carbon fluxes at the crop level.

Keywords: electrical conductivity (EC), nutrient solution, nutrient uptake, soilless production, solar radiation

Introduction

The soilless cultivation of crops is increasingly being done in closed re-circulating systems where the nutrient rich water drained from the growing system is re-used. This reduces pollution of the surface and ground water and can result in substantial fertilizer savings (Raviv and Lieth 2008)**.** Continual nutrient recycling of the nutrient solution and control based only on the electrical conductivity of the nutrient solution results in nutrient imbalances since the concentration of ions will start deviating from the specific target values as a result of selective uptake of ions (Voogt 1993). Over time this imbalance will increase, resulting in a negative effect on plant growth and yield (Zekki et al. 1996; Carmassi et al. 2002). It may also results in a decrease in the nutrient use efficiency of the system as the applied nutrient quantities may exceed the needs of the crop (Elings et al. 2004). Nutrient uptake is not constant but is related to the growth rate of the crop (Marcelis et al. 2009). To adjust nutrient supply to crops, demand factors affecting crop growth and nutrient uptake should also be considered. This includes environmental conditions of which the radiation input or solar radiation level is one of the most important factors driving this (Voogt 1993). A limited supply of assimilates from the shoots to the roots can affect nutrient uptake and any environmental factor that will limit the production of assimilates, such as low light intensities can therefore have a negative effect on nutrient uptake. The water use of crops, due to transpiration, is also strongly linked to the solar radiation level (De Graaf and Esmeijer 1998) and an increase in the solar radiation level normally results in an increase in Water Use (WU) (Nemali and van Iersel 2004). But whereas nutrient uptake is driven by crop demand and growth rate, water uptake is driven by the difference in water-potential [Pa] and maintained by transpiration.

In practice, fertigation frequency in soilless systems is often determined from the water demand of plants which can be estimated from the solar radiation level. This includes the use of uptake concentrations (UC) (i.e., the ratio of ions to water taken up over time) to make recommendations regarding fertilizer applications (Sonneveld 2000) and modeling nutrient uptake using models for transpiration (Marcelis et al. 2009). This assumes that the requirements for water and for minerals are always interrelated. Although long-term data can support this hypothesis (Schacht and Schenk 1990; Bar-tal et al. 1994) short-term experiments indicate that the ratio of water to nutrients up-take differ with the time of day (Le Bot 1991; Ferrario et al. 1992; Delhon 1995; Li et al. 2013). In warmer climates growers also experience sudden increases in the rootzone EC which can potentially damage crops and often necessitates flushing of the growing media which results in a poor nutrient use efficiency (van Noordwijk 1990). This happens during times when the plant water demand increases more than the nutrient demand (Le Bot 1998). Studies with wheat and maize also showed that there is no direct correlation between the WU of these crops and nutrient uptake (Tanner and Beevers 1990; Barthes et al. 1995). Although transpiration drives the transport of most mineral ions from the soil layers to the roots, when modeling nutrient uptake in plants ion uptake and transport should be considered separately from water uptake as it is governed by separate physiological processes (Le Bot 1998). The N use of crops has been shown to be affected by the solar radiation level and independent of variations in transpiration (Delhon 1995). Martinez et al. (2004), found a correlation between the cumulated solar radiation and the NO_3^- uptake rate as well as a correlation between the NO_3^- uptake rate and nutrient solution temperature. Fruit yield is also directly proportional to the accumulated solar radiation. Cockshull et al. (1992) found that during the first 14 weeks of harvest 2.01 kg fresh weight of fruit was harvested for every 100 MJ of solar radiation incident on the crop and for the remainder of the growing period 2.65 kg fruit fresh weight per 100 MJ was obtained. Mechanistic models such as Michaelis–Menten kinetics are typically used to express ion uptake mathematically. This is based on the fact that ion transporters are specific membrane-bound proteins for each individual ion and in a similar way enzymes are for a specific substrate (Bassirirad 2000). The algorithm used by Papadopoulos and Liburdi (1989) to calculate the adjustments in nutrients in the standard nutrient solution based on the solar radiation level, relative humidity and temperature is an example of modeling nutrient uptake in relation to the micro-climate although still very general as it only takes into consideration average daily light integral, temperature and relative humidity.

In order to ultimately simulate crop nutrient demand necessary for model based regulation of water and fertilizer application to crops it is necessary to determine the effect of climatic factors, specifically solar radiation level, on the uptake of macro nutrients in a soilless system using tomato as a model crop. The aim of this study was therefore to investigate the rate of macro-nutrient and water uptake at different solar radiation levels and different nutrient solution concentrations under conditions where the rate of uptake is not limited by chemical or physical properties of a growing medium.

Material and methods

Plant material and growth conditions

Six week old tomato (*Lycopersicon esculentum* Mill. cvs. FA593, Sakata, South Africa) seedlings, germinated in a mix containing vermiculite, perlite and coco-peat were transplanted to 5L closed plastic containers filled with nutrient solution. The nutrient solution was aerated continuously. Trials were done in a temperature controlled glasshouse in Stellenbosch during winter, from 17th May 2010 to 25th July 2010 and during summer, from 13th October 2010 to 31st December 2010. During winter the glasshouse temperature was set to 18 / 24^{O}C (night / day temperature) and during summer to 20 / 28^{O}C (night / day temperature). Although there was a difference in the air temperatures between the seasons that could have affected the growth rate of the crops, the nutrient solution temperature remained at an average of 22 ^{O}C during both seasons, limiting direct effects of temperature on nutrient uptake from the solutions. The total daily solar radiation (PAR) (MJ m^2 day^{-1}) inside the glasshouse during winter ranged from 6 to 11 MJ PAR m^{-2} while it ranged between 18 and 26 MJ PAR m^{-2} during summer (figure 1). The relative humidity (RH) varied between 60 and 85% during the experimental period. Plants were pruned to a single stem with side shoots removed once a week. All trusses were pruned to six fruit per truss as soon as fruit set was complete.

Treatments

Plants were grown at different solar radiation levels during winter and summer by placing plants either under no shade (full sunlight), 20% shade netting or 40% shade netting during each trial. Due to the difference in solar radiation levels during winter and summer this in effect gave a range of six solar radiation levels. The solar radiation treatments were combined with five macro-nutrient solution concentrations (EC, mS cm^{-1}). Plants were supplied with a solution adjusted for re-circulating systems based on earlier trials, with the ratio between nutrients kept constant. The pH of the nutrient solution was 5.8 and the EC's were 0.8, 1.6, 2.4, 3.2 and 4.0 mS cm^{-1} at 25^{O}C (Table 1). Micronutrients were applied at a constant concentration of 40.6 µmol L^{-1} Fe^{3+}; 35.0 µmol L^{-1} $H_2BO_3^-$, 4.6 µmol L^{-1} Zn^{2+}; 3.6 µmol L^{-1} Cu^{2+}; 10.9 µmol L^{-1} Mn^{2+}. Since this trial was terminated at 71 days after planting and only fruit from the first two trusses were matured, the nutrient solution was kept at the formulation recommended for vegetative growth and not adjusted to a formulation suggested during fruit development (Voogt 1993).

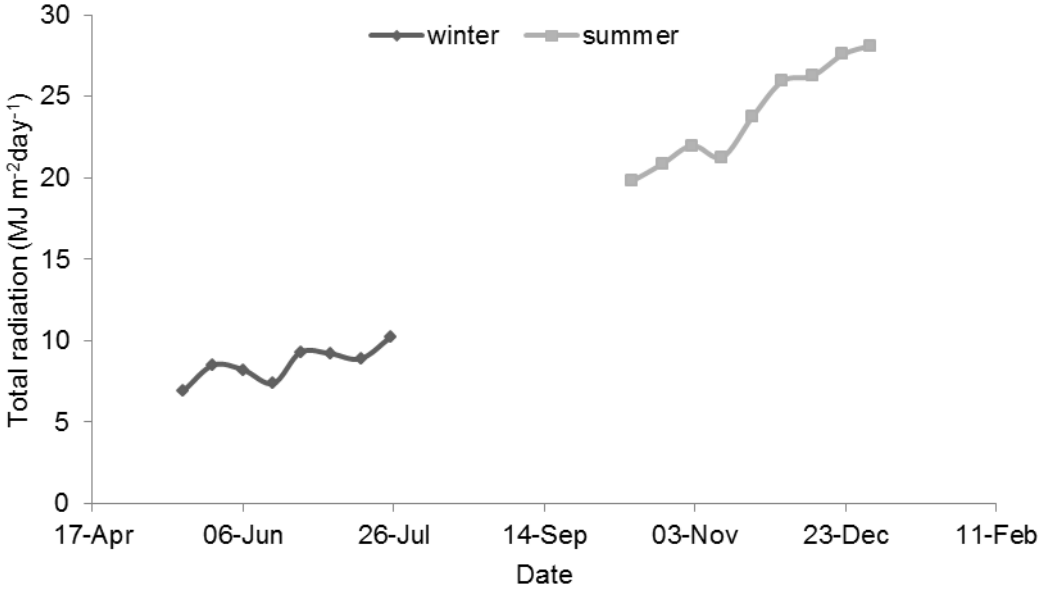

Figure 1. Total daily radiation (MJ m^{-2} day^{-1}) inside the glasshouse for the two seasons during which the trials were conducted. Points represent the mean of 10 days.

Water and nutrient uptake Nutrient uptake (Nu, mg m^2 hr^{-1}) and water uptake (Wu, ml m^2 hr^{-1}) was determined during week 3, 5 and 9 over a three hour period during midday (from 12:00 to 15:00). Nutrient uptake (Nu) was calculated by determining the depletion of macro-nutrients in nutrient solution sample through analysis using liquid chromatography (120 Dionex, USA). This was done for the starting and end solutions and Wu by determining the volume of nutrient solution needed to refill the container as there was no leaching and evaporation from the sealed containers was negligible.

At first the nutrient solution in the container was replaced with the reference nutrient solution every three days, after 3 weeks this was increased to every two days and after 5 weeks it was replaced daily. Changes in EC and pH were also recorded, prior to replacement of the solution. The frequent replacement of the nutrient solutions resulted in only minor variations in the pH and EC of the nutrient solutions.

Table 1. Macro-nutrient composition (meq L^{-1}) of the municipal water and the final nutrient solutions at different EC levels (mS cm^{-1}) used to determine the nutrient and water uptake of tomato plants.

	NH_4^+	**K^+**	**Ca^{2+}**	**Mg^{2+}**	**NO_3^-**	**$H_2PO_4^-$**	**SO_4^{2-}**
				Municipal water			
	0.05	0.01	0.17	0.03	0.01	0.01	0.04
EC (mS cm^{-1})				**Nutrient solutions**			
0.8	0.8	3.4	2.4	1.4	7.0	0.4	0.6
1.6	1.6	6.8	4.8	2.8	14.0	0.8	1.2
2.4	2.4	10.2	7.2	4.2	21.0	1.2	1.8
3.2	3.2	13.6	9.6	5.6	28.0	1.6	2.4
4.0	4.0	17.0	12.0	7.0	35.0	2.0	3.0

Using this data the Michaelis-Menten based model proposed by Mankin and Fynn (1996) relating individual nutrient uptake to intercepted photosynthetic photon flux density (PPFD) was evaluated. As radiation increases the rate of nutrient uptake follows a Michaelis-Menten type relationship (rectangular hyperbola). According to this model the actual plant nutrient uptake (U_n, mg m^2 hr^{-1}) can be calculated using the following equation:

$$U_n = U_{max}(PAR)/(K_m+PAR) \quad (1)$$

Where U_{max} = maximum rate of nutrient uptake (mg m^{-2} h^{-1})

PAR= solar radiation (µmol m^{-2} s^{-1})

K_m = Michaelis-Menten constant (the PPFD at ½U_{max})

The constant K_m, characteristic of each individual uptake rate, and U_{max} were determined by a reciprocal plot. The kinetic constants determined with the double-reciprocal plot were then used to draw the Michaelis-Menten plots for nutrient uptake.

The data collected on ion external concentration and uptake rates were fitted using nonlinear regression and to substantiate the correspondence between measured data and the Michaelis-Menten kinetics, nutrient uptake rates were analyzed by fitting the entire data set with Equation 1.

Statistical analysis and experimental design

Each treatment combination was repeated four times in a completely raqndomized trial. Multivariate analysis of variance (MANOVA) was used for evaluating data (STATISTICA 11.0, Statsoft (SA) Inc., Tulsa, Oklahoma, USA). Differences among the mean values were determined using using Fischer's LSD ($P<0.05$) equations.

Results and discussion

Uptake of macro nutrients in response to solar radiation

The uptake rate of individual macro nutrients as a function of the average solar radiation levels indicate that NO_3^- uptake increases with an increase in the solar radiation level and that the rate of the increase - the slope of the graph - is affected by the EC of the nutrient solution (Figure 2). At low solar radiation levels, up to 350 µmol m^{-2} s^{-1} the NO_3^- uptake rate increased more rapidly with an increase in available light whereas at higher solar radiation levels the uptake rate of NO_3^- tended to level off although a true leveling off was not observed during this trial. A decrease in photosynthesis, or the availability of sugars, transported from photosynthesizing leaves, has been linked to the control of NO_3^- uptake (Delhon et al. 1996). In another study it was observed that for crops with a low light requirement a maximum nitrogen uptake rate was observed at a relatively low PAR level of 400 µmol m^{-2} s^{-1} (Pang 1992). Although it is a C3 crop, tomatoes are adapted to high solar radiation levels and response curves show that net photosynthesis only approach light saturation at a photosynthetic photon flux density (PPFD) of 2200 µmol m^{-2} s^{-1} and photosynthesis tend to be linearly correlated with the leaf nitrogen content (Bolanos et al. 1991).

The phosphorus uptake rate also increased with an increase in the solar radiation level (Figure 2). The difference in $H_2PO_4^-$ uptake rate between the low and high nutrient solution EC was greater than for NO_3^-. As with the NO_3^- uptake rate, the solar radiation level through its effect on photosynthesis will influence the translocation of carbohydrates to the roots and this will also affect $H_2PO_4^-$ uptake since $H_2PO_4^-$ uptake is energy dependent and a portion of absorbed inorganic $H_2PO_4^-$ will be combined into organic molecules upon entry into the roots (Barker and Pilbeam 2007; Hammond and White 2011). Chang et al. (2014) also found $H_2PO_4^-$ uptake to increase with increasing solar radiation levels, under both P-sufficient and P-deficient conditions. Terabayashi et al. (1991) showed that the uptake of water and most macro-nutrients were higher in summer compared to winter in a temperature controlled greenhouse. Considering the results from the present study, the results shown by Terabayashi et al. (1991) might also be due to the higher solar radiation level during the summer.

A close relationship between the sulphate (SO_4^{2-}) uptake rate and solar radiation levels was also observed (Figure 2). Similar to what was seen with the other anions, the uptake of sulphate increased with an increase in solar radiation levels. Similarly to the uptake rate of NO_3^- and $H_2PO_4^{2-}$ the uptake rate appeared to start levelling off sooner when plants were grown at a lower EC level. Although the SO_4^{2-} uptake rate appeared to start levelling off at 600 µmol m^{-2} s^{-1} the maximum SO_4^{2-} uptake rate (U_{Smax}) determined with the Michaelis Menten equation will only be at 26.3 and 28.1 mg m^{-2} hr^{-1} at an EC of 0.8 and 4.0 mS cm^{-1} respectively.

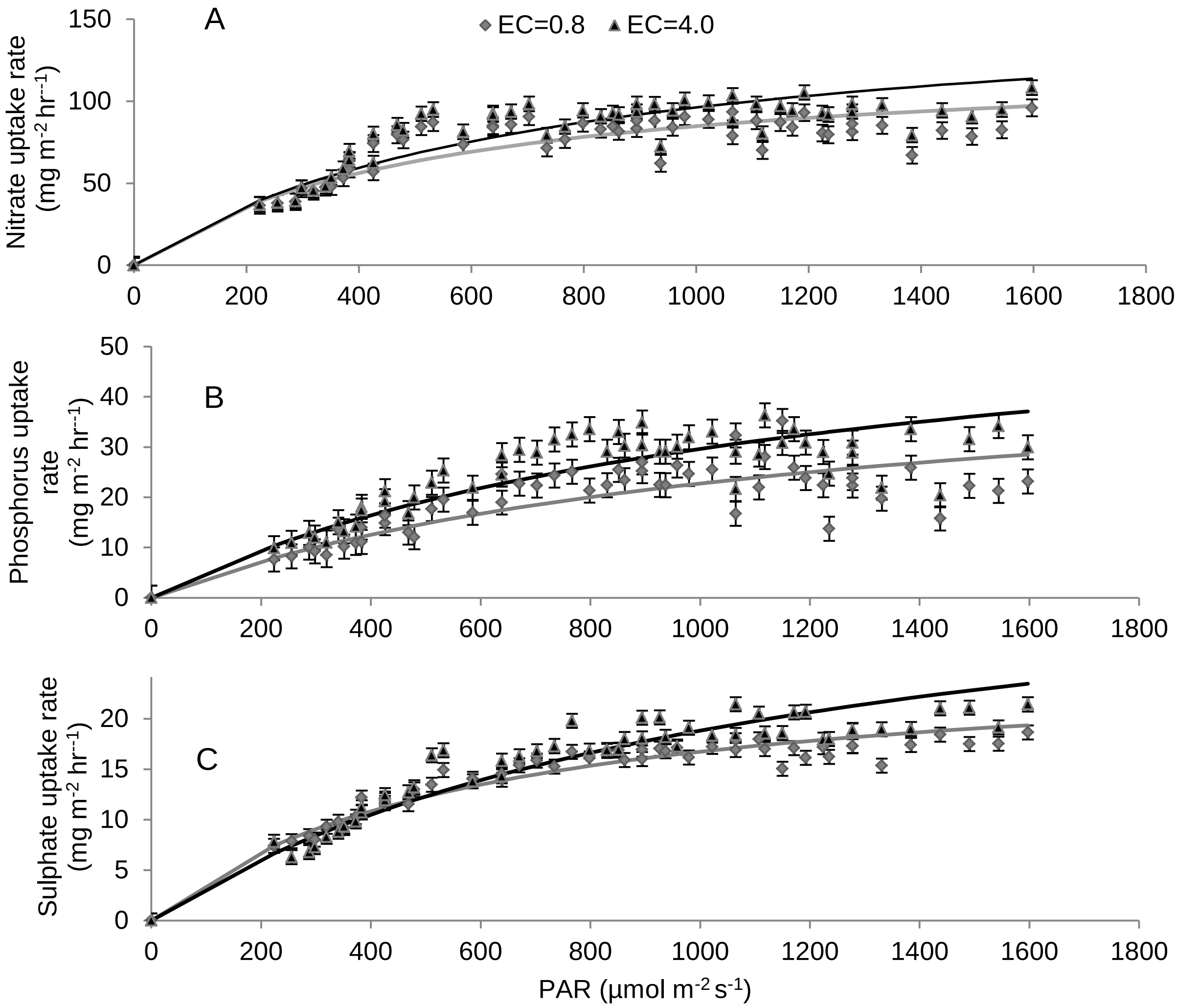

Figure 2. The uptake rate (mg m^{-2} hr^{-1}) of anions, A: nitrate (NO_3^-), B: phosphorus ($H_2PO_4^{2-}$) and C: sulphate (SO_4^{2-}) of young tomato plants at a two nutrient solution concentrations (EC 0.8 and 4.0 mS cm^{-1}) as a function of the solar radiation (µmol m^{-2} s^{-1}). Error bars indicate the LSD value at $p \leq 0.05$).

In agreement with findings by Adams and Grimmett (1986), a close relationship between the potassium (K^+) uptake rate by tomato plants and the solar radiation level was observed. The K^+ uptake rate increased with an increase in solar radiation levels but no significant difference was observed between the high and low EC treatments (Figure 3). The increase in K^+ uptake with an increase in solar radiation level was more linear compared to the nitrate uptake and no sign of levelling off was observed indicating that K^+ uptake will not saturate under these light conditions. Previous results did show a significant increase in the K^+ uptake with an increase in nutrient solution EC but in this study the K^+ uptake only tended to be higher for the high EC (4.0 mS cm^{-1}) nutrient solution at moderate light intensities (200 to 1200 µmol m^{-2} s^{-1}). Potassium absorption by plant roots are dependent on light energy as efflux of K^+ is observed from roots placed in the dark (Marschner 1995; Barker and Pilbeam 2007) but also K^+ influx into chloroplasts helps regulate the electron flow and thus increases the efficiency of transfer of light energy to chemical energy (Barker and Pilbeam 2007). The uptake of K^+ is therefore positively correlated to assimilate production in plants (Peoples and Koch 1979) and it can be expected that an increase in the rate of photosynthesis through an increase in available light will increase the uptake of K^+. The rate of photosynthesis and sugars in the shoot of Arabidopsis has also been linked to the rate of K^+ uptake by roots (Deeken et al. 2000) while Chu and Toop (1975) found that the diameter of tomato plant stems was affected significantly by K^+ levels and solar radiation level and a high K^+ level appeared to compensate for low light levels.

The magnesium (Mg^{2+}) uptake by the plants showed a response similar to that of other macronutrients to an increase in the solar radiation with uptake increasing with an increase in the light levels (Figure 3). There was however no significant difference between the low and high EC treatment and the Mg^{2+} uptake at both nutrient solution concentrations and the maximum Mg^{2+} uptake rate (U_{Mgmax}) determined with the Michaelis Menten equation was 15.1 and 15.6 mg m^{-2} hr^{-1} at an EC of 0.8 and 4.0 mS cm^{-1} respectively. As a central atom of the chlorophyll molecule it is expected that the uptake of Mg^{2+} will increase when factors promoting photosynthesis is enhanced, in this case available light energy. Illustrating the importance of Mg^{2+} to the plant as a part of the chlorophyll molecule, the proportion of the total plant Mg^{2+} bound in chlorophyll is in fact higher under low light conditions (Marschner 1995).

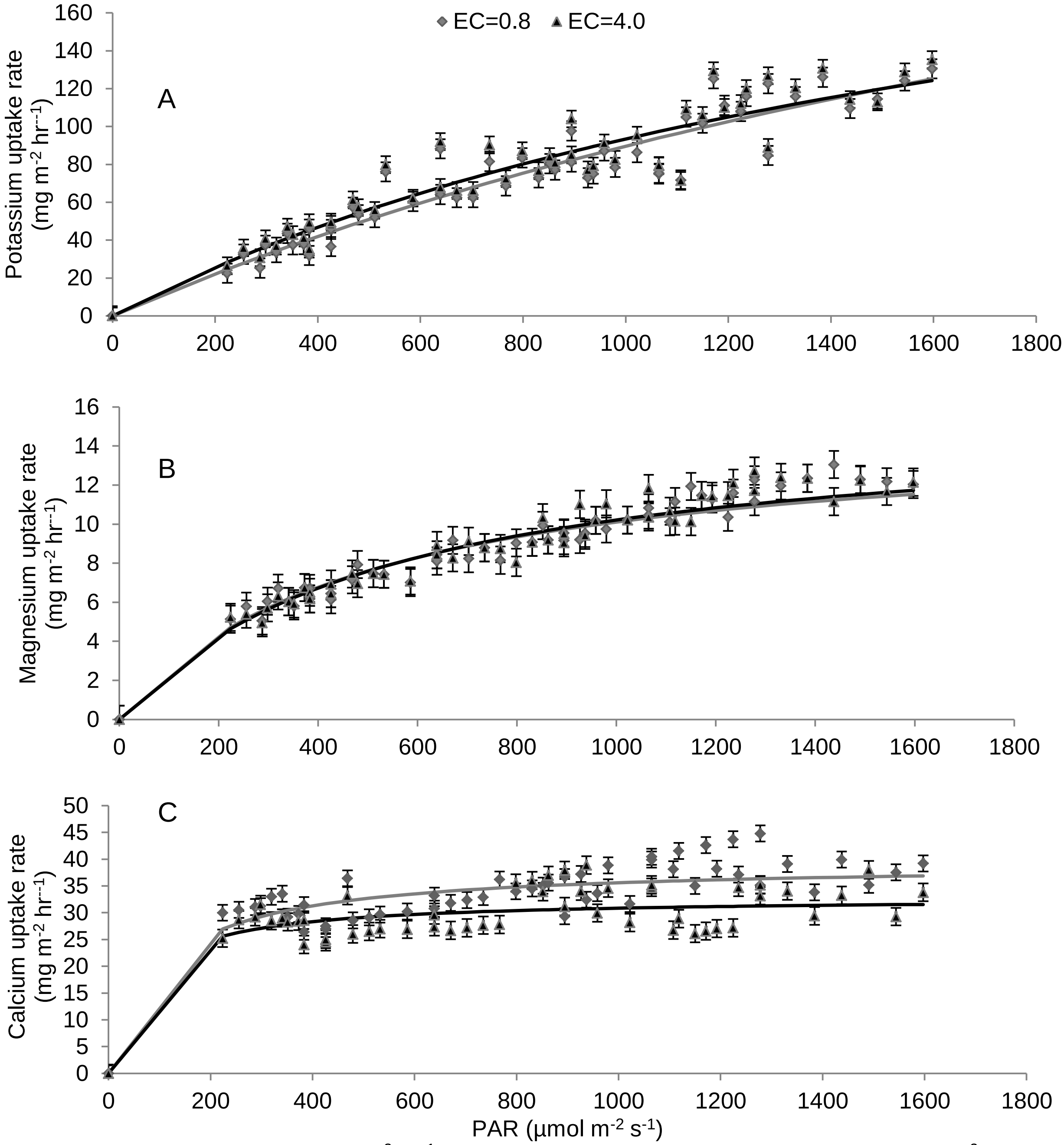

Figure 3. The uptake rate (mg m^{-2} hr^{-1}) of cations, A: potassium (K^+), B: magnesium (Mg^{2+}) and C: calcium (Ca^{2+}) of young tomato plants at a two nutrient solution concentrations (EC 0.8 and 4.0 mS cm^{-1}) as a function of the solar radiation (µmol m^{-2} s^{-1}). Error bars indicate the LSD value at $p \leq 0.05$).

The Ca^{2+} uptake showed a minor increase as the solar radiation level increased, which was not statistically significant (Figure 3). Although a reduction in Ca^{2+} uptake when the EC is increased is often found due to an increase in competing cations, especially K^+ (Sonneveld and Welles 2005) the Ca^{2+} uptake was also not significantly affected by the nutrient solution EC in this trial (Figure 3).

The findings above is supported by the correlation analysis of the data that revealed that during winter when the average daily solar radiation levels was 450 µmol m^{-2} s^{-1} the relationship between the solar radiation level and the uptake rate of all the macro-elements except for Ca^{2+} was strongly correlated (Table 2). However, during summer when the average daily solar radiation levels was significantly higher at 1250 µmol m^{-2} s^{-1} only the uptake rate of K^+ and Mg^{2+} showed a good relationship with the solar radiation levels (Table 2). Correlations between the uptake of the different macro nutrients and radiation levels were almost the same at low and high nutrient solution EC levels. At the higher solar radiation levels (summer) the correlation between Ca^{2+} uptake rate and solar radiation levels was a bit higher, also increased, but only at a the low EC levels.

Table 2. The coefficients of determination (R^2) denoting the variance between solar radiation levels and macro-nutrient uptake measured over a 3 hour period during midday during winter (May to July) and summer (October to December).

	Winter	
	EC 0.8 mS cm^{-1}	**EC 4.0 mS cm^{-1}**
NO_3^-	0.92	0.94
K^+	0.74	0.79
$H_2PO_4^-$	0.74	0.86
Mg^{2+}	0.72	0.86
SO_4^{2-}	0.92	0.92
Ca^{2+}	0.03	0.02
	Summer	
	EC 0.8 mS cm^{-1}	**EC 4.0 mS cm^{-1}**
NO_3^-	0.00	0.07
K^+	0.70	0.68
$H_2PO_4^-$	0.00	0.00
Mg^{2+}	0.88	0.78
SO_4^{2-}	0.47	0.50
Ca^{2+}	0.34	0.04

Ratio between water and nutrient uptake

The rate of water uptake by the plants was affected by the solar radiation levels as well as the EC of the nutrient solution (Figure 4). The water uptake rate increased with an increase in solar radiation only when plants were grown at a low EC of 0.8 mS cm^{-1}. At the relatively high EC (4.0 mS cm^{-1}), water uptake did not increase significantly with an increase in solar radiation levels. In their study

Schwarz and Kuchenbuch (1998) found a decrease in water uptake by tomato plants grown at different ECs (1 to 6 mS cm^{-1}). Under high solar radiation levels (22 MJ m^2 day^{-1}) this decrease in water uptake was greater than for plants at low solar radiation levels (9 MJ m^2 day^{-1}). They found that the reduction in water uptake at high EC levels was primarily caused by a reduction in the plant growth and especially the leaf area of the plants.

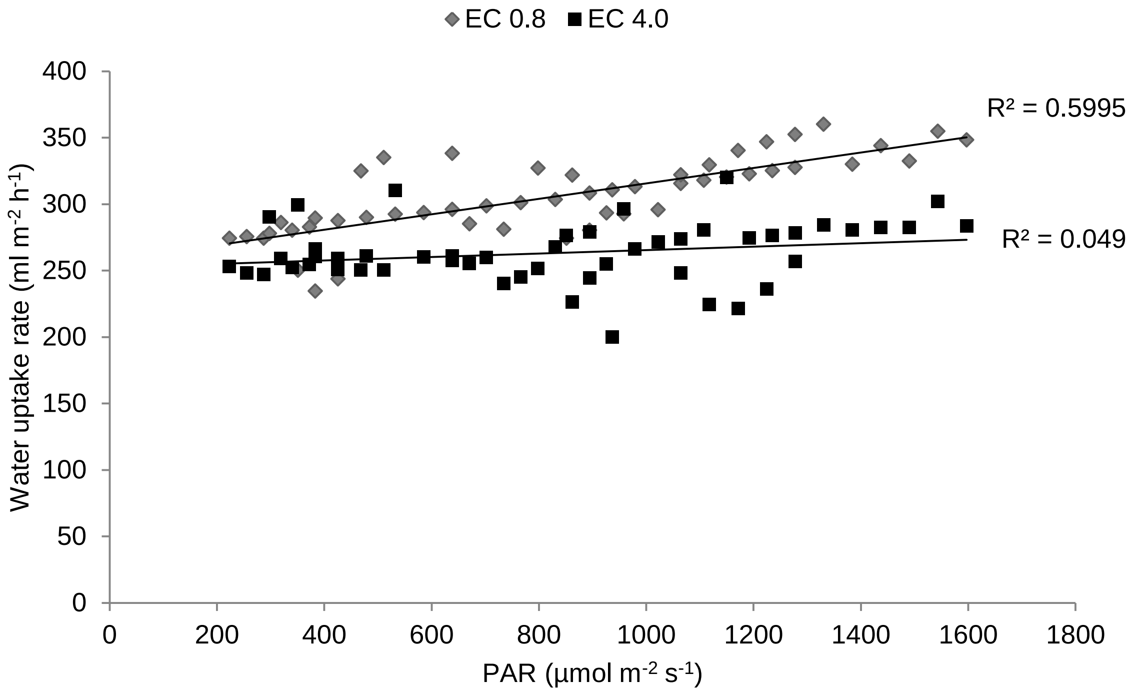

Figure 4. The water uptake rate (ml m^{-2} hr^{-1}) of young tomato plants at a two nutrient solution concentrations (EC 0.8 and 4.0 mS cm^{-1}) as a function of the solar radiation (µmol m^{-2} s^{-1}). Error bars indicate the LSD value at $p \leq 0.05$.

The water uptake rate over the 3-hour assay times did not show a good correlation with the uptake rates of most of the ions at either a high or low nutrient solution concentration (Figure 5 and 6). Although the water and ion uptake rate in this study was higher for plants at higher light intensities, the ion uptake rates tended to increase with an increase in EC unlike the water uptake rate that was lower at higher EC levels. This resulted in an inconsistency in the ratio between water and ion uptake ratios (mg ion taken up per ml of water over the same time period) (Figure 5 and 6).

While the NO_3^-, $H_2PO_4^{2-}$ and SO_4^{2-} uptake rate increased relatively fast with an increase in solar radiation during winter (solar radiation levels up to 480 µmol m^{-2} s^{-1}) and then started leveling off at higher solar radiation levels during summer (Figure 2), water uptake increased at a constant rate as the solar radiation levels increased (Figure 4). This resulted in the variation of the NO_3^-, $H_2PO_4^-$ and SO_4^{2-} uptake ratios as seen in Figure 5. The relationship between water and ion uptake has been debated for many years. Although Jensen (1962) found that NO_3^- and water absorption were positively correlated, others (Shaner and Boyer 1976; Schulze and Bloom 1984; Bower 2008) found that nitrate flux through the xylem was independent of the transpiration rate.

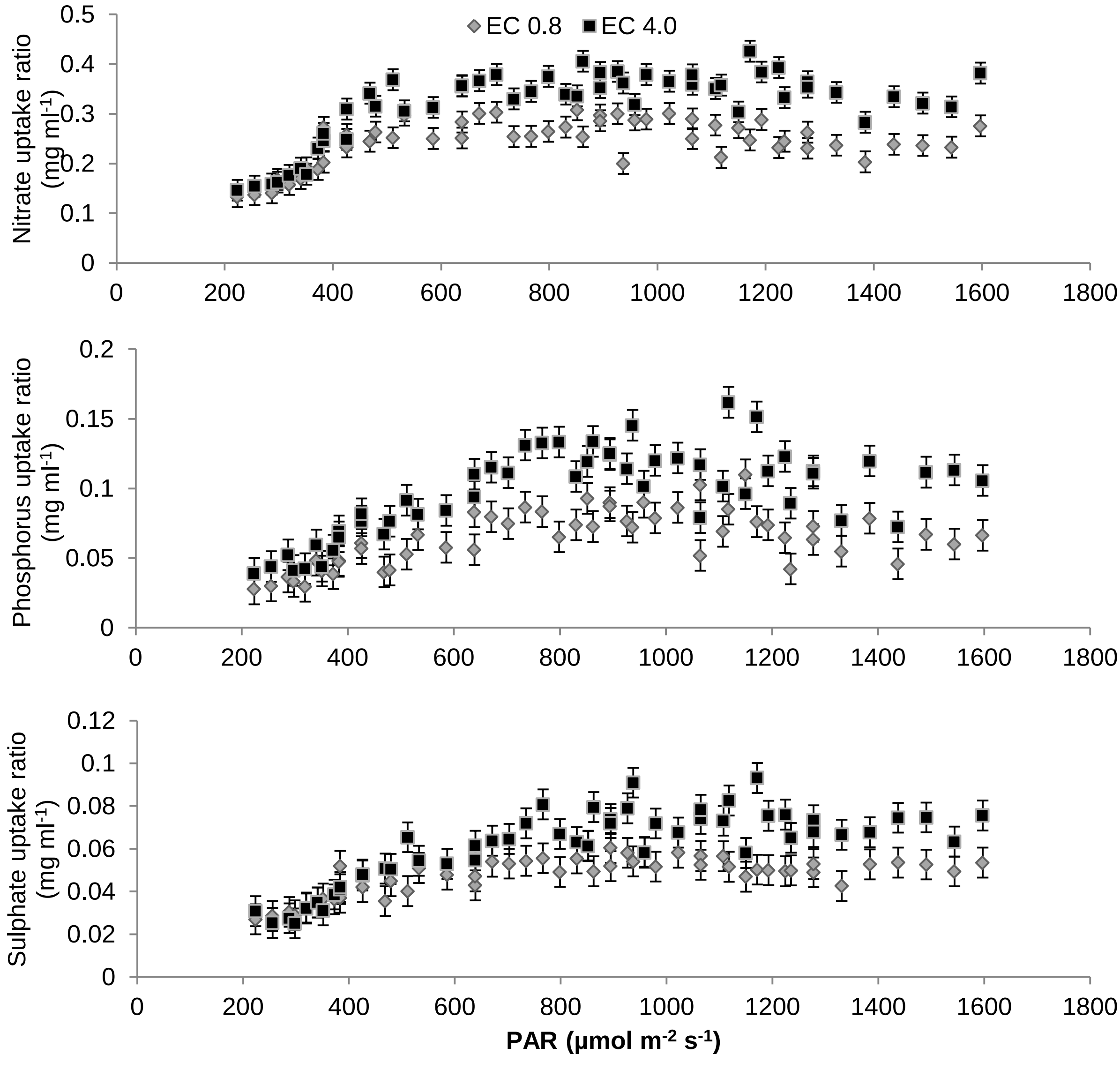

Figure 5. The relationship between the anion uptake and water uptake expressed as the uptake ratio (mg ion uptake per ml water uptake e). Graphs show the uptake ratios for A: nitrate, B: phosphorus and C: sulphate in relation to the solar radiation level (µmol m^{-2} s^{-1}) for young tomato plants at a two nutrient solution concentrations (EC 0.8 and 4.0 mS cm^{-1}). Error bars indicate the LSD value at $p \leq 0.05$).

The ratio between water and Ca^{2+} uptake gave a good correlation with the findings that the Ca^{2+} uptake ratio (mg Ca^{2+} taken up per ml water uptake) remained fairly constant over the range of solar radiation measurements (Figure 6) and appear slightly higher for plants at an EC of 4.0 mS cm^{-1}.

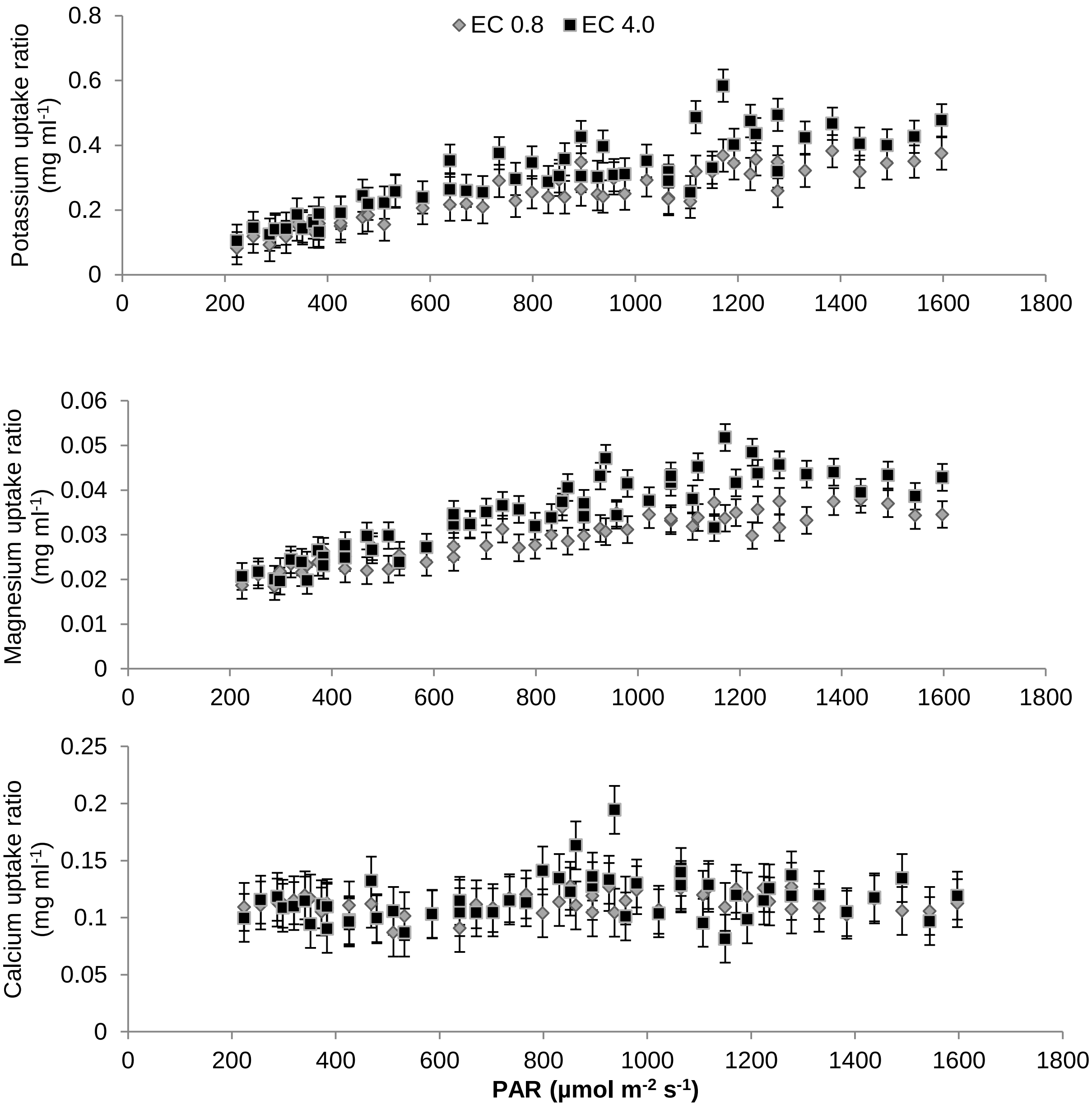

Figure 6. The relationship between the cation uptake and water uptake expressed as the uptake ratio (mg ion uptake per ml water uptake) in relation to the solar radiation level (µmol m^{-2} s^{-1}) for young tomato plants at a two nutrient solution concentrations (EC 0.8 and 4.0 mS cm^{-1}). Error bars indicate the LSD value at $p \leq 0.05$.

This can be expected since Ca^{2+} movement in the plant takes place almost exclusively via the xylem and once the Ca^{2+} entered the xylem it is transported via the transpiration stream and the rate and selectivity of Ca^{2+} transport to the shoot is therefore predominantly controlled via the symplastic pathway (White 2001; Barker and Pilbeam 2007). Conditions that enhance water uptake appear to also enhance the uptake and translocation of Ca^{2+} via the xylem to the leaves (Taylor et al. 2004). According to Barker and Pilbeam (2007) the link between Ca^{2+} uptake and transpiration can be purely incidental since the movement of Ca^{2+} in the symplasm of the endodermis is required for xylem loading. New cation exchange sites are made available in new tissue as the crop grow and Ca^{2+} uptake is therefore rather proportional to crop growth.

As Sonneveld (2002) points out, the uptake rate of most ions is curve linearly related with radiation input (similar to the relationship between photosynthesis and radiation input), while water uptake is merely linearly related with radiation input explaining the variation in uptake ratios of most of the ions tested. Establishing models to predict the changes in the nutrient solution composition of re-circulation systems can therefore clearly not just employ models of water uptake and the use of nutrient uptake ratios cannot be used without taking into account the effect of solar radiation and nutrient solution concentration.

In his study trying to simulate nutrient uptake in hydroponic systems Pardossi et al. (2005) found that nutrient uptake is not only linearly related to the water uptake but also that the uptake rates of different nutrients were closely inter-correlated. This would provide a simple method that will enable measurement of only some of the nutrients in the drained nutrient solution and by using a simple algorithm the levels of the other nutrients can be determined and adjusted accordingly. However when looking at the uptake of ions in this study it is clear that the relationship between the uptake of ions is not constant but is affected by both solar radiation levels and the nutrient solution concentration (Table 3 and 4).

During winter when the average solar radiation level was 450 µmol m^{-2} s^{-1} there was a good correlation between the uptake of the macro-nutrients apart from Ca^{2+} (Table 3). Only small differences were seen at different nutrient solution concentrations. However, during summer when the average daily solar radiation levels were 1250 µmol m^{-2} s^{-1} there was not a good correlation between the uptake of most macro-nutrients apart from the two cations Mg^{2+} and K^{+} (Table 4). When using the relationship between ions in the drained nutrient solution to model nutrient uptake to be used in a decision support system it will be essential to consider the average daily solar radiation levels.

Table 3. The coefficients of determination (R^2) depicting the correlation in macro-nutrient uptake (mg plant^{-1}) measured over a 3 hour period during midday during winter (May to July) when the average solar radiation levels was 450 µmol m^{-2} s^{-1}.

	EC 0.8 mS cm^{-1}				
	NO_3^-	**K^+**	**$H_2PO_4^-$**	**Mg^{2+}**	**SO_4^{2-}**
K^+	0.74				
$H_2PO_4^-$	0.68	0.64			
Mg^{2+}	0.70	0.66	0.35		
SO_4^{2-}	0.89	0.65	0.74	0.64	
Ca^{2+}	0.02	0.02	0.04	0.00	0.1
	EC 2.4 mS cm^{-1}				
	NO_3^-	**K^+**	**$H_2PO_4^-$**	**Mg^{2+}**	**SO_4^{2-}**
K^+	0.74				
$H_2PO_4^-$	0.79	0.69			
Mg^{2+}	0.79	0.77	0.71		
SO_4^{2-}	0.94	0.71	0.86	0.76	
Ca^{2+}	0.00	0.02	0.01	0.01	0.04
	EC 4.0 mS cm^{-1}				
	NO_3^{2-}	**K^+**	**$H_2PO_4^-$**	**Mg^{2+}**	**SO_4^{2-}**
K^+	0.72				
$H_2PO_4^{2-}$	0.85	0.71			
Mg^{2+}	0.77	0.74	0.76		
SO_4^{2-}	0.94	0.67	0.88	0.76	
Ca^{2+}	0.02	0.00	0.05	0.00	0.05

Table 4. The coefficients of determination (R^2) depicting the correlation in macro-nutrient uptake (mg plant^{-1}) measured over a 3 hour period during midday during summer (October to December) when the average solar radiation levels 1250 µmol m^{-2} s^{-1}. All coefficients are significant at 5% level.

	EC 0.8.4 mS cm^{-1}				
	NO_3^-	**K^+**	**$H_2PO_4^-$**	**Mg^{2+}**	**SO_4^{2-}**
K^+	0.00				
$H_2PO_4^{2-}$	0.00	0.00			
Mg^{2+}	0.00	0.65	0.00		
SO_4^{2-}	0.00	0.18	0.00	0.36	
Ca^{2+}	0.02	0.24	0.00	0.27	0.23
	EC 2.4 mS cm^{-1}				
	NO_3^-	**K^+**	**$H_2PO_4^-$**	**Mg^{2+}**	**SO_4^{2-}**
K^+	0.00				
$H_2PO_4^{2-}$	0.03	0.00			
Mg^{2+}	0.03	0.58	0.07		
SO_4^{2-}	0.06	0.17	0.04	0.37	
Ca^{2+}	0.00	0.06	0.11	0.14	0.18
	EC 4.0 Ms cm^{-1}				
	NO_3^-	**K^+**	**$H_2PO_4^-$**	**Mg^{2+}**	**SO_4^{2-}**
K^+	0.00				
$H_2PO_4^{2-}$	0.06	0.00			
Mg^{2+}	0.10	0.42	0.08		
SO_4^{2-}	0.14	0.13	0.04	0.59	
Ca^{2+}	0.00	0.01	0.05	0.10	0.11

Conclusion

Solar radiation levels, especially at the higher levels experienced during summer in this study has a significant effect on nutrient uptake although the extent of this effect as well as its interaction with the nutrient solution concentration is not constant. Except for Ca^{2+}, the macro-nutrient uptake is not linearly related to the water uptake and the uptake rates of most macro-nutrients also do not correlate well, especially at higher solar radiation levels. Basing crop nutrition on the use of models for transpiration or the use of uptake concentrations (the ratio between nutrient and water uptake) to maintain crop nutrition in soilless systems is therefore not accurate under all conditions and can result in yield and quality degradation for producers. The data obtained in these trials can be used to adjust existing nutrient uptake models to include the effect of solar radiation and nutrient solution concentration, two relatively easy parameters measured in most greenhouses already. These results have especially important implications for simulating nutrient uptake in areas with high solar radiation levels such as South Africa and points out that management practices needs to be adapted to these areas. Additionally these results provides some valuebel scientific knowledge on the correlation between the uptake of macro-nutrients and solar radiaton that needs to be investigated further.

These trials have been done in a water culture where the availability of ions was not affected by the chemical and physical properties of a growing medium. Further studies need to be done to determine if growing medium and the irrigation frequency (number of irrigation pulses per day), which will affect the availability of nutrients for uptake will result in differences in water and nutrient uptake under these climatic conditions.

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Article 4

The growth, biomass partitioning and water and nutrient uptake of soilless grown tomato plants in relation to solar radiation levels and nutrient solution concentration.

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Abstract

In a soilless system where the drained nutrient solution is re-used it becomes essential to test and adjust the composition of the nutrient solution in order to prevent yield losses due to nutrient levels that fall outside the optimum range. Though water uptake appears to be linked to solar radiation level the uptake mechanisms differ and the ratio between water and nutrient uptake may therefore differ under certain circumstances. In this study, hydroponically grown tomato plants growth were evaluated during two seasons and under modified solar radiation levels as well as different nutrient solution concentrations. The total dry matter production tended to increase with an increase in solar radiation level and at low solar radiation levels the total plant dry weight was significantly higher at higher EC levels. While root dry weight decreased with an increase in nutrient solution EC, the nutrient uptake per root dry weight increased resulting in an increase in uptake efficiency for nitrate, phosphate and calcium. Leaf area however decreased with an increase in solar radiation level and with an increase in nutrient solution EC. Water uptake at the low solar radiation levels was affected by the nutrient solution EC but at higher solar radiation levels there was no difference in water uptake for plants grown at different nutrient solution ECs.

Keywords: biomass partitioning, electrical conductivity (EC), nutrient uptake, soilless production, solar radiation

Introduction

Soilless crop production in a protected environment such as a greenhouse is becoming increasingly popular in many parts of the world (Massa et al. 2011). It allows the production of food and ornamental crops year-round, even out of season and in areas where it would otherwise not be possible. It helps to ensure food security and provides economic opportunities to the local populations, also in peri-urban areas where traditional agricultural production may not be possible. Crops grown hydroponically are normally grown with particularly high nutrient levels in order to maintain optimal concentrations of nutrients in the rootzone at all times. Unfortunately only 30 to 80 % of the nutrients supplied to crops in an open hydroponic system is used by crops (Rácz 2007) and up to 1000 kg N ha^{-1} per year can be lost in traditional drain to waste soilless production systems (van Noordwijk 1990). When the system is designed to be able to re-use all the drained nutrient rich water it is referred to a closed or re-circulating system. This increases the ecological and economical sustainability of the system (Raviv 2007). However, continued re-use of the nutrient solution without adequate adjustments will result in nutrient imbalances since the composition of the nutrient solution will start deviating from the specific target values (Voogt 1993). These imbalances can result in a negative effect on plant growth and yield (Zekki et al. 1996, Carmassi et al. 2002). Nutrient uptake is not constant but is closely related to the growth rate of the crop (Vos et al. 2009) and also correlates to above ground biomass partitioning patterns, for instance, nitrate uptake rates are strongly reduced by defoliation (Macduff and Jackson 1992). Plant nutrient uptake rate is therefore often calculated as the product of net uptake rate per root unit as a function of the root size, root:shoot ratio (RSR) or root:whole plant ratio (RWR) According to Le Bot et al. (1998) the rapid variations in uptake rates cannot be explained by changes in the root system size or by synthesis of new transporters but indicate feedback control via respiration and thus the flow of carbon compounds from leaves to roots. In young tomato plants the relative growth rate (RGR) decreases sharply at low daily solar radiation integrals (Bruggink and Heuvelink 1987).

To adjust nutrient supply to crop demand, crop growth and nutrient uptake should be related to environmental conditions, especially the radiation input (Voogt 1993). Together with temperature, solar radiation determines the growth rate of crops and changes in environmental conditions will cause plants to modify their growth, development and physiology, including modifications in the photosynthetic apparatus enabling plants to acclimatize photosynthetically to the reigning light environment (Walters et al. 2003). Although solar radiation drives plant growth, an excess can also lead to photoinhibition (Powles 1984; Taiz and Zeiger 1998) and high solar radiation levels can reduce tomato leaf area (Heuvelink 2005). Apart from solar radiation levels, nutrient supply can also have significant effects on biomass allocation patterns of plants (Poorter and Nagel 2000). Although a low nutrient supply result in a decrease in the plants rate of photosynthesis per unit leaf mass, plant growth is decreased to an even greater extent (Poorter and Nagel 2000). According to Heuvelink (2005) a linear relationship between cumulative intercepted photosynthetically active radiation (PAR) and tomato dry mass (DM) production exist and a minimum light requirement of 4.6 mol m^{-2} for fruit set and growth exists. Fruit yield is also directly proportional to the accumulated solar radiation. Cockshull et al. (1992) found that during the first 14 weeks of harvest 2.01 kg fresh weight of fruit was harvested for every 100 MJ of solar radiation incident on the crop and for the remainder of the growing period 2.65 kg fruit fresh weight per 100 MJ was obtained.

Many of the studies looking at the effect of solar radiation levels on the growth, development and biomass partitioning have only been done at relatively low solar radiation levels (Bruggink and Heuvelink 1987; Ingestad et al. 1994). In order to simulate crop nutrient demand necessary for model based regulation of water and fertilizer application to crops it is necessary to quantify the effect of climatic factors, specifically high solar radiation levels, on the growth and development of crops, which will affect the uptake of macro nutrients. The aim of this study was therefore to investigate the water to nutrient uptake in relation to the crop growth and biomass partitioning as affected by the solar radiation levels and nutrient solution concentrations.

Material and methods

Plant material and growth conditions

Tomato seeds (*Lycopersicon esculentum* Mill. cvs. FA593, Sakata, South Africa) were germinated in a seedling mix consisting of vermiculite, perlite and coco-peat and seedlings were transplanted at six weeks to 5L closed plastic containers. The containers were filled with nutrient solution and was aerated continuously. Trials were completed in a temperature controlled glasshouse from 17th May 2010 to 25th July 2010 (winter) and from 13th October 2010 to 31st December 2010 (summer). The glasshouse temperature was set to 18 / 24^{O}C (night / day temperature) during winter and to 20 / 28^{O}C (night / day temperature) during summer. The nutrient solution temperature however remained at an average of 22 ^{O}C during both seasons, limiting direct effects of temperature on nutrient uptake from the solutions. The total daily solar radiation (PAR) (MJ m^{-2} day^{-1}) inside the glasshouse extended from 6 to 11 MJ PAR m^{-2} while it ranged between 18 and 26 MJ PAR m^{-2} during summer (figure 1). The relative humidity (RH) remained between 60 and 85% during the trial. Plants were pruned to a single stem and side shoots were removed weekly. All trusses were pruned to six fruit per truss immediately after fruit set was complete.

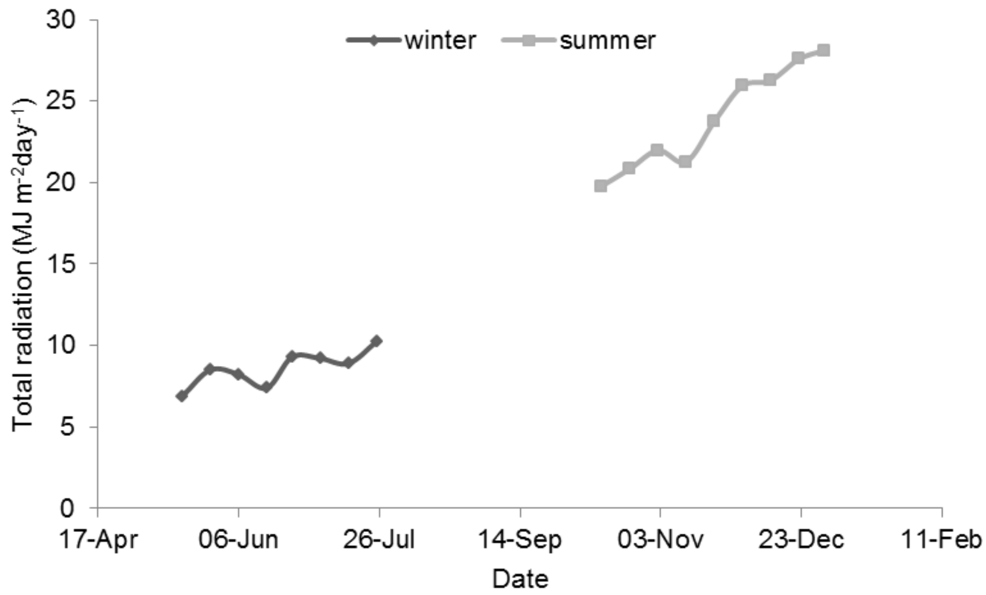

Figure 1. Total daily solar radiation (MJ m^{-2} day^{-1}, PAR) inside the glasshouse during the winter and summer seasons during which the trials were done. Points represent the mean of 10 days.

Treatments

The solar radiation levels the plants were grown at were manipulated by placing plants either under no shade (full sunlight), 20% shade netting or 40% shade netting during each trial, winter and summer. This resulted effectively in a range of six solar radiation levels due to seasonal effect. In combination with the solar radiation treatments, plants were placed in five different nutrient solutions, differing in their macro-nutrient concentrations (EC, mS cm^{-1}). The solutions used were adjusted for re-circulating systems based on earlier trials. The ratio between nutrients was kept constant, the pH was 5.8 and the EC's were 0.8, 1.6, 2.4, 3.2 and 4.0 mS cm^{-1} at 25 ^{O}C (Table 1). A constant concentration of micronutrients were applied: 40.6 µmol L^{-1} Fe^{3+}; 35.0 µmol L^{-1} $H_2BO_3^-$, 4.6 µmol L^{-1} Zn^{2+}; 3.6 µmol L^{-1} Cu^{2+}; 10.9 µmol L^{-1} Mn^{2+}. The nutrient solution was not adjusted to a formulation recommended for reproductive growth (Voogt 1993) later in the season since this trial was completed at 71 days after planting and only the first two trusses were ripened.

Table 1. Macro-nutrient composition (meq L^{-1}) of the municipal water and the final nutrient solutions at different ECs used to determine the nutrient and water uptake of tomato plants.

	NH_4^+	K^+	Ca^{2+}	Mg^{2+}	NO_3^-	$H_2PO_4^-$	SO_4^{2-}
				Municipal water			
	0.05	0.01	0.17	0.03	0.01	0.01	0.04
EC ($mS\ cm^{-1}$)				**Nutrient solutions**			
0.8	0.8	3.4	2.4	1.4	7.0	0.4	0.6
1.6	1.6	6.8	4.8	2.8	14.0	0.8	1.2
2.4	2.4	10.2	7.2	4.2	21.0	1.2	1.8
3.2	3.2	13.6	9.6	5.6	28.0	1.6	2.4
4.0	4.0	17.0	12.0	7.0	35.0	2.0	3.0

Growth and development parameters

At 71 days after planting (DAP) the leaf area (LA) was measured with a Li-Cor model 300 leaf area meter (Li-Co., Lincoln, NB) and fresh weights (FW) of the roots, stems and leaves determined. After drying in an oven for 72 hours at 80 ^{O}C to constant weight, the dry weight (DW) of all plant parts were determined. This was then used to determine the assimilate partitioning in the plants as a percentage of the total dry weight. The leaf area and shoot dry weight of the side shoots were also determined with every pruning. The specific leaf area (SLA, $m^2\ kg^{-1}$) was determined as the total plant leaf area per leaf dry weight.

Water and nutrient uptake

Total daily water uptake ($Wu_{dt} = Wu_{day} + Wu_{night}$, ml m^{-2} day^{-1}) and total daily nutrient uptake ($Nu_{dt} = Nu_{day} + Nu_{night}$, g m^{-2} day^{-1}) was determined during day time (07:00 to 18:00 during winter or 06:00 and 20:00 during summer) and during the night (18:00 to 07:00 during winter or 20:00 to 06:00 during summer). This was done through chemical analysis of samples taken at the beginning and end of this time period. At first the residual nutrient solution in the container was replaced with the reference nutrient solution every three days, after 3 weeks this was increased to every two days and after 5 weeks daily. This frequent replacement of the residual nutrient solutions lead to only minor differences in the pH and EC of the nutrient solutions as observed with each replacement of the solution.

The total nutrient uptake (Nu, g $plant^{-1}$) over the duration of the trial was also determined through plant chemical analysis. The K^+, Ca^{2+}, Mg^{2+} and $H_2PO_4^-$ content of the dried and ground root, stem, leaf and fruit samples were determined after HCl extraction from the plant material and ash drying at 550^{O}C for 5 hours. The $H_2PO_4^-$, SO_4^{2-} and NH_4^+ concentrations were determined colorimetrically using a spectrophotometer at 460nm for $H_2PO_4^-$ and for SO_4^{2-} and NH_4^+ at 640nm. The total-N in the leaf samples was determined using the Kjeldahl method and the concentrations of K^+, Ca^{2+}, Mg^{2+} was determined by atomic absorption spectrophotometry. The nutrient content was determined as the tissue concentration (%) * dry weight (g). The nutrient use efficiency (NUE) was calculated as the mg of any given element per shoot dry weight (DWs, mg).

Statistical analysis and experimental design

Each treatment combination was repeated four times in a completely randomized design. Multivariate analysis of variance (ANOVA) was used for evaluating data (STATISTICA 11.0, Statsoft (SA) Inc., Tulsa, Oklahoma, USA). Differences among the mean values were determined using using Fischer's LSD ($P<0.05$) equations.

Results and discussion

Growth, development and biomass partitioning

The leaf area of the plants was significantly affected by the nutrient solution concentration as well as the solar radiation levels (Figure 2). The total leaf area of plants were significantly lower at an EC of 3.2 and 4.0 mS cm^{-1} compared to EC levels of 0.8 and 2.4 mS cm^{-1} and decreased with an increase in daily solar radiation (DSR, MJ m^{-2} day^{-1}) levels during summer, when the average daily radiation levels was on average between 15 and 26 MJ m^2 day^{-1}. During winter (DSR levels below 10 MJ m^{-2} day^{-1}) the leaf area was however not significantly affected by the solar radiation levels (Figure 2). For tomato plants the relationship between leaf area and crop growth and biomass production can be described as a negative exponential function (Heuvelink 2005). A reduction in the leaf area would therefore be expected to result in a decrease in the relative growth rate (RGR) of the plants if it is assumed that the photosynthetic rate remained constant. It is suggested that the RGR is directly related to the uptake rate of nutrients and therefore global radiation is used in crop growth models and could possibly also be applied in nutrient uptake models (Mankinn and Fynn 1996; Gallardo et al. 2009).

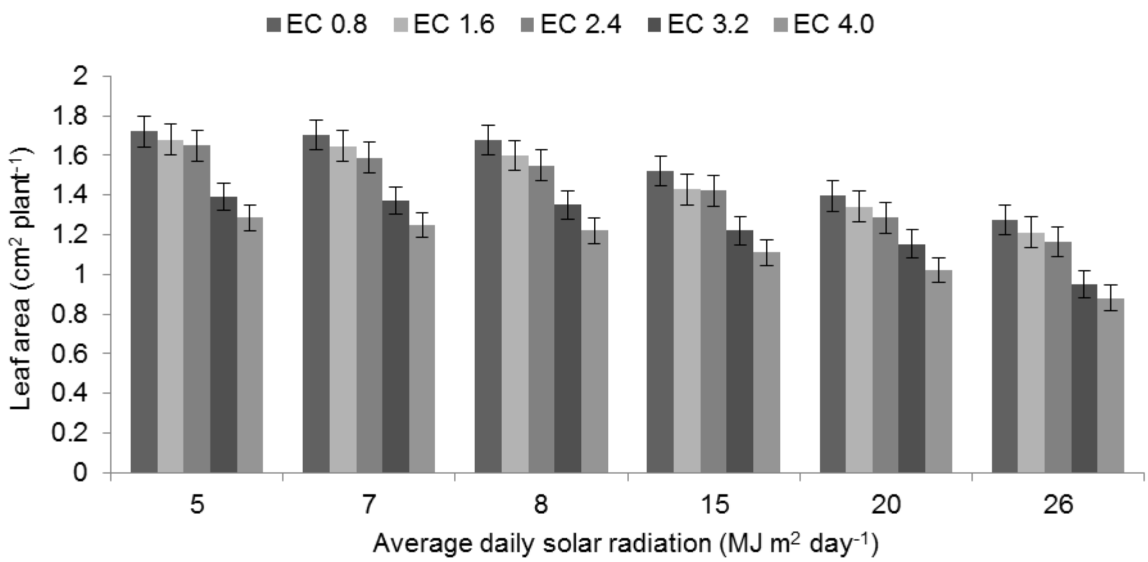

Figure 2. The total leaf area (m^2 $plant^{-1}$) of tomato plants at 70 DAP in relation to the average solar radiation levels during the growing period and the nutrient solution concentrations (EC, mS cm^{-1}). (Error bars indicate the LSD value at $p \leq 0.05$).

The high solar radiation levels during the summer trial could have resulted in a reduced sink/source ratio (overproduction of assimilates) which can possibly be linked to a reduction in the length of leaves and consequently also the specific leaf area (SLA) of tomato plants (Figure 3) (Taiz and Zeiger 1988; Heuvelink 2005). There is consequently a good correlation between the SLA and the average daily radiation levels over the vegetative growth period of these tomato crops (R^2 = 0.82). This is in agreement with other studies where it was shown that a decrease in SLA occurs with an increase in solar radiation levels (Mezaine and Shipley 1999; De Groot et al. 2002). Heuvelink (1995) also found a sinusoidal relation between the average crop SLA and season. During summer it was between 175 and 250 cm^2 g^{-1} and in early spring, late autumn and winter it was between 300 and 400 cm^2 g^{-1}. The SLA was however not significantly affected by the nutrient solution EC which can be attributed to a lower leaf dry weight at the higher ECs (data not shown). The SLA relates dry matter production to leaf area development and light interception and is therefore an important variable in many crop growth models.

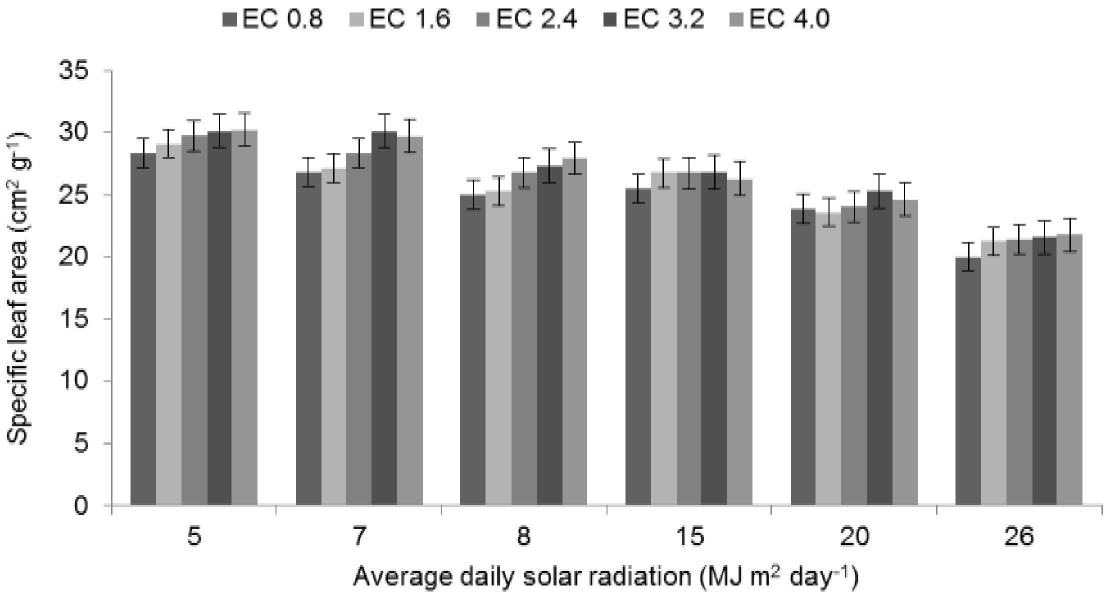

Figure 3. The specific leaf area (cm^2 leaf area g^{-1} leaf dry weight) of tomato plants at 70 DAP in relation to the average solar radiation levels during the growing period and the nutrient solution concentrations (EC, mS cm^{-1}). (Error bars indicate the LSD value at $p \leq 0.05$).

The total dry weight production of the plants was significantly affected by the nutrient solution concentration as well as the solar radiation levels (Figure 4). At low solar radiation levels plant dry weight tended to increase with an increase in the nutrient solution EC. This effect was significant for plants at an EC of 3.2 and 4.0 mS cm^{-1} grown at solar radiation levels of 5 and 7 MJ m^{-2} day^{-1}. Plants grown at a lower EC (2.4 mS cm^{-1} and below) showed a significant increase in total plant dry weight as the solar radiation levels increased. However the total plant dry weight of plants at the higher EC levels tended to increase up to a daily solar radiation level of 8-15 MJ m^{-2} day^{-1} and then decrease dry weight did not differ significantly between the different EC treatments except for plants at an EC of 2.4 mS cm^{-1}. Root dry weight was nonetheless only significantly affected by the nutrient solution EC (Figure 5). Increasing the nutrient solution EC resulted in smaller roots for plants regardless of the solar radiation levels they are grown under. The slight increase in total plant dry weight with an increase in solar radiation levels could therefore be attributed to an increase in the above-ground biomass alone. This may possibly affect nutrient uptake since the uptake rate of nutrients is often calculated as the product of net uptake rate per root unit as a function of the root size (Le Bot et al. 1998). Biomass partitioning between roots and shoots should therefore also be considered as it may correlate to the uptake rate of nutrients.

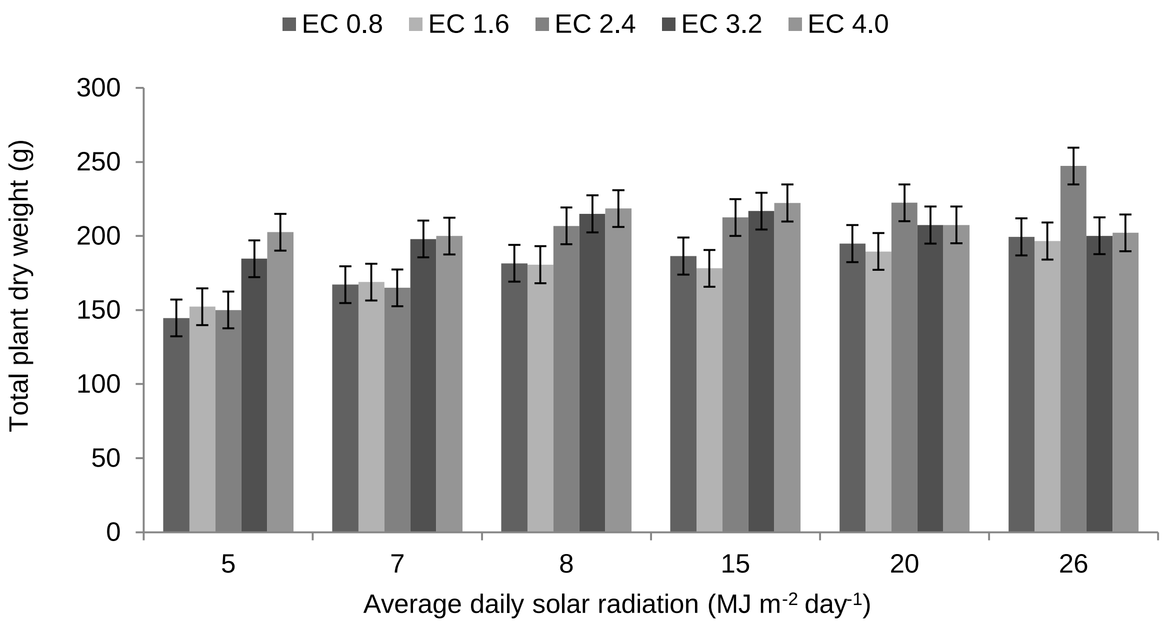

Figure 4. The total plant dry weight (DW, g plant^{-1}) of tomato plants at 70 DAP in relation to the average daily solar radiation levels during the growing period (DSR, MJ m^{-2} day^{-1}) and the nutrient solution concentrations (EC, mS cm^{-1}). (Error bars indicate the LSD value at $p \leq 0.05$).

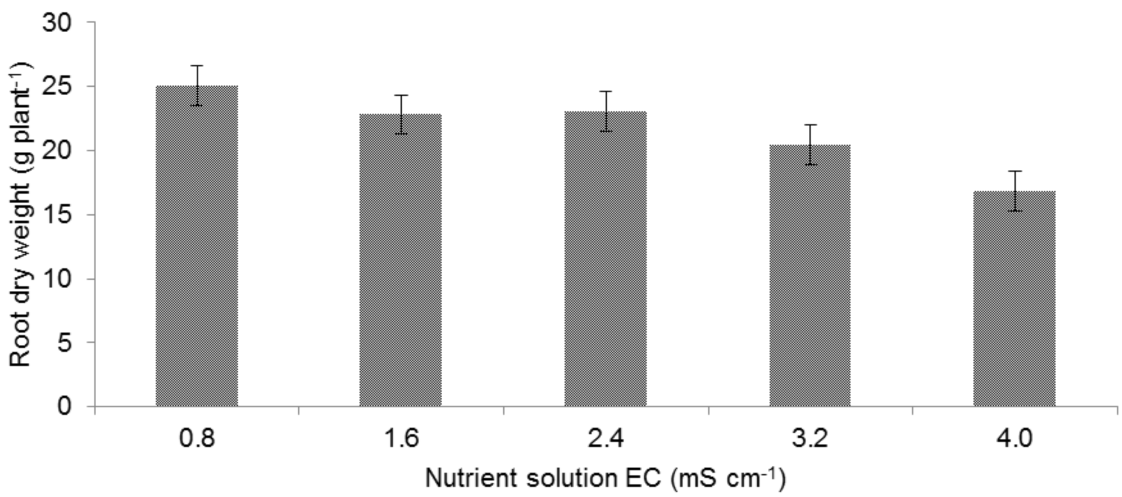

Figure 5. The root dry weight (g plant^{-1}) of tomato plants at 70 DAP in relation to the nutrient solution concentrations (EC, mS cm^{-1}). (Error bars indicate the LSD value at $p \leq 0.05$).

. This was in fact evident from these results where the dry matter partitioning to the shoots was higher and to the roots lower at a higher nutrient solution EC (Table 2). Although the increase in solar radiation level did not significantly affect the biomass partitioning to the shoots, biomass partitioning to the roots decreased significantly with an increase in solar radiation levels, especially for plants at the low EC level of 0.8 mS cm^{-1}. Under low nutrient availability (EC of 0.8 mS cm^{-1}) and low assimilate availability as a result of low solar radiation levels, biomass partitioning was the highest compared to all other treatments (Table 2). The shoot: root ratio varies between species, plant development stages and can be modified by external conditions. According to the functional equilibrium approach that states that dry matter distribution between root and shoot will be regulated by an equilibrium between root activity and shoot activity, i.e. the availability of carbon and nutrients (Marcelis and Heuvelink 2007). This concept has been shown in several previous studies (Le Bot et al. 1998; Henriques and Marcelis 2000; Poorter and Nagel 2000; de Groot et al. 2002). An increase in leaf activity and carbon concentration as a result of increased solar radiation levels should therefore result in a decrease in partitioning to the leaves. In the same way an increase in the nutrient availability should result in a decrease in biomass allocation to the roots

Part of the crop growth model TOMSIM (Heuvelink 1995) is a model for the simulation of dry matter distribution between reproductive and vegetative plant parts. Dry matter distribution is primarily controlled by the sinks and the sink strength of an organ is defined by its RGR (Heuvelink and Marcelis 1989). The dry matter distribution in indeterminate crops however changes dynamically making a simulation of plant nutrient relationships incorporated in a mechanistic model for crop growth and development potentially very complex (Marcelis et al. 1989, Marcelis et al. 2004). In the model the nutrient demand for each organ is calculated as the product of dry weight growth and required nutrient concentration. However, according to Marcellis and Hevelink (2007), the simulation of carbon allocation among plant organs is still one of the weakest features of crop growth models and consequently the most appropriate concept will depend on the species studied.

Water- and nutrient uptake

The water uptake during the day as a function of the plants total dry weigh was highest for plants at the highest solar radiation levels (no shade during summer, average 24.3 MJ m^{-2} day^{-1}) except at the lowest EC where there was no significant difference in water uptake due to total solar radiation levels (Figure 7). A large percentage of water and macro-nutrients has been reported to be taken up during the night (Le Bot 1991; Cárdenas-Navarro et al. 1998), so although it is important to look at the short term influence of light on nutrient uptake for the rapid management of nutrient levels in the rootzone, a wider analysis is also needed to help prevent damage to the roots or growth limitation.

Table 2. The biomass partitioning (%) to the shoots and roots of tomato plants at 70 DAP in relation to the average solar radiation levels during the growing period at a nutrient solution concentration of 0.8 and 4.0 mS cm^{-1}.

EC (mS cm^{-1})	**Daily solar radiation levels (MJ m^{-2} day^{-1})**	**Root**	**Shoot**	**Fruit**
0.8	5	0.21a	0.77b	0.02d
	7	0.18b	0.80b	0.02d
	8	0.15c	0.81b	0.04b
	15	0.15c	0.81b	0.04b
	20	0.14cd	0.83ab	0.03c
	26	0.12de	0.85ab	0.03c
4.0	5	0.10e	0.87ab	0.03c
	7	0.09e	0.87ab	0.04b
	8	0.08ef	0.88a	0.04b
	15	0.08ef	0.88a	0.04b
	20	0.08ef	0.88a	0.04b
	26	0.07f	0.88a	0.05a
LSD ($p \leq 0.05$)		0.021	0.070	0.005

Significant differences between cultivars for means are indicated by different letters in superscript.

At the high solar radiation level water uptake was only significantly lower at an EC of 0.8 mS cm^{-1} while at the low solar radiation levels water uptake decreased significantly with an increase in nutrient solution EC. When the daily solar radiation levels was high, the night time water uptake also remained fairly constant at about 12% of the total daily water uptake (day and night) and was also not significantly affected by the EC of the nutrient solution. For plants grown at the lowest light level (40% shade, during winter, average of at 3.1 MJ m^{-2} day^{-1}), water uptake decreased as the nutrient solution EC increased during the night time. At an average of 19%, the night-time water uptake also comprised a larger % of the total water uptake of the plants compared to plants grown at high light intensities (Table 3).

Significant night-time transpiration was found for several C3 and C4 species at different growing conditions and the higher night-time transpiration were found to correlate with higher daytime values (Snyder et al. 2003). Daytime conditions and photosynthetic rates can influence stomatal conductance during the night. Day length and light intensity can affect the speed and degree to which stomata close at night with higher light intensity during the day resulting in faster stomatal closure at night (Blom-Zandstra et al. 1995).

Table 3. The daytime and night time water uptake (ml g^{-1} day^{-1}) of tomato plants grown at four nutrient solution concentrations (EC, mS cm^{-1}) during two seasons with different shade levels applied. For clarity, only the treatments resulting in the highest solar radiation levels (summer, no shading) and lowest solar radiation levels (Winter, 40% shade) is included.

		Water uptake (ml g^{-1} day^{-1})	
Daily solar radiation levels (MJ m^{-2} day^{-1})	**EC (mS cm^{-1})**	**Day**	**Night**
5	0.8	3.52bc	0.83a
	1.6	3.64b	0.85a
	2.4	3.30c	0.77b
	3.2	3.04c	0.71b
	4.0	2.65d	0.62c
26	0.8	3.54bc	0.43e
	1.6	4.02a	0.54d
	2.4	3.73ab	0.51d
	3.2	3.83ab	0.52d
	4.0	3.72b	0.51d
LSD ($p \leq 0.05$)		0.29	0.07

Significant differences between cultivars for means are indicated by different letters in superscript.

According to Caird et al. (2007) it is possible that a byproduct of starch metabolism result in a greater stomatal opening at night when starch levels are high. It is not clear however if this night-time water use is essential to plants or if it is merely a by-product of insufficient stomatal closure. The relevance to this study is the potential effect that night time water use will have on the total water uptake by the plant and how this correlates to the total nutrient uptake by plants. Although it was shown in previous trials that over the short term there is no correlation between water uptake and the uptake of most macro-nutrients it is possible that the correlation over a 24 hour period is sufficient thus allowing the use of uptake concentrations in adjusting the nutrient solutions a nd in predicting nutrient uptake by crops.

In previous studies (Article 1 and 2) a reduction in water uptake at high EC levels was found. It was probably caused by a reduction in the plant growth and especially the leaf area of the plants (Schwarz and Kuchenbuch 1998). Although the plants in this study did show a decrease in leaf area when the nutrient solution EC was increased it is also clear that the water uptake per leaf area increased both with an increase in nutrient solution EC and an increase in solar radiation levels (Figure 6). The decrease in leaf area due to an increase in nutrient solution EC and solar radiation levels is therefore far greater than the reduction in water uptake indicating that leaf area alone cannot be used to predict water uptake of crops.

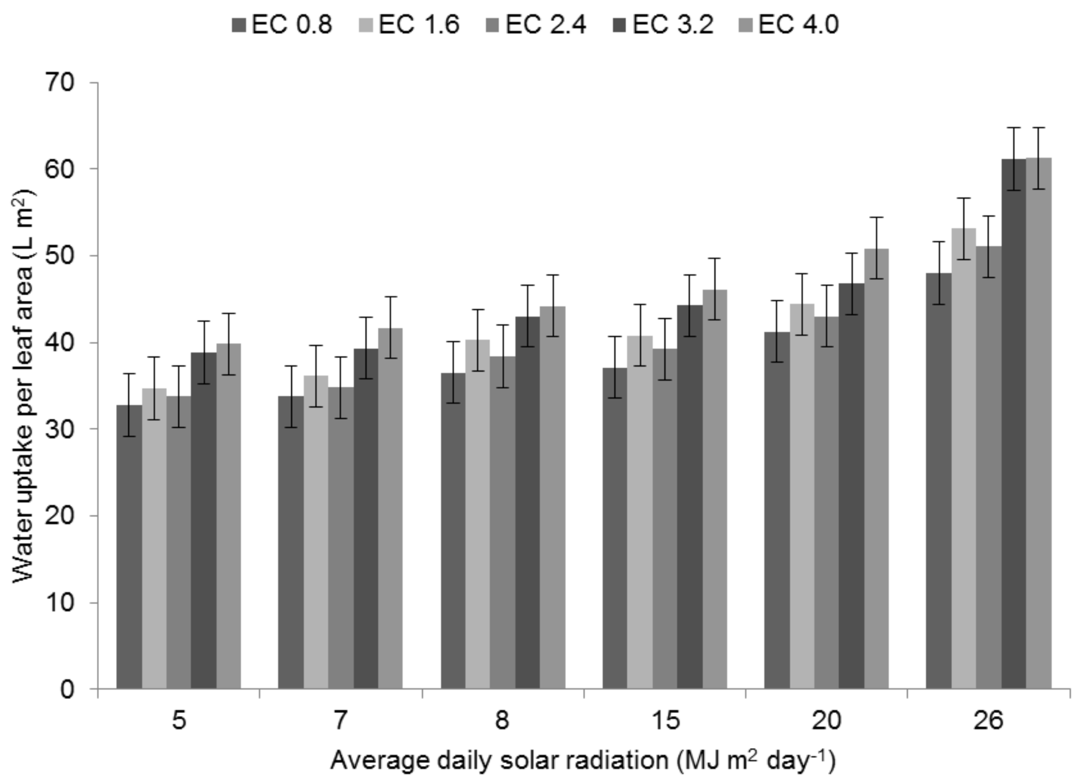

Figure 6. The water uptake per leaf area ($L\ m^2$) of tomato plants at 70 DAP in relation to the average solar radiation levels during the growing period and the nutrient solution concentrations (EC, $mS\ cm^{-1}$). (Error bars indicate the LSD value at $p \leq 0.05$).

Although the uptake of all nutrients were analysed, for the sake of brevity in this article only the uptake of nitrate (NO_3^-), calcium (Ca^{2+}) and phosphate ($H_2PO_4^-$) will be discussed as these showed the most variability in previous trials. Nutrient uptake during both the day and at night was not constant for plants during different seasons and grown at different nutrient solution ECs. Nitrate (NO_3^-) uptake during the day was significantly lower at the lowest nutrient solution EC of 0.8 $mS\ cm^{-1}$ regardless of the solar radiation levels (Figure 9). During nighttime the NO_3^- uptake also tended to increase with an increase in EC although this difference was not significant. The night-time nitrate uptake was however considerably higher than the uptake of water during the night. The night-time nitrate uptake comprised on average a total of 35% of the total daily nitrate uptake and no significant difference was observed as a result of varying solar radiation levels. Calcium (Ca^{2+}) uptake decreased slightly at an increase in nutrient solution EC during periods with a high solar radiation and this effect was observed during both day and night-time (Figure 7). The total Ca^{2+} uptake during the night was lower during the winter and tended to decrease with an increase in the nutrient solution EC. Hower the % of Ca^{2+} taken up durigng the night was higher at a total of 48% of the total Ca^{2+} uptake compared to 41% uptake of Ca^{2+} at night during summer. Of all the ions, the phosphate ($H_2PO_4^-$) showed the highest night-time uptake rates with the result that there was little variation between day- and night-time nutrient uptake. On average 45% of the total $H_2PO_4^-$ was taken up during the night- time both during the winter and summer periods (Figure 7).

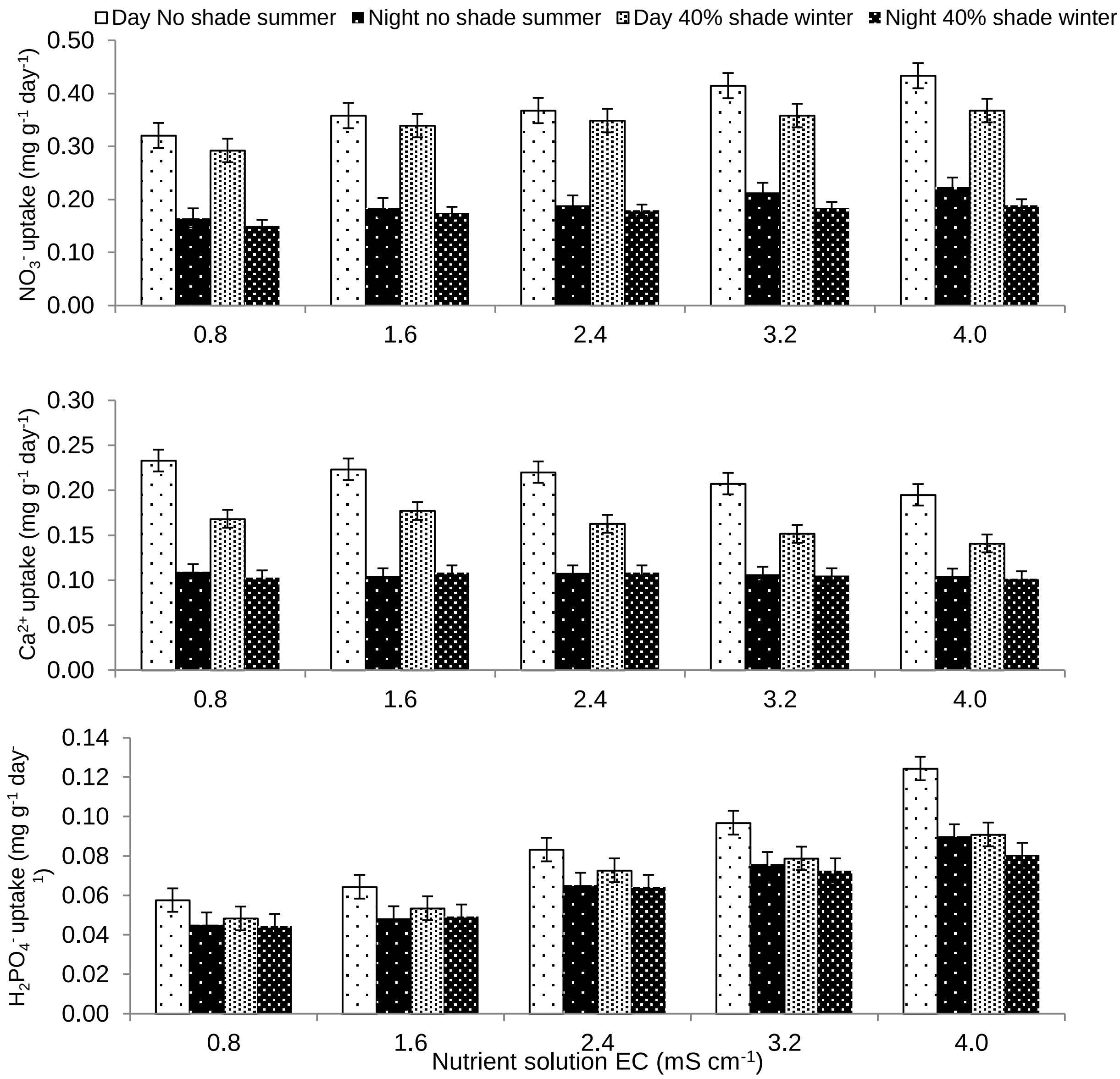

Figure 7. The daytime and night time nitrate, calcium and phosphorus uptake (mg g^{-1} day^{-1}) of tomato shoots grown at four nutrient solution concentrations (EC, mS cm^{-1}) during two seasons with different shade levels applied. Only the treatments resulting in the highest solar radiation levels (Summer, no shading) and lowest solar radiation levels (Winter, 40% shade) is shown. (Error bars indicate the LSD value at $p \leq 0.05$).

This corresponds to findings in other studies (Masuda 1989; Terabayashi et al. 1991). Phosphate ($H_2PO_4^-$) uptake is known to be inhibited at low root zone temperatures. These results have several significant implications of which one of the most important is in terms of the management of nutrient application to crops. Under normal growing media based growing crops are rarely fertigated during the night but it might be possible to increase nutrient uptake and possibly crop growth rate and even quality if nutrients are made available for uptake during the night. It should be verified in a media based system if the % of night-time water and nutrient uptake will be comparable to this pure water culture where the availability of nutrients were kept optimal. The variability in uptake during day and night and under variable environmental conditions raises questions on the effectiveness of using uptake concentrations to predict nutrient uptake in re-circulating soilless systems.

The uptake of NO_3^-, Ca^{2+}, $H_2PO_4^-$ per root dry weight (RDW) (mg g^{-1}) revealed a similar response in reaction to nutrient solution EC and solar radiation levels (Figure 8). For all three macro-nutrients the uptake per RDW tended to increase with an increase in nutrient solution EC and was highest under a combination of high solar radiation and high nutrient solution EC. This can possibly be attributed to the increased availability of assimilates during times with a total daily higher solar radiation providing energy for active ion uptake. According to Le Deunff and Malagoli (2014), an increase in nutrient uptake can be the result of interactions between shoot N demand and N supply (EC of nutrient solution) or variations in environmental variables such as temperature and PAR resulting in either the addition of new transporters or a change in the affinity of transporters for the specific ions. These results also imply that the plants with the smaller root systems, mainly as a result of an increase in nutrient solution EC, were more efficient in taking up these macro-nutrients. The NO_3^- uptake per RDW was however significantly lower during low solar radiation and low nutrient availability whereas the uptake per root DW was not affected by solar radiation levels at low EC levels for Ca^{2+} and H_2PO_4. The decrease in biomass partitioning of roots at the high solar radiation levels also did not limit the uptake of these ions although the correlation between the uptake of Ca^{2+} per root dry weight was more linear under both summer and winter conditions than that of NO_3^- and $H_2PO_4^-$. This reaffirms that the dry weight of the roots alone is not an accurate estimation of nutrient uptake.

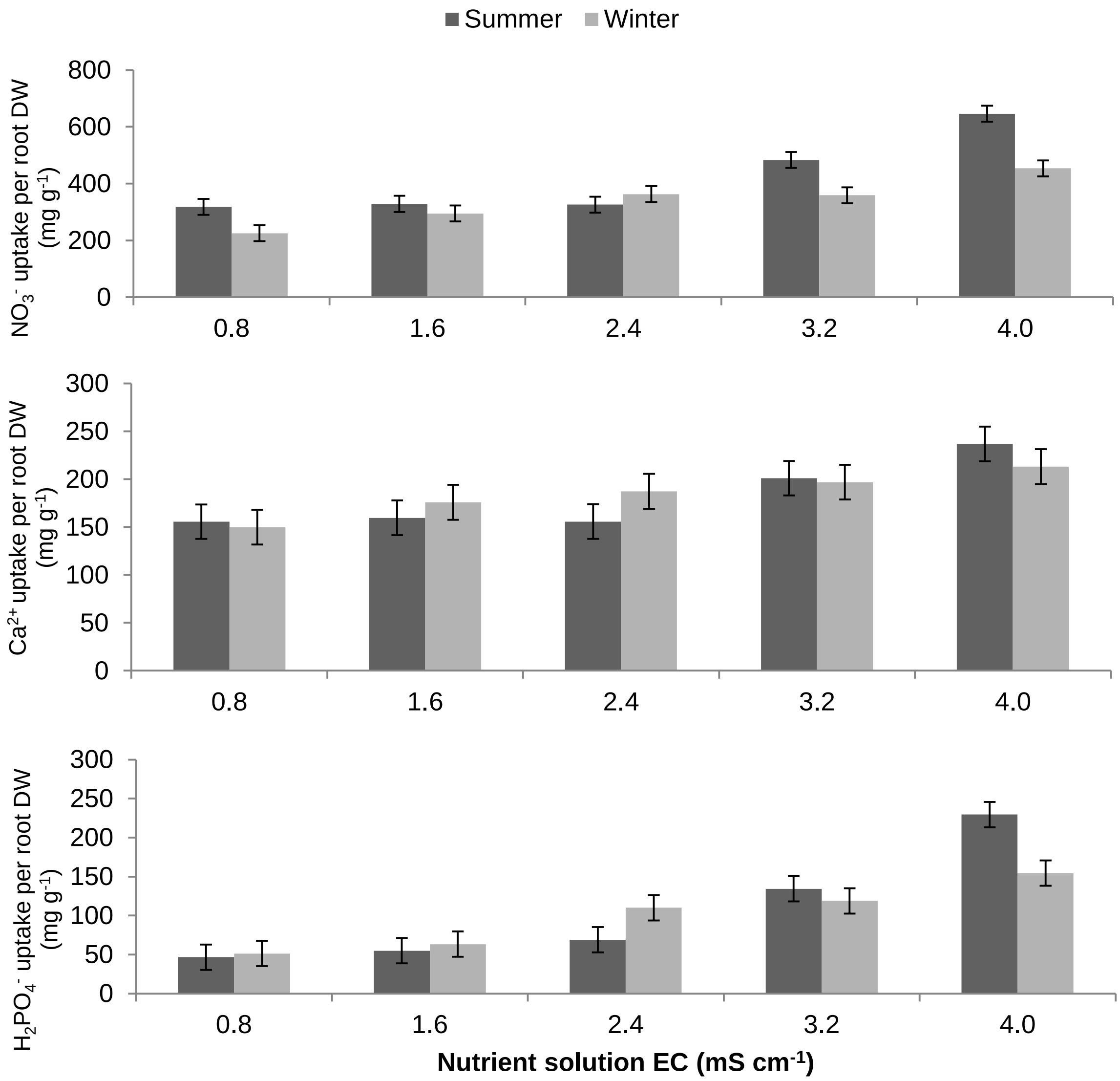

Figure 8. The NO_3^-, Ca^{2+} and $H_2PO_4^-$ uptake per root dry weight (mg g^{-1}) of tomato plants grown at four nutrient solution concentrations (EC, mS cm^{-1}) during two seasons with different shade levels applied. Only the treatments resulting in the highest solar radiation levels (Summer) and lowest solar radiation levels (Winter) is shown. (Error bars indicate the LSD value at $p \leq 0.05$).

Conclusion

Solar radiation levels and nutrient solution concentration will affect growth and biomass partitioning within the tomato plant. This will not only affect the yield for the producer but will also have effects on the rate of nutrient uptake which can affect composition of nutrient solution intended for re-use. The data obtained in these trials can be used in nutrient uptake models to predict the composition of the nutrients drained from the grow bags although there are not necessarily a linear response between the uptake of macro-nutrients and biomass production and allocation. It is also clear that the leaf area alone cannot be used to predict water and by implication nutrient uptake of crops without taking into account the effect of nutrient solution EC and solar radiation levels. Specifically important for management in Mediterranean climates is that water uptake has been shown to be affected by the EC of the nutrient solution to a larger extent during periods with high solar radiation than when the solar radiation levels are lower. A significant amount of the total daily nutrient uptake can be accounted for by night-time uptake of nutrients although this also varies between ions and is affected in some instances by the solar radiation levels and nutrient solution concentration.

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Chapter 4

The irrigation scheduling affects the nutrient uptake as well as the biomass partitioning and fruit quality of hydroponically grown tomatoes.

Article 5

Nutrient and water use of a tomato crop is affected by the irrigation scheduling in hydroponic systems.

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Abstract

The continuous re-use of the drained nutrient solution can result in yield and quality reductions of crops. Whereas the norm is to drain 25 – 30% of the applied nutrient solution in open or drain to waste hydroponic systems it is possible to increase the leaching fraction in a re-circulating system since no waste or pollution will occur. Tomato plant growth, biomass production, fruit yield and quality were assessed by cultivating tomato in a coir growing medium with either a full strength or half strength nutrient solution and at 3 different irrigation frequencies. An increase in irrigation frequency can increase biomass production and partitioning to the shoots while root development is reduced. Fruit yield was also increased at the higher irrigation frequencies while no significant difference was observed at the high irrigation frequency when a half strength nutrient solution was used. The low irrigation frequency resulted in smaller fruit but an increase in fruit dry matter %, total soluble solids (TSS) and titratable acidity. Water uptake was largely determined by the concentration of the nutrient solution and not significantly affected by irrigation frequency under these conditions. Large variations in the specific ion concentrations in the rootzone were observed indicating the importance of managing the specific composition and not just the EC of the nutrient solution.

Keywords: fertigation frequency, fruit quality, nutrient uptake, soilless production, water use efficiency

Introduction

The demand for out of season fruit and vegetables is popularising the use greenhouse production as well as soilless growing methods. Most greenhouse crops grown hydroponically are planted and fertigated in a growing medium instead of soil. The most important advantages of these growing media include improved control over water and nutrient availability, aeration, and disease management. The nutrient status in the growing medium should be kept optimal for the specific crop under the existing growing conditions (Sonneveld and Straver 1994). If managed properly, soilless production allows for accurate water and nutrient management resulting in better crop growth and yield. There is however major differences in water, air and nutrient distribution in the restricted rootzone of soilless grown crops which will affect root and shoot growth and development (Poorter et al. 2012). Compared to soil-grown crops, crops in a growing medium, grown hydroponically have a restricted root volume and a high shoot:root ratio (Sonneveld 1981). A limited nutrient reserve and a restricted buffering capacity for water and nutrients will also result in a rapid depletion of nutrients in the root medium (Bar-Tal 1999; Sonneveld 2000). Additionally the physiological capacity of the root system may also become a limiting factor for the uptake of water and nutrients by the plant, ultimately affecting dry matter production (Bar-Tal 1999). Potentially this can result in a reduction in growth and an increase in nutrient deficiencies and physiological disorders such as blossom end rot of tomatoes. However Bar-Tal (1999) cites several studies where nutrient uptake was not affected or even increased when the root volume was reduced through pruning of the roots but that it was the nutrient concentration at the rootzone that was crucial. Although container size was found to be a key determinant of the rate of nutrient uptake an increase in the nutrient solution concentration was in some cases able to compensate for the negative effect of a decrease in container size. This necessitates the accurate control of irrigation frequency of soilless production systems to ensure that the water and nutrient uptake is not limited by availability between irrigation events.

The rate of diffusion of an ion in the growing medium increases with an increase in temperature and also depends on the moisture content of the rootzone since the diffusion pathway becomes longer when the moisture content of the growing medium is low (Barber 1995). Tilling et al. (2007) showed that a tomato crops response to fertilizer N is strongly affected by the water supply and Santos (2009) showed that with sufficient irrigation the N application rates can be reduced from 336 to 224 kg N ha^{-1} without a significant drop in yields. This is the result of an increase in the availability of N when there is adequate soil moisture (Kim et al. 2008). Less mobile elements such as P and K can become unavailable for plant uptake through adsorption and precipitation. Increasing the irrigation frequency have however been shown to maintain higher dissolved P and K concentrations in the substrate solution and can therefore increase their uptake (Silber and Bar Tal 2008). Approximately 90% of water taken up by the plant is lost again through transpiration (Li et al. 2001) and irrigation is therefore often controlled through measurements of transpirations rates. Although the irrigation frequency is primarily controlled to ensure that the crops water demand is met, Bar-Tal et al (1993) also showed that the availability of other nutrients can be increased by increasing the fertigation frequency. Low rootzone oxygen conditions often occur when over-irrigation occurs and the growing medium becomes waterlogged. Since the uptake of ions is dependent on energy from respiration, low oxygen levels in the rootzone can also affect nutrient uptake (Hopkins et al. 1950).

In a closed hydroponic system where the drainage solution is re-used imbalances between the ratio of nutrients can occur rapidly resulting in a negative effect on crop growth, yield and fruit quality (Roorda van Eysinga and Smilde 1981). Increasing the application frequency of nutrient solution supplied to the crops can potentially decrease the rate of change in composition of the nutrient solution to be re-used and therefore limit the negative effects due to these imbalances. To determine the possibility of increasing the nutrient use efficiency of a system, it is necessary to determine the effect of different nutrient application rates on crop dry matter and production, fruit yield and nutrient accumulation.

The aim of this study was to assess the effect of a coir growing medium under different irrigation frequencies and different nutrient solution concentrations (EC) on the availability of nutrients for uptake by tomato plants grown in coir.

Methods and materials

Plant material and growth conditions

Trials were conducted in a naturally ventilated greenhouse at Welgevallen Experimental farm, Stellenbosch University (Stellenbosch, South Africa). Six week old tomato (*Lycopersicon esculentum* Mill. cvs. MFH 9343, Sakata, South Africa) seedlings, were transplanted to 10 L bags filled with coconut fibre (coir) at a planting density of 2.5 plants m^{-2}. Trials were conducted from September 2008 to March 2009 (summer/autumn) and repeated from September 2009 to March 2010 (summer/autumn). Climatic variables inside the greenhouse were logged throughout the duration of the trials. Air temperatures (T) varied between a minimum of 12 and maximum of 37 ^{O}C and the total daily solar radiation (R) (PAR) (MJ m^{-2} day^{-1}) inside the greenhouse ranged from 6 - 14 MJ PAR m^{-2}.

Treatments

Plants were irrigated by drip irrigation with two emitters per bag at a frequency of 4, 8 and 16 times a day, labelled as L1 (low irrigation frequency, 4xdaily), L2 (standard irrigation frequency, 8xdaily) and L3 (high irrigation frequency, 12xdaily). A modified nutrient solution, adjusted according to the growth stage at either full strength (S1) or half s trength (S2) was applied to plants (Table 1). The concentration of the micronutrients was however kept constant throughout the trial and the same for the full-strength and half-strength nutrient solutions. The irrigations start and stop times was automated and the total volume of water received per plant was the same for all treatments and calculated in order to maintain a variation from the stock nutrient solution of less than 20% in the EC of the drained nutrient solution of the plants irrigated eight times a day with the full strength nutrient solution. Edge rows were grown on the margins to reduce the border effect.

Table 1. Full strength nutrient solution concentration (EC, mS cm^{-1}) and macro-nutrient composition (meq L^{-1}) of the municipal water and final nutrient solutions used to fertigated the tomato plants at different growth stages. Nutrient solutions contained the following concentrations of micronutrients: 40.6 µmol L^{-1} Fe^{3+}; 35.0 µmol L^{-1} $H_2BO_3^-$, 4.6 µmol L^{-1} Zn^{2+}; 3.6 µmol L^{-1} Cu^{2+}; 10.9 µmol L^{-1} Mn^{2+}.

	EC	**NH_4^+**	**K^+**	**Ca^{2+}**	**Mg^{2+}**	**NO_3^-**	**$H_2PO_4^-$**	**SO_4^{2-}**
	mS cm^{-1}				**meq L^{-1}**			
		Municipal water						
	0.02	0.05	0.01	0.17	0.03	0.01	0.01	0.04
		Full strength nutrient solutions						
At planting	1.2	0.8	5.9	3.5	1.8	9.3	0.8	1.9
From 3rd Truss	2.6	1.2	14.3	6.9	3.6	20.2	1.7	4.1
From 5th Truss	2.6	1.2	16.5	5.5	2.8	20.2	1.7	4.1
		Half strength nutrient solutions						
At planting	0.6	0.4	2.9	1.8	0.9	4.7	0.4	0.9
From 3rd Truss	1.3	0.6	7.2	3.5	1.7	10.2	0.8	2.0
From 5th Truss	1.3	0.6	8.3	2.7	1.4	10.2	0.8	2.0

Measurements

Plants were trained to a single stem and all side shoots were removed weekly as is standard practise. The stomatal conductance of leaves was determined once a week on sun-exposed fully expanded leaves, 5th from the top between 12:00 and 14:00. Four plants per treatment were harvested during the vegetative growth part (45 days after planting (DAP)), after the 3rd truss formation (75 DAP), after the 5th truss formation (100 DAP) and at final harvest (168 DAP).

The leaf area and dry weight of the shoots was also determined. Crop nutrient uptake was determined through the chemical composition of leaves 3 to 5 of samples from every destructive harvest. The composition of the nutrients in the rootzone was determined from a water sample extracted with a large syringe from 3 areas within the rootzone. The volume of water (daily total) drained from the bags and the pH and EC were determined for four plants per treatment twice a week and a full chemical analysis of the macro-nutrients in the drainage done every four weeks. For every fertigation treatment four bags without plants were included. Leachate from these bags was also monitored for changes in pH, EC and chemical composition. The physiological water use efficiency (WUE) was calculated as the ratio of total fruit yield (g) to water use (WU). The use efficiency of each macro-nutrient was determined separately by determining the volume and concentration of each ion in the nutrient solution.

Fruit were harvested twice weekly starting on 60 days after planting (DAP) and separated into marketable and unmarketable and the average fruit weight was determined for fruit in each category. The percentage of fruit with blossom end rot was noted as well as cracked fruit. The total soluble solid (TSS, ^{O}Brix) content was determined using a refractometer (Atago, Japan) and the titratable acidity (TA) was determined as citric acid in fresh juice by titration of tomato juice with 0.1 M sodium hydroxide using a 862 compact titrosampler (Metrohm 862, Herisau, Switzerland) (Cliff et al.2012). To determine the dry matter percentage of the fruit a subsample was oven dried 70^{O}C 72 hours. The experiment was terminated 168 DAP.

Statistical analysis and experimental design

A factorial design with eight randomized blocks was established with irrigation frequency as main effect and nutrient solution concentration as sub effect repeated four times within each block. Each treatment combination consisted of 20 plants at a density of 2.5 plants per m^2. Analysis of variance (ANOVA) was used for evaluating data (STATISTICA 11.0, Statsoft (SA) Inc., Tulsa, Oklahoma, USA). Differences among the mean values were determined using using Fischer's LSD ($P<0.05$) equations.

The data was also analysed for treatment effects by means of a general linear model procedure and a stepwise procedure to obtain the relationship between the nutrient concentrations in the leaves and the growth parameters.

Results

Plant growth and yield

Results indicated that the leaf area index (LAI) and total biomass production, aboveground as well as the roots was affected by the nutrient solution concentration and the irrigation frequency (Table2). During the vegetative growth and early fruit set phase (H1 and H2) the dry weight of the shoots as well as the LAI was significantly lower for the plants that were only irrigated 4 times daily. There was however no difference in shoot weight or leaf area for plants irrigated 8 or 12 times daily. At the low irrigation frequency the dry weight of the shoots and the LAI was also significantly lower for plants grown with the half strength nutrient solution (S2) while there was no difference in dry matter accumulation when the irrigation frequency was increased to 8 or 12 times a day. This indicated the possibility that the increase in irrigation frequency to 8 or 12 times per day facilitated an increase in water and/or nutrient uptake by the plants and that it may be possible to use a lower nutrient solution concentration if the frequency of application is increased.

In contrast to the shoot dry weight the root DW of plants was decreased by the more frequent fertigations (L2 and L3) as well as the higher nutrient solution concentration (S1) resulting in the significant differences in the root:shoot ratio of plants at all the harvest stages. This is in agreement with other researchers who also found that an increase in the nutrient availability will increase the biomass allocation to the leaves and decrease in biomass allocation to the roots (Le Bot 1998; Poorter and Nagel 2000; de Groot et al 2002). The differences in biomass allocation can be the result of differences in nutrient availability but can in turn affect the uptake of nutrients which will affect the composition of the nutrient solution to be recycled.

Table 2. The interaction of irrigation frequency and nutrient solution concentration on the shoot dry weight, Leaf area index (LAI) and root:shoot ratio of tomato plants. Plants were fertigated at 3 different irrigation frequencies (L1: 4xdaily, L2: 8xdaily and L3:12xdaily) with a nutrient solution at either full strength (S1) or half strength (S2). Plants were harvested at four different growth stages; H1, vegetative growth; H2, after the 3rd truss formation; H3, after the 5th truss formation; H4 at final harvest, 168 DAP.

	Dry weight of shoots (g)				**Leaf area index (LAI)**				**Root:shoot ratio ($g\ g^{-1}$ DW)**			
	H1	H2	H3	H4	H1	H2	H3	H4	H1	H2	H3	H4
Treatment												
L1S1	12.5b	36.8b	58.6a	98.6a	1.3b	2.6b	3.6a	4.2a	0.59a	0.57a	0.50a	0.48a
L1S2	10.9c	30.2c	48.2b	79.3b	1.1c	2.0c	3.1b	3.5b	0.58a	0.55a	0.49a	0.46a
L2S1	12.6b	35.4b	57.6a	94.6a	1.8a	3.1a	3.7a	4.1a	0.51b	0.52a	0.44b	0.35b
L2S2	12.2b	33.8b	55.8a	93.2a	1.8a	2.6b	3.6a	4.1a	0.57a	0.55a	0.49a	0.45a
L3S1	15.8a	40.9a	59.1a	101.1a	1.9a	3.0a	3.9a	4.4a	0.45c	0.36b	0.22d	0.22c
L3S2	15.4a	39.2a	57.4a	95.2a	1.8a	2.8a	3.6a	4.2a	0.50b	0.41b	0.38c	0.37b
LSD ($p \leq 0.05$)	0.98	3.15	4.26	8.56	0.19	0.35	0.46	0.51	0.05	0.06	0.04	0.05

Significant differences between cultivars for means are indicated by different letters in superscript.

Fruit yield was affected by the nutrient solution concentration as well as the fertigation frequency. The total marketable fruit yield was significantly higher at the high irrigation frequency of 12 irrigation pulses per day (Figure 1) compared to either 8 or 4 pulses per day. At the low irrigation frequency of only 4 pulses per day the total marketable fruit yield was significantly lower when a half strength nutrient solution was used (Figure 1). Increasing the fertigation frequency to 8 or 10 times a day however resulted in marketable fruit yields not differing significantly between the full strength and half strength nutrient solutions. At only 4 irrigation pulses a day the number of unmarketable fruit was also significantly higher than at the higher irrigation frequencies of 8 or 12 pulses per day, especially for the plants grown at the half strength nutrient solution (Figure 1). When irrigating plants 12 times a day not only were the number of unmarketable fruit reduced but there was also no difference in the number of unmarketable fruit between the plants grown at the full of half strength nutrient solution.

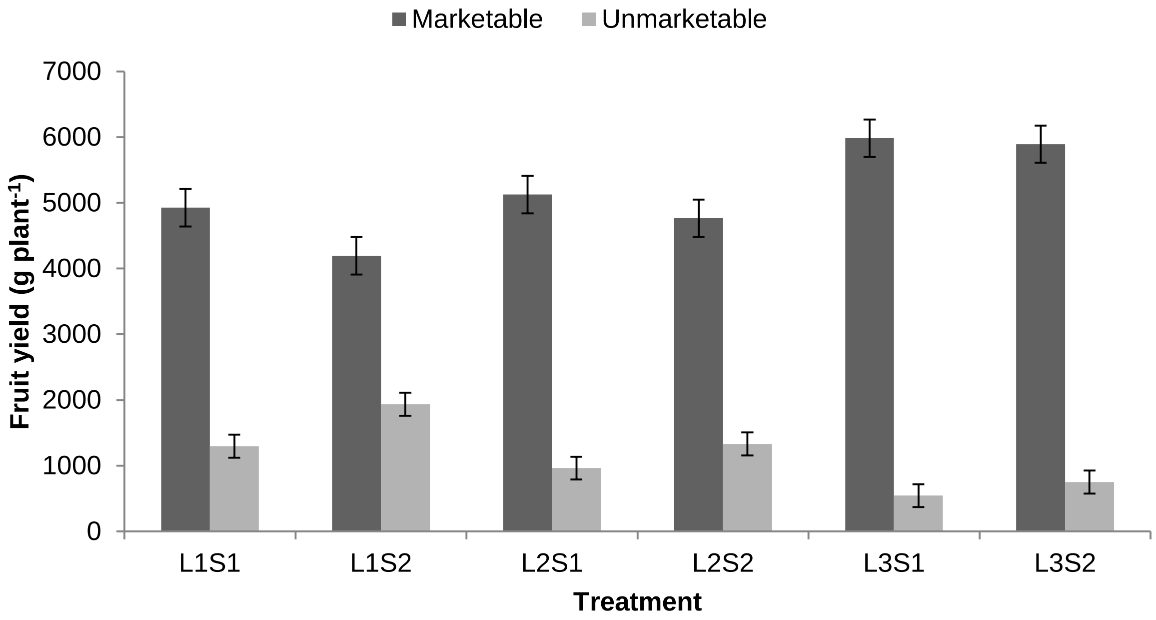

Figure 1. The interaction of irrigation frequency and nutrient solution concentration on the total marketable an unmarketable fruit yield (g plant^{-1}) of tomato plants fertigated at 3 different irrigation frequencies; L1: 4xdaily, L2: 8xdaily and L3:12xdaily with either a full strength nutrient solution (S1) or a half strength nutrient solution (S2). (Error bars indicate the LSD value at $p \leq 0.05$).

The number of fruit as well as the average fruit weight was also affected by the irrigation frequency and nutrient solution concentration (Table 3). Increasing the number of irrigation pulses per day resulted in an increase in the number of marketable fruit and decreased the number of unmarketable fruit. While at the low irrigation frequencies the number of marketable fruit was lower when using a half strength nutrient solution there was no difference in the number of marketable and unmarketable fruit when plants received 12 irrigation pulses per day (Table 3). A restriction of water transport into the fruit can also affect yield through a decrease in average fruit size and number of fruit per truss. This can be seen either when the availability of water is decreased or when there is an increase in the rootzone EC to more than 2.9 mS cm^{-1} due to either a high nutrient solution concentration being applied or a build-up of nutrients in the medium sometimes due to water uptake being higher than nutrient uptake (Adams 1991; Li et al. 2001; Passam 2007). From Table 3 it is also evident that the average fruit size increased with an increase in fertigation frequency and tended to be higher at the lower nutrient solution concentration although this difference was not statistically significant.

Table 3. The interaction of irrigation frequency and nutrient solution concentration on the number of marketable and unmarketable fruit per plant and average fruit size of tomato plants fertigated at 3 different irrigation frequencies (L1: 4xdaily, L2: 8xdaily and L3:12xdaily) with a nutrient solution at either full strength (S1) or half strength (S2).

	Number of fruit		**Average fruit weight (g $fruit^{-1}$)**	
Treatment	**Marketable**	**Unmarketable**	**Marketable**	**Unmarketable**
L1S1	40.2b	15.2b	123.13bc	86.35c
L1S2	34.6c	24.6a	125.34bc	80.62d
L2S1	43.2ab	12.4c	119.22c	80.28d
L2S2	35.5c	14.8b	136.16ab	94.96c
L3S1	45.1a	5.2d	132.98ab	108.72b
L3S2	42.7ab	5.4d	140.30a	149.86a
LSD ($p \leq 0.05$)	3.5	1.8	12.5	10.6

Significant differences between cultivars for means are indicated by different letters in superscript.

The unmarketable fruit was mostly as a result of cracking, blossom end rot and fruit being smaller than the minimum allowed size of 30 mm in diameter. The fertigation frequency and nutrient solution concentration also had an effect on the percentage of unmarketable fruit in each of these classes (Figure 2). The percentage of fruit with blossom-end rot increased with an increase in the fertigation frequency to 12 pulses per day. Blossom-end rot (BER) is generally regarded as a ‘calcium-related disorder’ but can be aggravated by either under- or over-irrigation (Saure 2001). The highest percentage of fruit cracking was observed for fruit at the low irrigation frequency of 4 pulses per day and this was highest for plants irrigated with a half strength nutrient solution. According to Hao et al. (2000), tomato fruit have a lower susceptibility to fruit cracking under high ECs. Abrupt changes to the EC in the growing medium are also known to negatively affect the plant water status and therefore tomato fruit quality (Shi et al. 2000). This was more likely when plants were only irrigated four times a day and the nutrient solution in the rootzone therefor not replenished as often leading to large fluctuations in ion concentrations in the rootzone.

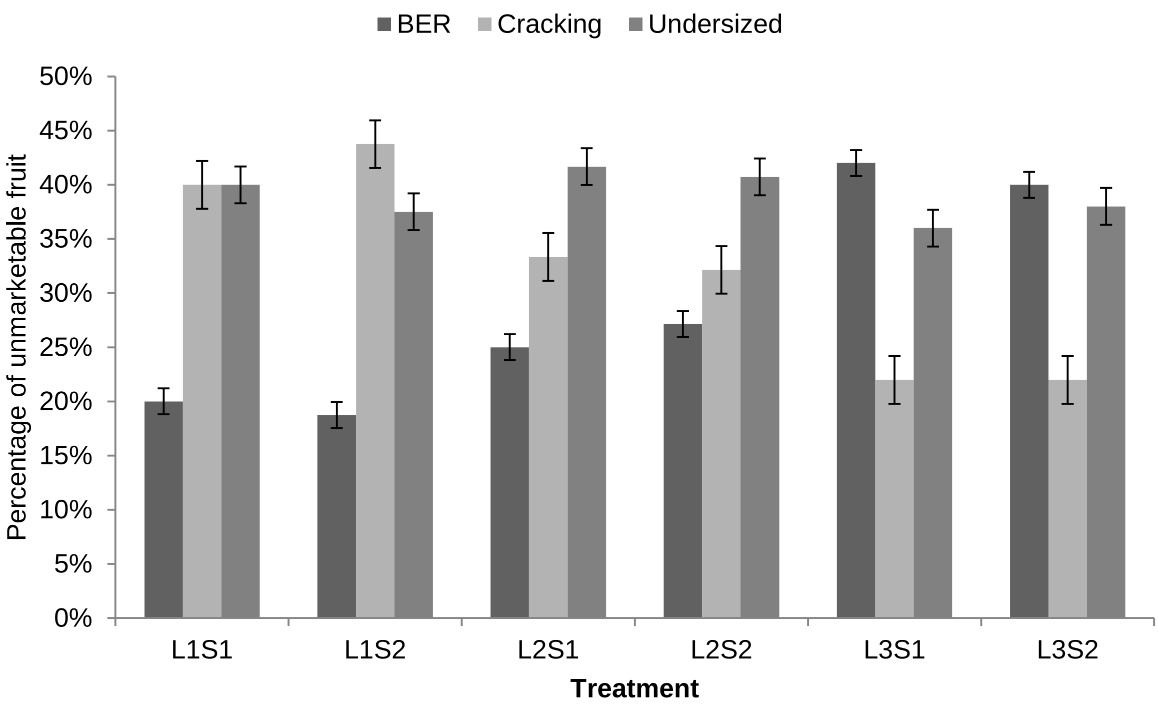

Figure 2. The interaction of irrigation frequency and nutrient solution concentration on the percentage of unmarketable fruit with blossom-end rot (BER), cracking and classified as undersized for tomato plants fertigated at 3 different irrigation frequencies; L1: 4xdaily, L2: 8xdaily and L3:12xdaily with either a full strength nutrient solution (S1) or a half strength nutrient solution (S2). (Error bars indicate the LSD value at $p \leq 0.05$).

Fruit quality

Fruit quality was affected by the nutrient solution concentration as well as the irrigation frequency. The fruit from the lowest irrigation frequency treatment combined with the half strength nutrient solution produced fruit with the lowest dry matter content (Table 4). It has been reported before that a decrease in the water availability, sometimes achieved through an increase in the EC in the root environment, will enhance the dry matter content of tomato fruit through a restriction of water transport into the fruit (Plaut et al. 2004). Since all other treatments besides the low concentration low frequency treatment showed minimal differences in the fruit dry matter content it indicates that an increase in fertigation frequency can overcome the negative effects low EC is known to have on tomato fruit quality. Similarly the total soluble solids of the fruit were highest under the low irrigation frequency treatment for plants at the full strength nutrient solution and lowest at the combination of low irrigation frequency and low nutrient solution concentration (Table 4). As a result of less water being absorbed the sugar content of tomato fruit can also be increased by an increase in nutrient solution EC (Combrink 1998). The titratable acidity (TA) of tomato fruit, which is an important contributor to the tomato taste and flavour, was affected by the concentration of the nutrient solution but not by the irrigation frequency (Table 4).

Table 4. The interaction of irrigation frequency and nutrient solution concentration on the dry matter content, total soluble solids and titratable acidity of tomato fruit from plants fertigated at 3 different irrigation frequencies (L1: 4xdaily, L2: 8xdaily and L3:12xdaily) with a nutrient solution at either full strength (S1) or half strength (S2).. Data given is from fruit of truss 2 (T2), truss 4 (T4), truss 6 (T6) and truss 8 (T8).

	Dry matter content %				**Total soluble solids (TSS) (^{O}Brix)**				**Titratable acidity (TA) (mmol.L^{-1})**			
	T2	T4	T6	T8	T2	T4	T6	T8	T2	T4	T6	T8
Treatment												
L1S1	8.5a	8.7a	8.3a	7.1a	5.6a	6.5a	6.6a	5.8a	15.9a	16.3a	16.2a	15.6a
L1S2	5.2d	5.1d	5.1c	4.8b	4.2d	4.2c	4.1c	4.0c	13.2b	13.4b	13.4b	12.7b
L2S1	7.3bc	7.5bc	7.2ab	6.8a	5.2ab	5.2b	5.2b	5.0b	15.6a	16.2a	16.1a	15.5a
L2S2	6.8c	6.7c	6.5b	6.5a	4.8c	5.0b	4.9b	4.6b	13.1b	13.4b	13.1b	12.6b
L3S1	7.9ab	7.7b	7.7a	6.8a	5.3ab	5.2b	5.2b	4.8b	15.7a	15.9a	16.1a	15.4a
L3S2	7.3bc	7.3bc	7.1ab	6.9a	5.0bc	5.1b	5.1b	4.6b	13.3b	12.9b	12.7b	12.4b
LSD ($p \leq 0.05$)	0.9	0.9	0.8	0.7	0.4	0.6	0.6	0.5	1.2	1.4	1.3	1.3

Significant differences between cultivars for means are indicated by different letters in superscript.

Water and nutrient uptake by plants

The tissue analysis for all macro-nutrients was done but for the sake of brevity only that of nitrogen and phosphorus will be discussed. The leaf nitrogen (N) concentration as a % of the leaf dry weigh decreased during the early fruit development phase - harvest stage (H2), but increased again later in the season (Figure 3). The leaf N concentration however remained in the optimum range as recommended by Peet (2005) except at H2 for the half strength nutrient solution treatments at irrigation frequencies of 4 and 8 times a day. Although the N leaf levels appeared lower under the low irrigation frequency this difference was not statistically significant indicating that N uptake is still satisfactory at all growth stages even under low irrigation frequencies often employed by producers and recommended in open systems to reduce water loss.

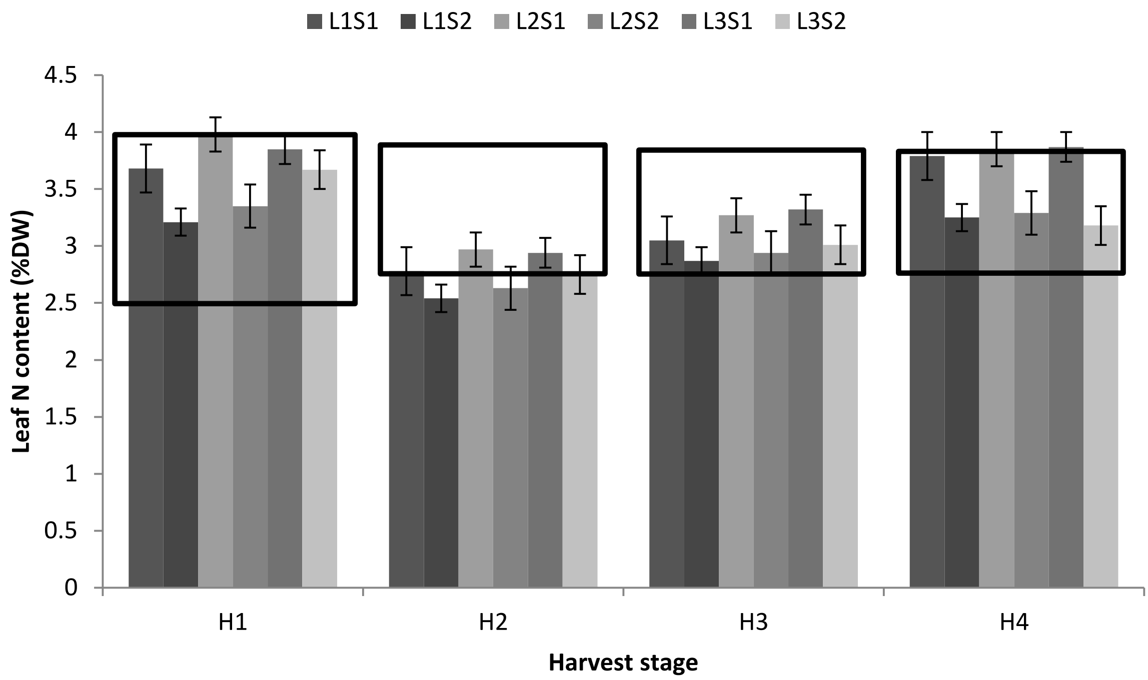

Figure 3. The interaction of irrigation frequency and nutrient solution concentration on the leaf nitrogen concentration (%DW) of tomato plants fertigated at 3 different irrigation frequencies; L1: 4xdaily, L2: 8xdaily and L3:12xdaily with either a full strength nutrient solution (S1) or a half strength nutrient solution (S2). Plants were harvested at four different growth stages; H1, vegetative growth; H2, after the 3rd truss formation; H3, after the 5th truss formation; H4 at final harvest, 168 DAP. Box indicates sufficient range. (Error bars indicate the LSD value at $p \leq 0.05$).

In contrast to nitrogen the leaf phosphorus (P) content increased later in the growing season when the plants transitioned from their vegetative phase to a fruit development phase (Figure 4). At the first harvest plants fertigated at the lower frequencies had a leaf P content lower than the recommended rate but at the third and final harvest the leaf P content was well above the recommended rate. This does however indicate that an increase in fertigation frequency early in the season can cause problems with P uptake possible due to a small root system and high concentrations of competing anions in the rootzone such as NO_3^- and SO_4^{2-}. Referring to several studies, Mankin and Fynn (1996) point out that maximal plant growth can be sustained under considerably lower concentrations than normally used in soilless production systems and according to Zheng et al. (2005) and Rouphael et al. (2008) nutrient solution concentrations can be reduced by up to 50% without a negative effect on biomass production and product quality for geraniums and gerberas. It appears thus that the nutrient demand seems more important than the supply and plant nutrient uptake will be determined by demand.

Less mobile elements such as P and K can often become unavailable for plant uptake through adsorption and precipitation. Increasing the irrigation frequency have however been shown to maintain higher dissolved P and K concentrations in the substrate solution and can therefore increase their uptake (Silber and Bar Tal 2008). Tilling et al. (2007) showed that a tomato crops response to fertilizer N is strongly affected by the water supply and Santos (2009) showed that with sufficient irrigation the N application rates can be reduced from 336 to 224 kg N ha^{-1} without a significant drop in yield. This is the result of an increase in the availability of N when there is adequate soil moisture (Kim et al. 2008).

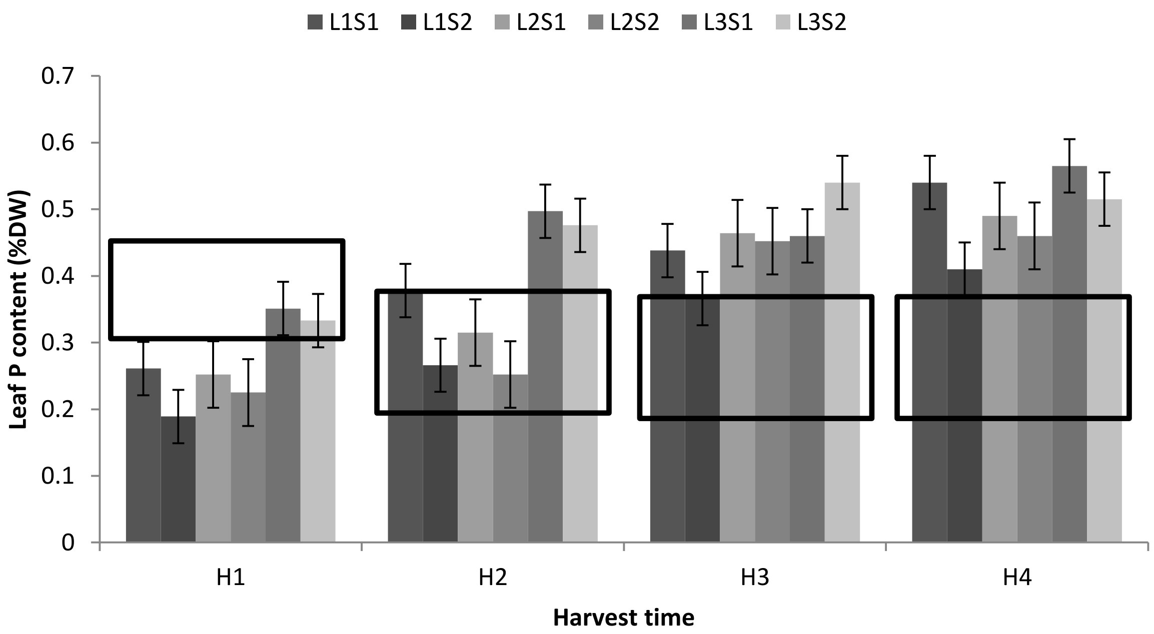

Figure 4. The interaction of irrigation frequency and nutrient solution concentration on the leaf phosphorus concentration (%DW) of tomato plants fertigated at 3 different irrigation frequencies; L1: 4xdaily, L2: 8xdaily and L3:12xdaily with either a full strength nutrient solution (S1) or a half strength nutrient solution (S2). Plants were harvested at four different growth stages; H1, vegetative growth; H2, after the 3rd truss formation; H3, after the 5th truss formation; H4 at final harvest, 168 DAP. Box indicates sufficient range. (Error bars indicate the LSD value at $p \leq 0.05$).

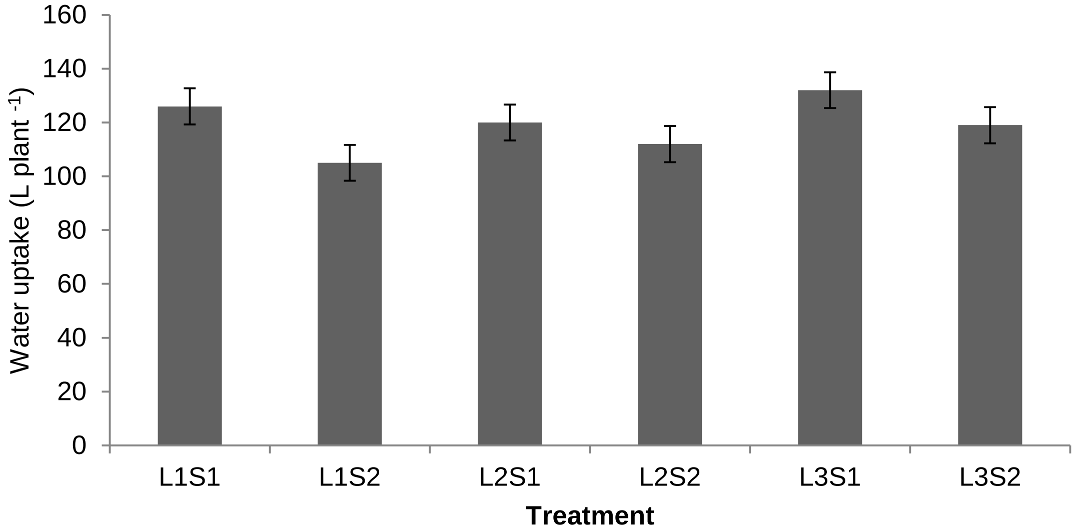

Figure 5. The interaction of irrigation frequency and nutrient solution concentration on water uptake (L water taken up per plant) of tomato plants fertigated at 3 different irrigation frequencies; L1: 4xdaily, L2: 8xdaily and L3:12xdaily with either a full strength nutrient solution (S1) or a half strength nutrient solution (S2). (Error bars indicate the LSD value at $p \leq 0.05$).

Water uptake was not significantly affected by the irrigation frequency and tended to be lower at the half strength nutrient solution for all the irrigation frequencies (Figure 5). This results in slightly higher water use efficiency for the plants grown at lower nutrient solution concentration although this effect was not statistically significant at the higher irrigation frequencies (Figure 6). Total shoot dry weight was however well correlated with water uptake with a coefficient of determination (R^2) higher than 0.91 which indicates that the nutrient solution concentration explained almost all the variation in water uptake.

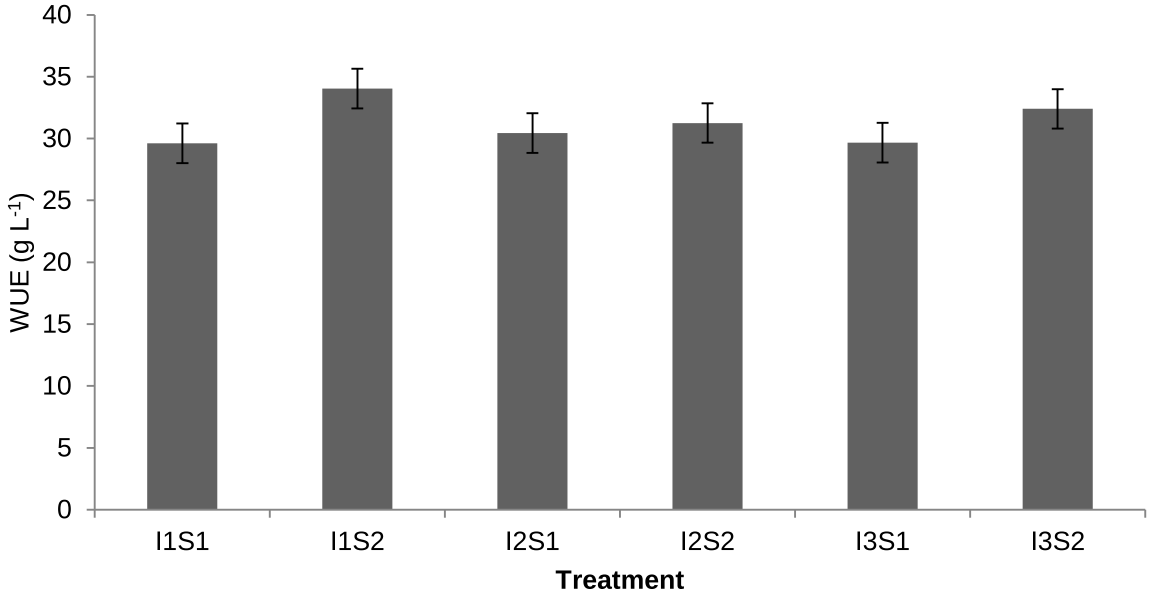

Figure 6. The interaction of irrigation frequency and nutrient solution concentration on water use efficiency (WUE) (g fruit per L water used) of tomato plants fertigated at 3 different irrigation frequencies; L1: 4xdaily, L2: 8xdaily and L3:12xdaily with either a full strength nutrient solution (S1) or a half strength nutrient solution (S2). (Error bars indicate the LSD value at $p \leq 0.05$).

A significant correlation was observed between the leaf P content and the aboveground biomass during the vegetative growth phase of the crop (Figure 7). This indicate that the positive effect the increase in fertigation frequency had on vegetative growth can be attributed to the positive effect it had on the uptake of P. Based on this regression, 95% of the variation in aboveground biomass production can be attributed to differences in the P content of the leaves. Frequent fertigation is known to reduce the role of diffusion in transporting nutrients towards the plants roots (Silber et al. 2003) enhancing nutrient and especially the uptake of P that is relatively immobile in the rootzone. The increase in P uptake as a result of an increase in fertigation frequency has also been linked to an increase biomass production and yield in lettuce and bell pepper (Silber et al. 2003; Silber et al. 2005). According to Silber et al (2005) the improvement of nutrient uptake through high frequency fertigation is the result of two mechanisms: 1) the regular renewal of nutrients in the rootzone area that becomes depleted soon after a fertigation event and 2) maintenance of a higher water content in the medium that facilitates the mass-flow of nutrients.

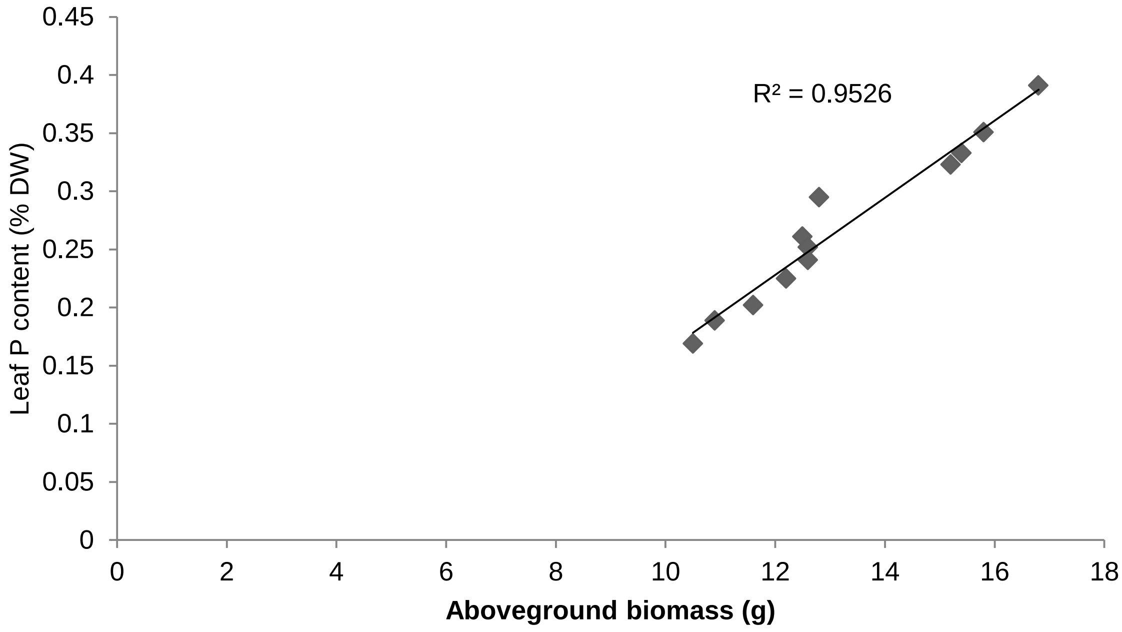

Figure 7. Relationship between the leaf P content and the aboveground biomass (leafs, stems and inflorescence) of tomato plants during the vegetative growth of the crop.

Analysis of the nutrient solution extracted from the rootzone during the vegetative growth phase revealed that although there was a small difference in the EC, the cation and anion concentrations varied significantly and was significantly affected by the irrigation frequency (Table 5). For the most part the composition of the rootzone solution for plants under the highest irrigation frequency changed less than that of the rootzones where plants were irrigated either 4 or 8 times a day. The concentration of cations NH_4^+ and K^+ decreased in the rootzone compared to the starting solution while that of Ca^{2+} and Mg^{2+} increased. NO_3^- levels were also severely reduced in the rootzone compared to the starting solution while that of SO_4^{2-} increased. There was very little change in the $H_2PO_4^-$ concentration in all of the treatment combinations.

Table 5. Concentration and composition of the nutrient solution extracted from the rootzone of coir grown tomato plants during the early vegetative growth of the crop. Plants were fertigated at 3 different irrigation frequencies (L1: 4xdaily, L2: 8xdaily and L3:12xdaily) with a nutrient solution at either full strength (S1) or half strength (S2).

	EC ($mS\ cm^{-1}$)	**NH_4^+**	**K^+**	**Ca^{2+}**	**Mg^{2+}**	**NO_3^-**	**$H_2PO_4^-$**	**SO_4^{2-}**
				meq L^{-1}				
S1 - Starting Solution	1.2	0.8	5.9	3.5	1.8	9.3	0.8	1.9
L1S1	1.1a	0.2b	3.4b	6.1a	3.2a	4.1b	0.9a	3.9a
L2S1	1.1a	0.2b	3.9a	5.4b	2.8a	5.8a	0.8a	3.6ab
L3S1	1.1a	0.4a	4.2a	4.6c	2.1b	6.2a	0.8a	3.2b
LSD (p≤0.05)	0.15	0.18	0.35	0.42	0.43	0.48	0.19	0.45
S2 - Starting Solution	0.6	0.4	3.0	1.8	0.9	4.7	0.4	1.0
L1S2	0.5a	0.1b	1.5b	3.2a	1.7a	1.8c	0.5a	1.8a
L2S2	0.5a	0.2ab	1.8b	2.6b	1.3b	2.5b	0.5a	1.9a
L3S2	0.6a	0.3a	2.4a	1.9c	0.9c	3.8a	0.4a	1.5b
LSD (p≤0.05)	0.11	0.19	0.38	0.38	0.37	0.35	0.12	0.21

Significant differences between cultivars for means are indicated by different letters in superscript.

These results again re-affirm that it is important to do a full nutrient analysis when managing the nutrient solution either in an open drain to waste or re-circulating hydroponic system. The practice of only managing the nutrient solution based on EC readings can result in large ion imbalances in the rootzone that can cause a decrease in nutrient uptake, crop growth and yield. When attempting to maintain the nutrient levels at a set amount in the applied nutrient solution the variability of evapotranspiration and nutrient absorption must also be considered as this will also have an effect on the nutrient concentrations in the rootzone. Since the uptake of ions is energy dependant and this energy is dependent on respiration, low oxygen levels in the rootzone can affect nutrient uptake. In follow-up trials the water content as well as the oxygen content of the mediums should also be evaluated.

Conclusion

In soilless growing systems where the size of the rootzone is often limited, the irrigation frequency can play a significant role in the availability of nutrients for crop uptake. Under high irrigation frequencies (12 pulses per day) the frequent replenishment of ions in the rootzone can result in an increase in the dry matter content and fruit yield although several fruit quality parameters might be negatively influenced under these conditions. When using a nutrients solution with a low EC producers can therefore increase nutrient uptake through increasing the irrigation frequency which can result in a significant cost reduction and increase in profitability.

It is also evident that the nutrient composition in terms of the cation and anion ratios and not only the concentration in the growing medium should be assessed regularly to keep it within and optimal range for the specific crop under the existing growing conditions.

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Chapter 5

Simulating water and nutrient uptake for tomatoes in a soilless production system

Article 6

Modelling water and nutrient uptake of soilless grown tomatoes grown in coir.

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Abstract

In a closed soilless production system the continual recycling of the nutrient solution requires careful monitoring and control of ion levels to prevent yield losses due to nutrient imbalances. This paper presents possible methods for predicting the macro-nutrient and water uptake of tomato (*Solanum lycopersicum* L.) in a coir growing medium. The models for water and nutrient uptake was calibrated and validated with 3 separate trials during 2011 and 2012. In these, different fertigation methods were applied; no re-circulation (FM1), re-circulation through topping up the re-circulation water with a full strength nutrient solution (FM2) or re-circulating using topping up to a desired EC level (FM3). The fertigation method had no effect on the crops biomass production but the fruit yield and quality was affected, mainly as an increase in total soluble solids (TSS) and titratable acidity (TA) in fruit from FM2. Although the water uptake per plant was not significantly affected by the fertigation method the water use efficiency (WUE) was lower in FM2 and FM3. The proposed models were able to accurately predict leaf area development and water and nutrient uptake. Although nutrient uptake was affected by the fertigation method it was possible to predict the concentration of macro-nutrients in the nutrient solution drained from the growbags fairly accurately using these equations. A close relationship between the uptake of certain macro-nutrients was observed and can also be explored further as a method to predict and adjust nutrient concentrations in semi-closed growing systems.

Keywords: electrical conductivity (EC),nutrient solution, nutrient uptake, soilless production, solar radiation

Introduction

An intensive production system that is still gaining ground is soilless crop production in a protected environment such as a greenhouse (Sonneveld and Voogt 2009). Growing plants in soilless culture is a method of cultivating crops in any growing medium different than soil where all the nutrients are added to the irrigation water (Raviv and Lieth 2007). A wide variety of crops can be grown in soilless systems including vegetables such as tomatoes, lettuce and cucumbers and flowers including roses, tulips and potted plants such as cyclamens (Van Os et al. 2008).The drained nutrient solution from crops grown in a soilless system in the greenhouse is more often being re-used in order to reduce the risk of pollution but also to increase the sustainability and the water and nutrient use efficiency of the system (Raviv 2007). Besides the risk of pathogen build-up, one of the main impediments of a wider application of this method is the possible yield reductions caused by an unbalanced nutrient solution or even the build-up of all or certain ions in the re-circulated solution (Giuffrida and Leonardi 2012). This is the result of plants not taking up ions at a constant rate or at the same rate as applied in the nutrient solution (Voogt 1993). When re-using drained nutrient solutions for fertigating crops several techniques can be used to manage the nutrient application. Two of the most widely used techniques are to either automatically adjusting the electrical conductivity (EC) of the nutrient solution to a set value or by adding the set nutrient solution to the drain water (De Kreij et al. 1996; Bugbee 2003). The nutrient solution is then re-circulated until the EC or the concentration of a specific ion reaches a maximum threshold level (Baas and van den Berg 1999).To be able to recirculate the nutrient solution for as long as possible adjustments to the nutrient solution to maintain ion concentrations as well as the total salt concentration as close as possible to the norm values is required. This necessitates frequent chemical analyses either by submitting samples and determining the composition of the new solution based on the % deviation of ions in the drained nutrient solution or through the use of specific algorithms (Combrink and Kempen 2011). Another method is through on-line ion-sensing which requires using an expensive chemosensor-based control system (Gieling et al. 1988).

An alternative method of calculating the addition level of nutrients in a re-circulating system is based on using nutrient uptake models. Using nutrient uptake models can assist producers in managing their nutrient solutions without being dependent on frequent lab analysis of the recirculated irrigation water, which in some instances can take several weeks. However, the traditional nutrient uptake models used for field grown crops are not adequate to describe nutrient uptake in a soilless system which is characterized by a restricted root volume and high rootzone nutrient concentrations (Sonneveld and Voogt 2001; Silberbush et al. 2005). Recently various modeling tools intended to describe and/or predicting the processes related to plant nutrition has been developed (Le Bot et al. 1998). Several authors have suggested the use of uptake concentrations (UC) defined as the ratio between nutrient ions (mmol) and water (L) taken up by plants during the same time interval in crop models used for fertigation control mainly for its ease of use and few input parameters (Magán et al. 2005; Savvas et al. 2008; Gallardo et al. 2009; Massa et al. 2011). These models are not always able to accurately simulate nutrient uptake under diverse conditions (Massa et al. 2011). In previous trials (Article 1, p44) it was observed that the UC of macro-nutrients was affected by the nutrient solution EC and that nutrient uptake is not linearly related to the water uptake. The use of mechanistic models should therefore rather be considered as a means of predicting more accurately the nutrient uptake of plants in soilless growing systems. An example of a simulation where nutrient uptake is linked to nutrient demand is the Michaelis-Menton based model proposed by Mankin and Fynn (1996) and was used in a previous study (Article 3, p82) to successfully relate individual nutrient uptake to intercepted photon flux density (PPFD). Several simulation models for water and mineral uptake in soilless systems which was developed by other authors (Carmassi et al. 2007, Massa et al. 2011). However they do not take the effect of nutrient solution concentration and solar radiation levels into account.

The aim of this study was to simulate nutrient and water uptake and thus also the the composition of the drained nutrient solution, in soilless systems using tomatoes as a model crop. This was done through using both existing models and models developed through stepwise multiple regression using data from previous trials on the uptake of water and nutrients as affected by the availibitity and crop demand (article 1 to 5 in this thesis). These models were then calibrated and validated in the trials described in this article. In these trials tomatoes were cultivated in a coir growing medium using different fertigation methods; both an open and two different semi-closed fertigation methods.

Material and methods

Plant material and growth conditions

Trials were conducted in an evaporatively cooled greenhouse at Welgevallen Experimental farm, Stellebosch University (Stellenbosch, South Africa). Six week old tomato (*Lycopersicon esculentum* Mill. cvs. Tinker, Sakata, South Africa) seedlings, were transplanted to standard (1m long) coir growbags at a planting density of 2.8 plants m^2. Trials were conducted from January to May 2011 (summer/autumn) and repeated from August to December 2011 (spring/summer) for calibration of the models and again from January to May 2012 (summer/autumn) for validation of the models. Climatic variables inside the greenhouse were logged throughout the duration of the trials. Air temperatures (T) varied between a minimum of 14 and maximum of 36^{O}C but day temperatures was on average 26^{O}C during summer/autumn 2011, 28^{O}C during spring/summer 2011-2012 and 26^{O}C during summer/autumn 2012. The daily solar radiation levels (R) (PAR)(MJ m^2 day^{-1}) inside the greenhouse during spring/summer 2011 ranged from 7 -11 MJ PAR m^{-2} while it ranged between 8 and 14 MJ PAR m^{-2} during summer/autumn 2012 and from 7 - 12 MJ PAR m^2 during spring/summer 2012. The CO_2 concentration inside the greenhouse was measured using a K-33 ELG sensor.

Crops were cultivated for 115 days from transplanting to final harvest. Three plants were transplanted to each growbag with one dripper per plant. The plants were trellised vertically and all side shoots were removed weekly as is standard practise in commercial greenhouses. Plants were topped after fruit set of the 10th fruit truss.

Treatments

Plants were fertigated with the same nutrient solution of which the composition and concentration was varied according to the growth stage of the crops (table 1). Plants were fertigated at a high frequency of 8 times a day (8:00, 9:30, 11:00, 12:30, 14:00, 15:30, 17:00 and 18:30) resulting in a high leaching fraction of between 30 and 50% being maintained. The frequent irrigations and high leaching fraction ensured that the ion concentrations in the rootzone did not deviate much from the concentration of the nutrient solution as was observed in earlier trials (Article 5, p122).

To calibrate and validate the models, data was gathered in each trial from three different fertigation approaches that may be applied by soilless growers:

Fertigation method 1 (FM 1): A traditional drain-to-waste system as is still currently widely used in South Africa. The drainage water volume EC and chemical composition was measured but none was collected for re-use.

Fertigation method 2 (FM 2): A re-circulating system where the drained nutrient solution was collected, volume, EC and chemical composition determined before collection in a drainage tank. This drainage water was not continuously fed into the main nutrient solution tank but rather when the main nutrient solution tank needed to be replenished, water from this larger collection tank was used as feeding water which was topped up with the full strength starting nutrient solution. This resulted in a gradual increase in the nutrient solution EC over time. When the EC increased by more than 40% of the baseline solution EC it was flushed out and replaced by a new nutrient solution.

Fertigation method 3 (FM 3): A re-circulating system where the drained nutrient solution was collected, volume, EC and chemical composition determined before being pumped back to the main nutrient solution tank. The main nutrient solution tank was topped up daily with fresh water and then the EC was adjusted to the desired level by addition of concentrated solutions. Although the EC remained relatively constant the macro-nutrient ratios started to deviate necessitating the tank being flushed on four occasions during the growing season.

Each of the growing systems representing a fertigation approach consisted of 4 rows of 84 plants each, 336 plants in total.

Table 1. Macro-nutrient composition (meq L^{-1}) of the municipal water and final nutrient solutions used to fertigate tomato plants at different growth stages. Nutrient solutions contained the following concentrations of micronutrients: 40.6 µmol L^{-1} Fe^{3+}; 35.0 µmol L^{-1} $H_2BO_3^-$, 4.6 µmol L^{-1} Zn^{2+}; 3.6 µmol L^{-1} Cu^{2+}; 10.9 µmol L^{-1} Mn^{2+}.

	EC (mS cm^{-1})	**NH_4^+**	**K^+**	**Ca^{2+}**	**Mg^{2+}**	**NO_3^-**	**$H_2PO_4^-$**	**SO_4^{2-}**
					meq L^{-1}			
		Municipal water						
	0.02	0.05	0.01	0.17	0.03	0.01	0.01	0.04
		Nutrient solutions						
At planting	1.2	0.8	5.9	3.5	1.8	9.3	0.8	1.9
From 3rd Truss	2.6	1.2	14.3	6.9	3.6	20.2	1.7	4.1
From 5th Truss	2.6	1.2	16.5	5.5	2.8	20.2	1.7	4.1

Measurements

Crop growth and fruit yield parameters

Destructive harvesting of four tomato plants was conducted every week. Plants were separated into leaves, stems and fruits. The leaf area and all plant parts fresh weights were obtained before oven drying at 80˚C for 3 days and determination of the dry weight.

From 60 days after planting (DAP) fruit were harvested, graded as marketable or unmarketable where the unmarketable fruit were determined as fruit with any discernible physical deformities or disorders or less than 30mm in diameter. Marketable fruit were separated into marketable and unmarketable, and divided into the following size classes; small (31-55 mm), medium (56-72 mm) and large (>73mm) The Brix of fruit from four plants per treatment were determined at every harvest using a handheld refractometer (Atago, Japan) and on 112 DAP on 71 DAP fruit were oven dried at 70^{O}C for 72 hours to determine the dry weight and the elemental concentration.

Water uptake (U_w) and nutrient uptake (U_n)

Daily water uptake (Uw) was measured by calculating the difference between the amount of water applied through the drippers and the amount of water drained from the grow bags daily. Since closed grow bags with only a 5cm x 5cm hole at the top for the stem was used, evapotranspiration was assumed to be negligible. The nutrient solution was analysed in the laboratory at the beginning of each experiment and the EC and pH levels were checked daily throughout the trial period. The pH levels in the two re-circulating systems (FM 2 and FM 3) were adjusted with nitric acid when necessary to remain between 5.5 and 6.5. Nutrient uptake (U_n) was calculated as the difference between the concentration in the applied nutrient solution and the concentration from the solution extracted with a syringe from the rootzone. Total plant nutrient uptake was assessed through chemical analysis of plants from every destructive harvest.

Simulation of water and nutrient uptake

Water uptake (Uw, L m^{-2} day^{-1}) was simulated as a function of crop transpiration using a simple linear regression model, which reflected the radiation intercepted by the crop as a function of the crop leaf area (Carmassi et al. 2007):

$$Uw = 0.946(1-\exp^{-k\mathrm{LAI}})^{*} (\mathrm{DLI}/\lambda) + 0.188 \quad (1)$$

Where DLI is the daily light integral (cumulative solar radiation, MJ m^{-2}), λ is the latent heat of vaporization (2.45 MJ kg^{-1}). The canopy light extinction coefficient (*k)* is dimensionless and was determined using the following equation from Carmassi et al. (2007):

$$R/R0 = \exp^{-k\mathrm{LAI}} \quad (2)$$

Where R and R0 are the solar radiation levels measured above and below the crop canopy. This was determined three times; once when the leaf area index (LAI) was 1.05, then when the LAI was 2.54 and again when the LAI was 3.12. The values of 0.59 obtained for the light extinction coefficient (*k)* within the crop canopy is somewhat lower than the values obtained by Marcelis et al (1998) and Massa (2008) for greenhouse crops but higher than the value reported by Jovanovic and Annandale (2000) for 3 open field produced tomatoes.

Carmassi et al. (2007) and Massa (2008) assumed LAI to obey a sigmoid function and used leaf area and temperature data (incorporated as growing degree days (GDD) to model the LAI. The leaf area of individual leaves is however also strongly affected by assimilate availability. Where there is good a correlation between temperature and solar radiation levels it is acceptable to follow this approach but in greenhouses the correlation between temperature and radiation is however small compared to open field conditions and it would therefore be more accurate to use solar radiation levels when modelling leaf area development of greenhouse crops (Heuvelink and Marcelis, 1996). Based on data from previous work that found a good correlation between the LAI and the solar radiation levels (article 4, p102) as well as the age of the plant best described in the form of photo-thermal units (PTU, ^{O}C MJ m^{-2}) (Pardossi et al. 2005) which is the product of the growing degree days (GDD, ^{O}C calculated on the basis of mean daily air temperature, with a base temperature of $8^{O}C$) (Thornley and Johnson, 1990) and the mean solar radiation level (R, MJ m^{-2}) the following original equation was formulated and used to estimate the LAI during these trials:

$$LAI = (-6.94*10^{-10}*(PTU)^2) + (1.17*10^{-4}*(PTU)) -0.405 \quad (3)$$

As radiation increases the rate of nutrient uptake follows a Michaelis-Menten type relationship (rectangular hyperbola). To estimate the macro-nutrient uptake (U_n, mg m^{-2} hr^{-1}) a mechanistic high-affinity, active uptake Michaelis-Menten based model was therefore used which takes into consideration the intercepted photosynthetic photon flux density (PPFD):

$$U_n = U_{max}(PAR)/(K_m+PAR) \quad (4)$$

Where U_{max} = maximum rate of nutrient uptake (mg m^{-2} h^{-1})

PAR= solar radiation (µmol m^2 s^{-1})

K_m = Michaelis-Menten constant (the PPFD at ½Umax)

The constant K_m, characteristic of each individual uptake rate, and U_{max} is usually determined by a reciprocal plot. The values for U_{max} and K_m will however be affected by the internal as well as external conditions (Massa 2008). This effect can be either incorporated through a sub-model relating the effect of environmental conditions on biomass production and thus on nutrient uptake direct as was done by Wheeler (1998) or by measurements and calculations of U_{max} and K_m at different environmental conditions (Sago et al 2011). The approach used in this study was to calculate the U_{max} and K_m values for each of the macro-nutrients from data generated in previous studies (article 3, p82) where correlations was established between the uptake of macro nutrients and the EC of the nutrient solution as well as the mean solar radiation level (R, MJ m^{-2} day^{-1}) through the age of the plant defined in the form of photo-thermal units (PTU, ^{O}C MJ m^{-2} day^{-1}) and (Table 2).

Since the uptake of calcium is mostly passively driven by the transpiration stream the following additional equation was adjusted as suggested by Silberbusch et al (2005):

$$U_n^{Ca} = U_{max}^{Ca}(PAR)/(K_m^{Ca}+PAR) + ß*((T_t*a*LAI_t)/(RA_t))*C^{Ca} \quad (5)$$

Where ß is the fraction of water influx active in Ca uptake and assumed constant (0.25), T_t is the water losses due to transpiration obtained from the following equation:

$$Tt = Trel*Tmax*LAI \quad (6)$$

where Tmax is the maximal temporal transpiration rate during midday of 4mm day^{-1} (Silberbusch et al, 2005).

Table 2. *Coefficients used to simulate ions' uptake*

Ion	U_{max}		K_m	
NO_3^-	0.0002*(EC*PTU)+122.09	R^2 = 0.77	0.001(EC*PTU)+506.24	R^2 = 0.77
K^+	0.0007*(EC*PTU)+241.491	R^2 = 0.67	0.006(EC*PTU) + 2198.3	R^2 = 0.71
$H_2PO_4^-$	0.0001*(EC*PTU)+54.235	R^2 = 0.72	0.0006(EC*PTU)+429.14	R^2 = 0.68
Mg^{2+}	-0.00003*(EC*PTU)+18.893	R^2 = 0.65	0.00002(EC*PTU)+18.035	R^2 = 0.74
SO_4^{2-}	0.00006*(EC*PTU)+26.841	R^2 = 0.70	0.0017*ES*PTU) + 701.99	R^2 = 0.81
Ca^{2+}	-0.00012*(EC*PTU)+48.538	R^2 = 0.76	0.0003(EC*PTU) + 112.9	R^2 = 0.69

Using these equations the total daily ion uptake per plant could be calculated as well as the concentration of each ion remaining in the drainage water (C_{dr}, meq L^{-1}) if the volume of the irrigation water, volume of drainage water and ion concentration in the applied nutrient solution is known.

$$C_{dr}= ((C_{NS}*V_I)-U_{nT}) / V_{dr} \qquad (7)$$

Where C_{NS} (meq L^{-1}) is the concentration of the specific ion in the nutrient solution supplied to the crops (concentration of ions in fertilizer as well as from the feeding water), V_I is the volume of irrigation water supplied (L m^{-2} day^{-1}), U_{nT} (meq m^{-2} day^{-1}) is the total daily nutrient uptake. V_{dr} (L m^{-2} day^{-1}) is the volume of the drainage water.

Lastly the EC (mS cm^{-1}) of the drainage water could be calculated from the total cation concentration (C^{CAT}, meq L^{-1}) using the formula proposed by Sonneveld (2000):

$$EC = 0.19 + (0.095*C^{CAT}) \qquad (8)$$

Using these equations it is also possible to simulate the effect the leaching fraction may have on the ion concentration and EC of the drained nutrient solution for re-use.

Statistical analysis and experimental design

Each treatment combination was repeated four times in a completely randomized trial. Multivariate analysis of variance (ANOVA) was used for evaluating data (STATISTICA 11.0, Statsoft (SA) Inc., Tulsa, Oklahoma, USA) and the statistical significance of the results was analysed by the t-test ($p \leq 0.05$). The development of nutrient uptake models was performed through stepwise multiple regression (MR) analysis of data sets derived from previous experiments (Chapter 2, 3 and 4). Most of the variables were calculated daily basis and then linear equations were generated from regression analysis between simulations and observations.

Results and discussion

Crop growth and fruit yield parameters

No significant differences were observed during both years in total shoot biomass production or the leaf area of the plants as a result of the different fertigation methods used (data not shown). As previous results (Article 2, p63) indicated that variations in EC and nutrient solution composition can have a significant effect on tomato crop growth and development this indicates that management of these solutions with regards to replacement of the solutions at certain times was sufficient to prevent deviations that can affect crop growth. A good correlation was found between the simulated and measured leaf area index (LAI) using the proposed model that incorporates the effect of plant age as a function of temperature and solar radiation levels (Figure 1). Although it has been reported that an EC of up to 5 mS cm^{-1} will not affect the LAI (Massa et al. 2010), this might be cultivar dependent since previous trials with this cultivar did show an effect of nutrient solution concentration on leaf area development (unpublished data). It is therefore recommended that this factor should also be incorporated into this model to further improve the accuracy of its predictive capability.

Both the marketable and unmarketable fruit yield was similar regardless of the fertigation methods applied (Table 3). The marketable yield was however lower during the second season but not the unmarketable yield resulting in a higher unmarketable fruit % during the second season.

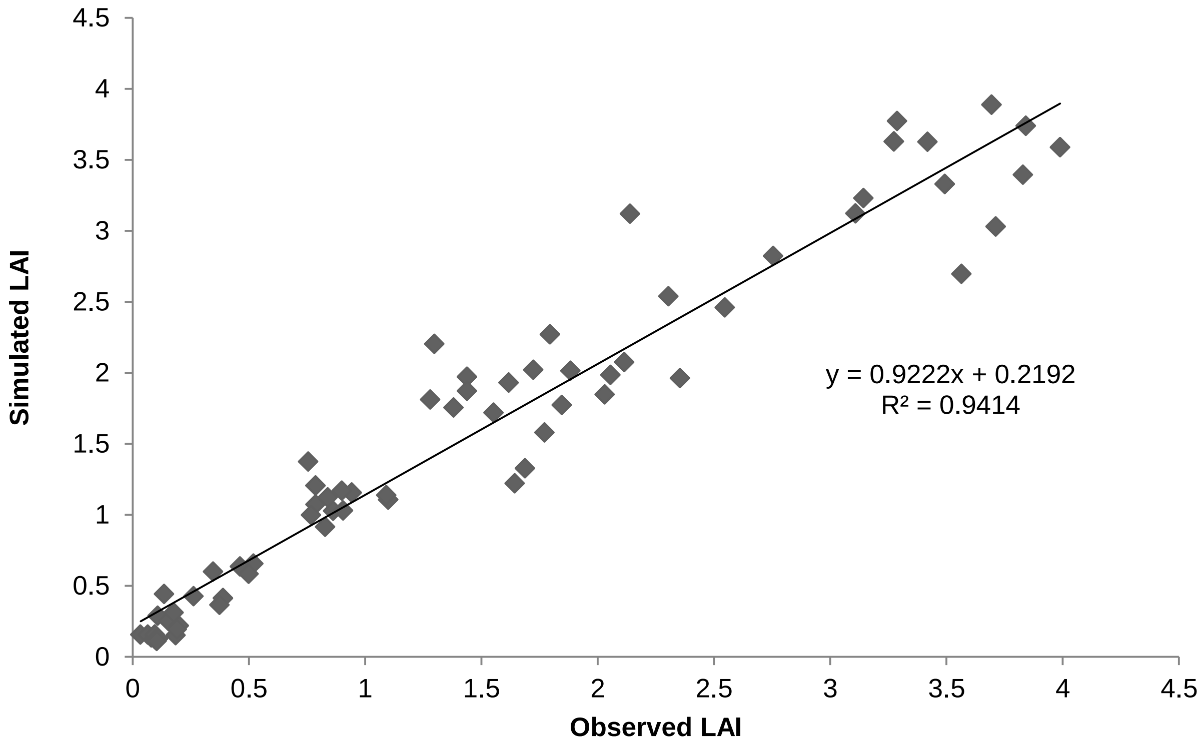


Figure 1. Observed and simulated LAI of tomato plants grown hydroponically in a coir medium during 2011 and 2012. Each value represents the mean of three replicates. The line represents the linear regression (equation is reported inside the graph).

During both seasons the fruit quality in terms of the total soluble solids (TSS) and titratable acidity (TA) was however higher for the fruit from FM2 where the nutrient solution was periodically topped up with the full strength starting nutrient solution which resulted in a gradual increase in the nutrient solution EC over time. An increase in EC is well known to result in an increase in tomato fruit quality (Adams 1992; Ehret and Ho 1986; Dorais et al 2001). Since yield was not significantly lower for these plants the increase in the TSS of fruit can in part be attributed to enhanced sucrose unloading to the developing fruits (Heuvenlink, 2005) and not just the restriction of water transport to fruits (Adams, 1992). Total water uptake was however lower for plants where the irrigation water was re-circulated (FM2 and FM3) compared to the drain to waste system (FM1) (Figure 2).

Table 3. Fruit yield as affected by the fertigation method used. Fertigation method 1 (FM1), no re-use of nutrient solution; Fertigation method 2 (FM2), re-use of drained nutrient solution and topping up with a full strength nutrient solution; fertigation method 3 (FM3), re-use of drained nutrient solution and topped up to target EC level. In each row of measurements different letters indicate a LSD significant difference of p<0.05.

	Marketable fruit yield (kg plant $^{-1}$)	**Unmarketable fruit yield (kg plant $^{-1}$)**	**Dry matter content %**	**Total soluble solids (TSS) (^{O}Brix)**	**Titratable acidity (TA) (mmol L^{-1})**
		Season 1 (Summer/Autumn)			
FM1	6.46a	0.86a	6.3a	6.5b	13.2b
FM2	5.98a	0.91a	6.7a	7.1a	14.7a
FM3	6.19a	0.75a	6.1a	6.1b	12.9b
		Season 2 (Spring/Summer)			
FM1	5.21b	0.79a	6.1a	6.1b	12.9b
FM2	4.85b	0.83a	6.2a	6.9a	14.5a
FM3	5.13b	0.74a	6.4a	6.2b	12.6b
LSD (p≤0.05)	0.65	0.21	0.71	0.52	1.12

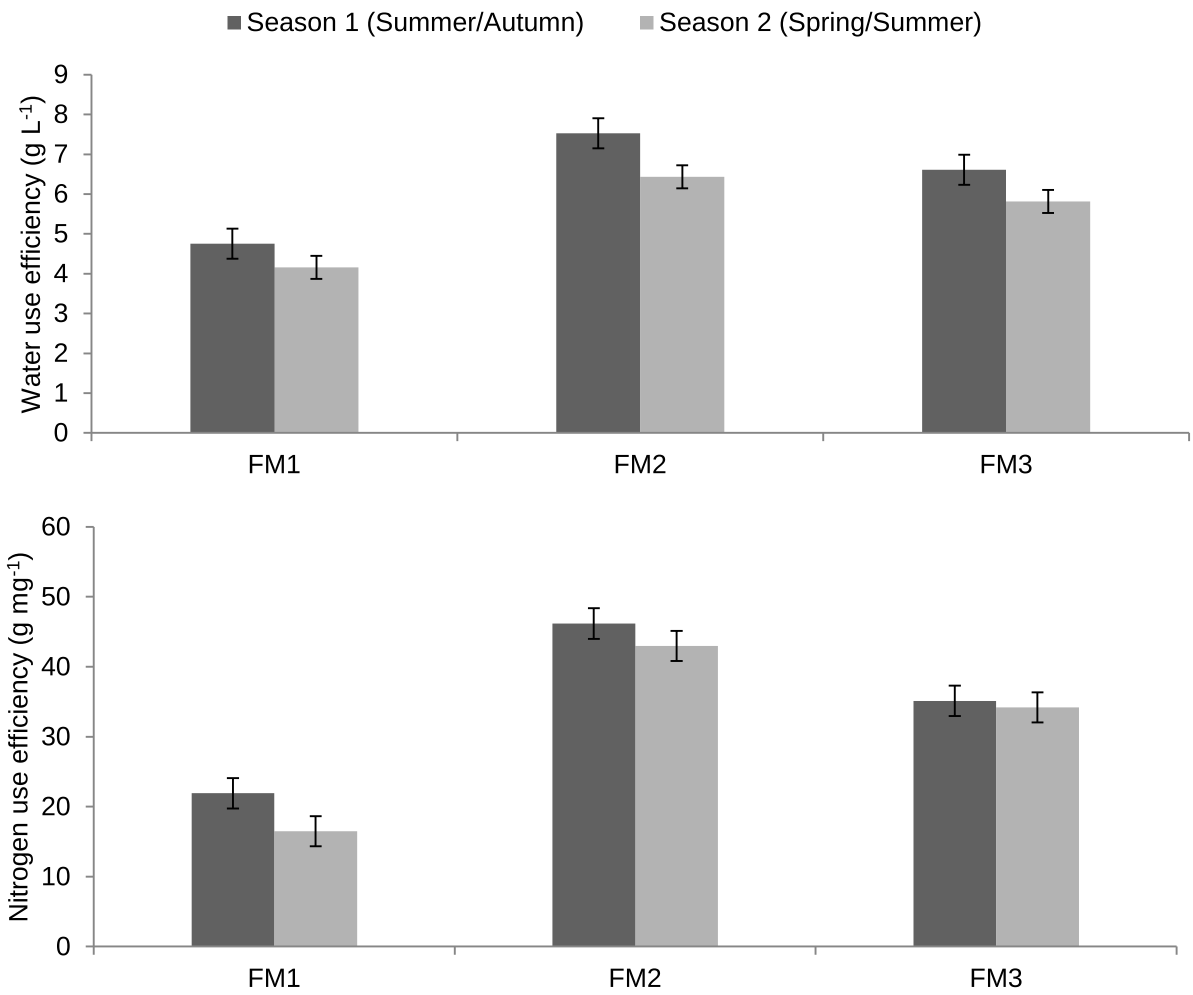
Water and nutrient uptake

Water uptake per plant did not differ significantly between the different fertigation methods within each season but there was a significant difference between the seasons with more water taken up per plant during the spring/summer season that was significantly warmer during the latter part of the season (Table 4). For most of the macro nutrients there was some variation in the uptake either due to the fertigation method used or the growing season (Table 4). Potassium (K) uptake was higher during the summer/autumn season in the two re-circulating systems whereas calcium (Ca) uptake was higher during the warmer spring summer season in both of the re-circulating systems (Table 4). This correlates with previous results (Article 3, p82) showing the correlation between water and Ca uptake. Magnesium (Mg) and sulphate (SO_4) uptake was however higher in the drain to waste system during both seasons which could be the result of other ions that accumulate in the re-circulating systems inhibiting the uptake of these ions. Nitrogen uptake was relatively constant except for plants in the drain to waste system during the warmer spring/summer season. During both seasons the P uptake was significantly higher for plants where the nutrient solution was re-circulated through topping up to the desired EC level. Schwarz et al.(1993) observed that the total amount of N and K absorbed by a tomato crop grown in NFT closely matched the amount of these nutrient supplied to the crops.

Table 4. Water (U_w) and macro-nutrient uptake of tomato plants as affected by the fertigation method during two growing season. Season 1; January to May 2011 (summer/autumn) and season 2; August to December 2011. Fertigation method 1 (FM1), no re-use of nutrient solution; Fertigation method 2 (FM2), re-use of drained nutrient solution and topping up with a full strength nutrient solution; fertigation method 3 (FM3), re-use of drained nutrient solution and topped up to target EC level. In each row of measurements different letters indicate a LSD significant difference of p<0.05.

	Nutrient uptake (g plant^{-1})						
	U_w (L plant^{-1})	**K**	**Ca**	**Mg**	**N**	**P**	**S**
Season 1 (Summer/Autumn)							
FM1	467.6b	59.3b	31.6c	14.3a	30.1a	5.7c	19.4a
FM2	471.2b	66.8a	30.1c	11.2c	32.2a	6.9b	17.6bc
FM3	466.3b	65.2a	35.2b	12.6b	29.3a	8.3a	17.2c
Season 2 (Spring/Summer)							
FM1	511.4a	51.3c	38.2b	12.8b	24.2b	4.6d	18.3ab
FM2	506.3a	55.6bc	45.3a	10.9c	33.4a	5.7c	15.2d
FM3	501.5a	49.7c	48.1a	11.4c	31.4a	7.1b	16.3cd
LSD (p≤0.05)	28.5	4.5	3.3	1.1	4.2	0.75	1.5

In terms of the total water use (water uptake plus water drained) the water use efficiency (WUE) and nitrogen use efficiency (NUE) was higher in the two systems where the drained nutrient solution was re-used. During season 1 the WUE and NUE was highest for the system employing fertigation method 2 while during season 2 the WUE was similar in FM1 and FM2 but the NUE remained higher in FM2



(Figure 2). Using FM2 the drained nutrient solution was mixed with a complete starting nutrient solution (full strength or half strength) before re-use and flushed whenever the EC exceeded 3.5 mS cm^{-1}. The EC of the drained nutrient solution using this method did not increase as fast as was noticed in previous trials (Article 1, p 44 and other unpublished data) when a higher starting EC was used. This resulted in only 6 flushings throughout the growing season compared to fertigation method 3 where the entire volume of nutrient solution was flushed out 10 times per growing season.

Figure *2*. The water use efficiency (g fruit yield per water applied) and nitrogen use efficiency (gram fruit yield per milligram Nitrogen applied) for tomato plants grow in during 2011 and 2012 a soilless production system using 3 different fertigation methods; FM1, FM2 and FM3. Each value represents the mean of four replicates.

During the Summer/autumn season of 2012 there was a good relationship between the simulated and actual water uptake for crops in all three fertigation approaches (Figure 3). This can to a large extent be attributed to the fairly accurate determination of the LAI using the adjusted equation that incorporates photo-thermal units (PTU).

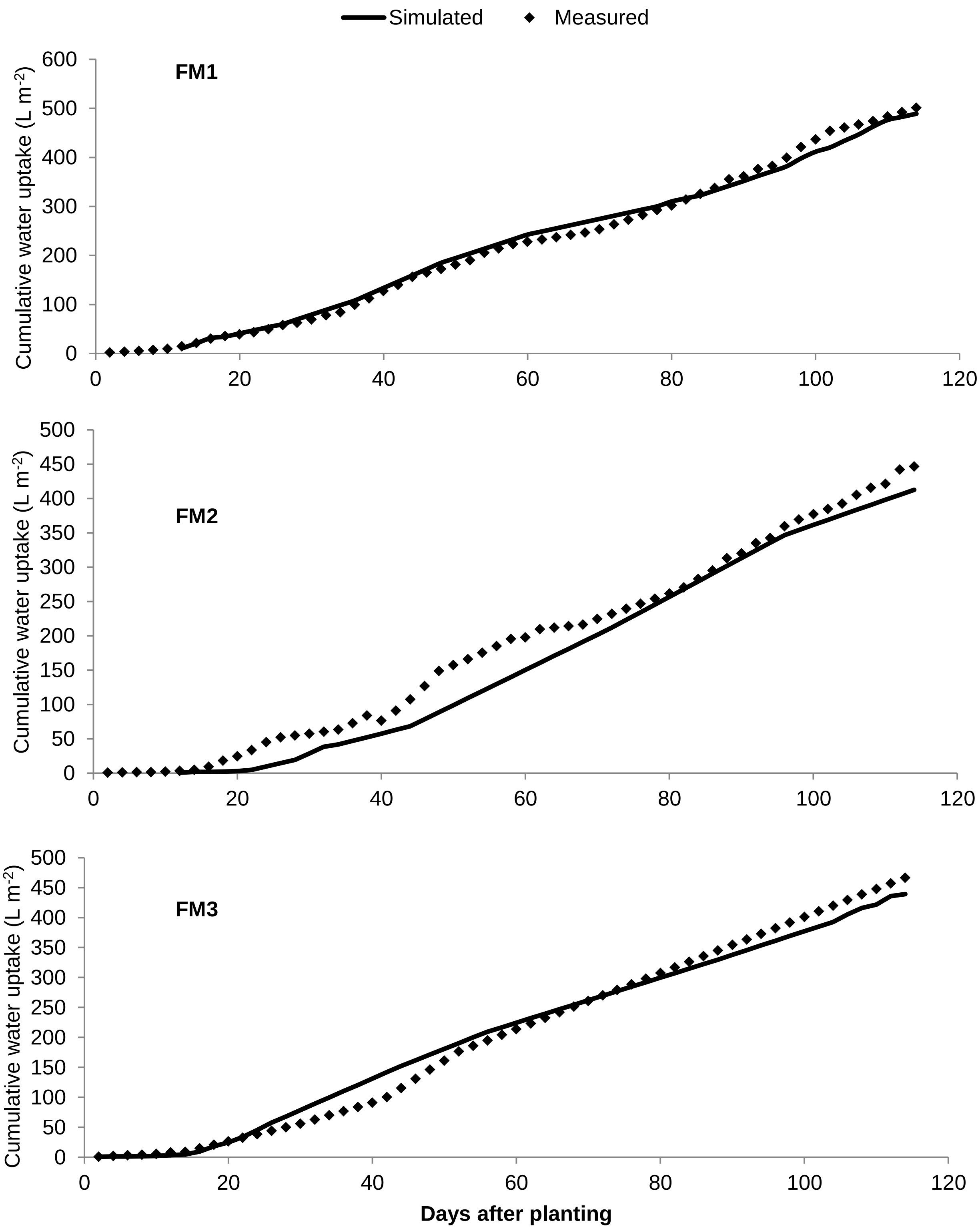


Figure 3. The measured and simulated cumulative crop water uptake (L m^2) of tomato plants in relation to three different fertigation strategies, FM1, FM2 and FM3. Each value represents the mean of three replicates.

Composition of drained nutrient solution

Apart from some small discrepancies, a relatively accurate prediction of the NO_3^- and Ca^{2+} concentrations in the drained nutrient solution was obtained using the proposed model (Figures 4 and 5). The main differences between the simulated and observed NO_3^- concentration in the drainage water was observed in the later part of the season on occasions when a sharp decrease in the NO_3^- levels occurred, usually just prior to flushing of the system. This resulted in the measured values were lower than the predicted values. Similarly for Ca^{2+}, the main differences occurred just prior to flushing of the system when the Ca^{2+} concentration in the drainage water started increasing considerably. This indicates that as long as the nutrient ratios remain close to the ratios in the starting nutrient solution, uptake and therefore levels of residual nutrients can be accurately predicted using this model. Further calibration of the model will be needed under conditions where there is a larger difference on the nutrient ratios of the nutrient solutions. The nutrient uptake models used was also largely based on data gathered during the vegetative and early flowering and fruiting phase of tomatoes resulting in more differences later in the season when the rate of nitrate uptake usually decrease (Voogt 1993).

Adams and Ho (1993) reported Ca uptake for fruiting tomato of 1.67 mmol Ca per l transpired water which is considerably lower than the average of 2.4 mmol Ca per l transpired water obtained during these trials. The contribution of transpiration to Ca uptake and transport in plants however differs widely, determined genetically and influenced by environmental conditions. Various models have been developed that can accurately simulate dry matter production and yield of hydroponically grown crops. These can be incorporated with the current models to enable growers to manage the nutrient solutions and crop production. The effect of sodium and chloride accumulation in closed soilless systems on nutrient uptake has not been considered in this study since it has been thoroughly researched already and several models exist to describe these effects. These could be added as submodels to the existing models in cases where the Na^+ and Cl^- concentrations in the feeding water will result in negative effects on cation and anion absorption.

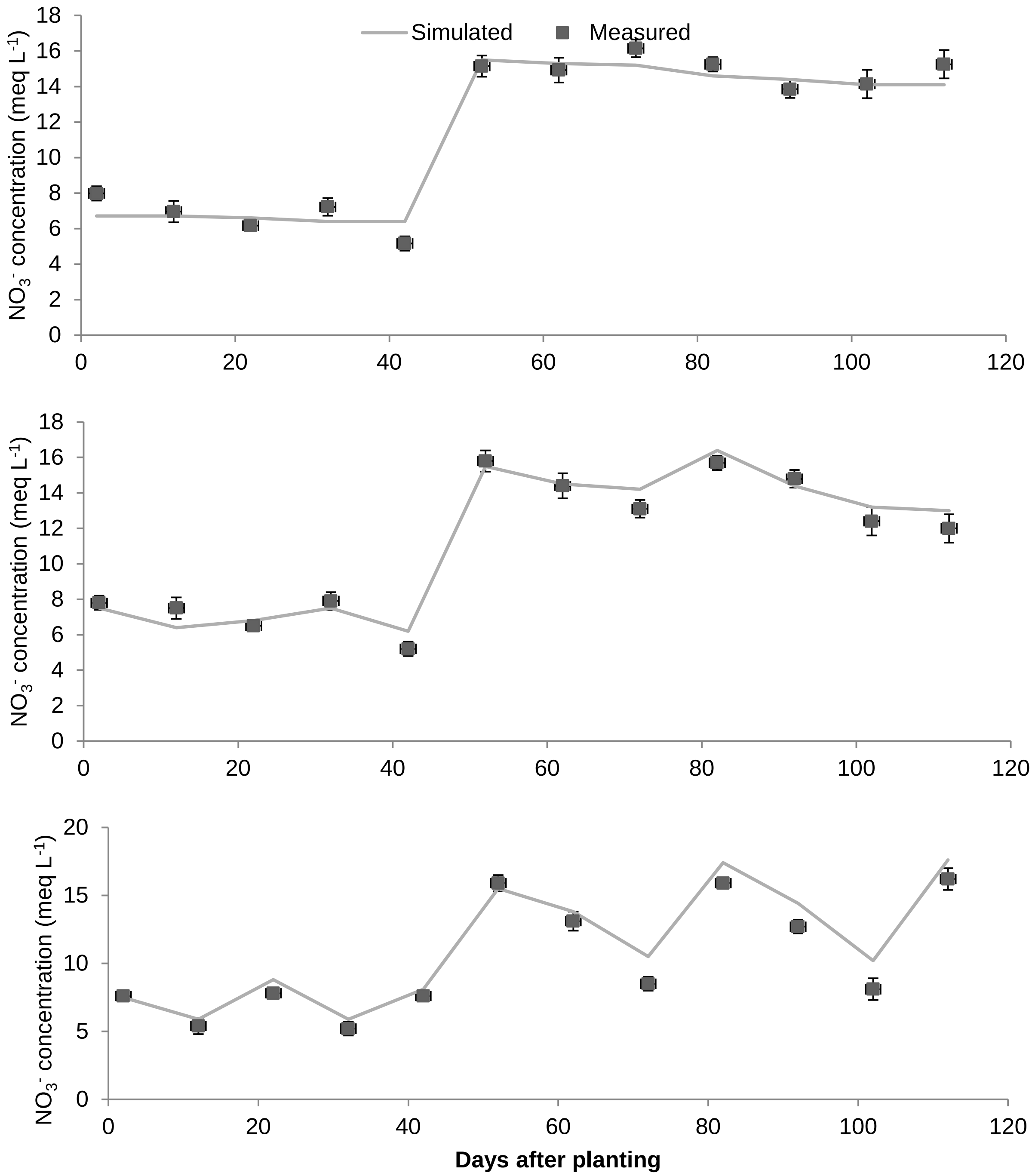


Figure 4.Concentration of nitrate (NO_3^-, meq L^{-1}) in the drainage water obtained from three alternative fertigation methods; FM1, FM2 and FM3. Symbols represent the observed values and the line the simulated values. The sharp increase was when the nutrient solution was adjusted according to the growth stage of the crop. Each value represent the mean of three replicates.

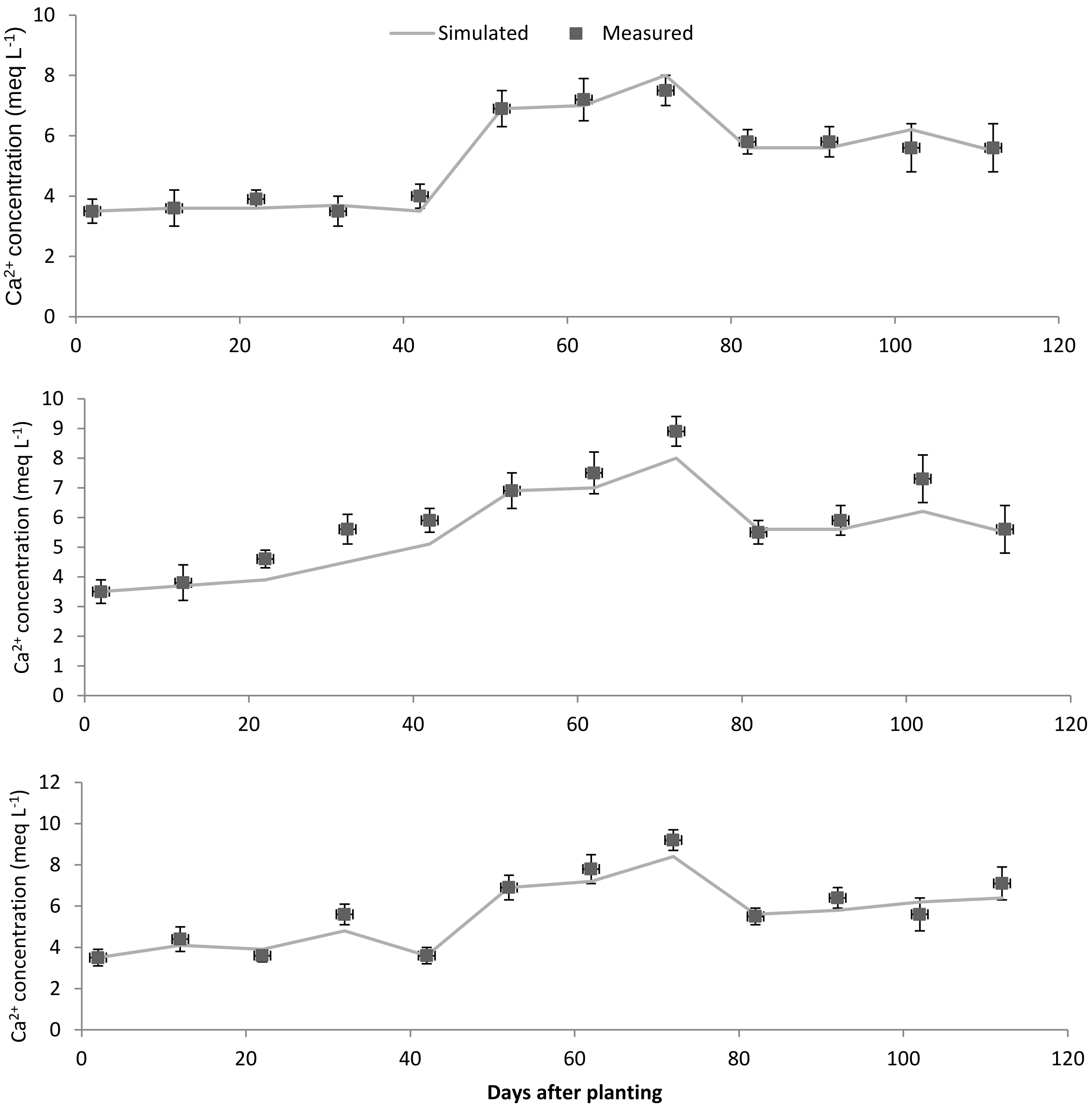


Figure 5. Concentration of Calcium (Ca^{2+}, meq L^{-1}) in the drainage water obtained from three alternative fertigation methods; FM1, FM2 and FM3. Symbols represent the observed values and the line the simulated values. The sharp increase was when the nutrient solution was adjusted according to the growth stage of the crop. Each value represents the mean of three replicates.

In a closed soilless system the aim is to maintain the concentrations of the ions in the rootzone as close as possible to their pre-determined norm values even though re-use of the nutrient solution will result in accumulation of some and depletion of other ions. For this reason regular testing and adjustment of the application rate of certain macro-nutrients is necessary. A simple method for analysing the concentration of ions in the nutrient solution is through the use of test-strips or handheld devices. If a good correlation exists between the uptake of certain ions it would be possible to test for only some of these ions or possibly a single guide-ion which can then be used to predict and adjust the levels of the other ions as well. The best correlation was found between the uptake of SO_4^{2-} and NO_3^- also between SO_4^{2-} and $H_2PO_4^-$, and SO_4^{2-} and Mg^{2+}. Further examination of these correlations may lead to the development of a simple and practical method of managing nutrient application in closed soilless systems where frequent laboratory analysis is not feasible. However there was some variation in the correlations due to the fertigation method used (Table 5). This can most likely be attributed to the changes in EC and nutrient ratios occurring in these systems as a result of re-using the drained nutrient solution.

Table 5. The coefficients of determination (R^2) depicting the correlation in macro-nutrient uptake (g plant^{-1}) for tomato plants in a soilless production system using three different fertigation methods, measured over the duration of the growing season.

Fertigation method 1:

	NO_3^-	**K^+**	**$H_2PO_4^-$**	**Mg^{2+}**	**SO_4^{2-}**
K^+	0.84				
$H_2PO_4^-$	0.78	0.72			
Mg^{2+}	0.65	0.65	0.49		
SO_4^{2-}	0.92	0.75	0.82	0.74	
Ca^{2+}	0.10	0.25	0.21	0.16	0.32

Fertigation method 2:

	NO_3^-	**K^+**	**$H_2PO_4^-$**	**Mg^{2+}**	**SO_4^{2-}**
K^+	0.71				
$H_2PO_4^-$	0.76	0.76			
Mg^{2+}	0.82	0.77	0.64		
SO_4^{2-}	0.95	0.71	0.83	0.76	
Ca^{2+}	0.12	0.02	0.27	0.19	0.23

Fertigation method 3:

	NO_3^-	**K^+**	**$H_2PO_4^-$**	**Mg^{2+}**	**SO_4^{2-}**
K^+	0.65				
$H_2PO_4^-$	0.75	0.77			
Mg^{2+}	0.81	0.77	0.69		
SO_4^{2-}	0.95	0.71	0.83	0.76	
Ca^{2+}	0.16	0.02	0.31	0.21	0.27

Conclusion

There is need to convert more drain to waste production systems to re-circulating systems in order to reduce water and nutrient use. Results from these trials show that if managed properly a closed system where drain water is re-used will have no negative effect on tomato crop growth and yield and that water and nutrient use efficiency will be greatly improved. This can be related into substantial economicic gains for the soilless producer. In areas where growers are still hesitant to convert to a re-cycling system, this second fertigation approach (FM 2) can be an easy method to convert standard drain to waste systems to a re-circulating system in greenhouses without the need for state-of-the-art fertilizer injection systems to bet used.

To assist producers in converting to a closed growing system alternative methods are however still needed to help manage the crop nutrition in these systems. The models proposed here show a fair capability of predicting the water and nutrient uptake in three different systems. Although the proposed model simplifies several processes, it seems detailed enough to simulate water and nutrient uptake of tomato plants in a coir growing medium. It may therefore be a useful tool managing crop nutrition in soilless systems. Further investigation is however needed to improve the accuracy of these simulations under non-standard conditions and include other parameters that may affect the availability of nutrients for uptake.

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Chapter 6: General discussion and conclusion

Soilless production systems are known for the high concentrations of nutrients that are supplied to plants and often a large percentage of the supplied nutrients are drained to waste when the traditional open system is used. In semi-closed systems the nutrient solution can be re-used as long as the concentration and composition of the nutrient solution will sustain crop nutrient demands and product quality. Maintaining the optimum nutrient concentrations in the re-circulating nutrient solution is however one of the biggest constraints towards a more wide-spread adoption of this technique. Regular analysis of the ion concentrations in the rootzone is required as well as the appropriate algorithms to calculate adjustments based on the degree of variation between the input concentration and the desired norm values in the rootzone. An alternative or additional method for regulating fertigation is through the use of crop models where plant physiological functions and climatic parameters are used to simulate plant growth, the water and nutrient requirements as well as the nutrient concentration in the root zone of a soilless system. Before this approach can however be effectively applied as a tool in decision support systems, knowledge of all relevant parameters need to be incorporated into these mathematical models and these models need to be vigorously validated, under different growing conditions.

In this study eight successive trials were conducted to evaluate the effect of nutrient solution composition, solar radiation levels and irrigation frequency on the uptake of water and nutrients and also crop growth, fruit yield and quality.

Water uptake

Water uptake is affected by the composition of the nutrient solution (Article 1) as well as the solar radiation levels (Article 3). Water uptake increased at a constant rate as the solar radiation levels increased while it decreased with an increase in nutrient solution concentration. Specifically important for management in Mediterranean climates is that water uptake has been shown to be affected by the EC of the nutrient solution to a larger extent during periods with high solar radiation than when the solar radiation levels are lower. Part of the reduction in water uptake at higher nutrient solution concentrations can be attributed to morphological adaptations plants make when grown at a higher external salt concentration although this correlation is not linear. The EC of the nutrient solution had a greater effect on the leaf area, than on the water use of the plant (Article 1). In article 6 water uptake (Wu, L m^{-2} day^{-1}) was simulated as a function of crop transpiration using a simple linear regression model as a function of the crop leaf area. Since a good correlation between the LAI and the s olar radiation levels was observed in article 4, this was incorporated into the estimation of the LAI instead of basing this equation purely on temperature data. Since the correlation between temperature and radiation is small in greenhouses compared to open field conditions it is considered more accurate to use solar radiation levels when modelling leaf area development of greenhouse crops. A large percentage of the total water use by plants can be attributed to water being taken up during the night (Article 4) and during periods with high solar radiation levels the night-time water uptake comprised a larger % of the total water uptake compared to plants grown during periods with low solar radiation levels. This is relevant for two reasons; Firstly additional night time irrigation can benefit crop growth during periods with high solar radiation levels which could lead to a reduction in growth due to closure of stomata during the day. Also if the ratio between night-time water uptake is significantly higher than nutrient uptake or vice versa it can result in changes in the ion concentration on the rootzone that can negatively affect nutrient uptake until the following irrigation event.

Nutrient uptake

The composition of the nutrient solution will affect the uptake of nutrients, but plants do not take up nutrients at the same quantity or ratio as that supplied resulting in an increase or depletion relative to other elements in the nutrient solution to be re-used (Article 1). Since a close relationship between nutrient and water uptake has been reported some authors suggested that this relationship can be used as a method of determining nutrient uptake and the composition of the nutrient solution to be re-used. These uptake concentrations (UC, mmol L^{-1}) of different nutrients has been determined for several crops but there is however a large difference in UC between crops not only attributed to the variation in water use, but also as a result of different nutrient solution compositions (Article 1). Results from this study therefore indicate that nutrient uptake is not linearly related to the water uptake and that the composition of the nutrient solution affects water and nutrient uptake, but not necessarily to the same degree. Although water and nutrient uptake is linked to solar radiation level, different physiological processes are involved in water and nutrient uptake. The only macro-nutrient showing a good correlation with water uptake was calcium (Ca^{2+}) (Article 3). Since the uptake of Ca^{2+} is mostly passively driven by the transpiration stream an alternative method, based on measurements of the rate of transpiration was used to simulate Ca^{2+} uptake (Article 6).

The uptake most macro-nutrients is often higher in summer compared to winter. Since nutrient uptake is not constant but is related to the growth rate, radiation input is a key driving factor influencing the uptake of nutrients. In Article 3 it is shown that the uptake of most macro-nutrients increases with an increase in the solar radiation level and that for the anions (NO_3^-, $H_2PO_4^-$, SO_4^{2-}) the rate of the increase - the slope of the graph - is affected by the EC of the nutrient solution. (This correlated with the findings in article 1 which showed that total-N, $H_2PO_4^-$, and SO_4^{2-} uptake tended to increase with an increase in nutrient solution concentration from 0.8 to 4.0 mS cm^{-1}). As radiation increases the rate of nutrient uptake follows a Michaelis-Menten type relationship (rectangular hyperbola). The data from Article 3 was used to determine by a reciprocal plot the components needed (Km, Michaelis Menten constant and U_{max} = maximum rate of nutrient uptake (mg m^{-2} h^{-1})) to estimate the macro-nutrient uptake (Un, mg m^{-2} hr^{-1}) using a mechanistic high-affinity, active uptake Michaelis-Menten based model. This model was adjusted to take into consideration the concentration of the ions in the nutrient solution as well as the intercepted photosynthetic photon flux density (PPFD) to simulate nutrient uptake (Article 3 and 6).

Another factor that can affect the uptake of nutrients is the irrigation frequency. In soilless production systems with the small root volumes this needs to be managed to maintain sufficient nutrients, as close as possible to the pre-determined ratios, to ensure that the water and nutrient uptake is not limited by availability. In a closed hydroponic system where the drainage solution is re-used imbalances between the ratio of nutrients can occur rapidly resulting in a negative effect on nutrient uptake and in this case the simulation of nutrient uptake. In article 5 it was observed that by increasing the frequency of nutrient solution application to the crops, the rate of change in composition of the nutrient solution can be minimized and should therefore not have a significant effect on the simulation on nutrient uptake as was done in article 6.

A large percentage of macro-nutrients are also taken up during the night and the exact percentage was influenced by the daytime solar radiation levels (Article 4). Especially interesting was that the nighttime $H_2PO_4^-$ uptake almost the same as the daytime uptake. This is important to note since few growers actually irrigate during the night and this can result in large deviations in the composition of the solution in the rootzone and also of the re-cycled nutrient solution that needs to be adjusted before re-use.

The proposed model in article 6 gave a relatively accurate prediction of the NO_3^- and Ca^{2+} concentrations in the drained nutrient solution as long as the nutrient ratios remained close to the ratios in the starting nutrient solution, and uptake and therefore levels of residual nutrients can be accurately predicted using this model.

Water and nutrient use efficiency

As expected, the water use efficiency (WUE) and nutrietn use efficiency (NUE) was higher in the two systems where the drained nutrient solution was re-used (Article 6). It might be possible to increase nutrient uptake when using a nutrient solution with a low EC. By increasing the irrigation frequency. In article 5 it was shown that the uptake of P especially, which is one of the less mobile elements, can be increased when the irrigation frequency is increased even when using a half-strength nutrient solution. In a closed system this will allow for an increase in the nutrient use efficiency (NUE) but also an increase in the water use efficiency (WUE) since it will be possible to re-circulate the nutrient solution for longer before having to flush it. When the nutrient solution was mixed with a complete starting nutrient solution before re-use and flushed whenever the EC exceeded an upper limit, the EC of the drained nutrient solution also increased very slowly, reducing the number of times it was necessary to flush the whole system (Article 6).

Crop yield and fruit quality

The composition of the nutrient solution will also affect the yield and quality of crops as it is strongly related to nutrient uptake. When re-using drained nutrient solution the concentration (EC) as well as the balance between the ions will start deviating from the specific target values due to the selectivity in uptake of ions by plant roots. As the time period of recirculation increases, the imbalance will intensify resulting in osmotic effects and antagonism between ions, reducing the ability of a plant to take up water and nutrients. Adjusting the concentration and composition of the nutrient solution might limit these deviations (Article 1) but it should still allow for optimal growth, yield and tomato fruit quality. Results from this study (Article 2) showed that a rootzone EC of 3.2 mS cm^{-1} and 4.0 mS cm^{-1} can result in smaller fruit but an increase in fruit dry matter %, total soluble solids (TSS), titratable acidity (TA) and lycopene content. It was also observed that adjusting the nutrient solution in a re-circulating system through increasing the total-N and K^+ concentration and reducing the SO_4^{2-} concentration in the nutrient solution can also result in an increase in these fruit quality parameters.

The adjusted nutrient solutions used in most of these trials had a significantly lower Ca^{2+} concentration and a higher K^+ and total-N. This could result in a reduction in Ca^{2+} uptake and as a result an increase in the incidence of blossom end rot (BER) a physiological disorder often associated with greenhouse tomatoes linked to a reduction in Ca^{2+} transport to the distal part of the fruit. However this was not observed (Article 2) and the only incidence of BER was in article 5 where an increase in fertigation frequency to 12 pulses per day significantly increased the number of unmarketable fruit with BER.

In article 5 an increase in fertigation frequency is shown to be able to overcome the negative effects low EC is known to have on tomato fruit dry matter % but under high irrigation frequencies the fruit total soluble solids (TSS) and titratable acidity (TA) decreased significantly. Although these fruit quality parameters are at this stage not regulated or tested for except for fruit destined for processing, it should be noted.

Future considerations

Although the effect of solar radiation levels was included in the equation to estimate the crops water uptake, a further improvement will be to also include the effect of EC since the decrease in leaf area due to an increase in EC was in fact greater than the reduction in water uptake.

Biomass partitioning between roots and shoots in the plant can also affect nutrient uptake since root size for instance can be linked to the rate of nutrient uptake. In this thesis the effect of nutrient solution composition and also solar radiation levels on biomass partitioning was investigated but these parameters was not successfully incorporated into the models used to simulate nutrient uptake. One of the reasons was that there seemed to be an interaction between the effects of biomass partitioning, nutrient solution composition and solar radiation levels on nutrient uptake. The dry matter distribution in indeterminate crops however changes dynamically making a simulation of plant nutrient relationships incorporated in a mechanistic model for crop growth and development potentially very complex. This should however be investigated further.

The use of test-strips or handheld devices provides a simple method for analysing the concentration of ions in the nutrient solution and If a good correlation exists between the uptake of certain ions it would be possible to test for single ions which can be used to predict and adjust the levels of the other ions as well. In article 3 and article 5 correlations was found between the uptake of certain macro-nutrients, especially SO_4^{2-} and NO_3^- also between SO_4^{2-} and $H_2PO_4^-$, and SO_4^{2-} and Mg^{2+}, and this should be explored further in future studies.

In conclusion this study managed to simulate the water and nutrient uptake of soilless grown tomato plants based on biological and physiological deductions derived from these trials. Valuable new knowledge with regards to the effect of solar radiation levels on the uptake of specific macro-nutrients as well as the correlations between their uptakes was generated as well as crop physiological responses to the treatment combinations. The proposed models can be used to predict the change in composition of drained nutrient solution before re-use and incorporates both the effect of nutrient availability (concentration and ratios) and nutrient requirement for growth (solar radiation levels) which up until now was not reflected in most nutrient uptake models. In future these models can be further calibrated and extended to include other factors such as the physical and chemical properties of the rootzone and the relative humidity in the greenhouse to improve their accuracy. These models can now also be evaluated and adjusted for other greenhouse crops.