Analysis of humidity effects on growth and production of glasshouse fruit vegetables

Promotor: Dr. Ir. H. Challa, hoogleraar in de tuinbouwplantenteelt,
in het bijzonder de beschermde teelt.

J.C. Bakker

Analysis of humidity effects on growth and production of glasshouse fruit vegetables

Proefschrift

ter verkrijging van de graad van
doctor in de landbouw- en milieuwetenschappen,
op gezag van de rector magnificus,
Dr. H.C. van der Plas,
in het openbaar te verdedigen
op woensdag 13 november 1991
des namiddags te vier uur in de aula
van de Landbouwuniversiteit te Wageningen

Voor Jeanette, Jessica en Esther.

NN0870 1, 1499

Stellingen

Recent gepubliceerde onderzoeksresultaten, gebaseerd op in het verleden blootgestelde populaties, laten geen eenduidig antwoord toe op de vraag hoe groot het risico op CARA is voor de tegenwoordig beroepsmatig aan luchtverontreiniging blootgestelde populatie in Nederland.
(Dit proefschrift)

De uitspraak dat effecten van een beroepsmatige stofblootstelling op de luchtwegen zich vooral bij rokers manifesteren is een grove generalisatie en niet in overeenstemming met onderzoeksresultaten.
(Jacobsen M. Smoking and disability in miners. Lancet 1980; ii: 740)

Preventieve maatregelen met het doel CARA ten gevolge van een beroepsmatige blootstelling aan luchtverontreiniging te voorkomen zijn nu al mogelijk op basis van recent verzamelde blootstellingsgegevens en bestaande grenswaarden voor luchtverontreiniging op de arbeidsplaats.

Een MAC-waarde voor endotoxinen, gebaseerd op acute longfunctieveranderingen, moet op korte termijn worden overwogen gezien de consistentie in de onderzoeksresultaten.
(Palchak RB et al. Airborne endotoxin associated with industrial scale production of protein products in gram-negative bacteria. Am Ind Hyg Assoc J 1988; 49:420-421)

Voordat men in de epidemiologische onderzoekzoekspraktijk overgaat op de door K.R. Popper voorgestelde procedures om hypothesen te toetsen moet meer aandacht aan de critici van Popper, waaronder P. Feyerabend, worden gegeven.
(P. Feyerabend. Science in a free society. Schocken Books, New York, 1978)

De slechte karakterisering van een beroepsmatige blootstelling in veel epidemiologische studies is het gevolg van een verwaarloosbaar kleine inbreng van arbeidshygiënische principes.
(Checkoway H, JM Dement, DP Fowler, RL Harris, SA Lamm & TJ Smith. Industrial hygiene involvement in occupational epidemiology. Am Ind Hyg Assoc J 1987; 48:515-523)

Indien de verzameling en beoordeling van longfunctiegegevens in de bedrijfsgezondheidszorg niet op een gestandaardiseerde wijze plaatsvinden, kunnen deze tienduizenden metingen per jaar beter achterwege blijven.

Smith karakteriseert epidemiologisch en toxicologisch onderzoek respectievelijk als 'exposure poor, species right', 'exposure satisfactory, species wrong'. Het waardeoordeel 'the score poor plus right wins over satisfactory plus wrong' geeft de plaats van de epidemiologie ten behoeve van risicoanalyses duidelijk aan.
(Smith AH. Epidemiologic input to environmental risk assessment. Arch Env Health 1988; 43: 125-127)

NNO8201, 1499

De uitspraak van Kroes "Casuïstisch en epidemiologisch onderzoek hebben in verband met het opstellen van advieswaarden relatief weinig betekenis" is volstrekt onjuist gezien de veelvuldige toepassing van epidemiologische gegevens bij de onderbouwing van milieu- en arbeidshygiënische grenswaarden.
(Kroes R. Normstelling voor chemische verbindingen. In: Stumpel ARJ, R van den Doel. Medische milieukunde. Bohn, Scheltema & Holkema. Utrecht /Antwerpen 1989, p.171)

De bevinding dat een grote opzichtige postzegel op een antwoordenvelop van een postenquête tot een statistisch significant verhoogde respons leidt, kan een nieuwe impuls geven aan het werk van de ontwerpafdeling van de PTT.
(Choi, BCK, AWP Pak, JT Purdham. Effects of mailing strategies on the response rate and time in a questionnaire among nurses. Seventh International Symposium on Epidemiology in Occupational Health, Tokyo, 1989)

Autouitlaatgassen zijn milieuhygiënisch gezien pas schoon als ze aangewend kunnen worden voor de interieurventilatie van de auto.

Stellingen behorend bij het proefschrift:
Epidemiological studies of the relationship between occupational exposures and chronic non-specific lung disease. Dick Heederik
18 april 1990

Abstract

Bakker, J.C. (1991). Analysis of humidity effects on growth and production of glasshouse fruit vegetables. Dissertation, Agricultural University, Wageningen, The Netherlands; 155pp; 27 figs.; 63 tables; English and Dutch summaries.

Air humidity is a climate factor that can modify final yield and quality of crops through its impact on processes with a short as well as with a long response time. This thesis primarily deals with the long term responses of growth and production of glasshouse cucumber, tomato, sweet pepper and eggplant to humidity in the range of 0.3 to 0.9 kPa Vapour Pressure Deficit. Knowledge of these responses is essential to optimize environmental control for glasshouse crop production.

The influence of humidity on leaf photosynthesis was estimated from its effect on stomatal conductance. Within the range investigated, humidity had limited effects on stomatal density (morphological component) and this did not significantly influence leaf conductance. The relative response of leaf conductance to vapour pressure deficit (dynamic component) was equal for the four species. From simulation it was concluded that the effect of humidity on leaf photosynthesis under normal growing conditions in moderate climates is limited to about 10% which was of the order of actual observations with young tomato plants.

Long term exposure to high humidity significantly increased the leaf area of cucumber through a higher rate of leaf formation whilst with tomato leaf area was reduced due to severe calcium deficiency.

Humidity had no significant effect on dry matter distribution between leaves, stem and fruits but a marginal gain in shoot/root dry weight ratio was observed at high humidity. Dry matter content of leaves and fruits was unaffected by humidity.

Flowering was unaffected by humidity and only limited effects on fruit set were observed. Seed set of tomato was lower at high humidity and closely related to the effects of humidity on pollen dehiscence and adhesion to the stigma. Fruit maturation rate was not influenced by humidity.

Final yield of cucumber was higher at high humidity by day whilst yield of tomato was lower at continuously high humidity. Yield of sweet pepper was unaffected, yield of eggplant was slightly lower at high humidity. Keeping quality was generally lower at high humidity. For each crop practical guidelines for humidity control in glasshouses are presented.

It is concluded that the major effect of high humidity on yield is mediated through its impact on light interception resulting from either the enlargement (through number of leaves and leaf expansion) or the decrease of the LAI (through calcium deficiency) and the (marginal) effect on photosynthesis as such. The results are discussed in the view of current humidity control and the development of environmental control strategies.

Key words: air humidity, Vapour Pressure Deficit, glasshouse climate, cucumber, tomato, sweet pepper, eggplant, *Cucumis sativus*, *Lycopersicon esculentum*, *Capsicum annuum*, *Solanum melongena*, stomata, dry matter production, dry matter distribution, growth, flowering, pollination, fruit growth, production, quality.

Voorwoord

De totstandkoming van dit proefschrift is mede mogelijk gemaakt door de medewerking en steun van een reeks van personen. Dit voorwoord biedt een goede gelegenheid om hen persoonlijk te bedanken.
Mijn promotor Prof. Dr. Hugo Challa dank ik voor de zorg die hij besteedde aan de diverse manuscripten. Zijn begeleiding, kritiek en suggesties zijn van grote waarde geweest.
Het bestuur en de direktie van het Proefstation voor Tuinbouw onder Glas dank ik voor de mogelijkheid die zij mij geboden hebben voor het schrijven van dit proefschrift.

Binnen het PTG hebben een aantal mensen een duidelijk stempel gedrukt op dit werk. Met name de inbreng van Chris van Winden en Gerard Welles in de discussies en hun commentaar op de verschillende manuscripten waren zeer waardevol. Verder ben ik dank verschuldigd aan mijn direkte collega's binnen de sectie kasklimaat van het PTG. Vooral de opbouwende kritiek van Ad de Koning en Elly Nederhoff heb ik zeer gewaardeerd. Pieter van de Sanden van het CABO dank ik voor zijn bijdrage aan de uitvoering en dataverwerking van de metingen van de stomataire geleiding. Bij het uitvoeren van de vele waarnemingen is veel medewerking verleend door stagiaires en diverse onderzoeksassistenten waarvan ik met name Gonnie Bergman wil noemen.
Een grote bijdrage is geleverd door Willem van Winden, die, ondanks de aanhoudende stroom van onderdelen van het proefschrift en vaak onder tijdsdruk, het volledige proefschrift nauwgezet gecorrigeerd heeft wat betreft de engelse tekst en de referentielijsten. Dr. Bernard Bailey van het AFRC Silsoe Research Institute heeft gezorgd voor een nog verdere perfectionering van het engelse taalgebruik.
Het zal duidelijk zijn dat er naast deze met name genoemde collega's nog vele anderen hebben bijgedragen aan de uitvoering van het onderzoek. Een dankwoord aan de statistici, informatici, de technische dienst en het tuinpersoneel van het PTG is hier dan ook zeker op zijn plaats. De in dit onderzoek gebruikte vruchtgroenten zijn op schitterende wijze in beeld gebracht door Theo van Gaalen die de foto op de omslag verzorgde.

Het is zeer wel mogelijk dat dit proefschrift nooit geschreven zou zijn als ik niet aan het einde van de middelbare school met de glastuinbouw in contact gekomen was. Op het bedrijf van de familie Timmers in Barendrecht werd mijn interesse in dit vakgebied gewekt en mede daardoor mijn studierichting aan de Landbouwuniversiteit bepaald. Mijn ouders dank ik voor het in mij geschonken vertrouwen en hun steun tijdens mijn studie en in de achterliggende periode.

Tenslotte, Jeanette, Jessica en Esther, bedankt voor de steun en het geduld in de periode waarin dit werk voltooid werd en waarin ik vaak wel aanwezig maar toch ook 'afwezig' was. Ik draag dit proefschrift daarom graag aan jullie op.

"Remember what Christ taught and let his words enrich your lives and make you wise"

Colossians 3:16, Living Bible.

Contents

Account

The following papers cover parts of this thesis:

2.2 Bakker, J.C., 1991. Effects of humidity on stomatal density and its relation to leaf conductance. Scientia Horticulturae, in press.

2.3 Bakker, J.C., 1991. Leaf conductance of four glasshouse vegetable crops as affected by air humidity. Agricultural and Forest Meteorology, 55: 23-36.

4.3 Bakker, J.C., 1989. The effects of air humidity on flowering, fruit set, seed set and fruit growth of glasshouse sweet pepper (*Capsicum annuum* L.). Scientia Horticulturae, 40: 1-8.

5.1 Bakker, J.C., Welles, G.W.H., Uffelen, J.A.M. van, 1987. The effects of day and night humidity on yield and quality of glasshouse cucumbers. Journal of Horticultural Science, 62: 361-368.

5.2 Bakker, J.C. and Sonneveld, C., 1988. Calcium deficiency of glasshouse cucumber as affected by environmental humidity and mineral nutrition. Journal of Horticultural Science, 63: 241-246.

5.3 Bakker, J.C., 1989. The effects of air humidity on growth and fruit production of sweet pepper (*Capsicum annuum* L.). Journal of Horticultural Science, 64: 41-46.

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

5.5 Bakker, J.C., 1990. Effects of day and night humidity on yield and quality of glasshouse eggplant (*Solanum melongena* L.). Journal of Horticultural Science, 65: 747-753.

1. General introduction

The greenhouse environment differs considerably from the environment outside. In general, radiation and CO_2 (without control) levels are lower, while humidity and air temperature are increased. Each of these changes has its own impact on growth, production and quality of the greenhouse crop, some of them being detrimental (Heggestad et al., 1986).

It has been known for a long time that humidity affects plant growth and development. However, in early controlled environment studies humidity received little attention (Went, 1957), most probably this was due to the limited possibilities for humidity control in controlled environment facilities. This situation lasted for several decades until about 1970. It was then clearly shown that growth and yield of crops could differ because of humidity effects (e.g. Hoffman, 1979). Among glasshouse growers, humidity continued to receive little attention, except for its effects on fungal diseases (e.g.: Winspear et al., 1970).

After the oil crisis the need for energy saving increased rapidly. One of the major consequences of the energy saving measures such as lower temperature setpoints, reduced air leakage and natural ventilation, double cladding and thermal screens, was an increase of glasshouse air humidity. Growers were facing the challenge of growing crops under entirely different environmental conditions, and humidity as an environmental factor gained interest, stimulating research in this field during the early eighties. At the same time, the development of automatic climate control systems enabled more accurate modification of the environment.

Originally the climate control of greenhouses was primitive: only extreme conditions were avoided and the actuators (heating, ventilation and later on thermal screens, CO_2 enrichment and artificial lighting) were operated manually. Later advances in electronics led to the development of more refined control procedures which were primarily based on the common practice of climate control by "good" growers (Strijbosch and van de Vooren, 1975). With the introduction of digital computers the greater flexibility allowed other control procedures to be implemented easily, without changing the hardware. A number of objectives, e.g. efficient use of energy, high yield and quality, avoidance of diseases and disorders, play a role in relation to climate control. But the ultimate goal is the optimal use of inputs in relation to the (economic) output.

The main problem with climate control is that there is no simple relation between actuators, environmental factors inside the greenhouse, short term response and long term results (Figure 1.1).

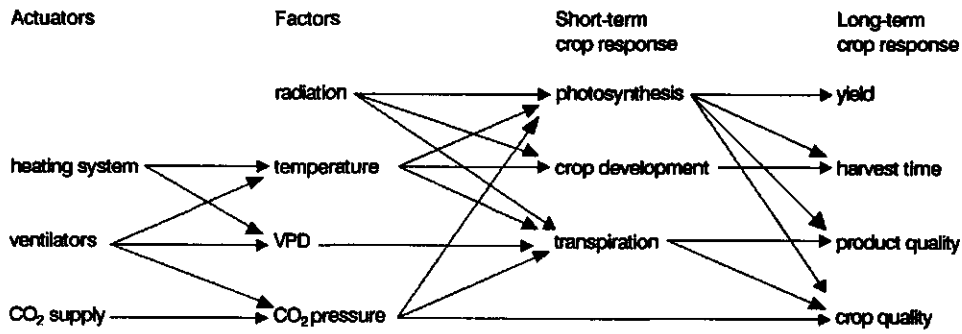

Figure 1.1
Some important relations between actuators, factors and short- and long-term crop response (v.p.d. = vapour pressure deficit of the greenhouse air). From Challa, 1990.

Optimization of greenhouse climate management may be achieved by defining a hierarchical set of three subsystems, where each subsystem is optimized within the limits dictated by the higher levels (Challa, 1985). At the highest level (referred to as level 2), crop responses with a long (> 24 h) relaxation time are considered. At this level processes that play a role include the distribution of assimilates, morphogenesis, growth, flowering, fruiting, production and quality. Combining this with information from the grower (crop status, price expectations) enabled long term average optimal (blueprint) climate control strategies to be formulated (Krug and Thiel, 1984; Liebig, 1985).

At the intermediate level (level 1) crop responses with a short relaxation time (hours, minutes), such as crop photosynthesis, transpiration or pollination, are considered. Here the required microclimate is defined.
These two highest levels can also be characterized by the term: 'control strategy', that is the required sequence of set points based on the influence of environmental factors during each day as well as during the total growth and production period.

At the lowest level (level 0) the actuation of the climate set-points is dealt with, taking into account the performance of the greenhouse in response to the weather and control actions. At this level the technical facilities for the control of single factors are available, thanks to research already performed in the field of climate control and greenhouse climate simulation (e.g. Tantau, 1989; Bot, 1989). However, the knowledge of crop responses, and especially humidity effects, is still insufficient to optimize the utilization of the techniques and the long term return for the grower (Challa, 1985).

This work attempts to contribute to the knowledge required in both levels 1 and 2 with respect to humidity responses but it is also intended to provide information valuable for commercial horticultural practice. Recent observations show that commercial tomato growers ventilate up for to 75% of the time. A major part of this is attributed to minimum ventilation, used frequently to overcome 'expected adverse effects of high humidity on plant development', and it is questionable whether this is necessary in all cases. A better understanding of humidity responses may therefore not only contribute to a better control of the production process and of the quality, but also to the reduction of energy consumption and as a result, of global environmental pollution.

1.1 Terminology

The humidity of the air can be measured in different ways: as the mass of water in unit volume, or in unit mass of air, or as the partial pressure of water vapour in the air. At any temperature, there is a maximum or saturated water vapour pressure (e_s, in kPa) which is a function of temperature. The difference between saturation value and the actual vapour pressure (e) is the Vapour Pressure Deficit (= e_s - e, abbreviation: VPD), expressed in Pascal. In the temperature range used in glasshouses (10 to 30 °C), the VPD normally varies within the range 0 to 2.5 kPa, most of the time being below 1.0 kPa.

For calculating fluxes of water into and out of the glasshouse (e.g. Bakker, 1986) the use of mass units (kg m^{-3} or kg kg_{air}^{-1}) to express humidity is required. However, when considering plant responses to humidity, VPD is the most useful of the various humidity measures because of its relation with transpiration (Cockshull, 1988).

The actual humidity of the air can also be expressed as a proportion of the saturation value measured in the same units. This proportion is the relative humidity (RH) and it is usually expressed as a percentage (RH = e/e_s x 100%). Relative humidity is widely used in commercial horticultural practice. However, its value is of limited importance because it is not directly related to the drying power of the air. Besides this, an additional advantage of the Vapour Pressure Deficit is that it is a more sensitive indicator of the water vapour conditions and varies over a wider range with temperature change than relative humidity.

1.2 Vapour balance and humidity control in glasshouses

In glasshouse cultivation the main source for water vapour is crop transpiration. Evaporation from the soil may also contribute, but when the crops are grown in substrates with the soil surface covered, this source can be

neglected. The transpiration of the crop is primarily determined by the intercepted shortwave radiation, the air temperature and the air humidity (Stanghellini, 1987). The water loss of leaves is governed by the vapour pressure gradient from the leaf to the surrounding air and this mainly depends on the VPD of the air. Humidity in the glasshouse therefore not only results from transpiration, but it also affects transpiration, being the output as well as the input signal in a feed back system. The water vapour leaves the glasshouse through (leakage) ventilation and condensation, both mass fluxes being dependent on the glasshouse air humidity. At an equilibrium humidity level, crop transpiration equals vapour transport by ventilation and condensation (Bakker, 1986).

All measures or variations in ambient conditions, that affect either the amount of radiation, ventilation or condensation, thereby affect transpiration and the humidity level achieved in the glasshouse. As condensation cannot be controlled directly and de-humidifiers are seldom used, lowering humidity is based on the principle of manipulation of the vapour transport by ventilation. Although the commonly used procedure (simultaneous heating and ventilation) does not always lead to a permanent decrease of the vapour content of the air, because of the resulting higher transpiration rates (Stanghellini, 1987), it is still the most widespread technique of lowering humidity in glasshouses.

To increase the humidity, especially in floriculture, humidification systems are used (De Bakker, 1988). However, during periods when one might want to increase the humidity level (i.e. spring and summer conditions) the effects of these systems are limited due to the generally high ventilation rates during these periods (Bakker, 1990).

1.3 Previous humidity research with glasshouse crops

Studying the literature on humidity in protected crop production reveals that in this field the majority of the research has been conducted in growth chamber experiments.

Increasing stomatal conductance at high humidity has been observed with many species (cf. Lösch and Tenhunen, 1981) showing effects on both transpiration and photosynthesis (e.g.: Jarvis and Morison, 1981). There are various examples in which a decrease of VPD results in an increase of photosynthesis rate (Acock, et al., 1976; Bunce, 1984; Hall and Milthorpe, 1978) which is ascribed to the higher stomatal conductance at low VPD. The most pronounced effects of humidity on stomatal aperture and leaf conductance are supposed to occur at high VPD levels (Lösch and Tenhunen, 1981), which are above the levels to which glasshouse crops are generally exposed (0.1-1.0 kPa). Although in this range the influence of low VPD on carbon assimilation is supposed to be small the effects are beneficial.

Depending on the humidity range, most reported responses of vegetative

growth (expressed as length, leaf area, fresh and dry weight) of various crops indicate enhanced growth at high humidity (Hoffman, 1979; Papenhagen, 1986). However, the majority of these results have been obtained with young plants in short term (of the order of 4 to 5 weeks) growth chamber experiments.

In the field of reproductive development research has concentrated on pollen germination and pollination (Van Koot and Van Ravestijn, 1963; Picken, 1984), flowering (Papenhagen 1986; Gislerød and Nelson, 1989), fruit set and seed set (Baër and Smeets, 1978). The available information indicates that the influence of humidity on the process of pollination and fruit set seems to be of primary importance and that high humidity may have detrimental effects.

In contrast to growth chamber experiments almost no glasshouse experiments covering a long growth and production period have been described. Among the few exceptions are the studies of Lipton (1970), Swalls and O'Leary, (1976) and, very recently, that of Holder and Cockshull (1990), all considering tomatoes. It is striking that both Swalls and O'Leary and Holder and Cockshull report responses to high humidity (i.e. reduced growth and production) opposite to those obtained in growth chamber experiments (Swalls and O'Leary, 1975; Hoffman, 1979).

Long term suppression of transpiration rate by high humidity may lead to local calcium deficiency of plant tissues (Bakker, 1985). Conversely reduced transpiration at night promotes root pressure (Bradfield and Guttridge, 1984) which improves calcium transport into fruits. This may on the one hand reduce the risk of calcium deficiency in fruits but on the other hand lead to excess of calcium causing other quality disorders (Roorda van Eijsinga et al., 1973; Janse, 1988). In general, most of these symptoms require relatively long periods of exposure to various environmental conditions before becoming visible.

Besides the aspects of external quality of the marketable product, keeping quality should be mentioned. Information on this aspect was and still is extremely limited as in the few glasshouse experiments this aspect was not investigated.

Apart from the effects of humidity on growth, production and quality, humidity is a major environmental factor in the incidence and development of fungal diseases (e.g. Winspear et al., 1970; Van Steekelenburg, 1986). Compared to the responses of growth and production in relation to humidity, in this area much more information is available. High humidity promotes the germination of most of the fungi but in many cases free water is necessary (Fölster, 1986). Avoidance of condensation on the leaves and high humidity is therefore the key to preventing these diseases, and several techniques of heating and ventilation have proven to be effective (Van Steekelenburg, 1986).

1.4 Aim and outline of the present study

From the preceding review the majority of the work on humidity appears to confine itself to growth chamber experiments. Consequently it is restricted to short term processes and growth of seedlings. Generally growth was improved by higher humidity but the few exceptions where the plants were grown under glasshouse conditions for longer periods of time showed different effects. In addition, in contrast to temperature research, effects of humidity by day are rarely separated from effects of humidity by night (the only exception noticed being the work of Bradfield and Guttridge, 1984), which is another major deficiency in the available information on the effects of humidity.

This work primarily aims to contribute to the knowledge of long term responses of growth, production and quality and most information is therefore obtained from large scale glasshouse experiments. Glasshouse environmental research is extremely costly due to both the large scale and the time period of the experiments. By way of illustration: the work described here includes almost four years continuous use of eight glasshouse compartments each of 200 m^2. Under the research capacity and financial restrictions imposed, this could only be justified by a combination with practical research. As a consequence of this the data-sets obtained are not entirely consistent which may modify the final analysis. However, this had to be accepted beforehand.

In glasshouse horticulture a wide range of crops are cultivated. This work confines itself to the four major Dutch fruit vegetable crops, tomato (*Lycopersicon esculentum* Mill.), cucumber (*Cucumis sativus* L.), sweet pepper (*Capsicum annuum* L.) and eggplant (*Solanum melongena* L.). Analyzing several crops improves the possibilities of extrapolating the results to other crops and secondly, it produces information valuable for a large group of growers, which was another major objective of this study.

Crop production may be considered as an integrated system of both short term and long term responding processes. The essence of a plant production system with indeterminately growing crops as used in this study is presented in the relational diagram in Figure 1.2.
From the available literature it can be deduced that humidity as an external variable can modify transpiration, photosynthesis (both through leaf conductance), growth, the rate of fruit formation and thereby possibly the partitioning of biomass within the crop. The influence on transpiration was not included in this study but is added in Figure 1.2 because of its relationship to humidity.

Although this work is primarily aimed at the long term responses of growth and production, two processes with short relaxation times, stomatal behaviour and pollination, were also investigated as information in the literature indicates these are important in determining the final yield.

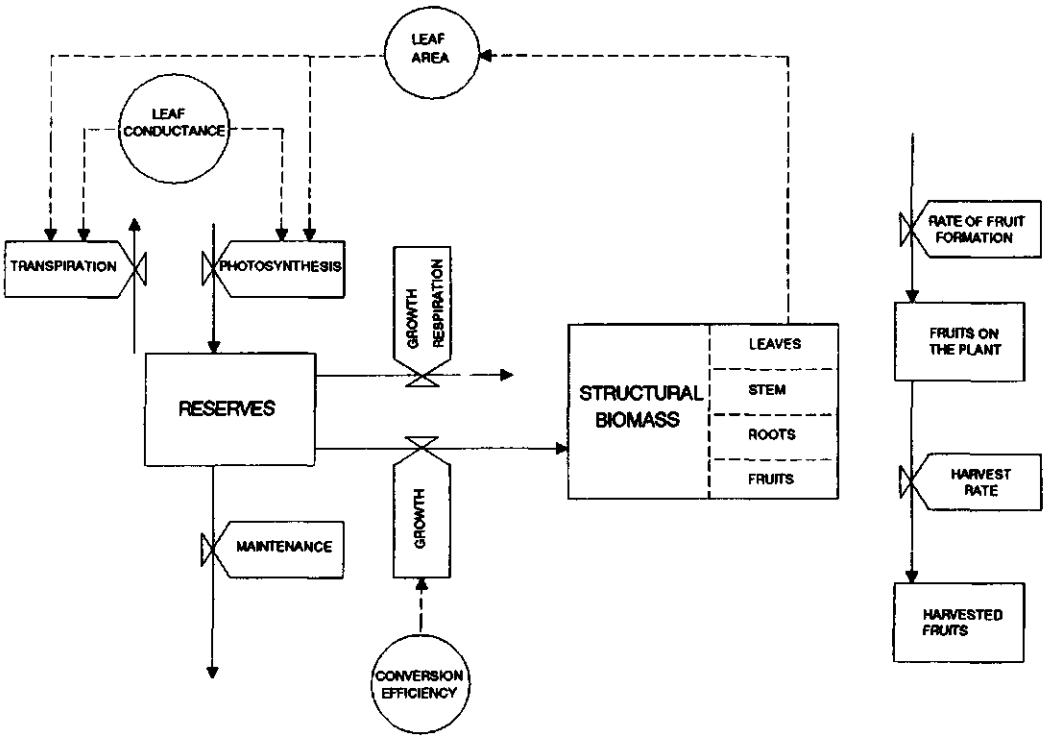

Figure 1.2
Simplified relational diagram of a production system of an intermediately growing crop

After this general introduction, the humidity effects on the stomatal response (Chapter 2) and pollination (Chapter 4), both expected to be essential short term responding processes in the determination of final production, are described. The long term processes dealt with are adaptation (stomatal density, Chapter 2), growth, dry matter production and distribution (Chapter 3), flowering, fruit set, seed set and fruit growth (Chapter 4), and production and quality aspects (Chapter 5). In Chapter 5 additional information is presented on the interaction effects of humidity and mineral nutrition on the occurrence of calcium deficiency in leaves. Finally a general discussion is given in Chapter 6.

1.5 References

Acock, B., Charles-Edwards, D.A. and Hand, D.W., 1976. An analysis of some effects of humidity on photosynthesis by a tomato canopy under winter light conditions and a range of carbon dioxide concentrations. J. Exp. Bot., 27: 933-941.

Baër, J. and Smeets, L., 1978. Effect of relative humidity on fruit set and seed set in pepper (*Capsicum annuum* L.). Neth. J. Agric. Sci. 26: 59-63.

Bakker, J.C., 1985. Physiological disorders in cucumber under high humidity conditions and low ventilation rates in greenhouses. Acta Hort., 156: 257-264.

Bakker, J.C., 1986. Measurement of canopy transpiration or evapotranspiration in greenhouses by means of a simple vapour balance model. Agric. For. Meteorol., 37: 133-141.

Bakker, J.C., 1990. Klimaatregeling door luchtbevochtigingssystemen. Vakblad voor de Bloemisterij, 45 (3): 78-81.

Bakker, C. de, 1988. Fijne nevelinstallaties houden luchtvochtigheid op peil. Vakblad voor de Bloemisterij, 43 (38): 50-51.

Bradfield, E.G. and Guttridge, C.G., 1984. Effects of night-time humidity and nutrient solution concentration on the calcium content of the tomato fruit. Scientia Hort., 22: 207-217.

Bot, G.P.A., 1989. Greenhouse simulation models. Acta Hort., 245: 315-325.

Bunce, J.A., 1984. Effects of humidity on photosynthesis. J. Exp. Bot., 35: 1245-1251.

Challa, 1985. Report of the working party "Crop growth models". Acta Hort., 174: 169-175.

Challa, H., 1990. Crop growth models for greenhouse climate control. In: R. Rabbinge, J. Goudriaan, H. van Keulen, F.W.T. Penning de Vries and H.H. van Laar, Eds., Theoretical production ecology: reflections and prospects. Simulation monographs 34, Pudoc, Wageningen: 125-145.

Cockshull, K.E., 1988. The significance of high humidity in energy-saving greenhouses. In: K.E. Cockshull, Ed., The effects of high humidity on plant growth in energy saving greenhouses. Report EUR 11261, Office for Official Publications of the European Communities, Luxembourg: 3-7.

Fölster, E., 1986. Wie und wann die Luftfeuchte Krankheiten begünstigt. Gärtnerbörse und Gartenwelt, 36: 1315-1317.

Gislerød, H.R. and Nelson, P.V., 1989. The interaction of relative air humidity and carbon dioxide enrichment in the growth of *Chrysanthemum* x *morifolium* Ramat. Scientia Hort., 38: 305-313.

Hall, A.J. and Milthorpe, F.L., 1978. Assimilate source-sink relationships in *Capsicum annuum* L. III. The effects of fruit excision on photosynthesis and leaf and stem carbohydrates. Aust. J. Plant Physiol., 5: 1-13.

Heggestad, H.E., Bennett, J.H., Lee, E.H. and Douglass, L.W., 1986. Effects of increasing doses of sulfur dioxide and ambient ozone on tomatoes: plant growth, leaf injury, elemental composition, fruit yields, and quality. Phytopathology, 76: 1338-1344.

Hoffman, G.J., 1979. Humidity. In: T.W. Tibbits and T.T. Kozlowski, Eds., Controlled environment guidelines for plant research. Academic Press, New York: 141-172.

Holder, R. and Cockshull, K.E., 1990. Effects of humidity on the growth and yield of glasshouse tomatoes. J. Hort. Sci., 65: 31-39.

Janse, J., 1988. Goudspikkels bij tomaat: een oplosbaar probleem. Groenten en Fruit, 43 (39): 30-31.

Jarvis, P.G. and Morison, J.I.L, 1981. The control of transpiration and photosynthesis by the stomata. In: P.G. Jarvis and T.A. Mansfield, Eds., Stomatal physiology. Society for Experimental Biology, seminar series, 8: 247-279.

Koot, Y. van, and Ravestijn, W. van, 1963. The germination of tomato pollen on the stigma (as an aid to the study of fruit setting problems). Proceedings of the 16th International Horticultural Congress, 1962, 2: 452-461.

Krug, H. and Thiel, F., 1984. Effect of soil temperature on growth of cucumber in different air temperature and radiation regime. Acta Hort., 156: 117-126.

Levitt, J., 1980. Responses of plants to environmental stresses. Volume 2. Water, radiation, salt and other stresses. Academic Press, New York, 607 pp.

Liebig, H.P., 1985. Temperature control strategy to avoid bolting of kohlrabi with minimum energy requirement. Acta Hort., 174: 321-325.

Lipton, W. J., 1970. Growth of tomato plants and fruit production in high humidity and at high temperature. J. Amer. Soc. Hort. Sci., 95: 674-680.

Lösch, R. and Tenhunen, J.D., 1981. Stomatal responses to humidity - phenomenon and mechanism. In: P.G. Jarvis, P.G. and T.A. Mansfield, Eds., Stomatal physiology. Society for Experimental Biology, seminar series, 8: 137-161.

Papenhagen, A., 1986. Hohe Luftfeuchte hat auf Planzen begrenzten Einfluss. Gärtnerbörse und Gartenwelt, 36: 1343-1346.

Picken, A.J.F., 1984. A review of pollination and fruit set in the tomato (*Lycopersicon esculentum* Mill.). J. Hort. Sci., 59: 1-13.

Roorda van Eijsinga, J.P.N.L., Rodenburg, R. and Uffelen, J.A.M. van, 1973. Stip, een nieuw kwaliteitsprobleem bij rode paprikavruchten. Bedrijfsontwikkeling, 4: 733-734.

Stanghellini, C., 1987. Transpiration of greenhouse crops. An aid to climate management. Dissertation Agricultural University, Wageningen, 150 pp.

Steekelenburg, N.A.M. van, 1986. *Didymella bryoniae* on glasshouse cucumbers. Dissertation Agricultural University Wageningen, 105 pp.

Strijbosch, T. and Vooren, J. van de, 1975. Developments in climate control. Acta Hort., 46: 21-22.

Swalls, A.A. and O'Leary, J.W., 1975. The effect of relative humidity on growth, water consumption and calcium uptake in tomato plants. J. Ariz. Acad. Sci., 10: 87-89.

Swalls, A.A. and O'Leary, J.W., 1976. Growth, water consumption and salt uptake of tomato plants in high humidity-high carbon dioxide greenhouse environments. J. Ariz. Acad. Sci., 11: 23-26.

Tantau, H.J., 1989. Models for greenhouse climate control. Acta Hort., 245: 397-404.

Went, F.W., 1957. The experimental control of plant growth. Chronica Botanica, Waltham, Massachusetts.

Winspear, K. W., Postlethwaite, J. D. and Cotton, R. F., 1970. The restriction of *Cladosporium fulvum* and *Botrytis cinerea* attacking glasshouse tomatoes, by automatic humidity control. Ann. Appl. Biol., 65: 75-83.

2. Stomatal density and leaf conductance

2.1 Introduction

In Chapter 1 the relations between air humidity and crop production were analysed qualitatively (Figure 1.2 Chapter 1). The influence of humidity on photosynthesis through its effect on stomatal conductance is one of the potential points of action. A relational diagram of this subsystem is presented in Figure 2.1. The stomatal conductance to gas exchange is determined by a slowly changing morphological component (adaptation of stomatal density, form and size; Tichá, 1982) and a dynamic component reacting directly to environmental conditions.

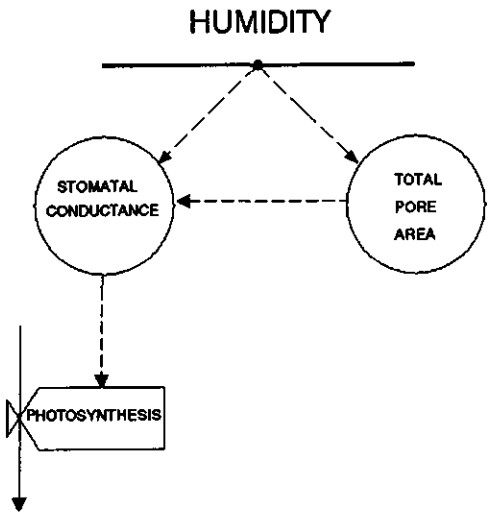

Figure 2.1
Relational diagram of humidity effects on photosynthesis through its effect on total pore area and momentary response of stomatal conductance.

The effects of humidity on adaptation of the total pore area to long term elevated humidity and its influence on leaf conductance were investigated under controlled environment and glasshouse conditions (section 2.2). The momentary response of leaf conductance of all four crops to environmental humidity is dealt with in section 2.3.

To provide an order of magnitude of the potential influence of humidity on growth, the effects on leaf and crop photosynthesis were estimated from the observed responses of leaf conductance. Although the relation between photosynthesis and crop growth is not a straightforward one, in this way it may be deduced to which extent humidity may potentially affect yield of the different crops (section 2.4).

2.2 Effects of humidity on stomatal density and its relation to leaf conductance.

Scientia Horticulturae, in press.

Abstract. The effect of air humidity in the range of 0.2 to 1.6 kPa vapour pressure deficit on stomatal density was investigated with glasshouse cucumber (*Cucumis sativus* L.), tomato (*Lycopersicon esculentum* Mill.), sweet pepper (*Capsicum annuum* L.) and eggplant (*Solanum melongena* L.). Stomatal density of tomato, eggplant and sweet pepper was higher at high humidity. The length of the pore increased at high humidity with cucumber, tomato and sweet pepper, the width was only affected with sweet pepper.

No significant differences in leaf conductances were observed between plants grown under different humidity pre-treatments. It is concluded that stomatal density and size as affected by humidity in the range investigated do not significantly influence leaf conductance.

2.2.1 Introduction

Stomatal density on leaves varies widely with species and environmental conditions, ranging from 60 to 1000 mm^{-2} (Kramer, 1983). Data of stomatal density of the four crops used in this study have been presented by Gay and Hurd (1975) for tomato, Schoch (1972) for sweet pepper, Daunay et al. (1986) for eggplant and Bressan et al. (1978) for cucumber. For mature leaves abaxial densities of these species are in the range of 100 to 500 per mm^2. Tichá (1982) presented a comprehensive review of the changes in stomatal density and sizes as induced by external and internal factors. In general stomatal density varies chiefly due to differences in the growth of epidermal cells, that is, to differences in the spacing of stomata rather than to differences in the proportion of stomata developed. The stomatal index (SI: number of stomata/[number of stomata+number of epidermis cells]) is relatively constant (Tichá, 1982). The more arid the conditions of plant growth, the higher the stomatal density usually is. On the other hand, at more humid conditions the stomatal density tends to be lower, while stomatal size usually changes in an opposite way. However, these statements (Tichá, 1982) are based on results with variations in soil moisture and water stress rather than on results with different air humidities. Recent results with variations in air humidity under controlled temperature and CO_2 conditions indicate a higher stomatal density

and an increase in size at high humidity (Gislerød and Nelson, 1989).

Stomatal densities and sizes are frequently used to estimate stomatal resistance (Tichá, 1982). However, although a higher density and larger sizes lead to a higher pore area per unit leaf area, this does not necessarily imply a higher leaf conductance (Prisco and O'Leary, 1973), transpiration (Rajapakse et al., 1988) nor a higher rate of photosynthesis. For example, Woodward and Bazzaz (1988) found that, for a range of species of trees, shrubs and herbs, photosynthesis remained almost constant despite an increase in stomatal density from 200 to 900 mm^{-2}.

To estimate the effects of long term elevated humidity on stomatal density and leaf conductance of glasshouse grown crops, measurements were done on plants grown in glasshouses and under controlled environments.

First, data were collected to investigate the effect of humidity in the range obtained in glasshouses under natural light conditions. Based on the results of this survey, this was followed by an experiment under controlled light and temperature conditions. Finally leaf conductance was measured on the plants which received these two different humidity pre-treatments. The objective was to check whether leaf conductance is determined primarily by prevailing humidity conditions or if pretreatment with different humidities results in after effects caused by differences in stomatal density.

2.2.2 Materials and methods

Measurement of stomatal density and size

Stomatal density and size were determined with the "replicate technique" (Sampson, 1961). Impressions of the abaxial leaf epidermis were made with silicone rubber (Xanthopren L Blue and Elastomer activator, Bayer). Replicas of the rubber impressions were made with polystyrene and mounted on a microscope slide.

Cell number and number of stomata were counted with three replications on each leaf impression, in an area of 0.032 or 0.1875 mm^2 using a Zeiss microscope with a 40 × (for cucumber and stomatal size) or 16 × (for eggplant, sweet pepper and tomato) objective lens. The microscopic view was displayed on a Sony colour video monitor (PMV-9000ME) using a Panasonic colour CCTV camera (type WV-CD 130 L/G). The overall magnification on the video display was 800 or 320 ×, for the 40 and 16 × objective lens, respectively.

As stomata are initiated from leaf unfolding and cell division and expansion continues leaf until the leaf reaches 10 to 60% of its final size, impressions were made only on mature leaves to avoid differences in stomatal density influenced by differences in leaf age. Furthermore the impressions were made at the same location on each leaf to prevent differences due to heterogeneity of stomata on the leaf blade.

Glasshouse experiments

In autumn 1984, spring 1989 and autumn 1989 leaf impressions were made of leaves of cucumber (cv. 'Lucinde'), tomato (cv. 'Spectra') and eggplant (cv. 'Dobrix'). The plants were grown on rockwool (salinity level: 2.5-3.0 dS m^{-1}) with a density of 2.5 plants m^{-2}. Four different day/night humidity treatments were replicated in separate glasshouse compartments. Humidity could be increased by a humidification system of water baths and closing a polythene thermal screen. To reduce humidity the humidification system was switched off and the polythene screen was opened for 15%. Screened and aspirated psychrometers were used to measure temperature and calculate vapour pressure deficit (VPD) with a sample time of one minute. A high or low relative humidity by day was combined with either a high or a low humidity by night. Treatment symbols are h/h and l/l for the continuously high or low humidities and h/l and l/h for the alternating high and low humidities.
The 24-h average humidity in these experiments ranged from about 0.3 to 0.9 kPa VPD, respectively, for the h/h and l/l treatment. In general the treatments were applied in the period from planting until after the start of harvest. More details of the exact periods of treatment and growing conditions for cucumber are presented by Bakker et al. (1987), for tomato by Bakker (1990[a]) and for eggplant by Bakker (1990[b]).

With cucumber leaf impressions were made of the 20th leaf at the centre of the leaf near the main vein. Impressions of tomato leaves were made at the centre of the second basal leaflet of the first leaf above the third and fifth truss. The impressions of eggplant leaves were made at 2 cm from the leaf edge in the middle of mature leaves. With all crops impressions were made on 20 mature leaves per humidity treatment.

Stomatal size of tomato (total length and width of the guard cells) was measured for 80 stomata from the 5th truss leaf from the continuously high or low humidity treatment.

Controlled environment experiment

Seeds of cucumber (cv. 'Corona'), sweet pepper (cv. 'Evident') and tomato (cv. 'Calypso') were sown in perlite and propagated in rockwool under standard conditions (day/night temperature 20/20 °C, nutrient solution: EC 2.5 dS m^{-1}). At the third leaf stage 5 selected plants of each species were transferred to two controlled environment cabinets (Karl Weiss ZK 2200E/+4JU-P-S), dimensions: l×w×h=1.2×1.2×1.5m, lamps: 90% Philips number 33 fluorescent lamps and 10% Philips Philinea linear lamps. The position of the growing point was labelled to discriminate leaves developed during propagation from those developed in the growth cabinets. The plants were grown for four weeks at 20 °C (day/night), a radiation level of 150 μmol m^{-2} s^{-1} (PAR), a day length of 12 h and a VPD of 0.2 kPa and 1.0 kPa, respectively.

At the end of the four weeks in the controlled environment cabinets the plants from both humidity treatments were transferred to a single growth chamber (dimensions l×w×h= 7×4.25×2.1 m, lamps: SON-T), to investigate the pretreatment effects on leaf conductance. Leaf conductance was measured with a steady state diffusion porometer (Li-Cor 1600C) on the first leaf which developed entirely under the different humidity pretreatments. The measuring conditions were: darkness at 20 °C and 0.2 kPa or 1.0 kPa; and 150 μmol $m^{-2}s^{1}$ (PAR), 22 °C and 0.8 kPa or 1.6 kPa VPD. The plants were allowed to adjust to the new environmental conditions for at least 4 hours before leaf conductance was measured. Immediately after these measurements leaf impressions were made on the same leaves.

2.2.3 Results and discussion

Stomatal density of eggplant and the first leaf above the fifth truss of tomato was significantly higher at the continuously high humidity. (Table 2.1). With tomato, the stomatal index also differed significantly between the treatments with a high or low humidity by day. With cucumber, stomatal density did not differ significantly among the treatments neither in the glasshouse (Table 2.1) nor in the controlled environment experiment (Table 2.2). Also the stomatal density of the first leaf above the third truss of tomato did not significantly respond to humidity (Table 2.1), but the tendency observed, a higher density at low VPD, is similar to those found in tomato and sweet pepper (Table 2.2), and eggplant (Table 2.1).

Table 2.1
Stomatal density (SD, number per mm^2) and stomatal index (SI, stomata/ [stomata + epidermis cells]) of cucumber, tomato and sweet pepper grown under different humidity treatments in glasshouses. (h=high humidity, l=low humidity). LSD values from Students' T-test; p=0.05.

day/night treatment	Cucumber	Tomato				Eggplant	
		3rd truss		5th truss			
	SD	SD	SI	SD	SI	SD	SI
h/h	460	105	0.177	153	0.215	182	0.196
l/h	437	91	0.168	113	0.175	136	0.182
h/l	402	103	0.177	128	0.204	171	0.202
l/l	425	90	0.163	103	0.174	137	0.212
LSD 5%	n.s.	n.s.	n.s.	15	0.018	42	n.s.

Table 2.2
Stomatal density (SD, number per mm^2) and stomatal index (SI, stomata/ [stomata + epidermis cells]) of cucumber, tomato and sweet pepper grown at two different humidity levels under controlled environments. LSD values from Students' T-test; p=0.05.

treatment	Cucumber		Tomato		Sweet pepper	
	SD	SI	SD	SI	SD	SI
0.2 kPa VPD	552	0.196	208	0.238	262	0.207
1.0 kPa VPD	523	0.210	144	0.225	168	0.215
LSD 5%	n.s.	n.s.	33	n.s.	36	n.s.

Stomatal density generally increases with leaf number (Gay and Hurd, 1975), and the sensitivity to environmental factors, especially those related to the water content of the leaf, is greater for leaves higher on the shoot (Tichá, 1982). Furthermore in the glasshouse experiment with tomato the differences in humidity between the different humidity treatments (Bakker, 1990[a]) were less pronounced than in the growth chamber experiment. This may possibly explain why in the glasshouse no significant difference in stomatal density was found on the lower leaf in contrast to the response of the upper leaf.

The stomatal index was not affected except for the upper leaf of tomato (Tables 2.1 and 2.2). As the replicas were made on mature leaves it is unlikely that this is the result of differences in leaf ontogeny. The leaves above the 5th truss, however, were suffering from calcium deficiency (Bakker, 1990[a]). In the cucumber experiments stomatal index also tended to be higher on leaves showing calcium deficiency induced by enveloping leaves with transparent plastic bags (Bakker, 1985). As variations in stomatal index are due to internal factors (Tichá, 1982), this may be the cause of the observed significant effect of humidity on stomatal index of tomato, especially as in the growth chamber experiment no calcium deficiency nor an effect on stomatal index was observed.

Stomatal length of tomato in the glasshouse experiment was slightly increased by high humidity (26 μm compared to 23 μm at low humidity; LSD 5%: 1.8), but stomatal width and length × width did not differ significantly. In the growth chamber experiment the stomatal length of all three species investigated was increased by low VPD, width was only significantly affected by humidity for sweet pepper. For all species investigated the length × width was higher at high humidity (Table 2.3). The observed effect of humidity on stomatal size concurs with the results of Gislerød and Nelson (1989). The response of width is less pronounced than that of length while stomatal size of tomato is least affected.

Table 2.3
Stomatal length (l, μm), width (w, μm) and length × width of cucumber, tomato and sweet pepper grown at two different humidity levels in controlled environments. LSD values from Students' T-test; p=0.05.

treatment	Cucumber			Tomato			Sweet pepper		
	l	w	l×w	l	w	l×w	l	w	l×w
0.2 kPa VPD	16.1	10.0	162	24.5	14.0	351	24.3	16.8	409
1.0 kPa VPD	13.9	9.5	135	20.1	13.3	267	20.4	14.6	299
LSD 5%	1.4	n.s.	22	2.6	n.s.	n.s.	1.8	1.5	53

The overall effect of humidity on stomatal density and size with all crops is a higher total pore area per unit leaf area at higher humidity. However, despite this effect, no significant differences in leaf conductance were found between the high or low VPD pre-treatment (Table 2.4). Differences in stomatal density and size in this range therefore seems unimportant in the determination of leaf conductance and consequently for water and CO_2 exchange. From this it is suggested that the observed effects of humidity on yield and quality of the various crops (e.g. Bakker et al., 1987 for cucumber; Bakker, 1990[a], for tomato and Bakker, 1990[b], for eggplant) are not influenced by differences in stomatal density.

Table 2.4
Influence of high or low humidity pre-treatment (VPD 0.2 or 1.0 kPa) on leaf conductance (cm s^{-1}) of cucumber, tomato and sweet pepper at four radiation/humidity treatments. Each value presented is the mean of 15-20 measurements (significance at Students' T-test; p=0.05).

	Cucumber				Tomato				Sweet pepper			
VPD:	0.2		1.2		0.2		1.2		0.2		1.2	
	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
darkness												
0.2 kPa	0.335	.030	0.409	.029	0.407	.029	0.439	.023	0.191	.019	0.165	.006
1.0 kPa	0.193	.012	0.224	.014	0.359	.035	0.264	.035	0.130	.010	0.108	.008
150 μmol m^{-2} s^{-1}												
0.8 kPa	0.359	.009	0.317	.008	0.448	.022	0.512	.023	0.451	.026	0.350	.025
1.6 kPa	0.206	.007	0.200	.009	0.347	.021	0.406	.024	0.170	.008	0.175	.008
mean	0.270		0.276		0.390		0.408		0.237		0.206	
significance	n.s.				n.s.				n.s.			

Stomatal density has not only been investigated in relation to gas exchange, but also in relation to plant diseases. A higher stomatal density may cause a higher incidence of diseases caused by pathogens which penetrate through the pore such as bacteria (Ramos and Volin, 1987) and some fungi as downy mildew (Royle and Thomas, 1971) and *Cladosporium fulvum* (Rich, 1963). However, most fungi can penetrate the outer barriers of the intact leaf (Rich, 1963) and the increase of most fungal diseases under high humidity conditions is attributed primarily to the more favourable conditions for germination of spores (Grange and Hand, 1987). A high humidity does not generally predispose leaves to infection, e.g. infection of *Didymella bryoniae* did not differ between cucumber leaves grown under high or low humidity (van Steekelenburg, 1986). However, the increase in stomatal density at high humidity may possibly be one of the underlying processes responsible for the observation in commercial practice that plants grown under high humidity are "weak", i.e. less resistant to some diseases (de Jong, 1987).

2.3 Leaf conductance of four glasshouse vegetable crops as affected by air humidity.

Agricultural and Forest Meteorology, 55: 23-36.

Abstract. Porometer measurements were conducted on eggplant, cucumber, sweet pepper and tomato in a glasshouse during day and night conditions at different levels of air vapour pressure deficit.

The response of leaf conductance was described as an empirical non-linear function of vapour pressure deficit at leaf surface (D_0) and solar radiation.

Leaf conductance at night clearly responded to D_0. Highest conductance was observed with tomato and cucumber. It is argued that effects of humidity on cuticular conductance may contribute to the increased leaf conductance at low D_0 but also that stomata respond to D_0 at night.

If both day and night measurements are combined into one model, relative response of leaf conductance to vapour pressure deficits is equal for the four species.

2.3.1 Introduction

Stomata are the major pathways for the efflux of water from the mesophyll of leaves into the atmosphere and for the influx of CO_2. During diurnal cycles, stomatal conductance varies in response to light, humidity and temperature, thus affecting the processes of transpiration and CO_2 assimilation (Schulze and Hall, 1982). In glasshouse cultivation, plants are exposed to a range of temperature and humidity conditions which, in general, is small compared to ambient conditions because of accurate environmental control. Under these

conditions, the dynamic responses of stomata may be expected to be substantially reversible (Schulze and Hall, 1982).

In natural environments the stomata strongly respond to vapour pressure deficit and temperature, but when the effects of temperature and humidity are separated, leaf conductance increases with temperature at a level above the optimum for photosynthesis (Hall, et al., 1976). As a result stomatal responses to temperature per se have often be confused with responses to vapour pressure deficit. Stomatal responses to humidity have been observed with most species that have been examined (eg. Kaufmann, 1982; Schulze, 1986; El-Sharkawy and Cock, 1986; Munro, 1989) and their importance in controlling the rate of photosynthesis has been demonstrated with various crops, eg. tomatoes (Acock, et al., 1976) and peppers (Hall and Milthorpe, 1978). In models of water relations and photosynthesis of glasshouse vegetable crops, incorporation of the effects of humidity on stomatal behaviour may improve simulation (Marcelis, 1989) and provide information to explain long term humidity effects on growth and yield of glasshouse vegetable crops (Bakker et al., 1987; Bakker, 1990[a]). The major objective of this study was to examine the response of leaf conductance to vapour pressure deficit of four glasshouse vegetable crops under natural winter light conditions and normal temperature regimes.

2.3.2 Materials and methods

Plant materials and glasshouse facilities

Four different species were used in this study: eggplant (*Solanum melongena* L., cv. 'Dobrix'), cucumber (*Cucumis sativus* L., cv. 'Lucinde'), sweet pepper (*Capsicum annuum* L., cv. 'Delphin') and tomato (*Lycopersicon esculentum* Mill., cv. 'Spectra'). Plants were grown on rockwool in a recirculation system at a salinity level of 2.5-3.0 dS m^{-1} (equivalent to a water potential of the root environment of -0.1 MPa).

All data were collected in 1989 in eight glasshouse compartments (dimensions 15 × 12.8 m) of a multispan Venlo type glasshouse covered with double glass and equipped with a polythene thermal screen and a humidification system (water baths with an area of 7 m^2; Bakker et al., 1987). Environmental conditions (temperature, humidity and CO_2 concentration) were measured once a minute and were controlled by a distributed computer system (Bakker et al., 1988). Different humidity levels (day and night) were obtained in the separate compartments by using the thermal screen and the humidification system. To increase the humidity, the screen was kept closed and the humidification system turned on. To reduce humidity, the screen was partly opened and the humidification system set off. In manipulating the screen in this way, light differences between the various humidity treatments were restricted to less than 2% of measured overall light transmission (Bakker,

1990[a]). Temperature differences between the treatments were minimized by adjusting (every minute) the setpoint for heating in the compartments with low humidity treatment to the temperature achieved in the compartment with the high humidity treatment (i.e. the compartment with the highest temperature because of the extra heat gain from the humidification system). The glasshouse atmosphere was enriched with pure CO_2 and controlled at a level of 450 cm^3 m^{-3}. Leaf temperatures and the irradiance at leaf surface were only measured in combination with the porometer observations.

Conductance measurements

Leaf conductance (cm s^{-1}) was measured with a steady-state diffusion porometer (Li-Cor 1600C, Li-Cor, Inc., Lincoln, NE, USA) on the underside of selected and marked leaves of 12 mature plants of eggplant and tomato, 12 seedlings of cucumber (5 weeks) and sweet pepper (8 weeks) in each glasshouse compartment. The plants were located around the sensors for the measurement and control of the glasshouse temperature, humidity and CO_2 concentration. Leaf conductance was measured on leaves at sensor level within a crop layer, 20 cm high. Measurements were made for several days and nights on one crop, followed by a similar cycle on the next crop in the sequence: tomato, eggplant, cucumber and finally sweet pepper. The measuring routine consisted of 12 readings in a compartment with a high humidity, alternated with 12 readings in a compartment with a low humidity. A complete measuring cycle including the eight compartments took about 1.5 h. Radiation (PAR) at leaf level was measured with a quantum sensor (LI-190S-1, Li-Cor, Inc., Lincoln, NE, USA) attached to the porometer sensor head. Final data analysis was performed with a Genstat-5 program package on a VAX-3600 computer system.

Dataprocessing and fitting routines

In general, leaf conductance is affected by the following environmental variables: radiation, temperature, humidity and CO_2. However, the influence of temperature in the range obtained here (20 - 27 °C) is considered to be of minor importance (Takakura et al., 1975; Hall et al., 1976; Avissar et al., 1985; Stanghellini, 1987). The effect of the small differences in glasshouse ambient CO_2 (400 - 500 cm^3 m^{-3}) on leaf conductance was assumed to be negligible. This assumption is based on the results of Stanghellini (1987) who was unable to demonstrate any significant effect of CO_2 on leaf conductance of tomato up to 700 cm^3 m^{-3}; thus confirming the statement of Raschke (1975) that stomata of plants grown in a well-watered environment are not sensitive to CO_2 concentration.

As the major objective of this study was to examine the response of leaf conductance to vapour pressure deficit (VPD), this response has been described as an empirical function of PAR and VPD, assuming that these are the two

major variables (Thorpe et al., 1980; Jarvis et al., 1981; Kaufmann, 1982). The sensitivity of leaf conductance to leaf to air water vapour pressure difference ($e_{leaf} - e_{air}$; D_l) depends on the leaf boundary layer conductance (Bunce, 1985). Therefore the response of leaf conductance to humidity should most appropriately be described as a function of vapour pressure deficit at the surface of the leaf (D_o), rather than as a function of the leaf to air vapour pressure difference (Meinzer and Grantz, 1989). Assuming that the leaf is isothermal, D_o ($e_{leaf} - e_{surface}$) can be calculated by:

$$D_o = [\, r_l/(r_l + r_{bl})] \, (e_{leaf} - e_{air}) \qquad (2.1)$$

where r_l is the stomatal and cuticular diffusive resistance, r_{bl} is the boundary layer resistance, e_{leaf} is the water vapour partial pressure in the stomatal pores and e_{air} is the water vapour partial pressure of air outside the boundary layer.

In glasshouse vegetable crops such as tomato, under conditions with natural ventilation, mean air velocity within the canopy is about 0.1 m s^{-1} with minimal variations (Bot, 1983) and consequently the boundary layer conductance is almost constant for a given crop (Stanghellini, 1988). The boundary layer resistances for the four crops used in this study were calculated using the equation derived by Stanghellini (1987) for glasshouse conditions:

$$r_{bl} = 587\, l^{0.5}/(1\, |T_l - T_a| + 207\, u^2)^{0.25} \quad (s\ m^{-1}) \qquad (2.2)$$

where l is the characteristic dimension of the leaf (m), T_l and T_a are temperatures of leaf and air, and u is the wind velocity (which was taken as 0.1 m s^{-1}). The characteristic leaf dimensions for the four crops used in this study were: tomato, 0.05 m; pepper, 0.06 m; cucumber, 0.10 m; eggplant, 0.12 m.

The influence of the VPD on leaf conductance has been described by linear (Thorpe et al., 1980; Munro, 1989), exponential and hyperbolic functions (Kaufmann, 1982; Schulze, 1986; El-Sharkawy and Cock, 1986). In the fitting routines three regression models for the response of leaf conductance (g_l) to D_o were compared:

$$g_l = G \exp(a\, D_o) \qquad (2.3)$$

$$g_l = G + a\, D_o \qquad (2.4)$$

$$g_l = G / (a + D_o) \qquad (2.5)$$

where G is the maximum conductance and a is a parameter. The relationship between PAR and leaf conductance was considered a negative exponential function (Burrows and Milthorpe, 1976):

$$g_l = G' [1 - b \exp(-c\, Q_p)] \qquad (2.6)$$

where G' is the maximum conductance, Q_p is the photon flux density and b and c are parameters.

To describe the response of leaf conductance to radiation and VPD this model was combined with either eqn. (2.3), eqn. (2.4) or eqn. (2.5), under the simple hypothesis that there was no interaction between radiation and VPD (Jarvis et al., 1981). i.e. for the combination of eqns. (2.6) and (2.3) this results in:

$$g_l = G_{max} [1 - b \exp (-c\, Q_p)] [\exp (a\, D_0)] \qquad (2.7)$$

where b, c and a are parameters and G_{max} is equal to leaf conductance in saturating PAR with zero D_0.

Leaf conductances were obtained by calculating the arithmetic means of the 12 measurements of g_l within one compartment. These data were fitted to the average Q_p and D_0 during the period the 12 measurements were made. Although the proper humidity variable to relate g_l to is D_0, for the sake of comparison with most of the literature in this field, the coefficients for fits using the leaf to air vapour pressure difference (D_l) were also calculated.

2.3.3 Results

Environmental conditions

For all four crops, the environmental conditions obtained during the conductance measurements were similar, only the PAR flux densities during the tomato measurements being slightly lower. The ranges for temperature, PAR at leaf level, VPD of the glasshouse air (D_a) and carbon dioxide were 20 to 27 °C; 0 to 300 μmol s^{-1} m^{-2}; 0.1 to 1.8 kPa and 400 to 500 cm^3 m^{-3}, respectively. As the various humidities in the separate compartments were obtained independently of temperature and radiation, no significant intercorrelations between the four environmental parameters existed (Figures 2.2, 2.3 and 2.4).

Because of the relatively low irradiance levels, leaf temperatures were within 1 °C of the glasshouse air temperature. Results with glasshouse tomato also indicate that with well-watered plants, even under higher irradiance levels than obtained here, the difference between leaf and air temperature is almost negligible (Stanghellini, 1987), while simulation studies show leaf temperatures within 1 °C of air temperature below 300 W m^{-2} global radiation (Marcelis, 1989), approximately equivalent to 600 μmol s^{-1} m^{-2} PAR (Thimijan and Heins, 1983).

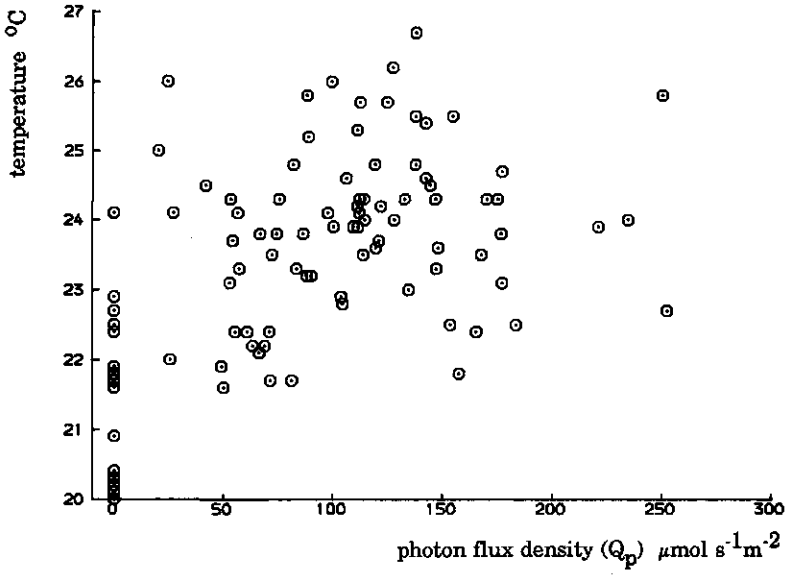

Figure 2.2
Glasshouse air temperature plotted against photon flux density.

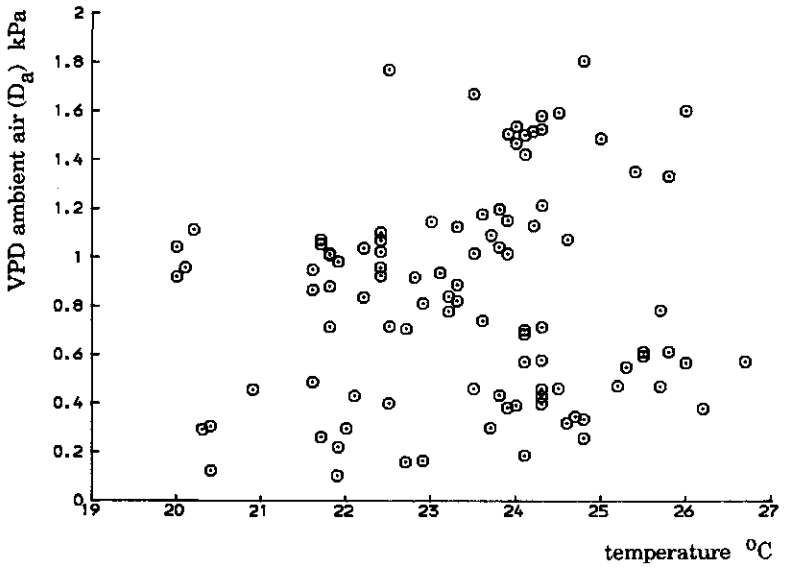

Figure 2.3
Vapour pressure deficit of glasshouse air (D_a) plotted against temperature.

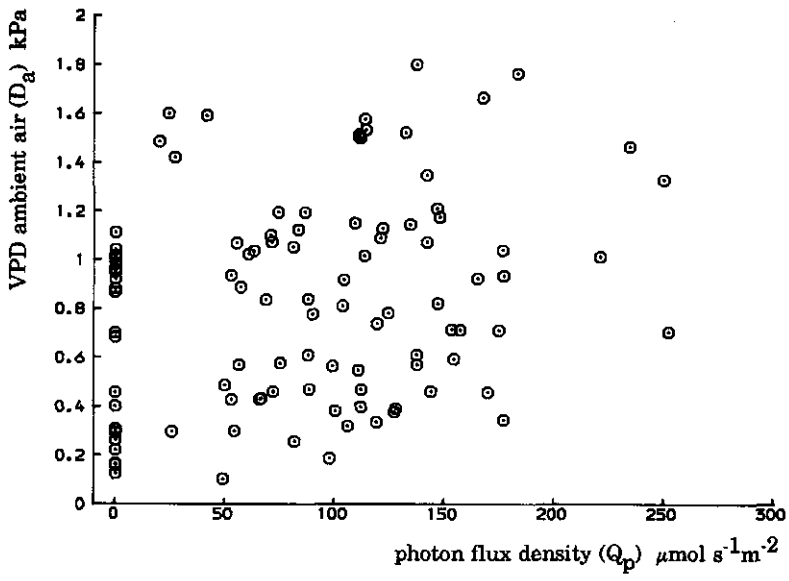

Figure 2.4
Vapour pressure deficit of glasshouse air (D_a) plotted against photon flux density.

Model fits night measurements

To describe the leaf conductance at night the measured conductances were fitted against D_0 (range at night 0.05 to 1.2 kPA) using eqns. (2.3) - (2.5). For all species, best fits were obtained with the non-linear relations. Highest percentages of variance accounted for were found with eqn. (2.3), whilst for three of the four species the linear relation gave the lowest correlations (Table 2.5).

Table 2.5
Percentage variance accounted for (r^2 adjusted) by three regression models to describe the effect of VPD at the leaf surface (D_0, kPA) on leaf conductance (g_l, cm s^{-1}) at night for four plant species.

model	eggplant	cucumber	pepper	tomato
$g_l = G \exp(a D_0)$	70.4	83.2	75.7	89.2
$g_l = G + a D_0$	67.6	77.7	73.3	85.2
$g_l = G / (a + D_0)$	70.0	82.2	70.6	87.4
Degrees of freedom	20	20	21	23

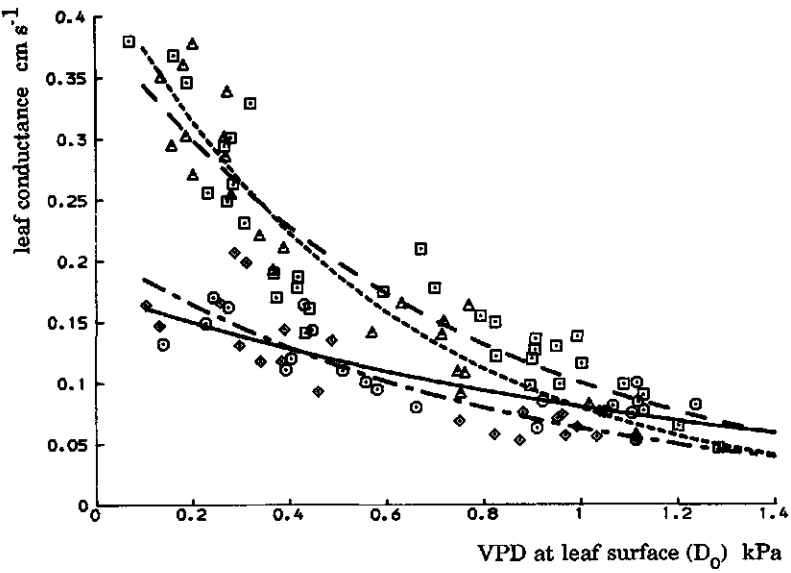

Figure 2.5
Leaf conductance at night of four species as a function of VPD at the leaf surface (D_0). Regression coefficients as in Table 2.6.
o—o , eggplant; □+−□ , cucumber; ◇-·-◇ , sweet pepper; △···△ , tomato.

In Figure 2.5 the fitted responses of leaf conductance at night are presented using eqn. (2.3), regression coefficients for the four species are given in Table 2.6. The maximum leaf conductances at night of tomato and cucumber were significantly higher than those of sweet pepper and eggplant (Table 2.6, coefficient G). Lowest values of leaf conductance were measured at high D_0 (around 1.2 kPa). For all species these values of g_l were between 0.02 and 0.05 cm s^{-1} and did not differ significantly. This indicates the that absolute sensitivity of g_l to D_0 (in cm s^{-1} kPa^{-1}) increases with increasing maximum conductance as found by Morison (1985). Furthermore, coefficient 'a' differed significantly (Students' T-test; p=0.01) only between tomato and eggplant (Table 2.6). This indicates that relative sensitivity of leaf conductance to D_0 at night does not vary much among the four species.

Using the leaf to air vapour pressure difference (D_l) in the fitting routines also gave best fits with the exponential function. In Table 2.7 the regression coefficients are presented for the relationship between g_l and leaf to air vapour pressure difference (D_l).

Table 2.6
Parameters of the function: $g_l = G \exp(a D_0)$ to describe leaf conductance (g_l, cm s^{-1}) at night as a function of VPD at the leaf surface (D_0, kPa) for four plant species (SE given in parentheses).

	G cm s^{-1}		a kPa^{-1}	
Eggplant	0.1755	(0.0123)	-0.778	(0.134)
Cucumber	0.3935	(0.0219)	-1.376	(0.180)
Pepper	0.2080	(0.0168)	-1.212	(0.169)
Tomato	0.4436	(0.0247)	-1.735	(0.196)

Table 2.7
Parameters of the function: $g_l = G_1 \exp(a_1 D_l)$ to describe leaf conductance (g_l, cm s^{-1}) at night as a function of leaf to air vapour pressure difference (D_l, kPa) for four plant species (SE given in parentheses).

	G_1 cm s^{-1}		a_1 kPa^{-1}	
Eggplant	0.1782	(0.0141)	-0.686	(0.120)
Cucumber	0.4200	(0.0284)	-1.211	(0.156)
Pepper	0.2127	(0.0199)	-1.097	(0.169)
Tomato	0.4812	(0.0344)	-1.574	(0.181)

Table 2.8
Percentage variance accounted for (r^2 adjusted) by three regression models to describe the effect of photon flux density (Q_p, μmol s^{-1} m^{-2}) and VPD at leaf surface (D_0, kPa) on leaf conductance (g_l, cm s^{-1}) for four plant species.

model type *	eggplant	cucumber	pepper	tomato
(i)	94.2	92.2	89.1	87.3
(ii)	93.9	91.5	88.3	86.7
(iii)	92.8	91.4	87.8	86.4
Degrees of freedom	92	90	86	53

*
(i): $g_l = G_{max} [1-b \exp(-c Q_p)] \exp(a D_0)$
(ii): $g_l = G_{max} [1-b \exp(-c Q_p)] (1 + a D_0)$
(iii): $g_l = G_{max} [1-b \exp(-c Q_p)] [1 / (a + D_0)]$

Model fits day and night measurements

Using the total dataset, for all species, best fits were obtained with the combination of eqns. (2.6) and (2.3), but the differences between the various equations were small. The percentage of variance accounted for (Table 2.8), was between 86.4 and 94.2, equivalent to multiple correlation coefficients from 0.93 to 0.97.

The regression coefficients for the best fit are presented in Table 2.9. Eggplant and cucumber show significantly higher maximum leaf conductances (G_{max}) than tomato and sweet pepper, but the relative response to D_0 does not differ significantly among the species (Table 2.9; coefficient a).

To visualize the differences in response to radiation for the four species, in Figure 2.6 the fraction: measured g_l / [G_{max} exp (a D_0)] is plotted against PAR together with the calculated [1 - b exp (-c Q_p)] using the regression coefficients in Table 2.9. This figure shows that for cucumber, sweet pepper and tomato fitted leaf conductance levels off at irradiances above 200 μmol s^{-1} m^{-2}, indicating PAR saturation, while for eggplant this irradiance is higher.

Table 2.9
Parameters of the function: $g_l = G_{max}$ [1-b exp (-c Q_p)] exp (a D_0) to describe leaf conductance (g_l, cm s^{-1}) in relation to photon flux density (Q_p, μmol s^{-1} m^{-2}) and VPD at leaf surface (D_0, kPa) for four plant species. (SE given in parentheses).

	G_{max} cm s^{-1}	b	c μmol^{-1} m^2 s	a kPa^{-1}
Eggplant	1.86 (0.18)	0.923 (0.012)	0.0050 (0.0009)	-1.004 (0.066)
Cucumber	1.89 (0.13)	0.805 (0.022)	0.0115 (0.0019)	-1.188 (0.079)
Pepper	1.11 (0.04)	0.833 (0.036)	0.0248 (0.0042)	-0.983 (0.072)
Tomato	1.13 (0.07)	0.687 (0.033)	0.0279 (0.0063)	-0.935 (0.121)

In Figure 2.7, the relative response to VPD is presented by plotting measured g_l / (G_{max} [1 - b exp -c Q_p]) against D_0, and the calculated exp (a D_0). From this figure it is evident that the four species show the same relative response of g_l to D_0.

When D_l was used instead of D_0, the best fits were also obtained with and D_l are presented in Table 2.10.

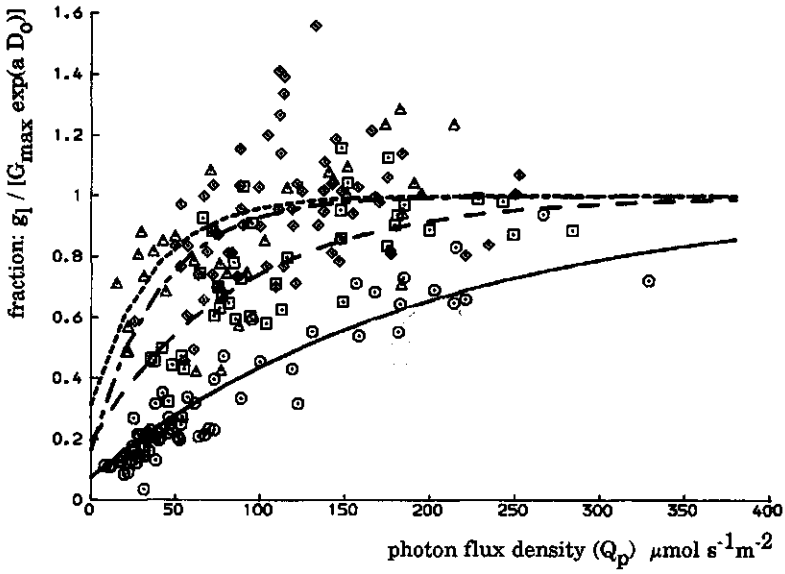

Figure 2.6
Fraction: measured g_l/ [G_{max} exp (a D_0)] and 1 - b exp (-c Q_p) plotted against photon flux density (Q_p) for four species. Regression coefficients as in Table 2.9. o—o , eggplant; □--□ , cucumber; ◇--◇ , sweet pepper; Δ···Δ , tomato. (for clarity data at Q_p=0 are omitted)

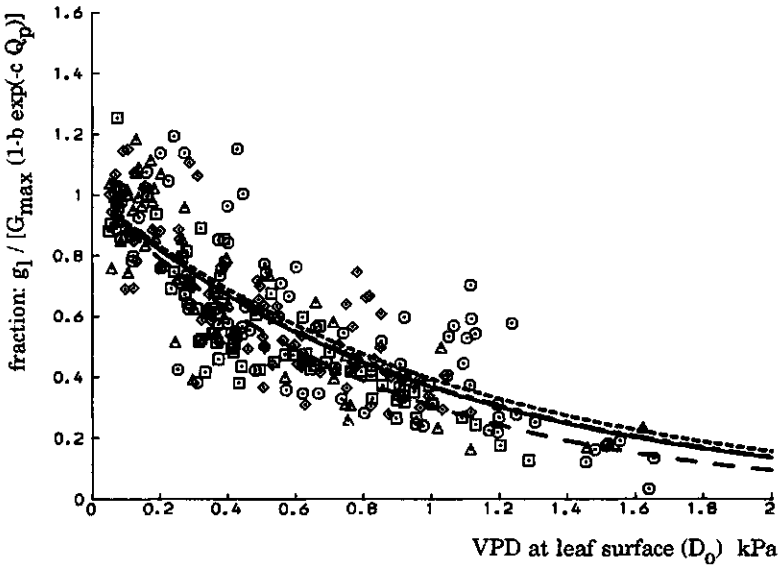

Figure 2.7
The fraction: measured g_l/ [G_{max} (1 - b exp -c Q_p)] and exp (a D_0) plotted against VPD at leaf surface (D_0) for four species. Regression coefficients as in Table 2.9. o—o , eggplant; □--□ , cucumber; ◇--◇ , sweet pepper; Δ···Δ , tomato.

2.3.4 Discussion

Leaf conductance in darkness is often assumed to be the cuticular conductance and its value is generally in the range from 0.025 to 0.1 cm s^{-1} (Kramer, 1983). For tomato cuticular conductance has been estimated as 0.05 cm s^{-1} (Kuiper, 1961). This value is in the same range as the lowest nighttime conductances measured (at a D_0 value of around 1.2 kPa; Figure 2.5), but significantly lower than the maximum conductances measured at night (at low D_0). Cuticular conductance is sensitive to VPD (Schönherr, 1982) and conductance of cuticles that lack stomata and trichromes increased by 1.2 to 1.6 when decreasing the VPD from 1.2 to 0.2 kPa, (Schönherr, 1982). In the same humidity range, fitted leaf conductance observed here, increased by a factor of 2.2, for eggplant and by a factor of 5.6 for tomato (Figure 2.5). Although no specific measurements of cuticular conductance were made, from the results of Schönherr (1982) it seems plausible to argue that the increase of cuticular conductance significantly contributed to the observed response of night-time leaf conductance to VPD. Observations of Kuiper (1961) and Shiraishi et al. (1978) indicate that stomata are not completely closed in darkness, and this may explain why the maximum values of leaf conductance observed with tomato and cucumber (Table 2.6 and Figure 2.5) are higher than may be expected from the response of cuticular conductance only. Furthermore it is possible that stomata also respond to VPD at night.

Table 2.10
Parameters of the function: $g_l = G_{1max} [1-b_1 \exp(-c_1 Q_p)] \exp(a_1 D_l)$ to describe leaf conductance (g_l, cm s^{-1}) as relation of photon flux density (Q_p, μmol s^{-1} m^{-2}) and leaf to air vapour pressure difference (D_l, kPa) for four plant species. (SE given in parentheses).

	G_{1max} cm s^{-1}	b_1	c_1 μmol^{-1} m^2 s	a_1 kPa^{-1}
Eggplant	2.12 (0.38)	0.956 (0.010)	0.0067 (0.0020)	-0.536 (0.050)
Cucumber	2.08 (0.21)	0.858 (0.021)	0.0098 (0.0020)	-0.555 (0.048)
Pepper	1.13 (0.05)	0.865 (0.035)	0.0236 (0.0043)	-0.519 (0.046)
Tomato	1.14 (0.08)	0.723 (0.035)	0.0292 (0.0072)	-0.548 (0.084)

The fitted leaf conductances of cucumber, tomato and sweet pepper saturated at PAR values above approximately 200 μmol s^{-1} m^{-2} (or about 100 W m^{-2} global radiation) in accordance with light saturation irradiances found by Behboudian (1977[a]) and Stanghellini (1987).

Information on the PAR saturation of eggplant stomata varies. A value of around 100 W m^{-2} was reported by Behboudian (1977[b]) but Daunay et al.

(1986) reported a decrease in leaf resistance of eggplant up to irradiances of 300 W m^{-2} and this does not contradict the results obtained here.

The fitted maximum conductances for the four species (Table 2.9) are within the range reported in the literature for glasshouse crops (Marcelis, 1989; Stanghellini, 1987). However, these values should be carefully interpreted, not only because maximal conductance varies with environmental history and age (Schulze and Hall, 1982) but also because of the relatively low maximum irradiance included in the fitting routines so that G_{max} is substantially extrapolated.

The sensitivity to VPD of stomata of the four species expressed on a relative scale is similar (Figure 2.7; Table 2.9, coefficient a). The average coefficient a for the four crops is -1.03 indicating a decrease of leaf conductance by about 65% at an increase of D_o by 1 kPa. With other species, Schulze and Hall (1982) also reported an equal relative decrease of stomatal conductance at an increase of the leaf to air vapour pressure difference (D_l) by 1 kPa. The results here confirm their statement that the sensitivity of stomata to humidity is not associated with either habitat or leaf type. This enables the use of this particular relationship in (multi-layer) simulation models for water relations and photosynthesis of glasshouse crops.

When D_l is used instead of the more proper variable D_o, the influence of g_{bl} on the relation between D_o and D_l is reflected in the difference between coefficient a (Tables 2.6 and 2.9) and a_1 (Tables 2.7 and 2.10). As the stomatal resistance is high at night, the ratio $r_l/(r_l+r_{bl})$ in eqn. (2.1) is close to unity. Consequently, D_o and D_l are almost equal, so the coefficients a and a_1 (Tables 2.6 and 2.7) do not differ significantly.
In circumstances of low stomatal resistances during the day, the ratio $r_l/(r_l+r_{bl})$ can be significantly lower than unity and D_o smaller than D_l. This is evident in coefficient a_1 (Table 2.10) which is much smaller than coefficient a (Table 2.9). However, as the coefficients a_1 (Table 2.10) did not differ significantly between the species, stomatal sensitivity to humidity of the four species is essentially similar.

2.4 Estimated effects on leaf and crop photosynthesis

It has been shown that variations in stomatal conductance are mainly caused by the instantaneous action of air humidity. Though these effects may be considerable, the resulting variations in photosynthesis may be much smaller (Goudriaan et al., 1985). To estimate roughly the potential effect of humidity on yield of the different crops by stomatal regulation of photosynthesis, both leaf and crop photosynthesis were estimated in the range of humidity levels used in the experiments.

leaf photosynthesis

The maximum effect of stomatal conductance will be obtained under non-limiting light conditions. The rate of leaf photosynthesis can be calculated using the following equation (Goudriaan et al., 1985):

$$P = (C_a - C_c) / (r_s' + r_b' + r_m') \qquad (2.8)$$

where P	= photosynthesis	mg m^{-2} s^{-1}
C_a	= ambient CO_2 concentration	mg m^{-3}
C_c	= CO_2 compensation point	mg m^{-3}
r_s'	= stomatal resistance for CO_2	s m^{-1}
r_b'	= boundary layer resistance for CO_2	s m^{-1}
r_m'	= mesophyll (carboxilation) resistance	s m^{-1}

The relative variations in P due to humidity are thus proportional to the relative variations in the total resistance chain r_t ($=r_s'+r_b'+r_m'$). The relative effect is evaluated as the ratio of r_t at 0 kPa/1 kPa VPD, under the following assumptions.

According to Jones (1983): $r_s' = 1.64\ r_s$. The stomatal resistance for water vapour $r_s = 1/g_l$ and g_l was estimated from the fitted responses of leaf conductance (section 2.2, Table 2.10). Furthermore $r_b' = 1.39\ r_b$. The boundary layer resistance for water vapour (r_b) was estimated using the equation (2.2) derived by Stanghellini (1987) with inputs: windspeed 10 cm s^{-1}, leaf temperature equal to air temperature, characteristic leaf dimensions of full-grown tomato, sweet pepper, cucumber and eggplant: 5, 6, 24 and 12 cm, respectively.

The mesophyll resistance (r_m') is assumed 250 s m^{-1} (Goudriaan et al., 1985), which is about the minimum level for C3 plants (Hay and Walker, 1989).

Table 2.11
Used values of resistances (s m^{-1}) for CO_2 and the ratio of the total resistance chain at 0 and 1 kPa VPD.

		cucumber	eggplant	sweet pepper	tomato
r_s'	0 kPa	79	77	145	144
	1 kPa	137	132	244	249
r_b'		334	236	167	157
r_m'		250	250	250	250
r_t	0 kPa/1kPa	0.92	0.91	0.85	0.84

The ratios of the total resistances (Table 2.11) indicate a reduction of maximum leaf photosynthesis in the order of magnitude between 10 and 20% when increasing the VPD from 0 to 1 kPa. This concurs with actual measured reductions in leaf photosynthesis for various glasshouse and field crops (eg. tomato: Acock et al., 1976; El-Sharkawy and Cock, 1986; ryegrass and white clover: Woledge et al., 1989).

crop photosynthesis

The estimated effects on leaf photosynthesis represent maximum effects, under non-limiting (light) conditions. Crop photosynthesis appears to be less affected by humidity. Using the above mentioned levels of boundary layer and stomatal resistances, crop photosynthesis at 250 Wm^{-2} (PAR) and 340 $\mu l\ l^{-1}$ CO_2 was simulated using the model and parameter values described by Challa (1990). Increasing the VPD from 0 to 1 kPa reduced simulated crop photosynthesis of all four crops with less than 5%.

Simulation of the effects of a reduction of stomatal conductance by 50% (from 2 to 1 cm s^{-1}) on crop photosynthesis by Gijzen (1990) also showed reductions of less than 5%. During periods with low light (winter conditions) the effect was (on average) in the order of 2 to 3% reduction of crop photosynthesis.

In glasshouse cultivation, even with artificial humidification, the average difference between high and low daytime humidity is restricted to less than 0.5 kPa (Bakker, 1990). Concomitant leaf conductance reductions will therefore probably be smaller than those used in the above mentioned calculations of maximum leaf photosynthesis and crop photosynthesis. This leads to the conclusion that photosynthesis of glasshouse crops under normal growing conditions in moderate climates is hardly affected by humidity.

2.5 References

Acock, B., Charles-Edwards, D.A., and Hand, D.W., 1976. An analysis of some effects of humidity on photosynthesis by a tomato canopy under winter light conditions and a range of carbon dioxide concentrations. J. Exp. Bot., 27: 933-941.

Avissar, R., Avissar, P., Mahrer, Y. and Bravdo, B.A., 1985. A model to simulate response of plant stomata to environmental conditions. Agric. For. Meteorol., 34: 21-29

Bakker, J.C., 1985. Invloed van klimaat en teeltbehandelingen op de huidmondjesdichtheid en chemische samenstelling van bladeren bij komkommer. Report no. 43, Proefstation voor Tuinbouw onder Glas, Naaldwijk, The Netherlands, 6pp.

Bakker, J.C., 1990[a]. Effects of day and night humidity on yield and fruit quality of glasshouse tomatoes (*Lycopersicon esculentum* Mill.). J. Hort. Sci., 65: 323-331.

Bakker, J.C., 1990[b]. Effects of day and night humidity on yield and fruit quality of glasshouse eggplant (*Solanum melongena* L.). J. Hort. Sci., 65: 747-753.

Bakker, J.C., Welles, G.W.H. and Uffelen, J.A.M. van, 1987. The effects of day and night humidity on yield and quality of glasshouse cucumbers. J. Hort. Sci., 62: 363-370.

Bakker, J.C., Van den Bos, L., Arendzen, A.J., and Spaans, L., 1988. A distributed system for glasshouse climate control, data acquisition and analysis. Comput. Electron. Agric., 3: 1-9.

Behboudian, M.H., 1977[a]. Water relations of cucumber, tomato and sweet pepper. Meded. LH 77-6, Wageningen, 85pp.

Behboudian, M.H., 1977[b]. Responses of eggplant to drought. II. Gas exchange parameters. Scientia Hort., 7: 311-317.

Bot, G.P.A., 1983. Greenhouse climate: from physical processes to a dynamic model. PhD. Dissertation, Agricultural University, Wageningen, 240pp.

Bressan, R.A., Wilson, L.G. and Filner, P., 1978. Mechanisms of resistance to sulfur dioxide in the Cucurbitaceae. Plant Physiol., 61: 761-767.

Bunce, J.A., 1985. Effect of boundary layer conductance on the response of stomata to humidity. Plant, Cell and Environment, 8: 55-57.

Burrows, F.J. and Milthorpe, F.L., 1976. Stomatal conductance in the control of gas exchange. In: T.T. Kozlowski, Ed., Water deficits and plant growth, vol. IV, Soil water measurement, plant responses and breeding for drought resistance. Academic Press, New York, pp. 103-152.

Challa, H., 1990. Crop growth models for greenhouse climate control. In: R.Rabbinge, J. Goudriaan, H. van Keulen, F.W.T. Penning de Vries and H.H. van Laar, Eds., Theoretical production ecology: reflections and prospects. Simulation monographs 34, Pudoc, Wageningen: 125-145.

Daunay, M.C., Malet, P. and Schoch, P.G., 1986. Facteurs agro-climatiques influencant la resistance stomatique de l'aubergine (*Solanum melongena* L.). Agronomie, 6 (7): 615-622.

Daunay, M.C., Schoch, P.G. and Malet, P., 1986. Fréquences stomatiques de l'aubergine (*Solanum melongena* L.) et relations avec le développement racinaire. Agronomie, 6: 523-528.

El-Sharkawy, M.A. and Cock, J.H., 1986. The humidity factor in stomatal control and its effect on crop productivity. In: R. Marcelle, H. Clijsters and M. Van Poucke, Eds., Biological control of photosynthesis. Martinus Nijhoff Publishers, Dordrecht. pp. 187-198.

Gay, A.P., Hurd, R.G., 1975. The influence of light on stomatal density in the tomato. New Phytol., 75: 37-45.

Gislerød, H.R. and Nelson, P.V., 1989. The interaction of relative air humidity and carbon dioxide enrichment in the growth of *Chrysanthemum* x *morifolium* Ramat. Scientia Hort., 38: 305-313.

Goudriaan, J., Laar, H.H. van, Keulen, H. van, and Louwerse, W., 1985. Photosynthesis, CO_2 and plant production. In: W. Day and R.K. Atkin, Eds., Wheat growth modeling. NATO ASI Series, serie A: Life Sciences, 86: 107-122.

Grange, R.I. and Hand, D.W., 1987. A review of the effects of atmospheric humidity on the growth of horticultural crops. J. Hort. Sci., 62: 125-134.

Gijzen, H., 1990. Greenhouse crop photosynthesis and dry matter production: some model investigations. Paper presented at N.J.F. seminar: From plant reactions to growth models. N.J.F.'s Utredninger-Rapporter, in press.

Hall, A.E., Schulze, E.D. and Lange, O.L., 1976. Current perspectives of steady state stomatal responses in controlled environment. In: O.L. Lange, L. Kappen, and E.D. Schulze, Eds., Water and plant life. Ecol. Studies, Vol. 19. Springer Verlag, Berlin. pp. 169-188.

Hall, A.J. and Milthorpe, F.L., 1978. Assimilate source-sink relationships in *Capsicum annuum* L. III. The effects of fruit excision on photosynthesis and leaf and stem carbohydrates. Aust. J. Plant Physiol., 5: 1-13.

Hay, R.K.M. and Walker, A.J., 1989. An introduction to the physiology of crop yield. Longman Scientific & Technical, Harlow, 292 pp.

Jarvis, P.G., Edwards, W.R.N. and Talbot, H., 1981. Models of plant and crop water use. In D.A. Rose and D.A. Charles-Edwards, Eds., Mathematics and plant physiology. Academic Press, London. pp. 151-194.

Jones, H.G., 1983. Plant and microclimate. Cambridge University Press, New York, 144pp.

Jong, J.Tj. de, 1987. Bacteriën in orchideeën te voorkomen en bestrijden door hygiëne. Vakblad voor de Bloemisterij, 42 (34): 34.

Kaufmann, M.R., 1982. Leaf conductance as a function of photosynthetic photon flux density and absolute humidity difference from leaf to air. Plant Physiol. 69: 1018-1022.

Kramer, P.J., 1983. Water relations of plants. Academic Press, New York, 489 pp.

Kuiper, P.J.C., 1961. The effects of environmental factors on transpiration of leaves, with special reference to stomatal light response. Meded. LH 61-7, Wageningen, 49 pp.

Marcelis, L.F.M., 1989. Simulation of plant-water relations and photosynthesis of greenhouse crops. Scientia Hort., 41: 9-18.

Meinzer, F.C. and Grantz, D.A, 1989. Stomatal control of transpiration from a developing sugarcane canopy. Plant, Cell and Environment, 12: 635-642.

Morison, J.I.L., 1985. Sensitivity of stomata and water use efficiency to high CO_2. Plant, Cell and Environment, 8: 467-474.

Munro, D.S., 1989. Stomatal conductances and surface conductance modelling in a mixed wetland forest. Agric. For. Meteorol., 48: 235-249.

Prisco, J.T. and O'Leary, J.W., 1973. The effects of humidity and cytokinin on growth and water relations of salt-stressed bean plants. Plant and Soil, 39: 263-276.

Rajapakse, N.C., Kelly, J.W. and Reed, D.W., 1988. Transpiration and water use of potted floricultural plants under low-light conditions. J. Amer. Soc. Hort. Sci., 113: 910-914.

Ramos, L.J. and Volin, R.B., 1987. Role of stomatal opening and frequency on infection of *Lycopersicon spp.* by *Xanthomonas campestris* pv. vesicatoria. Phytopathology, 77: 1311-1317.

Raschke, K., 1975. Stomatal action. Ann. Rev. Plant Physiol., 26: 309-340.

Rich, S., 1963. The role of stomata in plant disease. In: I. Zelitch, Ed., Stomata and water relations in plants. Bulletin 664, The Connecticut Agricultural Experiment Station, New Haven, 102-114.

Royle, D.J and Thomas, G.G., 1971. The influence of stomatal opening on the infection of hop leaves by *Pseudoperonospora humuli*. Physiol. Plant Pathol., 1: 329-349.

Sampson, J., 1961. A method of replicating dry or moist surfaces for examination by light microscopy. Nature, UK, 191: 932-933.

Schoch, P.G., 1972. Effects of shading on structural characteristics of the leaf and yield of fruit in *Capsicum annuum* L. J. Amer. Soc. Hort. Sci., 97: 461-467.

Schönherr, J., 1982. Resistance of plant surfaces to water loss: transport properties of cutin, suberin and associated lipids. In: O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler, Eds., Encyclopedia of plant physiology, new series, 12B. Springer Verlag, Berlin. pp. 153-179.

Schulze, E.D., 1986. Carbon dioxide and water vapor exchange in response to drought in the atmosphere and the soil. Ann. Rev. Plant Physiol., 37: 247-274.

Schulze, E.D. and Hall, A.E., 1982. Stomatal responses, water loss and CO_2 assimilation rates of plants in contrasting environments. In: O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler, Eds., Encyclopedia of plant physiology, new series, 12B. Springer Verlag, Berlin. pp. 181-230.

Shiraishi, M., Hashimoto, Y. and Kuraishi, S., 1978. Cyclic variations of stomatal aperture observed under the scanning electron microscope. Plant and Cell Physiol., 19: 637-645.

Stanghellini, C., 1987. Transpiration of greenhouse crops. An aid to climate management. PhD. Dissertation Agricultural University, Wageningen, 150 pp.

Stanghellini, C., 1988. The role of internal and external resistances in scheduling irrigation of a greenhouse crop. Acta Hortic., 228: 261-268.

Steekelenburg, N.A.M. van, 1986. *Didymella bryoniae* on glasshouse cucumbers. PhD. Dissertation Agricultural University, Wageningen, 105pp.

Takakura, T., Goudriaan, J. and Louwerse, W., 1975. A behaviour model to simulate stomatal resistance. Agric. Meteorol., 15: 393-404.

Thimijan, R.W. and Heins, R.D., 1983. Photometric, radiometric, and quantum light units of measure: a review of procedures for interconversion. Hortscience, 18: 818-822.

Thorpe, M.R., Warrit, B. and Landsberg, J.J., 1980. Responses of apple leaf stomata: a model for single leaves and a whole tree. Plant Cell and Environment, 3: 23-27.

Tichá, I., 1982. Photosynthetic characteristics during ontogenesis of leaves 7. Stomata density and sizes. Photosynthetica, 16: 375-471.

Woledge, J., Bunce, J.A. and Tewson, V., 1989. The effect of air humidity on photosynthesis of ryegrass and white clover at three temperatures. Ann. Bot., 63: 271-280.

Woodward, F.I. and Bazzaz, F.A., 1988. The responses of stomatal density to CO_2 partial pressure. J. Exp. Bot., 39: 1771-1781.

3. Growth, dry matter production and partitioning

3.1 Introduction

The effect of humidity on crop photosynthesis is likely to be small (section 2.4). Yet many observations indicate that growth (fresh or dry weight and leaf area) is enhanced by high humidity (e.g. Hoffman, 1979; Papenhagen, 1986). Even at equal crop photosynthesis yield may still vary because environmental humidity may affect dry matter distribution (e.g. Swalls and O'Leary, 1975 and 1976; Burrage, 1988). Therefore, as the next step, the effects of humidity on growth and dry matter distribution were investigated. A relational diagram of this subsystem is presented in Figure 3.1.

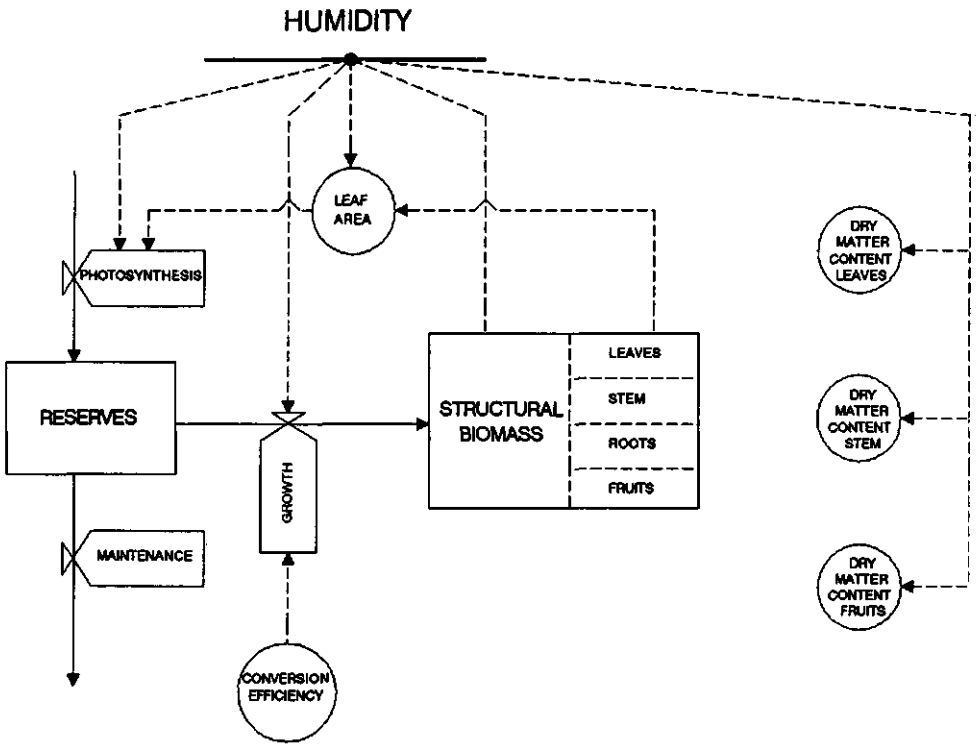

Figure 3.1
Simplified relational diagram of the influences of humidity on growth and dry matter distribution.

Within the feed back loop from leaf biomass to photosynthesis, the leaf area is an important link, which is possibly affected by humidity (e.g. Burrage, 1988).

Since for the vegetable species investigated in this study fresh fruits are harvested, variations of the dry matter content of fruits may, to a large extent, be responsible for differences in final fruit yield. The effects of humidity on the dry matter content of the various plant parts were therefore also the subject of investigation (Figure 3.1).

The effects of humidity on growth and dry matter production of tomato plants were examined by means of growth analysis. In this way effects mediated through leaf area (LAR) and those mediated through stomatal resistance (NAR) can be separated. The influence of humidity on dry matter distribution between leaves, stem and fruits and on the shoot/root ratio was investigated in tomato and eggplant.

3.2 Materials and methods

Table 3.1 shows in which experiments the various effects of humidity were investigated. In all experiments four day/night humidity regimes were duplicated in separate glasshouse compartments. A high or low relative humidity by day (sunrise to sunset) was combined with either a high or low relative humidity by night (sunset to sunrise). The treatment symbols used (day/night) are h/h and l/l for the continuously high and low humidities and h/l and l/h for the alternatingly low and high humidities. More details on the method of environmental control, humidity levels, planting dates, cultivars etc. are given in Chapter 5.

Table 3.1
Summary of the processes investigated with the various crops and the humidity treatments used for data collection.

	cucumber				eggplant		tomato			pepper		treatments
season and year	a83	s84	a84	s86	s88	a89	s85	a85	s89	a86	s87	
growth analysis	-	-	-	-	-	-	-	-	+	-	-	all
dry matter												
- content	+	+	-	+	+	+	+	+	+	+	+	h/h and l/l
- distribution	-	-	-	-	+	-	-	-	+	-	-	all
shoot/root ratio	-	-	-	-	-	+	-	-	+	-	-	h/h and l/l

a = autumn, s = spring

3.2.1 Growth analysis of tomato

Seedlings of *Lycopersicon esculentum* Mill. cultivar 'Spectra' were planted on 21 December 1988 on rockwool when the inflorescences of the first truss were just visible. The crop density was 2.5 plants m^{-2}. A standard nutrient solution for tomato (Sonneveld and de Krey, 1986) with an EC of 3.0 dS m^{-1} was applied with the aid of a trickle irrigation system, excess solution was recirculated. The average vapour pressure deficit and temperature during the growth period are presented in Table 3.2.

Table 3.2
Average vapour pressure deficit and mean temperature during the growth period of tomato (27 December 1988 - 20 February 1989). h= high humidity, l= low humidity. d = 10.00-16.00 h; n = 22.00-04.00 h; 24-h = 00.00-24.00 h.

treatment day/night	VPD kPa			temperature 24h mean
	d	n	24-h	
h/h	0.63	0.33	0.43	18.3
l/h	1.00	0.42	0.83	18.4
h/l	0.67	0.61	0.63	18.3
l/l	1.06	0.69	0.81	18.3

The VPD by day was generally higher than at night because more ventilation was necessary to control temperature. The difference of VPD by day, between the extreme humidity treatments (h/h and l/l), was slightly greater than at night. The day/night changes were made using the astronomical clock, and consequently the length of the periods with a high humidity by day gradually increased during the experimental period. From 27 December until 20 February, daylength increased by two hours from 8 to 10 hours with a corresponding decrease in nightlength. The average daily radiation integrals (outside) were 1.11, 2.32, 3.81 and 5.71 MJ m^{-2} day^{-1} for two week intervals.
From 27 December 1988 until 23 January 1989 four plants were harvested weekly, and on 6 and 20 February eight plants per compartment were harvested. The following parameters were determined for these plants: plant height, number of leaves >1 cm (length), leaf area, number of fruits and fresh and dry weight of leaves, stem and fruits. Dry weight in this experiment, and in all other experiments described in this Chapter was measured after 48 h drying at 80 °C.

Growth was analysed by means of Genstat-5 (Panye et al., 1987). Polynomials were fitted for the functions ln W (= total dry weight in gram)

and ln A (= leaf area in cm^2) versus time using stepwise selection of variables (Draper and Smith, 1981). Fitting was restricted to polynomials up to the second degree (Nilwik, 1981; Bruggink and Heuvelink, 1987). The various coefficients of the polynomials were analysed with an ANOVA.

3.2.2 Dry matter content of leaves and fruits

In the experiments indicated in Table 3.1 leaves and fruits were sampled near the end of the periods of treatment, from the extreme humidity treatments (h/h and l/l), to investigate dry matter content. In some experiments samples contained leaves and fruits from plants grown at different EC levels. In Table 3.3 the details of the time of sampling and the EC level are presented. Leaf samples contained about 150 gram fresh weight whilst fruit samples were in the order of 0.8 - 1 kg fresh weight. For some leaf samples (Table 3.3) the area was also measured to calculate SLA (Specific Leaf Area).

Table 3.3
Time of sampling and salinity levels used for leaf and fruit samples.

crop, season and year		sampling date leaves	sampling date fruits	EC dS m^{-1}
tomato	spring 1985	27/3	10/4	2.5 3.5 +
	autumn 1985	3/10	-	3.0
	spring 1989	18/4	21/4	3.0
pepper	autumn 1986	23/10	29/10	3.0
	spring 1987	3/3	14/4	3.0
cucumber	autumn 1983	28/10	27/10	2.0 6.0 +
	spring 1984	14/3	21/3	2.0 6.0 +
	spring 1986	12/3 *	17/4	3.0
eggplant	spring 1988	22/3	23/3	3.0
	autumn 1989	16/10 *	16/10	3.0

* = leaf area measured to calculate SLA (= area/leaf dry weight; $cm^2\ g^{-1}$)
+ = samples taken from two EC levels

3.2.3 Dry matter distribution of eggplant and tomato

The dry matter distribution between vegetative parts (excluding roots) and generative parts was determined in two experiments, one with eggplant (spring 1988) and one with tomato (spring 1989). Of 8 selected plants per compartment, all plant parts which were removed in accordance with normal practice (leaves, side shoots) and fruits harvested during the periods of treatment were collected and dried. At the end of the humidity treatments in both experiments (30

March 1988 and 20 March 1989, respectively), all plants were divided into vegetative and generative parts, and dried. Total dry matter production was calculated by adding the dry weight of the plants at the end of the treatments to the dry weight of removed leaves, side shoots and harvested fruits. If plant production had started after the period of treatment, only the dry weight of removed leaves and side shoots was added.

To determine the effect of humidity on the shoot/root ratio (excluding fruits) and the top/root ratio (which includes shoot and fruit components together; Richards, 1981), tomato and eggplant were grown in a water culture with recirculating nutrient solution. Humidity was either continuously high (h/h) or continuously low (l/l) in the spring tomato experiment in 1989 (section 5.3) and the autumn crop of eggplant in 1989 (section 5.4).

Five seedlings of *Lycopersicon esculentum* Mill. cv 'Spectra' and five seedlings of *Solanum melongena* L. cv. 'Dobrix', raised in rockwool cubes (10 × 10 × 6 cm) were planted in each compartment on 27 December 1988 and 1 September 1989, respectively. A standard nutrient solution for tomato in water culture (Sonneveld and de Krey, 1986) was used. Tomato plants were harvested on 20 March and the eggplants on 20 October 1989. With tomato the average vapour pressure deficits achieved over the growth period were 0.43 and 0.81 kPa for the h/h and l/l treatment respectively, and for eggplant 0.34 and 0.99 kPa. For all plants the roots grown in the nutrient solution were cut off below the rockwool cubes. Roots in the rockwool cubes were separated from the rockwool by means of washing with HCl (Brouwer and van Noordwijk, 1978).

3.3 Results

3.3.1 Growth analysis of tomato

Table 3.4 shows the measured values of all plant parameters for the four treatments at the final harvest on 20 February.

The total dry weight differed only between the continuous high and low humidity treatments. More than 50% of this difference can be ascribed to the difference in stem weights. The stage of development was not clearly affected. The number of leaves was lower at the l/h treatment but the number of trusses was not significantly different. The fruits accounted only for a minor fraction of the total dry weight as the plants were harvested at a relatively early stage of development. The total dry matter percentage (% dmt) was lower for the h/h than the l/l treatment. A high humidity by day resulted in a significantly higher Stem Weight Ratio (SWR = W_s/W).

Analysing the data of Table 3.4 with a two by two ANOVA showed that all significant main effects can be attributed to humidity by day, humidity by night had no significant effect whilst the interaction between day and night humidity was not significant for the parameters investigated except for the

number of leaves. Analysis of the total dataset using stepwise selection of variables showed that polynomials of degree one gave sufficient fits for the relations between ln W and ln A with time, indicating that growth was exponential over the 8 week period considered. The percentages of variance accounted for were 99.0 and 99.7 for ln W and ln A respectively. The coefficients for the relations between ln W and ln A and time are presented in Table 3.5.

Table 3.4
Measured and calculated plant parameters of young tomato after 8 weeks at four different day/night humidity regimes, h=high relative humidity, l=low relative humidity. (all data are means of 16 plants per treatment).
Abbreviations: W=dry weight (g), LAR=leaf area ratio ($cm^2\ g^{-1}$), RGR=relative growth rate (day^{-1}), A=leaf area (cm^2), SLA=specific leaf area, LWR=leaf weight ratio, SWR=stem weight ratio, l=leaf, s=stem, f=fruits, t=total, %dm=percentage dry matter.

	day/night humidity treatment				significance LSD 5%		
	h/h	l/h	h/l	l/l	day	night	day×night
W	24.83	21.98	23.63	21.54	2.68	n.s.	n.s.
Wl	15.26	14.34	14.78	12.98	n.s.	n.s.	n.s.
Ws	8.33	6.46	7.45	6.33	0.99	n.s.	n.s.
Wf	1.25	1.18	1.41	2.33	n.s.	n.s.	n.s.
SWR	0.337	0.295	0.317	0.295	0.018	n.s.	n.s.
LWR	0.612	0.651	0.626	0.604	n.s.	n.s.	n.s.
%dmt	7.85	8.44	8.15	8.21	0.30	n.s.	n.s.
%dml	8.43	8.92	8.73	8.86	0.25	n.s.	n.s.
%dms	7.37	7.68	7.36	7.44	n.s.	n.s.	n.s.
leaves	24.6	23.6	24.4	24.3	0.4	n.s.	0.4
A	5578	5261	5546	4803	n.s.	n.s.	n.s.
SLA	369.8	370.5	377.0	374.7	n.s.	n.s.	n.s.
LAR	225.2	240.2	236.0	226.0	n.s.	n.s.	n.s.
trusses	5.69	5.31	5.50	5.56	n.s.	n.s.	n.s.

Instantaneous values of NAR (Net Assimilation Rate, mg $cm^{-2}\ day^{-1}$) and LAR (Leaf Area Ratio, $cm^{-2}\ g^{-1}$) were calculated by means of the fitted responses of dry weight and leaf area (Figures 3.2a and 3.2b). NAR increased with time which should be attributed to the increasing radiation level (section 3.2.1) during the 8 week period. Two groups can be distinguished on the basis of the daytime humidity. On average the NAR was 0.214, 0.197, 0.211 and 0.197 mg $cm^{-2}\ day^{-1}$ for the h/h, l/h, h/l and l/l treatment, with a significant effect of daytime humidity (LSD 5%: 0.008). LAR gradually decreased from about 500 to 240 $cm^{-2}\ g^{-1}$ with no significant differences between the treatments (Figure 3.2b). Analysis of the original data instead of the fitted values with ANOVA

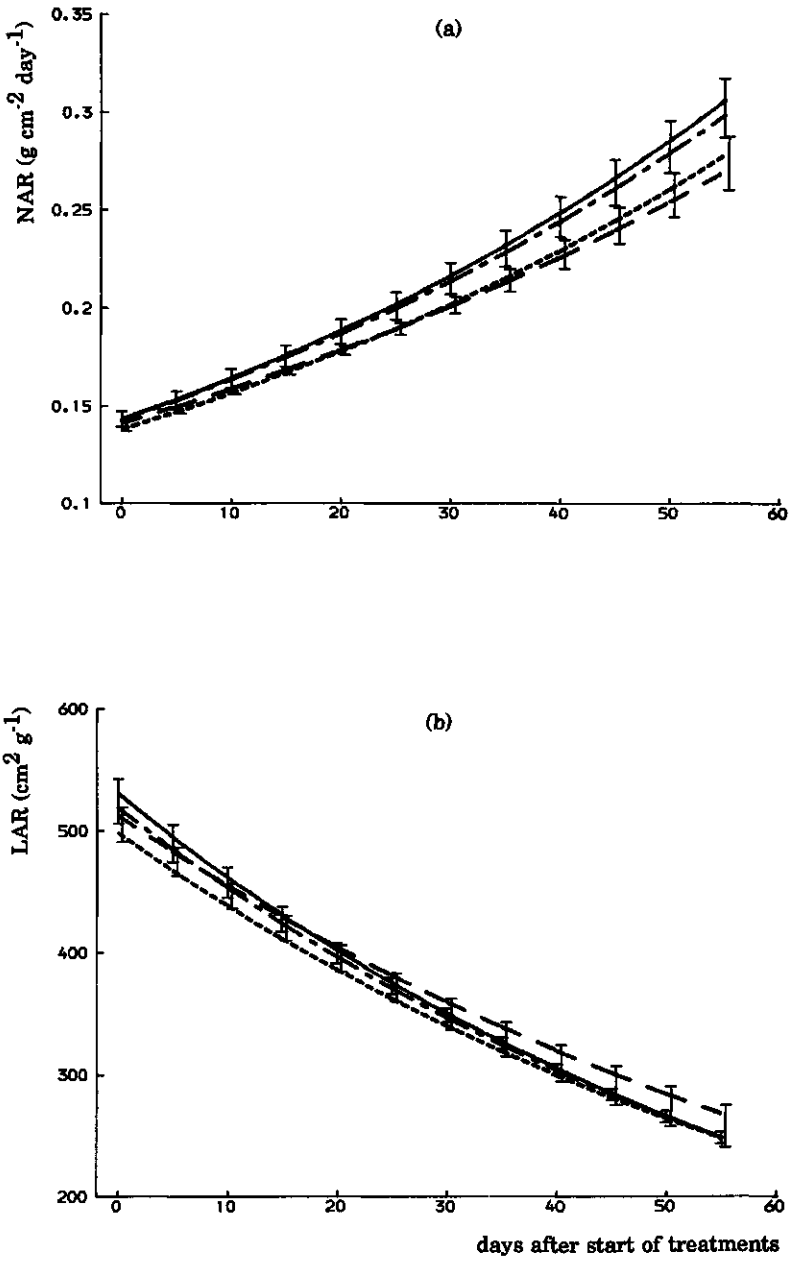

Figure 3.2
Progress curve of NAR (a) and LAR (b) of tomato grown at four day/night humidity treatments. Bars indicate 95% confidence limits for the high and low day humidity treatments.
h/h: ——— , l/h: – – – – , h/l: –·–·–·– , l/l: ····· .

confirmed that there were no significant effects of humidity on LAR at either harvest date.

Table 3.5
Growth analysis of young tomato plants grown under different day/night humidity treatments (h=high relative humidity, l=low relative humidity). LSD at P=0.05.
Relations: lnW = a + RGR time, lnA = c + d time.

	day/night humidity treatment				significance LSD 5%		
	h/h	l/h	h/l	l/l	day	night	day×night
a	-0.687	-0.691	-0.629	-0.489	n.s.	n.s.	n.s.
RGR*100	7.60	7.24	7.42	6.87	0.45	n.s.	n.s.
c	5.52	5.48	5.56	5.66	n.s.	n.s.	n.s.
d	0.062	0.061	0.061	0.056	n.s.	n.s.	n.s.

To provide an order of magnitude of the effect of humidity by day on the average RGR and NAR the relation with mean VPD by day (Table 3.2) was investigated by regression analysis. Under the assumption that high humidity (low VPD) improves growth (one sided t-test, 6 DF), both relations were significant at p=0.05:

RGR (g g^{-1} day^{-1}) = 0.083 - 0.0121 VPD day (kPA); r= 0.651
NAR (mg cm^{-2} day^{-1}) = 0.236 - 0.0379 VPD r= 0.625

Thus the estimated decrease in RGR and NAR due to an increase from 0 to 1 kPa in the daytime VPD is about 15%.

3.3.2 Dry matter content of leaves and fruits

Neither the dry matter content of leaves nor that of fruits differed significantly between the treatments in all experiments, except for the eggplant fruits in the autumn of 1989 experiment (Table 3.6). There was, however, a tendency for a "higher" dry matter percentage of fruits at low humidity (quotation-marks indicate a tendency and no statistically significant differences).

With eggplant no significant differences in SLA were found. With cucumber the SLA was significantly higher at the h/h treatment than at the l/l treatment, 660 and 620 cm^2 $gram^{-1}$, respectively. As the % dry matter was equal this suggests that cucumber forms thinner, larger leaves at high humidity.

Table 3.6
Dry matter content (%) of leaves and fruits of plants grown under continuously high or low humidity (averages of all samples taken during the periods of treatment).

experiment		leaves			fruits		
		h/h	l/l	LSD 5%	h/h	l/l	LSD 5%
tomato	spring 1985	13.1	12.7	n.s.	4.9	4.8	n.s.
	autumn 1985	11.5	11.4	n.s.	-	-	n.s.
	spring 1989	10.8	11.0	n.s.	4.9	5.0	n.s.
pepper	autumn 1986	14.7	14.6	n.s.	6.5	6.5	n.s.
	spring 1987	11.3	11.2	n.s.	8.4	8.5	n.s.
cucumber	autumn 1983	10.4	10.6	n.s.	2.9	2.9	n.s.
	spring 1984	10.3	10.5	n.s.	3.0	3.2	n.s.
	spring 1986	10.7	10.6	n.s.	3.0	3.2	n.s.
eggplant	spring 1988	12.6	12.5	n.s.	6.2	6.5	n.s.
	autumn 1989	10.6	11.0	n.s.	7.2	8.3	1.0

3.3.3 Dry matter distribution of eggplant and tomato

The production of total dry matter with eggplant from planting (7 December 1987) until 30 March 1988 was about 200 gram per plant, which did not vary significantly between the humidity treatments. Of this 200 gram, on average, 43 gram were in leaves and side shoots removed for cultural purposes. The distribution of the dry weight among the stem, leaves and fruits, as fractions of the total dry weight is presented in Figure 3.3a. There was no significant effect of humidity on stem weight ratio (SWR), leaf weight ratio (LWR) or fruit weight ratio (FWR). No significant relationships were found between the fractions of dry weight for the various plant parts and the average VPD by day, night or the 24-h mean during the period of treatment.

With tomato comparable results were obtained. The total dry weight was about 100 gram per plant on 20 March 1989. The LWR and FWR did not differ between the treatments (but the SWR was significantly higher at the h/h treatment than at the other three treatments; Figure 3.3b). The dry weight fractions showed no significant correlations to VPD by day, night or the 24-h mean, achieved during the periods of treatment (section 5.4) except for the relationship between VPD by day and the SWR.

It should be mentioned that these results were obtained from relatively young plants with consequently low FWR compared to mature producing plants.

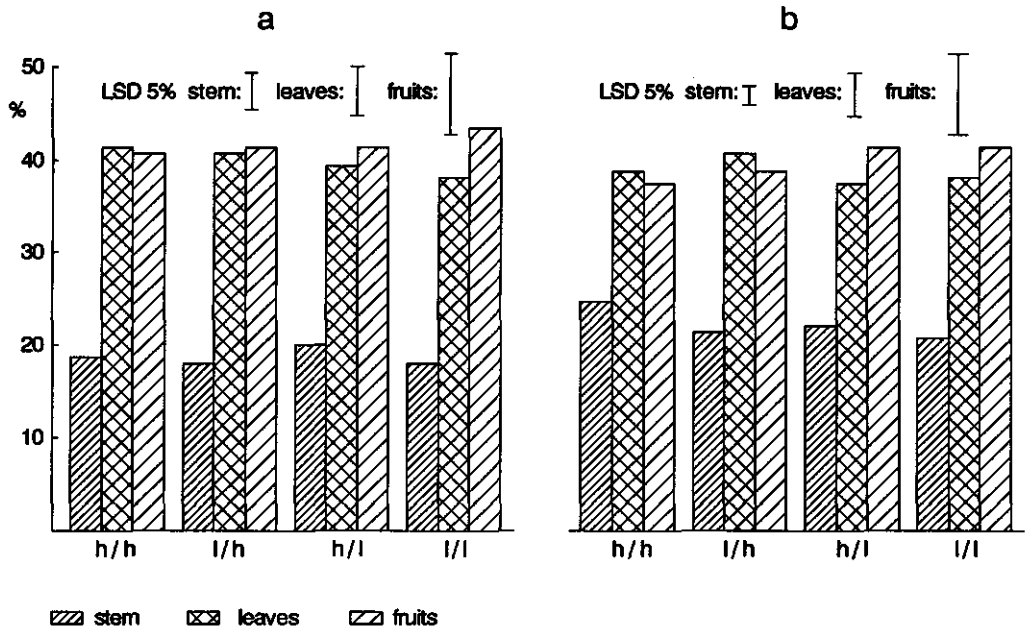

Figure 3.3
Distribution of dry matter as % of total dry weight between stem, leaves and fruits for eggplant (a) and tomato (b). Bars indicate 95% confidence limits (Students' t-test).

With tomato a lower shoot/root ratio at low humidity (high VPD) was found while eggplant showed a comparable tendency (not significant) (Table 3.7). With both crops the top/root ratio (including fruits) showed the same tendency but differences were not significant. Also the dry weight fraction of roots (RWR) did not differ significantly between the high and low humidities.

Table 3.7
Shoot/root ratio (s/r), top/root ratio (t/r) and root weight ratio (RWR = W_r/W) of tomato and eggplant grown at continuously low or high humidity.

treatment day/night	tomato			eggplant		
	s/r	t/r	RWR	s/r	t/r	RWR
l/l	7.88	17.51	0.055	8.70	10.19	0.092
h/h	10.42	21.37	0.045	11.21	11.48	0.083
LSD 5%	1.92	n.s.	n.s.	n.s.	n.s.	n.s.

3.4 Discussion

Humidity by day had a small but significant effect on the relative growth rate of tomato. As LAR was not affected, this effect should be attributed to NAR (Table 3.5). These results concur with those of Swalls and O'Leary (1975) but contradict later observations (Swalls and O'Leary, 1976; Burrage, 1988). However, in the cases where growth was reduced at high humidity, both Swalls and O'Leary and Burrage admitted that 'certain nutrient deficiencies' (of calcium and magnesium) occurred, which may have interfered with their results.

The estimated effects of humidity in the range of 0 to 1 kPa VPD on NAR of tomato are of the order of magnitude of the estimated effects on leaf and crop photosynthesis (section 2.4). However, the relationships between both NAR and RGR and humidity for tomato were only marginally significant, due to the relatively large scatter of the data.

The total dry weight of eggplant did not vary between the humidity treatments (section 3.3.3). Neither SLA nor LWR of eggplant were affected by humidity and as LAR is the product of SLA and LWR, it may be suggested that LAR of eggplant is also unaffected by humidity. From the calculations in section 2.4 it was concluded that leaf photosynthesis of eggplant is less sensitive to humidity than that of tomato. This may explain the absence of significant effects of humidity on total dry weight (and NAR) of eggplant.
In contrast to the reaction of tomato and eggplant, cucumber showed an increased SLA at high humidity. SLA is generally more sensitive to environmental changes than LWR (Hunt, 1982) and hence an increase of LAR for cucumber at high humidity may be anticipated. Unfortunately LAR was not determined in this experiment, but Van de Sanden and Veen (1991) observed that under low light conditions cucumber seedlings indeed have an increased LAR at high humidity caused by effects on SLA and LWR. Burrage (1988) observed similar responses of SLA and LAR to humidity without effects on LWR in tomato but, due to nutrient deficiency, the growth of tomato was significantly reduced under extremely high humidity. Whether this is also true for older plants and at higher radiation levels needs further investigation. However, of all crops investigated in this study, the leaf area of cucumber seems to respond most positively to increasing humidity due to an increased LAR and the formation of more leaves (Mortensen, 1986; section 5.1).

Between the species large differences exist in the dry matter content of fruits. Pepper and eggplant fruits have a dry matter content which is 2 to 3 times higher than that of cucumber fruits. Leaf dry matter content was almost equal for the four crops (Table 3.5). Humidity neither affected dry matter content of fruits nor that of leaves except in the early stage of tomato development (Table 3.3). This agrees with the results of Swalls and O'Leary (1975) and Mortensen (1986) who found lower total dry matter content and lower dry matter content of leaves of young tomato plants at high humidity.

With chrysanthemum Gislerød and Nelson (1989) observed comparable responses, high humidity decreased dry matter content of the early developed leaves but leaves developed in a later growth stage were affected less. CO_2 enrichment, although it improves photosynthesis and growth, has no significant effect on dry matter content either (Idso, Kimball and Mauney, 1988).

The distribution of dry matter is hardly affected by humidity (Figure 3.3) except for the slightly higher SWR of tomato at high humidity which concurs with results of Burrage (1988).

The distribution between shoot and roots is also not significantly affected by humidity (Table 3.7), but the tendency observed here (a higher shoot/root and top/root ratio at high humidity) is a general phenomenon (eg. Swalls and O'Leary, 1975, 1976; Burrage, 1988; Gislerϕd and Nelson, 1989). Although the results indicate a higher shoot/root ratio and a lower root dry weight at high humidity, the gain in shoot dry weight due to this change in distribution is only marginal and is used mainly for stem growth. The shoot/root ratio decreases if water is a limiting factor (Wilson, 1988). As in rockwool and NFT the water supply is excessive, a higher shoot/root ratio may be expected. This may explain the relatively high shoot/root and top/root ratios observed compared to those reported for fruiting tomato (Richards, 1981) and eggplant (Quast, 1977).

Dry matter distribution in crops is supposed to be regulated by the sinks (Heuvelink and Marcelis, 1989). When growth of fruits is restricted (due to fruit thinning or poor fruit set) the distribution among fruit, leaves, stem and roots changes (Quast, 1977; Heuvelink and Marcelis, 1989) reducing the top/root ratio, whilst improved fruit development increases the top/root ratio (Claussen, 1976). On the other hand, the distribution between leaves, stem and roots is usually independent of fruit load (e.g. Quast, 1977; Klapwijk, 1988; Heuvelink and Marcelis, 1989). It is therefore plausible to assume that humidity affects dry matter distribution between vegetative and generative parts through effects on fruit set. As the number of fruits was not or only slightly different (Chapters 4 and 5) this may explain the results observed.

As humidity had no effect on the dry matter content of the fruits and on dry matter distribution the occurrence of higher fruit yields must be associated with a higher total dry matter production. Hence the conclusion seems valid that no great effects are to be expected.

3.5 References

Brouwer, G. and Noordwijk, M. van, 1978. Het met zoutzuur vrijspoelen van wortels uit steenwol en het effect daarvan op het wortelgewicht. Rapport 4-78. Instituut voor Bodemvruchtbaarheid, Haren, 11 pp.

Bruggink, G.T. and Heuvelink, E., 1987. Influence of light on the growth of young tomato, cucumber and sweet pepper plants in the greenhouse: effects on relative growth rate, net assimilation rate and leaf area ratio. Scientia Hort., 31: 161-174.

Burrage, S.W., 1988. Growth and ion uptake in tomatoes grown in high and low humidities. In: K.E. Cockshull, Ed., The effects of high humidity on plant growth in energy-saving greenhouses. Report EUR 11261, Office for Official Publications of the European Communities, Luxembourg: 9-18.

Claussen, W., 1976. Einfluss der Frucht auf die Trockensubstanzverteilung in der Aubergine (*Solanum melongena* L.). Gartenbauwissenschaft, 41: 236-239.

Draper, N.R. and Smith, H., 1981. Applied regression analysis, Wiley, New York, 709 pp.

Gislerød, H.R. and Nelson, P.V., 1989. The interaction of relative air humidity and carbon dioxide enrichment in the growth of *Chrysanthemum* × *morifolium* Ramat. Scientia Hort., 38: 305-313.

Heuvelink, E. and Marcelis, L.F.M., 1989. Dry matter distribution in tomato and cucumber. Acta Hort., 260: 149-157.

Hoffman, G.J., 1979. Humidity. In: T.W. Tibbits and T.T. Kozlowski, Eds., Controlled environment guidelines for plant research. Academic Press, New York: 141-172.

Hunt, R., 1982. Plant growth curves. The functional approach to plant growth analysis. Edward Arnold, London, 248 pp.

Idso, S.B., Kimball, B.A. and Mauney, J.R., 1988. Atmospheric CO_2 enrichment and plant dry matter content. Agric. For. Meteorol., 43: 171-181.

Klapwijk, D., 1988. Wortelgroei en produktie: geen heldere relatie. Groenten en Fruit, 44 (16): 46-47.

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

Nilwik, H.J.M., 1981. Growth analysis of sweet pepper (*Capsicum annuum* L.). 1. The influence of irradiance and temperature under glasshouse conditions in winter. Ann. Bot., 48: 129-136.

Panye, R.W., Lane, P.W., Ainsley, A.E. et al., 1987. Genstat 5 Reference Manual. Statistics department, Rothamsted Experimental Station. Oxford University Press, Oxford, 749 pp.

Papenhagen, A., 1986. Hohe Luftfeuchte hat auf Pflanzen begrenzten Einfluss. Gärtnerbörse und Gartenwelt, 86: 1343-1346.

Quast, P., 1977. Verteilung von trockensubstanz, Kohlenhydraten und Gibberellin bei Tomaten-, Kartoffel- und Auberginenpflanzen ohne und mit Früchten bzw. Knollen. Gartenbauwissenschaft, 42: 97-105.

Richards, D., 1981. Root-shoot interactions in fruiting tomato plants. In: R. Brouwer et al., Eds., Structure and Functioning of Plant Roots. Martinus Nijhoff/Dr. W. Junk Publishers, Den Haag/Boston/London: 373-380.

Sanden, P.A.M.C. van de, and Veen, B.W., 1991. Effects of air humidity and nutrient solution concentration on growth, water potential and stomatal conductance of cucumber seedlings. Submitted to Scientia Hort.

Sonneveld, C. and Krey, C. de, 1986. Nutrient solutions for vegetables and flowers grown in water or substrates. Serie Voedingsoplossingen Glastuinbouw, 8, 5th ed., Proefstation voor Tuinbouw onder Glas, Naaldwijk, 30 pp.

Swalls, A.A. and O'Leary, J.W., 1975. The effect of relative humidity on growth, water consumption and calcium uptake in tomato plants. J. Ariz. Acad. Sci., 10: 87-89.

Swalls, A.A. and O'Leary, J.W., 1976. Growth, water consumption and salt uptake of tomato plants in high humidity-high carbon dioxide greenhouse environments. J. Ariz. Acad. Sci., 11: 23-26.

Wilson, J.B., 1988. A review of evidence on the control of shoot:root ratio, in relation to models. Ann. Bot., 61: 433-449.

4. Flowering, fruit set and fruit growth

4.1 Introduction

The production of horticultural crops is the overall result of a sequence of processes each affected to a greater or lesser extent by the environmental conditions. With fruit vegetable crops, yield depends on both the number and the weight of individual fruits. In Figure 4.1 a simplified relational diagram is presented to summarize the major processes related to both fruit number and fruit (fresh) weight.

The total number of harvested fruits is related to the number of flowers and regulated through fruit set, abortion, maturation rate and harvest rate. The rate of flowering is closely related to the rate of vegetative development (e.g. van Ravestijn, 1986) and it has been suggested that differences in flower number are influenced by the availability of carbon assimilates (Atherton and Harris, 1986).

In contrast to parthenocarpic fruits like cucumber, pollination and seed set are crucial processes in tomato (Rylski, 1979; Picken, 1984) and sweet pepper (Rylski, 1973; Rylski and Spigelman, 1982). Pollen transfer responds relatively quickly to variations in the environment. For example, pollen is more easily obtained by increasing the temperature for 2 or 3 hours on dull winter days (Picken, 1984). Though humidity is known to affect pollen transfer (Van Koot and van Ravestijn, 1963), the effects have not been quantified. Also germination, which generally takes place within a period of several hours can be considered as a quickly responding process in comparison with the rate of flower formation and fruit maturation and might be affected by humidity (cf. Henney, 1985). The extent of fertilization (i.e. seed number) is largely dependent on the number of pollen grains reaching the stigma and the effect of environmental factors on pollination and fertilization (Picken, 1984).

Seeds are important in the sink activity of individual fruits (Varga and Bruinsma, 1976), and thereby in the competition for assimilates within a truss or plant. The role of seeds in fruit growth has been demonstrated in several experiments (e.g. Rylski, 1973; Rylski, 1979; Imanishi and Hiura, 1977; Varga and Bruinsma, 1976). However, a high number of seeds does not always imply a higher fruit weight (Stenvers and Staden, 1976) because fruit weight also depends on the availability of assimilates, competition with other fruits (e.g. Fisher, 1977), competition between vegetative parts and fruits (Ho and Hewitt, 1986) and dry matter content of the fruit. A reduction of the number of fruits due to low fruit set therefore may give rise to a higher individual fruit weight.

Because the reproductive development plays an important role in determining yield of fruit crops this process, as related to humidity, was analyzed in more detail. The following processes were distinguished: flowering,

pollination, fruit set, fruit maturation rate and fruit-growth (Figure 4.1). The processes which are of major importance from a practical point of view (fruit set, weight and maturation rate) were investigated with all crops. A more detailed analysis (including growth of individual fruit diameters) was limited to tomato.

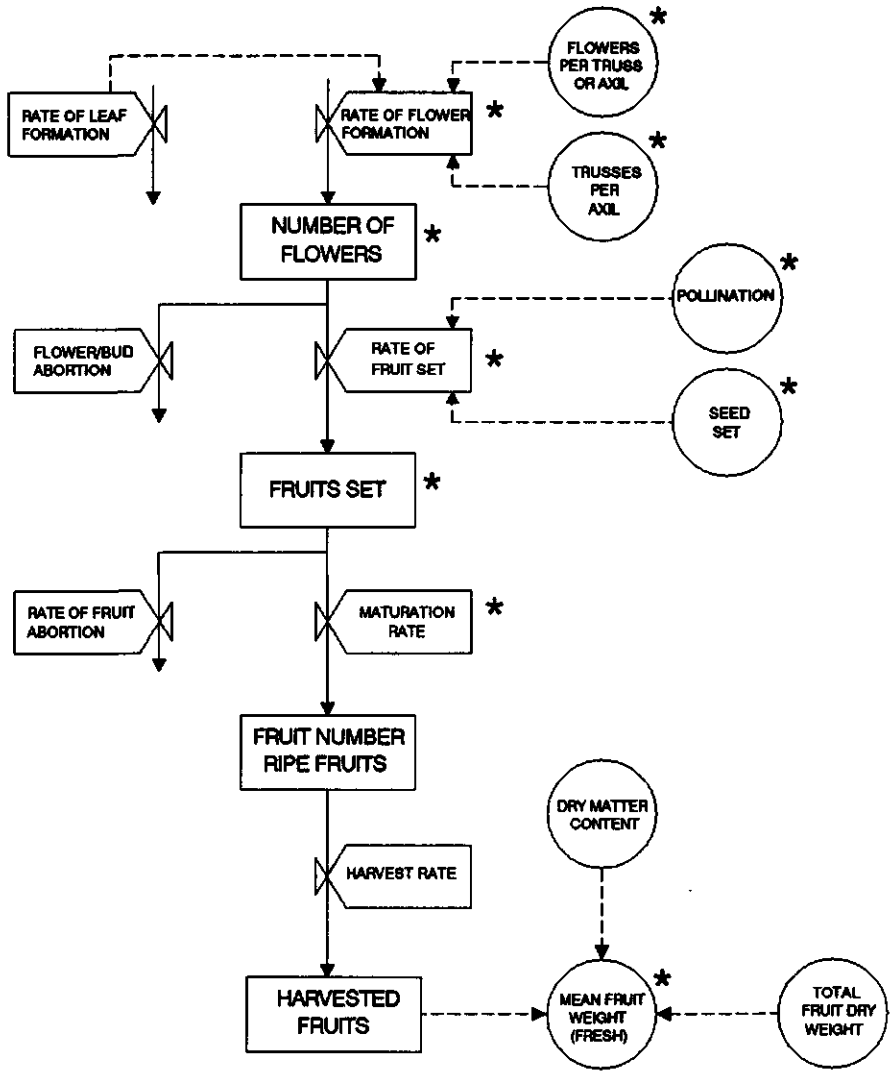

Figure 4.1
Relational diagram of important processes determining fruit number and fruit weight. Investigated influences of humidity are marked by *.

Table 4.1
Summary of investigated processes and rates with the various crops with respect to the reproductive development.

	flowering	pollen			seeds	fruit			maturation
		deh.	via.	adh.		set	size	weight	rate
cucumber	-	-	-	-	-	+	-	+	+
eggplant	+	+	+	-	-	+	-	+	+
tomato	+	+	+	+	+	+	+	+	+
pepper	+	+	+	-	+	+	-	+	+

deh. = dehiscence, via. = viability, adh. = adhesion to stigma

4.2 Materials and methods

4.2.1 Flowering

The rate of flowering was investigated in glasshouse experiments under natural light. In Table 4.2 the experiments in which flowering was recorded are presented. With eggplant and pepper the flowers were not only counted but also labelled to calculate the percentage of fruit set (see also sections 4.2.3 and 4.3). In the 1988 experiment with eggplant and in 1989 with tomato additional information was gathered on the number of flowers per axil and per truss.

In each experiment four day/night humidity regimes were duplicated in separate compartments. A high or low relative humidity by day was combined with either a high or low humidity by night (treatment symbols are h/h, l/h, h/l and l/l). The humidity range investigated was in the order of (24-h) 0.3 to 1.0 kPa VPD (Vapour Pressure Deficit). Data were collected on plants grown at an EC of around 3.0 dS m^{-1}. Further details of the environmental conditions, composition of the nutrient solution, planting dates, densities and cultivars used in the various experiments are presented elsewhere (sections 5.4 and 5.5 for tomato and eggplant; section 4.3 for sweet pepper).

Table 4.2
Experiments where flowering was recorded, recording method and period.

crop	year	method	period
tomato	1985	trusses	13/12/84 - 15/04/85
	1989	trusses and individual flowers	21/12/88 - 20/03/89
eggplant	1988	individual flowers	07/12/87 - 30/03/88
	1989	individual flowers	22/09/89 - 13/10/89
pepper	1987	individual flowers	02/12/86 - 09/05/87

4.2.2 Pollen transfer

During the spring of 1990, 20 plants of tomato (cv. 'Calypso'), eggplant (cv. 'Cosmos') and sweet pepper (cv. 'Mazurka') were grown on rockwool in three glasshouse compartments for 8, 20 and 20 weeks, respectively. On March 30, the plants were divided into two groups and transferred to two controlled environment growth chambers (7 × 4.25 × 2.1 m). There, the plants were grown (on rockwool at an EC of 2.5 dS m^{-1}) for two weeks at 85 W m^{-2} global radiation (SON-T) with a daylength of 20 h, at 20 °C and VPDs of 0.6 and 1.2 kPa (RH: 70 and 50%), respectively. Six times (every other day from 2 until 12 April), for each crop, all open flowers (10 to 50, dependent on the crop and day of measurement) were vibrated individually for two seconds with an 'electric bee' 6 hours after the onset of lighting. Both the period and moment of vibration were arbitrarily chosen, based on the information that vibration is most effective around midday (Picken, 1984) and that two seconds gives good results (van Koot and van Ravestijn, 1963). The pollen grains were collected in a glass tube mounted around the 'bee'. To estimate the pollen quantity, a method comparable to the one described by Trabelsi (1985) was used. When all flowers were tagged, a 12.5 ml suspension of pollen in 70% ethanol was made (ethanol was used instead of water to prevent aggregation of the pollen grains). The suspension was thoroughly mixed, and four samples were brought into a haemacytometer. The number of pollen grains within 0.2 mm^3 was counted for three replicates for each sample, using a Zeiss microscope with a 10 × objective lens and the camera and video display as described in section 2.2.2. The number of dehiscible pollen per flower was recorded. The humidity treatments were changed between the two growth chambers after each day of collecting pollen, to avoid possible confounding of humidity with chamber effects.

The same method of collecting and counting pollen grains was used for flowers of tomato (cv. 'Calypso') grown in a glasshouse at different environmental humidities. These measurements were done in glasshouse compartments equipped with a fogging system to humidify the air, resulting in VPDs as low as 0.2 kPa. Temperatures were slightly higher than in the growth chamber experiment and ranged from 22 to 25 °C. Pollen was collected from 20 flowers in 'humid' (0.2 to 0.6 kPa VPD; RH 85-95%) and 'dry' (0.5 to 1.2 kPa VPD; RH 65-88%) compartments two or three times a day for a series of days in the autumn of 1990 under natural light conditions and at equal temperatures (between the 'humid' and 'dry').

4.2.3 Pollen viability and adhesion to the stigma

Pollen of sweet pepper, eggplant and tomato was collected in glasshouse compartments with continuously high (h/h) or low humidity (l/l) in the spring of 1987, 1988 and 1989, respectively, to investigate the effects of humidity during

anther development on pollen viability. Details of the environmental treatments of these experiments are presented in Chapter 5. Pollen grains were collected on several days around 11.00, at least 3 hours after sunrise. The VPD at the time of collecting the pollen was between 0.2 and 0.5 kPa for the high humidity and between 0.6 and 0.8 kPa for the low humidity. In order to eliminate the influence of differences in desiccation, pollen was equilibrated for one hour at 100% relative humidity and 25 °C. In vitro germination of eggplant and pepper pollen was measured after 2.5 hours at 25 °C and 80% relative humidity on a 5% sucrose and 0.5% Bacto agar medium with 50 ppm H_3BO_3 and 145 ppm $CaCl_2$. The germination process was stopped by adding a drop of 1% acid fuchsine in lactophenol to the medium (Pet and Hornes, 1985).

With tomato, pollen germination was measured after 5 hours at 25 °C in a liquid medium containing 7% sucrose and 70 ppm boric acid (van Ravestijn, 1989, personal communication). Pollen germination of tomato was also measured in vivo. Therefore in the early morning 20 flowers were emasculated from two 'high' and 'low' humidity compartments. These flowers were hand pollinated the next day, around noon, with freshly collected pollen from flowers grown under the same environmental conditions. Pollen grains from the same sample were used in the in vitro germination. After 5 hours the stigmata of the pollinated flowers were collected, fixated and hydrolysed, and pollen tubes were stained with aniline blue. The total number of pollen grains (germinated and non-germinated) on the stigma was used as an estimate for the adhesion to the stigma. Observations were done with an ultra-violet microscope at 125 × magnification. The mean pollen tube length was calculated as the average of 5 randomly chosen tubes per style. Due to the set-up, the percentage germination obtained from the in vivo test represents both the overall effect of humidity on pollen viability and the effect of humidity on germination per se.

4.2.4 Fruit set, seed set and fruit maturation rate

Fruit set, seed set and fruit growth were investigated under the four day/night humidity regimes as described in section 4.2.1 in two spring (1988: eggplant; 1989: tomato) and two autumn (1984: cucumber, side shoots only; 1989: eggplant) experiments. Percentages of fruit set during the periods of treatment were calculated from harvested fruits and the number of open flowers. With cucumber the term 'fruit set' is used for non-aborted fruits. Tomato fruits were considered as set when larger than 2 mm. However, in commercial tomato growing, fruit set is often defined as the number of well shaped, normally developed fruits. For comparison with observations in commercial practice, and to facilitate the transfer of information obtained from the experiments described here, the percentage of fruits smaller than 15 mm was also recorded. All data were collected on 40 (eggplant and cucumber) or 48 (tomato) plants per

treatment. The salinity level of the nutrient solution was 3.0 dS m^{-1}, except for cucumber, which was grown at 2.5 dS m^{-1}.

Because fruit set may be affected by the degree of style exsertion (Levy, et al., 1978), the style length was measured (spring 1989) for 20 flowers of tomato (second flower of fifth truss) of the continuously high and low humidity treatments (h/h and l/l).

Seed number was counted for 84 tomato fruits (second fruit of trusses 1 to 7) per humidity treatment in spring 1989. The weight of these fruits was also measured. The day humidity levels at time of flowering of trusses 1 to 7 of tomato are presented in Table 4.3.

Table 4.3
VPD by day (week averages; kPa) at time of flowering of trusses 1 to 7.

treatment day/night	truss number						
	1	2	3	4	5	6	7
l/l	1.12	1.08	1.33	0.93	0.96	0.86	1.12
h/l	0.52	0.46	0.49	0.31	0.26	0.21	0.26
l/h	0.95	0.91	1.30	0.86	0.87	0.76	0.94
h/h	0.41	0.38	0.46	0.27	0.23	0.19	0.25

For trusses 1 to 4 the environmental humidities were generally lower than for trusses 5 to 7. For the latter trusses the humidities were on average 0.22 kPa and 0.96 kPa VPD for the high and low humidity treatments respectively.

With all crops the maturation rate of the fruits was measured in one of the experiments by recording the times of flowering and harvest of individual fruits (in total 256 cucumber, 635 eggplant, 480 tomato and 785 pepper fruits). More details on the various experiments are given in Chapter 5 and for pepper in section 4.3.

4.2.5 Fruit size and weight

With tomato (spring 1985 experiment) fruit diameter was measured with digital vernier calipers, three times a week, for 10 proximal, 10 middle and 10 distal fruits per humidity treatment on the 2nd, 5th and 8th truss. Diameters of individual fruits (with a final diameter > 20 mm) were analysed with a Genstat-5 program package using the Richards function:

$$\text{diameter} = a\,[1 + \exp^{-b\,(t-c)}]^{\,(1/(1-d))}$$

where a = final diameter (mm)
t = time after fruit set (days)
b,c and d are constants.

The coefficients a, b, c and d obtained from the fitting routines were then analysed with an ANOVA.

In the 1989 experiment with tomato size and weight of fruits sampled for seed content (second fruit of trusses 1 to 7; section 4.2.4) were also measured. Mean fruit weights (total yield) were calculated for all environmental treatments and in all experiments as described in Chapter 5.

4.3 The effects of air humidity on flowering, fruit set, seed set and fruit growth of glasshouse sweet pepper (*Capsicum annuum* L.).

Scientia Horticulturae, 40: 1-8.

ABSTRACT

The effects of day and night humidity on flowering, fruit set, seed set and fruit growth of sweet pepper (*Capsicum annuum* L.) cv. 'Delphin' were investigated in a glasshouse experiment. A continuously high or low humidity and alternating high and low humidities by day and night were applied during the early post-planting period from early December until mid-April. The vapour pressure deficit (VPD) of the glasshouse air varied from 0.33 to 0.66 kPa by day, from 0.27 to 0.86 kPa by night and the 24-h average from 0.30 to 0.75 kPa. Numbers of flowers and fruits showed a significant positive correlation with VPD by night. Fruit set and number of seeds per fruit were increased by low VPD by day. No significant effect of VPD was found on fruit shape (length/width ratio), number of cavities per fruit, pericarp thickness, dry matter content and fruit maturation rate.

INTRODUCTION

In the Netherlands sweet pepper is grown as a long season crop with planting dates in late November and early December and final harvest in October. Irregular fruit set is one of the main problems in glasshouse cultivation of sweet pepper. Flowering and fruit set are strongly affected by temperature (Rylski, 1972 and 1973; Rylski and Spigelman, 1982; Polowick and Sawhney, 1985). Differences in rate of flowering and fruit set, cause variations in fruit production and vegetative growth since these processes are closely correlated (Kato and Tanaka, 1971). Information on the effects of other environmental factors on flowering and fruit set is limited. High CO_2 levels promote fruit set as a result of improved photosynthesis (Nederhoff and van Uffelen, 1988). Baër and Smeets (1978) found that high 24-h average air humidity improved fruit set, but also enhanced flower abscission during the early production period in a growth chamber experiment. However, whether day and night humidity differ in their effect on fruit set of sweet pepper was not the subject of this study. With automatic environmental control in glasshouses different day and night humidity levels can be achieved. To gain maximum profit of environmental control, detailed knowledge of the effects of day and night humidity on growth, flowering, fruit set and yield is needed. In this research, the effects of day and night humidity on flowering, fruit set, seed set and fruit growth were investigated in a glasshouse experiment under normal growing conditions. Although humidity itself has no significant effect

on early and final yield of sweet pepper (Bakker, 1989) its control might be used to obtain a more uniform fruit set, and thereby reduce variation in production without reducing the final yield.

MATERIALS AND METHODS

Sweet pepper plants (*Capsicum annuum* L.), 'Delphin', were planted, at the 10-leaf stage, in 8 double glass compartments (15.0 x 12.8 m) of a Venlo-type glasshouse on 2 December 1986 (Table 1). Four day/night humidity treatments were applied with replication from planting until 14 April 1987. These were a continuously high (h/h) or low relative humidity (l/l) and alternating low and high relative humidities (l/h and h/l). Humidity could be increased (= decrease VPD), by a humidification system of water baths heated to 55 °C and closing a polythene thermal screen (light transmission: 80%). To reduce humidity (= increase VPD) the humidification system was switched off and the polythene screen was opened for 15% (= 45 cm). Screened and aspirated psychrometers were used to measure temperature and calculate VPD with a sample time of 1 min. Averages were calculated from these minute readings over the periods 10.00-16.00 h (day), 22.00-04.00 h (night) and 00.00-24.00 h (24h). Setpoints for (air) heating and ventilation, day/night, were 23/18 °C and 24/19 °C, respectively. Since temperature plays a major role in the vegetative growth (Bakker and van Uffelen, 1988) and fruit set of sweet pepper (Rylski and Spigelmann, 1982), attempts were made to minimize temperature differences between the treatments (Bakker, 1989). CO_2 concentration was controlled at 600 ml l^{-1} by applying pure CO_2.

Average daily photosynthetically active radiation (400-700 nm) in the glasshouses were 0.35, 0.59, 1.20, 2.22 and 3.56 MJ m^{-2} day^{-1} for December 1986, January, February, March and April 1987, respectively. The plants were grown on rockwool slabs placed in a gutter and irrigated with a nutrient solution of the following composition: NO_3^-, 12.25; $H_2PO_4^-$, 1.25; SO_4^{2-}, 1.25; NH_4^+, 0.25; K^+, 6.0; Ca^{2+}, 3.75; Mg^{2+}, 1.125 mmol l^{-1} and Fe, 10; Mn, 10; Zn, 4; B, 25; Cu, 0.5; Mo, 0.5 μmol l^{-1}. The electrical conductivity (EC) and pH were 3.0 dS m^{-1} and 5.5, respectively. Excess solution was recirculated. Root temperature was controlled at 20-21 °C.

The plants were trained with two main stems by applying pinching of lateral branches, which were restricted to 10-15 leaves. Flowers were removed from the first 10 axils as is commercially practised. On 20 plants $treatment^{-1}$ (10 $compartment^{-1}$) all open flowers were labeled 3 times a week. The dates of flowering and position of the flowers were recorded. No fruit thinning and artificial pollination were applied, all flowers were left to develop until fruit ripening or natural abortion. All fruits were harvested mature red, once a week. For all individual fruits the date of harvest and fruit weight were recorded.

On 7 April 1987, in each compartment the length, width, fresh and dry weight, pericarp thickness and number and dry weight of seeds were recorded on 25 (random check) mature red fruits.

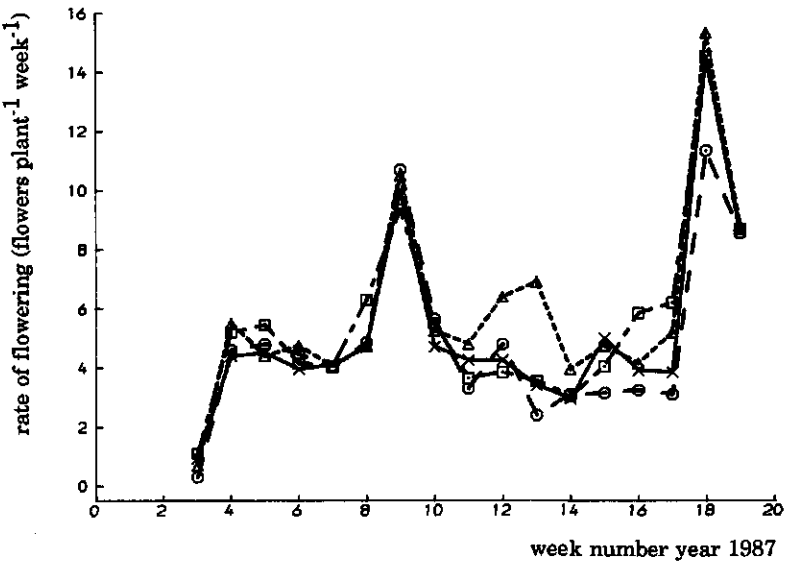

Fig. 1. Rate of flowering of sweet pepper 'Delphin', at four day/night air humidity treatments during spring 1987 (average of 20 plants). Week 1= 28 December 1986-3 January 1987.
l/l: △····△ , h/l: □-·-□ , l/h: ○——○ , h/h: ×——× .

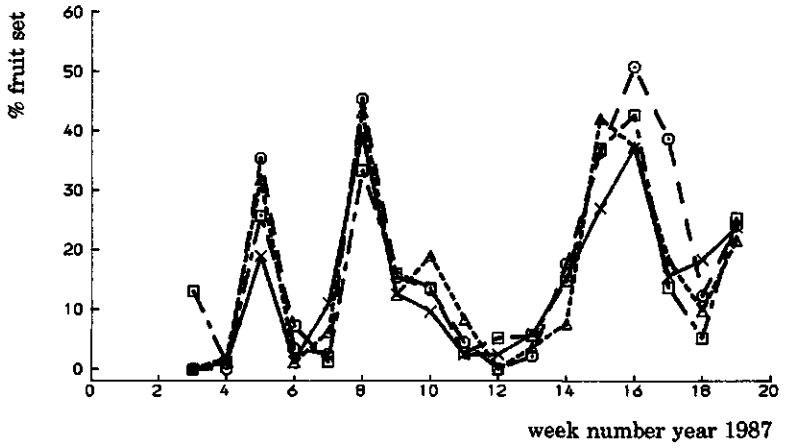

Fig. 2. Fruit set of sweet pepper 'Delphin', at four day/night air humidity treatments during spring 1987 (average of 20 plants).
l/l: △····△ , h/l: □-·-□ , l/h: ○——○ , h/h: ×——× .

RESULTS

Environment. - The average temperature and VPD by day, by night and for 24-h, measured over the period in which the humidity treatments were applied are presented in Table 1. The range of VPD observed during the night was greater than during the day. 24-h average temperature differences were not more than 0.2 °C.

Effects of humidity. - The four treatments showed a comparable pattern in flowering over the period from planting until week 19 (= 3-9 May, 1987), (Fig. 1). The climate treatments did not differ significantly in the total number of flowers counted until 14 April (Week 16) 1987 (Table 2). Peaks in fruit set occurred at alternating intervals (Fig. 2). First fruit set was obtained during the last week of January (Week 5) and in February (Week 8), followed by a period with relatively low fruit set. Fruit set increased again in April (Weeks 15 and 16), after the first fruits were harvested (Bakker, 1989). Over the period until 14 April (Week 16), the percentage fruit set was lowest at the l/l treatment (Table 2). The number of total fruits, mean fruit weight and fruit maturation rate were not significantly different between the treatments (Table 2). The number of seeds per fruit was lowest at the l/l treatment (Table 3). No significant differences were observed in percentage dry weight pericarp thickness, length/width ratio and number of cavities (Table 3).

Relationships between VPD by day, night and 24-h average and the parameters as presented in Tables 2 and 3 were investigated by calculation of correlation coefficients (Table 4). The percentage fruit set and number of seeds $fruit^{-1}$ were significantly correlated to the VPD by day. The numbers of flowers and fruits were positively correlated to VPD by night, while mean fruit weight was negatively correlated (Table 4). No other significant correlations were observed. For each humidity treatment and overall, the relationship between seed number and mean fruit weight was investigated. This relationship was only significant at the l/l treatment (Table 5).

DISCUSSION

Temperature plays a major role in the growth (Bakker and van Uffelen, 1988), flowering (Polowick and Sawhney, 1985) and fruit set of sweet pepper (Rylski and Spigelman, 1982). Since mean temperature differences for day, night and 24-h between the treatments were small (Table 1), the responses of flowering, fruit set, seed set and fruit growth were entirely ascribed to humidity.

TABLE 1

Average glasshouse temperature, relative humidity and vapour pressure deficit (VPD) for the period 2 December 1986 to 14 April 1987 at four humidity treatments by day (10.00-16.00h), night (22.00-04.00h) and 24h (00.00-24.00h).

Treatment day/night	Temperature (°C)			Relative humidity (%)			VPD (kPa)		
	Day	Night	24 h	Day	Night	24 h	Day	Night	24 h
1/1	24.4	20.2	21.7	78.4	63.7	70.4	0.66	0.86	0.75
h/1	24.7	20.1	21.8	87.1	69.4	77.9	0.41	0.72	0.56
1/h	24.3	20.5	21.9	79.2	82.5	81.0	0.63	0.42	0.50
h/h	24.9	20.0	21.9	89.6	88.5	88.9	0.33	0.27	0.30

TABLE 2

Total number of flowers, percentage fruit set, number of fruits, mean fruit weight (MFW) and fruit maturation rate (FMR) of fruits until 14 april 1987 for the four humidity treatments (means plant^{-1}).

Treatment day/night	Flowers	Fruit set (%)	Number of fruits	MFW (g)	FMR (days)
1/1	70.8	14.1	10.0	119.7	66.8
h/1	65.1	16.7	10.9	122.3	68.5
1/h	59.4	15.8	9.9	131.9	69.3
h/h	60.0	16.3	9.8	131.0	69.3
LSD 5%	NS	2.1	NS	NS	NS

TABLE 3

Number of seeds per fruit, percentage dry weight of fruits, pericarp thickness (mm), length/width ratio (l/w) and number of cavities at the four humidity treatments.

Treatment day/night	Seeds number	Dry weight (%)	Pericarp (mm)	l/w ratio	Cavities number
1/1	79.2	8.86	4.89	1.36	2.68
h/1	119.2	8.83	4.83	1.32	2.76
1/h	92.3	8.54	4.66	1.28	2.75
h/h	114.2	8.83	4.60	1.32	2.75
LSD 5%	33.3	NS	NS	NS	NS

No significant effect of humidity on vegetative growth of sweet pepper, in the range investigated was found (Baër and Smeets, 1978; Bakker, 1989) and since flower development is closely related to vegetative growth (Rylski, 1972; Van Ravestijn, 1986), similar crop reproductive development patterns might also be expected in the various humidity treatments. However, the number of opened flowers was significantly correlated to humidity by night (Table 4). A high humidity (low VPD) at night decreased the number of open flowers.

Although, with artificial pollination, Baër and Smeets (1978) did not find a significant effect of humidity on fruit set, under normal growing conditions and without artificial pollination fruit set is significantly increased by high humidity (low VPD) by day (Table 2 and 4). Depending on the light conditions, the anthers open 2-8 h after sunrise (Erwin, 1931; Kiss, 1970) to allow the pollen to fall to the stigma. At high humidity, tomato pollen tends to remain inside the anthers (van Koot and van Ravestijn, 1963). On the other hand, high humidity promotes pollen germination (Henny, 1985; van Ravestijn, 1986) and also improves pollen adhesion to the flower stigmatic surface (Van Koot and van Ravestijn, 1963; van Ravestijn, 1986). The observed improved fruit set at high humidity by day in this study (Tables 2 and 4) may therefore be attributed to improved pollen germination and adhesion to the stigma.

TABLE 4

Correlation coefficients for relations between vapour pressure deficit of air (between 28 December 1986 and 14 April 1987) by day (10.00-16.00h), night (22.00-04.00h) and 24-h (00.00-24.00h) and flowering, fruit set and fruit characteristics of sweet pepper.

Variable	Vapour pressure deficit		
	Day	Night	24-h
Number of flowers	NS	0.71	NS
Fruit set (%)	-0.73	NS	NS
Number of fruits	NS	0.71	NS
Fruit maturation rate	NS	NS	NS
Seeds per fruit	-0.76	NS	NS
Dry weight (%)	NS	NS	NS
Pericarp thickness	NS	NS	NS
Length/width ratio	NS	NS	NS
Number of cavities	NS	NS	NS
Mean fruit weight	NS	-0.79	NS

Significance level: P = 0.05: 0.71

TABLE 5

Coefficients a and b and correlation coefficient (r) for linear relations between seed number and mean fruit weight (MFW)[1] of sweet pepper at four humidity treatments[2].

Treatment	a	b	r
l/l	1.37	16.8	0.98
h/l	n.s.	n.s.	n.s.
l/h	n.s.	n.s.	n.s.
h/h	n.s.	n.s.	n.s.
Overall	n.s.	n.s.	n.s.

[1] MFW (g) = a.seed number + b
[2] Presented coefficients (a, b and r) are significant at $P<0.05$

The number of fruits per plant was increased by low humidity (high VPD) by night (Table 4). Since nighttime humidity did not significantly affect the percentage fruit set (Table 4), the greater number of fruits must therefore be a result of greater flower number. It may be concluded that the h/l treatment seems the most profitable from production point of view (Tables 2 and 4). Although not significant, crop production results also seem to support this conclusion (Bakker, 1989).

Further improvement of fruit set possibly might be obtained by maintaining a low humidity during the later part of the night and the early morning hours to improve the release of the pollen from the anthers, followed by a high humidity during the latter part of the day. To prevent fruit set, a low humidity by day could be combined with a high humidity by night. These response differences could be used, within limits, to optimize the total fruit production of sweet pepper, or to reduce variations in fruit production over the season. Within the humidity range investigated (24-h mean VPD: 0.30-0.75 kPa, i.e. normal growing conditions) pepper fruit maturation rate was not significantly affected by humidity (Table 2). This observation concurs with the results of Baër and Smeets (1978). Furthermore, the morphological characteristics and percentage dry weight of the fruits were not affected by humidity (Table 3).

Seed set was closely related to humidity by day (Table 4) and is in agreement with the results of Baër and Smeets (1978). As with fruit set, the explanation for this response should be considered in terms of improved pollination by high humidity by day and better pollen tube growth and fertilization (van Ravestijn, 1986).

For various fruit crops it is known that fruit size (weight) is influenced by the number of seeds (Rylski (1973) for pepper; Imanishi and Hiura (1977) for tomato). At the l/l treatment, the relation between number of seeds and mean fruit weight was significant, but no overall relation was observed (Table 5). Baër and Smeets (1978) also did not find a relation between seed set and fruit weight.

It can be concluded that, within a particular treatment (especially at low seed set), the number of seeds and fruit weight may be related (Table 5; Rylski, 1973), but that a higher number of seeds does not generally imply a higher fruit weight (Table 5) because different factors (competition between fruits, fruit thinning) affect the final fruit weight (Picken, 1984).

REFERENCES

Baër, J. and Smeets, L., 1978. Effect of relative humidity on fruit set and seed set in pepper (*Capsicum annuum* L.). Neth.J.Agric.Sci., 26: 59-63.

Bakker, J.C., 1989. The effects of day and night humidity on growth and fruit production of sweet pepper (*Capsicum annuum* L.). J.Hortic.Sci., 64: 41-46.

Bakker, J.C. and van Uffelen, J.A.M., 1988. The effects of diurnal temperature regimes on growth and yield of sweet pepper. Neth.J.Agric.Sci., 36: 201-208.

Erwin, A.T., 1931. Anthesis and pollination in *Capsicum*. Proc. Am. Soc. Hortic. Sci., 27: 309-310.

Henny, R.J., 1985. In vivo pollen germination of *Aglaonema* affected by relative humidity. HortScience, 20 : 142-143.

Imanishi, S. and Hiura, I., 1977. Relationship between fruit weight and seed content in the tomato (II). J. Jpn. Soc. Hortic. Sci., 46: 211-218.

Kato, T., and Tanaka, M. 1971. Studies on the fruit setting and development of sweet peppers. I. Fruiting behavior. J. Jpn. Soc. Hortic. Sci., 40: 359-366.

Kiss, A., 1970. Studies on pollen viability in the pepper variety collection at Tapioszele. Agrobotanika, 12: 53-60.

Koot, Y., van, and van Ravestijn, W., 1963. The germination of tomato pollen on the stigma (as an aid to the study of fruit setting problems). Proceedings of the 16th International Horticultural Congress, 1962, 2: 452-461.

Nederhoff, E.M. and van Uffelen, J.A.M., 1988. Effect of continuous and intermittent carbon dioxide enrichment on fruit set and yield of sweet pepper (*Capsicum annuum* L.). Neth. J. Agric. Sci., 36: 209-217.

Picken, A.J.F., 1984. A review of pollination and fruit set in the tomato (*Lycopersicon esculentum* Mill.). J. Hortic. Sci., 59: 1-13.

Polowick, P.L. and Sawhney, V.K., 1985. Temperature effects on male fertility and flower and fruit development in *Capsicum annuum* L. Scientia Hortic., 25: 117-127.

Ravestijn, W. van, 1986. Aanleg bloemen en verbeteren zetting bij paprika (Flower induction and improvement of fruit set in *Capsicum*). Groenten en Fruit, 41 (33): 32-35 (in Dutch).

Rylski, I., 1972. Effect of the early environment on flowering in pepper (*Capsicum annuum* L.). J. Am. Soc. Hortic. Sci., 97: 648-651.

Rylski, I., 1973. Effect of night temperature on shape and size of sweet pepper (*Capsicum annuum* L.). J. Am.Soc. Hortic. Sci., 98: 149-152.

Rylski, I. and Spigelman, M., 1982. Effects of different diurnal temperature combinations on fruit set of sweet pepper. Scientia Hortic., 17: 101-106.

4.4 Results

4.4.1 Flowering

Neither with tomato nor eggplant was flowering rate was affected by humidity (Table 4.4). Analysis of the tomato and eggplant data with a two by two analysis of variance did not show an effect of humidity by day or by night.

Table 4.4
Flowering of tomato and eggplant as affected by environmental humidity.
t = total number of flowering trusses per plant at end of treatments, f = average rate of flowering during period of treatment (flowers plant^{-1} week^{-1}).

treatment day/night	tomato			eggplant	
	1985 t	1989 t	1989 f	1988 f	1989 f
l/l	8.6	7.5	8.3	3.6	3.4
h/l	8.8	7.7	8.9	3.7	3.4
l/h	8.7	7.4	8.3	3.7	3.5
h/h	8.6	7.5	8.3	3.6	3.7
LSD 5%	n.s.	n.s.	n.s.	n.s.	n.s.

The patterns of flowering of tomato (1989) and eggplant (1988), measured over the entire treatment period are highly similar (Figure 4.2), and comparable to the results observed with sweet pepper (section 4.3). Holder and Cockshull (1990) also demonstrated an equal rate of flowering of tomato in a humidity range of 0.2 to 0.8 kPa VPD. Furthermore the number of flowers per truss (tomato, 1989) and the number of flowers per leaf axil (eggplant, 1988), were unaffected by humidity.

With sweet pepper, however, low nighttime humidity tended to increase the number of flowers (section 4.3) and after analysing the data with regression analysis, a minor positive effect (the correlation coefficient being equal to the significance level at P=0.05) of nighttime VPD on number of flowers was observed (section 4.3).

4.4.2 Pollen transfer

No significant differences between the humidity treatments on pollen transfer were observed (Table 4.5) in either the growth chamber or the glasshouse experiment. However, for pepper and in the glasshouse experiment with tomato, the number of pollen grains tended to be lower at high humidity (significant at P=0.10, or single sided test at P=0.05; Table 4.5).

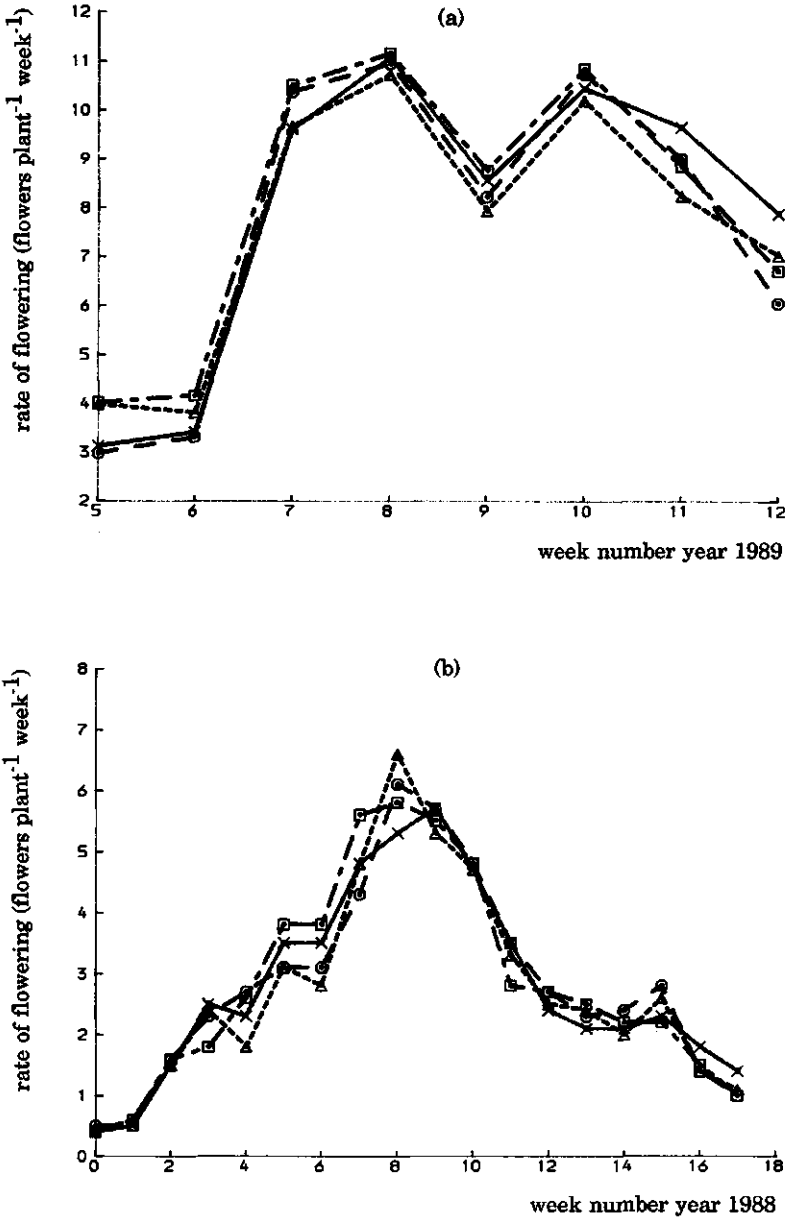

Figure 4.2
Rate of flowering of tomato (a) and eggplant (b) at four day/night humidity treatments (averages of 48 and 40 plants, respectively).
h/h: ×—× , l/h: o--o , h/l: □···□ , l/l: △····△ .

Table 4.5
Dehiscible pollen (number of pollen grains per flower × 10^4) at different humidity treatments in growth chamber and glasshouse experiments.

treatment	growth chamber			glasshouse
	tomato	eggplant	pepper	tomato
low humidity	8.4	32.2	6.3	8.3
high humidity	8.9	35.1	4.9	5.6
LSD 5%	n.s.	n.s.	n.s.	n.s.

In the glasshouse experiment the humidity varied between days, because of differences in the weather conditions and therefore a wider range of VPD was obtained compared to the growth chamber experiments. As high humidity tended to reduce the release of tomato pollen in the glasshouse experiment, the results were also examined with a regression analysis (Figure 4.3). The number of dehiscible pollen grains was significantly correlated to the VPD of ambient air ($r=0.639$ at 24 DF, $P=0.05$) but the variation was great. The lowest values were of the order of 20000 pollen grains per flower while the highest values reached 140000. On average the amount of pollen released ranged from about 60000 (tomato) to 350000 grains (eggplant) per flower (Table 4.5).

Although large differences exist between species, the values for tomato are in the order of magnitude of estimated total pollen quantity per flower (i.e. 160000; Trabelsi, 1985). The lower amount of pollen grains at low VPD in the glasshouse experiment agreed with the experience that it was difficult to collect enough pollen, for the in vitro germination tests, from the high humidity environments (with either tomato or eggplant). The results not only confirm that at very high humidity the pollen grains tend to remain inside, or stick to, the anthers (van Koot and van Ravestijn, 1963) but also provide quantitative information about the humidity effect.

4.4.3 Pollen viability and adhesion to the stigma

The viability of pollen was not significantly affected by humidity in the range investigated (Table 4.6). Pollen tube growth in vivo was unaffected by humidity, whereas the adhesion to the stigma was significantly better at high humidity (tomato).

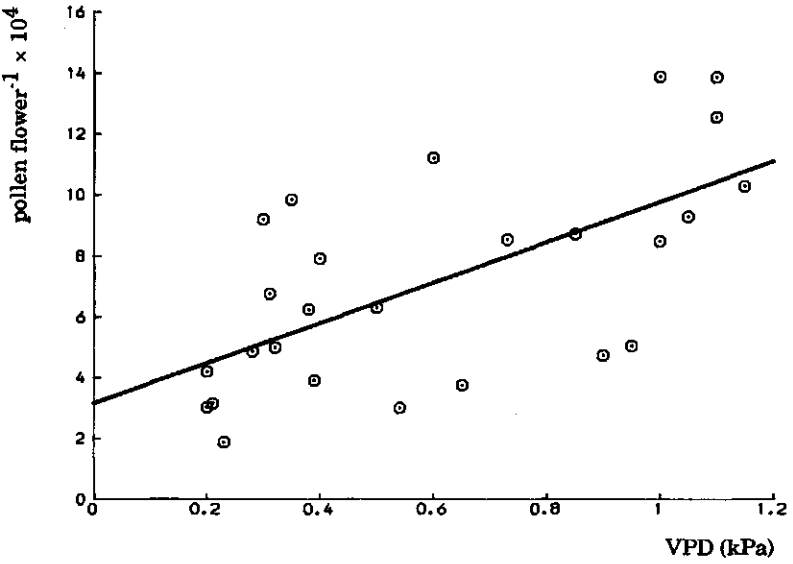

Figure 4.3
Dehiscible pollen of tomato (number of grains per flower) as affected by environmental humidity.
Number of pollen grains = $3.15 \times 10^4 + 6.62 \times 10^4$ VPD

Table 4.6
Effect of humidity on pollen viability (% germination; in vitro experiments) and the effect of humidity on germination, pollen tube growth and adhesion to the stigma of tomato pollen (in vivo). Presented averages are means of all collected data.

treatment day/night	pollen viability			tomato (vivo experiment)		
	eggplant %	pepper %	tomato %	pollen germination %	pollen tube growth $\mu m\ h^{-1}$	relative adhesion to stigma
1/1	14.5	14.5	21.6	93.4	153	100
h/h	13.5	14.0	17.2	90.6	174	167
LSD 5%	n.s.	n.s.	n.s.	n.s.	n.s.	58

4.4.4 Fruit set, seed set and fruit maturation rate

Fruit set

Fruit set of cucumber (side shoots) and tomato were not affected by humidity (Table 4.7). However, under low light conditions in spring, fruit set on the main stem of cucumber may be significantly reduced by low humidity, due to increasing fruit abortion (Hand, 1990). Fruit set of eggplant was significantly reduced by high humidity in the 1989 (autumn) experiment and in 1988 the same tendency was observed. Although fruit set of tomato was unaffected, the percentage of fruits smaller than 15 mm, generally the middle and the distal fruits, was clearly higher at continuously high humidity.

Table 4.7
Percentage fruit set of eggplant, cucumber and tomato, seed number per fruit of tomato and % tomato fruits < 15 mm at four day/night humidity treatments.

treatment day/night	eggplant		cucumber	tomato		
	1988 % set	1989 % set	1984 % set	% set	seed number fruit^{-1}	% fruits < 15 mm
1/1	17.6	21.6	57.8	90.1	162.9	7.5
h/1	16.9	18.8	55.0	90.7	158.3	14.1
1/h	17.1	19.6	59.8	90.6	165.0	8.2
h/h	15.1	16.4	57.8	89.1	140.3	24.4
LSD 5%	n.s.	2.9	n.s.	n.s.	17.6	9.6

Seed set

The average seed number of tomato was lower with the h/h treatment (Table 4.7) indicating lower seed set at high humidity. This overall effect arose from differences in seed number in the higher trusses. The seed number increased roughly from 90 (1st truss) to 180 (4th to 7th trusses) and the difference in seeds between the l/l and h/h treatment increased with the truss number (Table 4.8), being significant for trusses five to seven.
Based on the environmental conditions at the time of fruit set the ratio between pollen on the stigma at continuously high (h/h) and low (l/l) humidity (PShl) was estimated from pollen dehiscence (pdh, pollen per flower) and adhesion to the stigma. This ratio is considered a measure for the relative effect of humidity and was calculated by:

$$\text{Ratio PShl} = 1.67 \times [\text{pdh at h/h}] / [\text{pdh at l/l}]$$

Pollen dehiscence per flower (pdh) was calculated from the relation presented in Figure 4.3 (section 4.4.2) and average VPD by day at time of fruit set (Table 4.3). 1.67 is the estimated ratio of adhesion to the stigma between the high and low humidity (section 4.4.3). For trusses 1 to 7 the estimated ratios PShl are: 0.93, 0.92, 0.87, 0.89, 0.82, 0.83 and 0.77. These ratios are in good agreement with the seed ratios observed (Table 4.8).

Style length did not differ significantly between the extreme humidity treatments (high humidity: 6.45 mm, low humidity 6.35 mm); it is assumed therefore that the differences in fruit and seed set at different humidities are not caused by influences on style exsertion.

Maturation period

The maturation period of fruits of all crops did not differ significantly between the humidity treatments (Table 4.9). In general the maturation period is strongly affected by temperature (Hurd and Graves, 1985; Bakker, 1989) but in all experiments differences in 24-h average temperatures between the different humidity treatments were minimal (section 5.3). It is assumed therefore that a potential effect of humidity was not masked by temperature. As no significant differences in maturation period (flowering until picking) were observed with all crops, it is concluded that humidity has no effect on maturation period.

Table 4.8
Effect of humidity treatments on the number of seeds per fruit (second fruit of each truss) for trusses 1 to 7. R = ratio seeds at h/h divided by seeds at l/l treatment.

treatment day/night	truss number						
	1	2	3	4	5	6	7
l/l	93.6	139.4	156.3	178.4	188.8	184.7	203.6
h/l	88.1	137.0	151.4	189.7	182.4	178.2	174.6
l/h	98.2	138.7	154.4	191.3	187.7	196.8	188.3
h/h	89.6	126.1	150.9	168.8	154.8	142.9	145.6
LSD5%	n.s.	n.s.	n.s.	n.s.	32.3	41.0	47.6
R	0.96	0.90	0.96	0.94	0.82	0.77	0.72

Table 4.9
Maturation period of fruits grown under different day/night humidities (a=autumn, s=spring).

treatment day/night	cucumber a 1984	eggplant s 1988	tomato s 1985	pepper s 1987
1/1	15.3	39.8	54.8	66.8
h/1	14.3	40.3	52.8	68.5
1/h	15.4	38.4	53.5	69.3
h/h	14.6	39.3	52.7	69.3
LSD 5%	n.s.	n.s.	n.s.	n.s.

4.4.5 Fruit size and fruit weight

Fruit size (tomato)

The results of the ANOVA on the coefficients of the fitted diameter growth curves (Richards function) of tomato fruits are summarized in Table 4.10. Humidity only affected final diameter (parameter a), the other coefficients, related to the shape of the growth curve, were unaffected. Final diameter also differed significantly between the trusses (43.3, 46.9 and 47.9 mm for trusses 2, 5 and 8, respectively) and fruits (47.3, 46.7 and 44.3 mm for the proximal, middle and distal fruits).

Table 4.10
Average coefficients for Richards function (4.2.5) to describe fruit growth of tomato at four day/night humidity treatments.

treatment day/night	coefficients			
	a	b	c	d
1/1	47.1	0.112	63.6	1.51
h/1	48.5	0.110	65.3	1.56
1/h	45.6	0.111	64.7	1.54
h/h	43.1	0.118	64.8	1.55
LSD 5%	2.9	n.s.	n.s.	n.s.

In Figure 4.4 the fitted growth curves are presented for the four humidity treatments where time is expressed as days after fruit set (fruit diameter > 2 mm). Due to this time transformation the inflection point differs from

parameter c in Table 4.10. Diameter results here were slightly flattered as the smallest fruits (< 20 mm) were excluded.

From this figure and the coefficients presented in Table 4.10 it is clear that the pattern of fruit growth is almost unaffected by humidity. However, the final diameter (and consequently weight, see below) is lower at continuously high humidity.

By the middle of the growth period the rate of daily diameter growth is about 1.5 mm day^{-1} and at a fruit diameter of 25 mm this equals 2.5 mm^3 day^{-1} (under the assumption of a spherically shaped fruit). This is in the order of magnitude of maximum volume growth (2.2 ml day^{-1}) reported by Varga and Bruinsma (1976). The differences in diameter become visible in the second half of the growth period, during the phase with highest growth rate.

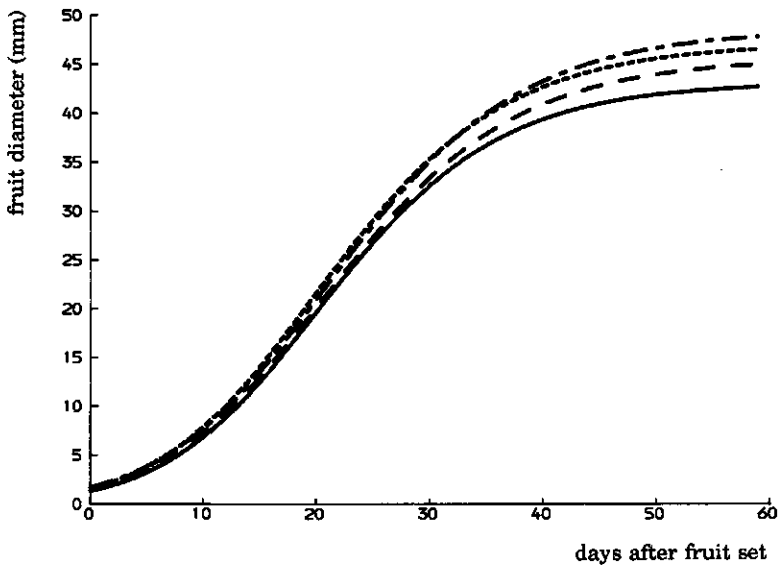

Figure 4.4
Growth curves of tomato fruits at four humidity treatments, time in days after fruit set.
h/h: ——— , l/h: – – – – , h/l: –·–·–· , l/l: ····· .

Fruit weight

In Chapter 5 (production) no fruit weights are presented for cucumber. Therefore this additional information is presented here (Table 4.11). The most striking result is a higher mean fruit weight at high humidity by day in two experiments (both 1984). In the 1983 experiment, the same tendency (significant at a single sided test at P=0.05) was observed. In the 1986 experiment fruit weight tended to be higher at both treatments with a low nighttime humidity, in accordance with Hand (1990).

Besides the average fruit weight of all crops, fruit weight of tomato was investigated in more detail in the 1989 experiment, from the fruits used for determination of seed set (section 4.4.4). In Table 4.12 the mean fruit weights of the second proximal fruit of trusses 1 to 7 are presented. The mean fruit weight gradually increased from the first to the seventh truss at the continuous low humidity (l/l). At the continuous high humidity, fruit weight was significantly lower for trusses five to seven.

Table 4.11
Average mean fruit weight of cucumber grown at four day/night humidity treatments (a=autumn, s= spring).

treatment day/night	experiment			
	a1983	s1984	a1984	s1986
l/l	419	375	421	448
h/l	441	389	448	450
l/h	435	379	418	440
h/h	436	453	453	440
LSD 5%	n.s.	13	23	n.s.

Table 4.12
Fruit weight (g) of second tomato fruit of trusses 1 to 7, grown under different humidity treatments.

treatment day/night	truss number						
	1	2	3	4	5	6	7
l/l	56.6	70.4	69.0	69.2	77.5	74.5	85.8
h/l	58.6	66.6	73.8	74.8	72.8	71.5	66.7
l/h	58.5	73.9	70.1	70.2	69.6	79.3	77.0
h/h	63.4	75.3	79.6	70.6	63.4	53.4	61.0
LSD 5%	n.s.	n.s.	n.s.	n.s.	13.7	20.7	23.2

The relation between fruit diameter and weight was investigated for these fruits using stepwise selection of variables in a multiple regression analysis. The best fit (percentage variance accounted for: 97.2) was obtained with the relation:

$$FFW = 16.9 - 1.563\ d + 0.0493\ d^2$$

where: FFW is the fresh fruit weight of tomato (g) and d is the diameter in mm

Based on this relation and the final diameter data presented in Table 4.10, the difference in mean fruit weight between the h/h and l/h treatment was estimated to be 16 g.

4.5 Discussion

Flowering

The rate of flowering is closely related to the rate of vegetative development (van Ravestijn, 1986). Since only minor effects of humidity on vegetative growth of tomato, pepper and eggplant were observed (Chapters 3 and 5), and because there was no effect on the number of flowers per axil or truss, similar flowering rates (Table 4.4) could be expected.

With tomato the rate of flower abortion (the complement of fruit set, Table 4.7) was unaffected. Abortion of pepper flowers, however, is increased in an early stage by low VPD (Baër and Smeets; 1978). Since only fully open flowers were counted, it is possible that the observed effect of humidity was due to abortion of young flowers (and possibly buds) at low VPD by night (section 4.3). It is concluded that the rate of flowering of these crops is not significantly affected by environmental humidity.

With cucumber flowering was not measured. De Lint and Heij (1982) and van der Vlugt (1983) observed, however, that the number of flowers per leaf axil is determined by temperature and pre-planting growth conditions. It is assumed that flowering is correlated to the rate of leaf(node) development. Since in cucumber high humidity enhances side shoot development and increases the number of leaves (Mortensen, 1986; section 5.1), a higher flowering rate with cucumber may be expected.

Pollination and seed set

Remarkably, only in the glasshouse experiment (tomato) an effect of humidity on pollen dehiscence was observed (section 4.4.2). According to Kretchman (1968) the effects of VPDs above 0.3 kPA (RH < 90%) are small. With tomato the difference between the glasshouse and growth chamber results therefore may be caused by the different ranges of humidity conditions achieved in these experiments.

The sensitivity of tomato to humidity in this respect may be attributed to the position of the anthers inside the flowers. Hoekstra and Bruinsma (1975) suggest that humidity around the anthers might be locally increased due to anther and flower transpiration and a low rate of air exchange. With eggplant and pepper the anthers are free from the calyx and hence local humidity will be less. Based on the observed tendency with pepper (Table 4.5) it is possible,

however, that at extremely high air humidity the dehiscence of pepper pollen is reduced, but further research should be directed to verify and quantify this effect. Also the difference in anther structure might be important. With pepper the anthers split longitudinally, with eggplant a small apical fissure is formed. Extremely high humidity conditions during ripening of pollen may reduce fertility (Hoekstra and Bruinsma, 1975; van Marrewijk and Visser, 1978) and very low humidity may cause rapid desiccation and hamper germination (Hoekstra and Bruinsma, 1975). In the humidity range obtained in the glasshouse experiments, however, neither viability nor germination were affected (Table 4.6) in accordance with the results of van Koot and van Ravestijn (1963). Since also the style length was not significantly affected by humidity within the humidity range investigated here, the adhesion to the stigma seems far more important than viability, germination, pollen tube growth and style exsertion.

The extent of fertilization (i.e. seed number) of tomato, and probably also of pepper, is largely dependent on the effect of humidity on pollination and fertilization (Picken, 1984). The relative effects of humidity on the estimated pollen quantity on the stigma (PShl; section 4.4.4) and on the actual seed number in tomato fruits (Table 4.8) were highly similar. Because of the absence of effects on pollen viability and germination it is concluded that the major effect of humidity on pollination and seed set of tomato, within the humidity range normally obtained in glasshouse production, is caused by its effect on pollen release and adhesion to the stigma. With tomato the number of seeds at high day humidity was lower than at low day humidity (Table 4.8). This indicates that the positive effect of humidity on adhesion was overruled by the negative effect on pollen release. For pepper the number of seeds at high humidity by day was, in contrast to tomato, (36%) higher than at low humidity (calculated from Table 3 in section 4.3). With pepper the effect on pollen viability can be excluded but the effect on in vivo germination requires further research. The higher seed number at high humidity by day (Table 3 in section 4.3), indicates that for pepper the positive effect of high humidity on adhesion and possibly germination, overrules any possible negative effect on pollen dehiscence.

Fruit set

Since fruit set was defined as the number of harvested fruits expressed as a percentage of open flowers, these figures represent the overall effect of humidity on fruit set, and flower- and fruit abortion. In general effects were small (eggplant, pepper) or absent (tomato, cucumber). The relatively low fruit set observed with pepper and eggplant demonstrates that the number of fruits of these crops is obviously not limited by the presence of flowers. Since the rate of flowering of these crops was not affected either (section 4.4.1) only minor

effects of humidity on the number of fruits can be expected. With tomato flowering and fruit set are unaffected by humidity and consequently no effect on the number of fruits was anticipated. In this research, in contrast to commercial practice, even the smallest tomato fruits were harvested, to discriminate effects on fruit set from effects on fruit growth. Although in fact fruit set is unaffected, for commercial application it is important that high humidity reduces the amount of harvestable fruits dramatically as the percentage of very small fruits is strongly increased.

With cucumber flowering was not measured. Since this crop responds to humidity with a higher rate of leaf node formation it is also likely that more flowers will be produced. Because fruit set was equal it is possible that humidity affects fruit production through an increased number of fruits.

Fruit size and weight

The size of tomato fruits is closely related to fruit weight (section 4.4.5). Differences in size gradually increase during the period with the highest growth rate (Figure 4.4). The final size of a tomato fruit is correlated to the number of seeds (Imanishi and Hiura, 1977) probably due to the higher sink activity created by the developing seeds (Varga and Bruinsma, 1976). The relation between seed number and fruit weight for a given cultivar, however, may differ in different environments (Rylski, 1979; section 4.3) and trusses (Ho and Hewitt, 1986). This relationship is probably influenced by e.g. assimilate supply (influencing the total fruit dry weight, Figure 4.1) and competition between fruits. Fruit thinning for example has little effect on the number of seeds but increases individual fruit weight (van Ravestijn and Molhoek, 1978). Both Verkerk (1957) and Rylski (1979) observed that each additional seed increased fruit weight by a progressively smaller amount. Various authors (e.g. Imanishi and Hiura, 1975; Varga and Bruinsma, 1979) assume that the relationship between seeds and fruit weight is causal. In these studies differences in seed number were induced by exclusively varying pollination whilst vegetative growth remained unaltered. In this study, however, due to the long term exposure to different humidities, not only pollination and seed set were affected, but also processes related to assimilate supply (stomatal behaviour, Chapter 2; vegetative growth, Chapters 3 and 5).

When the fruit weights are plotted against seed number, despite the large scatter, it is indeed clear that higher fruit weights are attained with higher seed numbers (Figure 4.5). Regression analysis revealed no significant differences between the humidity treatments (fitted lines in Figure 4.5). The relation between seed number and fruit weight for individual trusses (grown under comparable conditions) did not differ significantly between the environments and trusses with respect to the slope of the (linear) relationships. This means that the average increment of fruit weight with each additional

seed is equal for all trusses (0.35 g seed^{-1}) and higher (steeper lines, Figure 4.5) than expected from all trusses pooled. However, the average number of seeds increases with the height of the trusses (Table 4.8) possibly because of more favourable light conditions during pollination and seed set. This is reflected in the shifted lines for truss 6 compared to truss 2 (Figure 4.5) and means that fruits on higher trusses contain more seeds than fruits with the same weight on lower trusses. In accordance with Varga and Bruinsma (1976) it is assumed that the number of seeds determine the relative sink strength and competition among assimilates. So a high seed number does not necessarily imply a higher fruit weight. This indicates the danger of pooling data from different trusses when determining the absolute or relative effect of seed number on fruit weight (e.g. Verkerk, 1957; Rylski, 1979) and makes the conclusions at least debatable.

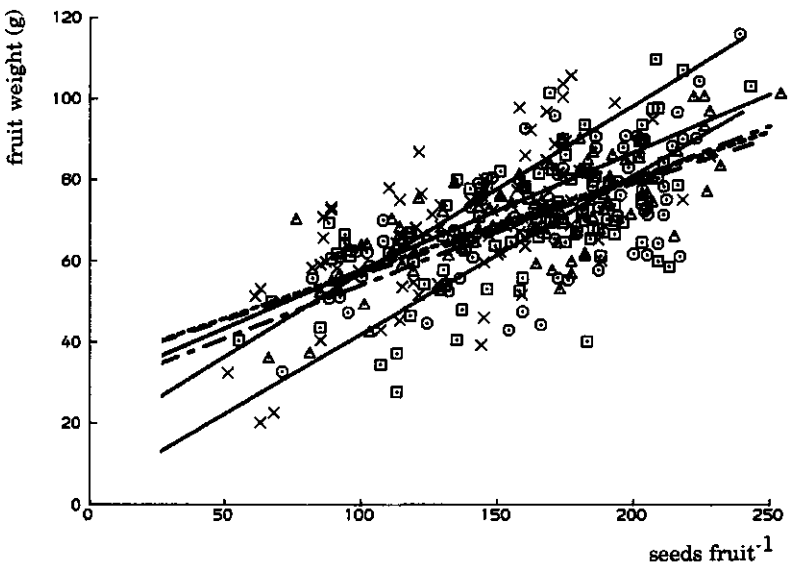

Figure 4.5
Fruit weight of tomato plotted against seed number (data of second fruit of trusses 1 to 7). The four lines with equal slope represent trends for the humidity treatments.
h/h: ×——× , l/h: o– –o , h/l: □–·–□ , l/l: △·····△ , the two steep lines represent fitted lines for truss 2 and 6 (for clarity other lines are omitted).

In contrast to the other crops under investigation, cucumber fruits of the (female flowering) cultivars used develop completely parthenocarpically. Consequently effects of humidity on pollination and seed set do not play a role.

The mean fruit (fresh) weight of cucumber was higher at high humidity by day and since the dry matter content of the fruits was unaffected (Chapter 3), this implies a higher mean fruit dry weight at high humidity by day. Also as the number of fruits is slightly higher at high humidity (van Uffelen, 1984) it is concluded that the total fruit dry weight of cucumber must have been higher at high humidity by day. The reason for this may be a higher photosynthesis due to stomatal effects (Chapter 2) and the gain in leaf growth (Chapters 3 and 5). In the 1986 experiment this was most likely counteracted by the severe calcium deficiency and associated reduction of leaf area (section 5.1).

Also with eggplant a gain in fruit weight at high humidity by day was observed (section 5.5). Tomato, however, showed a decreasing fruit weight at high average humidity, most likely a result of the severe leaf area reduction due to calcium deficiency at high humidity (section 5.4). A slightly positive effect of high nighttime humidity on fruit weight of sweet pepper was found (section 4.3). Fruit maturation period of all crops was unaffected by humidity, consequently no influences on yield through earliness are to be expected.

Combined with the effects of humidity on fruit number it is concluded that elevated humidity may affect the total yield of cucumber through both an increase of fruit number and fruit weight. With tomato the effect of high humidity on yield will be due to the decreasing fruit weight only. With both pepper and eggplant it is difficult, based on the results presented here, to deduce whether the number or weight is of major importance in the determination of final yield.

Conclusions

Flowering per se is unaffected by humidity. Based on the increased leaf number with cucumber an increase in number of flowers at high humidity can be expected.

High humidity affects the number of tomato seeds as a combined result of a decrease of pollen release and better adhesion to the stigma.

Fruit set of tomato and cucumber was unaffected. With pepper fruit set was slightly higher at high humidity by day whilst with eggplant high humidity decreased fruit set. It can be concluded that humidity may affect the yield of cucumber, pepper and eggplant because of fruit number, but not of tomato.

In general the fruit weight of cucumber and eggplant was increased at elevated humidity by day. Pepper fruits were heavier at high humidity by night, whilst fruit weight of tomato was lower at a high average humidity. The final yield of cucumber may be increased by high humidity through more fruits and a higher fruit weight whilst the yield of tomato may decrease due to a reduction of mean fruit weight.

The fruit maturation rate of all crops was unaffected by humidity so no effects on earliness are to be expected.

4.6 References

Atherton, J.G. and Harris, G.P., 1986. Flowering. In: J.G. Atherton and J. Rudich, Eds., The tomato crop. Chapman and Hall, London, 167-200.

Baër, J. and Smeets, L., 1978. Effect of relative humidity on fruit set and seed set in pepper (*Capsicum annuum* L.). Neth. J. Agric. Sci., 26: 59-63.

Bakker, J.C., 1989. The effects of temperature on flowering, fruit set and fruit development of glasshouse sweet pepper (*Capsicum annuum* L.). J. Hort. Sci., 64: 313-320.

Fisher, K.J., 1977. Competition effects between fruit trusses of the tomato plant. Scientia Hort., 7: 37-42.

Hand, D.J., 1990. The effect of humidity and calcium nutrition on the growth and yield of a long season cucumber crop. (Results at Efford Experimental Station). Lecture at the second annual cucumber conference, 25 september 1990, Stockbridge House, UK.

Henny, R.J., 1985. In vivo pollen germination of *Aglaonema* affected by relative humidity. HortScience, 20: 142-143.

Ho, L.C. and Hewitt, J.D., 1986. Fruit development. In: J.G. Atherton and J. Rudich, Eds., The tomato crop. Chapman and Hall, London, 201-239.

Hoekstra, F.A. and Bruinsma, J., 1975. Viability of *Compositae* pollen: germination in vitro and influences of climatic conditions during dehiscence. Z. Pflanzenphysiologie, 76: 36-43.

Holder, R. and Cockshull, K.E., 1990. Effects of humidity on the growth and yield of glasshouse tomatoes. J. Hort. Sci., 65: 31-39.

Hurd, R.G. and Graves, C.J., 1985. Some effects of air and root temperatures on the yield and quality of glasshouse tomatoes. J. Hort. Sci., 60: 359-371.

Imanishi, S. and Hiura, I., 1977. Relationship between fruit weight and seed content in the tomato II. J.Jap. Soc. Hort. Sci., 46: 211-218.

Koot, Y. van, and Ravestijn, W. van, 1963. The germination of tomato pollen on the stigma (as an aid to the study of fruit setting problems). Proc. 16th Intern. Hort. Congress, 2: 452-461.

Kretchman, D.W., 1968. A preliminary report of several aspects of fruit setting of greenhouse tomatoes. Research Summary of the Ohio Research and Development Center, 26: 5-8.

Levy, A., Rabinowitch, H.D. and Kedar, N., 1978. Morphological and physiological characters affecting flower drop and fruit set of tomatoes at high temperatures. Euphytica, 27: 211-218.

Lint, P.J.A.L. de, and Heij, G., 1982. Night temperature and number of nodes and flowering of the main stem of glasshouse cucumber (*Cucumis sativus* L.). Neth. J. Agric. Sci., 30: 149-159.

Marrewijk, N.P.A. and Visser, D.L., 1978. The effect of relative humidity on incompatibility and fertility in *Brassica oleracea* L. Neth. J. Agric. Sci., 26: 51-58.

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

Pet, G. and Hornes, M.A.P.F., 1985. Relatie tussen vroege vruchtzetting en stuifmeelkwaliteit bij paprika's. Zaadbelangen, 39 (4): 100-102.

Picken, A.J.F., 1984. A review of pollination and fruit set in the tomato (*Lycopersicon esculentum* Mill.). J. Hort. Sci., 59: 1-13.

Ravestijn, W. van, 1986. Aanleg bloemen en verbetering zetting bij paprika. Groenten en Fruit, 41 (33): 32-35.

Ravestijn, W. van, 1989. Proefstation voor Tuinbouw onder Glas, Naaldwijk, Netherlands, personal communication.

Ravestijn, W. van, and Molhoek, W.M.L., 1978. Effects of pollination on fresh and dry weight, size, number of seeds and harvest date of tomato fruits. Annual Report of the Glasshouse Crops Research and Expermental Station for 1977, Naaldwijk, 41.

Rudich, J., Zamski, E. and Regev, Y., 1977. Genotypic variation for sensitivity to high temperature in tomato: pollination and fruit set. Bot. Gaz., 138: 448-452.

Rylski, I., 1979. Fruit set and development of seeded and seedless tomato fruits under diverse regimes of temperature and pollination. J. Amer. Soc. Hort. Sci., 104: 835-838.

Stenvers, N. and Staden, O.L., 1976. Growth, ripening and storage of tomato fruits (*Lycopersicon esculentum* Mill.). III. Influence of vegetative plant parts and effects of fruit competition and seed number on growth and ripening of tomato fruits. Gartenbauwissenschaft, 41: 253-259.

Trabelsi, M., 1985. A reliable method for testing fruit setting ability in tomato using in vitro pollen germination. Med. Fac. Landbouww. Rijksuniv. Gent, 50/4: 1343-1356.

Uffelen, J.A.M. van, 1984. Herfstkomkommers: zowel een droog als een vochtig klimaat hebben voor- en nadelen. Tuinderij, 64 (18): 26-29.

Varga, A. and Bruinsma, J., 1976. Roles of seeds and auxins in tomato fruit growth. Z. Planzenphysiol. Bd. 80: 95-104.

Verkerk, K., 1957. The pollination of tomatoes. Neth. J. Agric. Sci., 5: 37-54.

Vlugt, J.F.L. van der, 1983. The effect of temperature on formation and abortion of flower buds in gynoecious cucumber plants. Scientia Hort., 20: 323-328.

5. Production and quality

5.1 The effects of day and night humidity on yield and quality of glasshouse cucumbers.

Journal of Horticultural Science, 62: 361-368

SUMMARY

The effects of different day and night humidity levels on autumn- and spring-grown cucumbers were examined in four glasshouse experiments. A high or low humidity during the day was combined with either a high or low humidity during the night to give four treatment combinations. The vapour pressure deficits achieved, over the total period, varied from 0.57 to 0.91 KPa by day, from 0.26 to 0.66 KPa by night, and the 24-h average varied from 0.43 to 0.75 KPa. Temperature differences between the treatments were less than 0.6 °C in each experiment. Vegetative growth was enhanced by either high day or night humidity but early yield was not related to either day, night, or 24-h average humidity. A significant negative correlation was found between vapour pressure deficit by day and final total yield in all but one experiment. Fruit quality, expressed as fruit colour, was reduced by a high 24h average humidity. Calcium deficiency in leaves was correlated with 24h average humidity. From the viewpoint of production, the best control procedure is to maintain a high humidity during the day but to avoid high 24h average humidity levels if good fruit quality is to be obtained.

HUMIDITY is an environmental factor that has received very little attention in research on glasshouse crops. The general effects of humidity on plant growth, transpiration, ion uptake and translocation have been reviewed by Grierson and Wardowski (1975) and Hoffman (1979), and some information is available on its effects on photosynthesis (Bunce, 1984; Acock *et al.*,1976). The humidity of the glasshouse environment can influence the incidence of fungal diseases (Winspear *et al.*, 1970; van Steekelenburg and van de Vooren, 1980), but information on its effects on the yield and quality of glasshouse vegetable crops is very limited (Lipton, 1970; Baër and Smeets, 1978). Humidity has become more important as an environmental factor in glasshouses since the introduction of energy saving measures such as thermal screens, double glazing and reduced ventilation. The increase in humidity caused by these measures, however, can have a detrimental effect on growth and production, and promotes the incidence of physiological disorders (Palzkill *et al.*, 1980; Bakker, 1984).

Until now, automatic control of the glasshouse environment has enabled growers to improve crop profitability. However, current humidity control programmes are largely based on growers' experience and are mainly chosen to prevent the incidence of fungal diseases and to maintain a favourable balance

between productivity and energy costs. The development of humidity control strategies which optimize glasshouse climate, however, is hindered by the lack of information on the effects of humidity on the production and quality of crops.

The purpose of this study was to examine the production and quality of autumn and spring cucumbers grown under different combinations of day and night humidity. The series of experiments described here was started in autumn 1983 and continued in 1984 and in the spring of 1986.

MATERIALS AND METHODS

The experiments were carried out in eight, double-glazed compartments of a Venlo type glasshouse, specially designed for research on the effects of energy-saving measures.

Each compartment (15.0 m × 12.8 m) was equipped with a mobile polythene thermal screen and a humidification system of water baths with a total area of 7 m^2. A Siemens computer system was used for environmental control. Temperature and humidity were measured using screened and aspirated psychrometers developed by the Technical and Physical Engineering Research Service (TFDL) in Wageningen. Different humidities were obtained by applying minimum ventilation and pipe temperature settings and by using the thermal screen and the humidification system as appropriate. A minimum ventilator setting, related to ambient temperature and wind velocity (van de Vooren and Strijbosch, 1980), and a minimum pipe temperature setting were maintained to reduce the humidity level. Humidity could be increased in daytime by heating the water baths to 50-60 °C, and at night, in addition to heating the water baths, the thermal screen was closed if the ambient temperature fell below 14 °C.

In all experiments, the root temperature was controlled at 20-21 °C and the addition of pure CO_2 was controlled by Siemens conductometric devices to maintain a level of 340 vpm by day and by night. Plants at the fifth-leaf stage were planted on rockwool slabs and irrigated with a complete nutrient solution with the aid of a trickle irrigation system. The volume nutrient solution applied was relative to evaporation and excess solution was recirculated. Within each compartment, 12 different nutrient solutions were applied with replication but as no significant interactions between environment and nutrition on production and quality of the fruits were found, only the effects of environment are presented.

Overall population density was 1.5 plants m^{-2}. The plants were grown as vertical cordons and were trained by the "umbrella" method. Main stem fruits were removed from the first ten leaf nodes and thereafter were restricted to one per leaf axil. Fruits were harvested twice a week, and their number, weight and market grade were recorded. Class 1 grade includes only well

shaped and well coloured fruits with a minimum length and weight of 30 cm and 300 g respectively.

The keeping quality of the fruits was regularly investigated, according to the criteria described by Janse and Welles (1984).

In Experiments 1, 2 and 3, leaf samples were taken from the main stem to measure leaf area differences. In Experiment 4 the total leaf area per plant was estimated from measurements of the leaf lengths of the individual leaves using the following equation for leaves longer than 10 cm:

$$A = 111 - 25.9\,L + 2.59\,L^2 - 0.0311\,L^3$$

where : A = leaf area in cm^2 and L is the leaf length in cm.

The total length of all the side shoots was used as a measure of side shoot development. Calcium deficiency in the leaves was assessed visually according to the scale described by Bakker (1984). In each experiment four combinations of day and night humidity were applied in duplicate. These were continuously high (h/h) or low (l/l) humidities and alternating low and high humidities (h/l and l/h).

The details of these experiments are listed in Table I. The water bath humidification system was not available for the first experiment and so humidity could only be increased during the night by using the thermal screen.

RESULTS

Environments.- The different environment treatments resulted in differences in vapour pressure deficit (Table II).

In all experiments, vapour pressure deficit during the night was generally lower than during the day and the difference in vapour pressure deficit between the high and low humidity treatment was generally greater during the night than the day. The range of vapour pressure deficits observed during the period of early (i.e. main stem) fruit production was generally similar to the range measured over the total production period, except in Experiment 4.

Despite the different control settings, temperature differences between treatments were small. Differences in 24-h average temperature were usually less than 0.6 °C (Table II).

TABLE I.
Details of the experiments.

Experiment number	Planting date	Cultivar	Day/night treatments						
			Symbol	Air temperature Heating °C	Air temperature Ventilation °C	Minimum setting Pipe temp. °C	Minimum setting Ventilation %	Screen + = closed	Humidification + = on
1	15/08/83	Milio	1/1	23/18	24/19	45/45	10/10	-/-	-/-
			h/1			0/45	0/10	-/-	-/-
			1/h			0/ 0	0/ 0	-/-	-/-
			h/h			0/ 0	0/ 0	-/+	-/-
2	20/12/83	Corona	1/1	23/20	25/25	0/ 0	40/40	-/-	-/-
			h/1			0/ 0	0/40	-/-	+/-
			1/h			0/ 0	40/ 0	-/+	-/+
			h/h			0/ 0	0/ 0	-/+	+/+
3	14/08/84	Lucinde	1/1	22/15	23/16	45/45	40/40	-/-	-/-
			h/1			0/45	0/40	-/-	+/-
			1/h			45/ 0	40/ 0	-/+	-/+
			h/h			0/ 0	0/ 0	-/+	+/+
4	14/01/86	Lucinde	1/1	25/20	26/21	0/ 0	10/10	-/-	-/-
			h/1			0/ 0	0/10	-/-	+/-
			1/h			0/ 0	10/ 0	-/+	-/+
			h/h			0/ 0	0/ 0	-/+	+/+

TABLE II

Average glasshouse temperature and vapour pressure deficit for two production periods. d = 10.00-16.00 h, n = 22.00-04.00 h, 24h = 00.00-24.00 h.

Treatment	Early fruit production period											
	Experiment 1			Experiment 2			Experiment 3			Experiment 4		
	d	n	24h	d	n	24h	d	n	24h	d	n	24h
						Temperature (°C)						
1/1	26.0	19.0	24.6	23.6	19.6	21.2	27.7	22.3	24.9	25.2	19.7	22.3
h/1	25.8	18.9	24.3	24.2	19.6	21.6	28.1	22.3	25.0	25.5	19.7	22.6
1/h	25.7	18.7	24.0	23.5	20.2	21.4	27.9	21.9	24.8	24.9	20.5	22.4
h/h	25.6	18.9	24.0	24.0	19.9	21.6	28.2	21.8	24.8	25.4	20.4	22.8
						Vapour pressure deficit (kPa)						
1/1	0.90	0.68	0.81	0.84	0.73	0.75	1.17	0.55	0.75	0.89	0.87	0.88
h/1	0.78	0.68	0.75	0.67	0.74	0.70	0.95	0.52	0.66	0.72	0.77	0.73
1/h	0.67	0.50	0.62	0.67	0.36	0.52	1.14	0.38	0.64	0.76	0.32	0.52
h/h	0.65	0.41	0.56	0.52	0.35	0.43	0.88	0.36	0.53	0.63	0.31	0.44
						Total period						
						Temperature (°C)						
1/1	23.9	18.8	22.1	24.2	19.7	21.6	26.6	21.9	24.0	24.9	19.0	21.6
h/1	23.7	18.6	21.9	25.2	19.7	22.0	27.2	21.8	24.1	25.5	19.5	22.2
1/h	23.2	18.0	21.3	24.2	20.2	22.2	27.3	21.5	24.0	24.8	19.7	21.9
h/h	23.6	18.4	21.5	24.6	20.2	22.2	27.3	21.5	24.0	25.1	20.0	22.2
						Vapour pressure deficit (kPa)						
1/1	0.82	0.61	0.75	0.82	0.63	0.72	0.91	0.51	0.66	0.90	0.62	0.74
h/1	0.73	0.61	0.69	0.71	0.66	0.68	0.70	0.48	0.56	0.77	0.55	0.59
1/h	0.62	0.44	0.55	0.72	0.26	0.50	0.89	0.35	0.55	0.85	0.25	0.50
1/h	0.60	0.35	0.47	0.57	0.27	0.42	0.73	0.31	0.43	0.75	0.27	0.44

Vegetative growth.- The plants grew well in all treatments. From their visual appearance, side shoot development and leaf area measurements (Table III) it was concluded that vegetative growth was enhanced by high humidity in the range investigated. The most serious detrimental effect observed was the occurrence of calcium deficiency in leaves, which was closely correlated with 24-h average humidity and so inversely correlated with vapour pressure deficit (Figure 1).

Analysis of the data of Experiment 4 showed that the number of leaves was not significantly affected by the humidity treatments but the higher 24-h average humidity resulted in a larger area per leaf and consequently a larger total leaf area per plant. On the other hand, leaf area in the continuously high humidity treatment was not as great, because serious calcium deficiency occurred in the side shoots.

TABLE III.
Vegetative growth, side shoot development (sh.dev.) and leaf area (leaf a.), expressed as % of the l/l treatment.

	Experiment 1		Experiment 2		Experiment 3		Experiment 4	
	sh.dev.	leaf a.	sh.dev.	leaf a.	sh.dev.	leaf a.	sh.dev.	leaf a.
l/l	100	100	100	100	100	100	100	100
h/l	117	102	123	105	164	106	102	97*
l/h	150	108	113	106	102	109	112	116
h/h	158	-	143	108	140	110	110	105
LSD (P=0.05)	48	2.4	n.s.	2.5	41	3.8	n.s.	16

* - reduced leaf area as a consequence of leaf necrosis

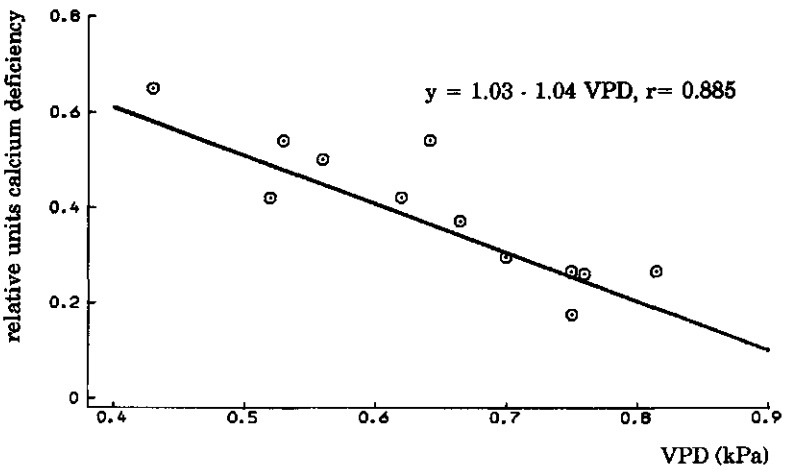

Fig. 1. Relationship between mean 24-h vapour pressure deficit and calcium deficiency symptoms in leaves.

Fruit production.- The treatments had no significant effect on the early yield (= main stem fruit) of either Class 1 fruit or of total fruit in total in any experiment. The proportion of Class 1 fruit was reduced, however, by high humidity in Experiments 3 and 4 (Table IV).

The final yields of Class 1 fruit and of total fruit were significantly increased by high humidity at night or continuously in Experiment 1, and by high humidity in the day, the night, or continuously in Experiment 2. No significant differences in final yield were observed in the other two experiments but the proportion of Class 1 fruit was reduced by continuously high humidities in Experiment 3 (Table IV).

The relations between yield, vapour pressure deficit and temperature were examined by linear regression analysis. With the early yield neither the yields of Class 1 fruit nor the yields of total fruit were related either to day, night or to 24-h average vapour pressure deficit; nor was there any relationship with temperature either.

A significant relationship ($P<0.01$) was found, however, between final total yield and daytime vapour pressure deficit in all but Experiment 4 (Table V).

The relationship between daytime vapour pressure deficit and final total yield for Experiment 2 is presented in Figure 2. The production of Class 1 fruit was also significantly related to daytime vapour pressure deficit in Experiment 1 and 2. The correlation coefficients for relationships between final yield and % Class 1 fruit and day, night and 24-h average vapour pressure deficit are presented in Table V. No significant correlation was found between final yield (total as well as Class 1 grade) and night vapour pressure deficit except in Experiment 1, where the correlation between yield and 24h average vapour pressure deficit was also significant.

With respect to the % Class 1 grade, a significant relation with vapour pressure deficit (night and 24-h average) was found only in Experiment 3.

TABLE IV.
Early and final yields, Class 1 (C1), total and % Class 1 (% C1).

	Experiment 1			Experiment 2			Experiment 3			Experiment 4		
	C1	total	% C1	C1	total	% C1	C1	total	% C1	C1	total	% C1
Early yield kg m^{-2}												
l/l	3.40	3.42	99.5	4.49	4.49	100	3.04	3.19	95.3	5.27	5.53	95.4
h/l	3.45	3.47	99.5	4.79	4.79	100	3.64	3.74	97.3	5.45	5.78	94.4
l/h	3.60	3.62	99.5	4.90	4.90	100	2.77	2.94	94.2	5.13	5.95	86.2
h/h	3.70	3.71	99.8	4.93	4.93	100	3.38	3.68	91.8	5.97	5.99	90.6
LSD (P=0.05)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	2.3	n.s.	n.s.	2.9
Final yield kg m^{-2}												
l/l	6.82	6.88	98.4	22.66	23.36	97.9	5.46	6.15	88.8	21.25	24.38	87.2
h/l	7.76	7.81	98.7	27.38	28.05	97.6	6.27	7.06	88.9	22.28	25.21	88.4
l/h	8.77	8.84	98.4	26.08	26.64	97.9	5.41	6.32	85.7	23.27	27.06	86.0
h/h	8.91	8.99	98.4	28.56	29.00	98.5	5.55	7.12	78.0	22.50	26.04	86.4
LSD (P=0.05)	1.03	1.04	n.s.	2.06	2.09	n.s.	n.s.	n.s.	2.7	n.s.	n.s.	n.s.

TABLE V.
Correlation coefficients of relations between final yield (total, Class 1, and % Class 1) and day, night and 24h average vapour pressure deficit.

		Total		Class 1		% Class 1	
Experiment 1	day	-0.981	<1%	-0.978	<1%	0.030	n.s.
	night	-0.800	5%	-0.791	5%	0.268	n.s.
	24-h	-0.926	<1%	-0.922	<1%	0.110	n.s.
Experiment 2	day	-0.895	<1%	-0.906	<1%	-0.428	n.s.
	night	-0.451	n.s.	-0.473	n.s.	-0.516	n.s.
	24-h	-0.658	n.s.	-0.679	n.s.	-0.548	n.s.
Experiment 3	day	-0.835	<1%	-0.660	n.s.	0.295	n.s.
	night	-0.289	n.s.	0.265	n.s.	0.846	<1%
	24-h	-0.663	n.s.	-0.134	n.s.	0.826	5%
Experiment 4	day	-0.282	n.s.	-0.318	n.s.	-0.179	n.s.
	night	-0.687	n.s.	-0.594	n.s.	0.564	n.s.
	24-h	-0.604	n.s.	-0.565	n.s.	0.249	n.s

Significance levels: 1%: 0.834, 5%: 0.708

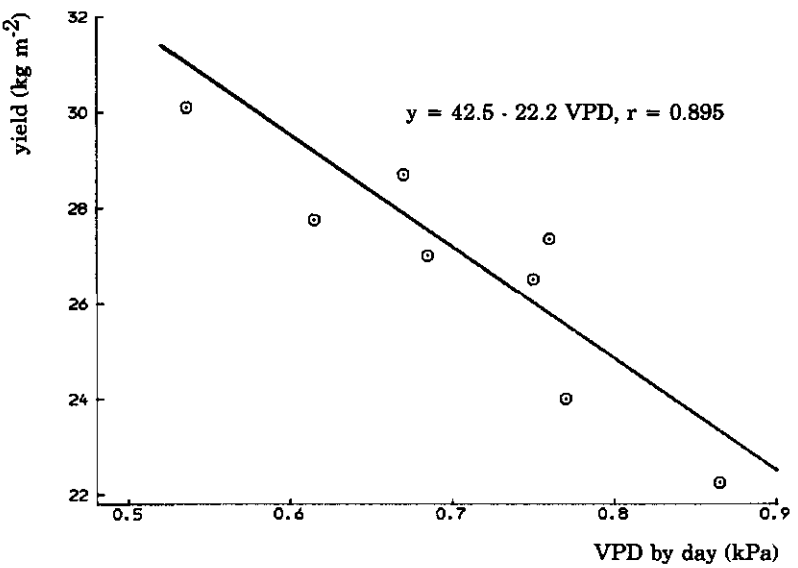

Fig. 2. Effect of daytime vapour pressure deficit on final yield (Experiment 2).

Fruit quality.- The results of the assessments of quality are presented in Table VI. A high humidity during the production phase reduced fruit colour at harvest and after 14 days' storage. Colour reduction during storage was similar in each treatment but was slightly enhanced by very high humidities during the production phase in Experiment 2 and 4.

TABLE VI.

Keeping quality of fruits (expressed as fruit colour). Colour scale: 9 = dark green, 1 = completely yellow, 6 = minimum colour Class 1 grade. C0 = colour at harvest, C14 = colour after 14 days' storage at 20 °C and 90% RH.

Treatment	Experiment 1		Experiment 2		Experiment 3		Experiment 4	
	C0	C14	C0	C14	C0	C14	C0	C14
1/1	7.1	5.1	7.2	5.6	7.0	4.9	8.0	6.6
h/1	6.8	4.9	-	-	-	-	-	-
1/h	6.9	4.9	-	-	-	-	7.7	6.0
h/1	6.8	5.0	7.0	5.0	6.5	4.4	7.4	5.5
LSD (P=0.05)	0.2	0.2	0.1	0.2	0.2	0.3	0.1	0.2

DISCUSSION

Since temperature plays a major role in the earliness of fruit production and hence significantly affects the final yield (van de Vooren, 1981; Slack and Hand, 1983) attempts were made to minimize temperature differences between the treatments. This is one of the major problems which need to be overcome in humidity research. Despite the different control settings in each treatment, temperature differences were relatively small in all experiments and should have had little effect on early yield. Since temperature is of minor importance during the production stage (van de Vooren *et al.*, 1978), the effect of these temperature differences on final yield was probably negligible.

The most remarkable result of this study is the very close relationship between final total yield and daytime humidity in three of the four experiments. Since production is closely related to canopy photosynthesis, this phenomenon might be explained by two different effects of humidity. Firstly, net photosynthesis is enhanced by high humidity (Acock *et al.*, 1976; Bunce, 1984) and secondly, high humidities increase leaf area (Table III). Both effects of humidity result in an increase in the potential production capacity of the plant. However, a continuously high humidity increases the occurrence of calcium deficiency (Figure 1) which reduces leaf area. Thus, photosynthesis is probably improved by high daytime humidity while nighttime humidity has no

direct effect. Leaf expansion and calcium deficiency, however, are correlated to 24-h average humidity, in which night-time humidity plays an important role. The explanation for the absence of a correlation between production and daytime humidity in Experiment 4 could be that the improvement of the photosynthesis by the high daytime humidity was counteracted by a reduction in leaf area, which was mainly due to calcium deficiency. Furthermore, the differences in daytime humidity obtained in this experiment were small compared to the other experiments, especially in the side-shoot production stage. The risk of calcium deficiency can be reduced by increasing the calcium content of the nutrient solution (Bakker, 1984) and this has no adverse effect on fruit production up to a level of 2.5 mmol Ca l^{-1} (Aalbersberg, 1984).

Fruit quality at harvest was reduced by the high humidity levels, so part of the extra production at high humidity is of poorer quality and consequently of lower monetary value. The differences in % Class 1 fruit between the four experiments were, besides humidity, mainly the result of differences in light level and cultivar. The best control strategy, from the point of view of production, seems to be to maintain a high daytime humidity. When this is combined with a high night-time humidity, however, keeping quality is reduced and also the internal fruit quality may be reduced due to the incidence of fruit rot caused by *Didymella bryoniae* (van Steekelenburg and van de Vooren, 1980; van Uffelen, 1985).

A combination of high daytime humidity and relatively low nighttime humidity, therefore, seems to be the best recommendation for optimum fruit production and quality.

It has been shown that day and night humidity differ in their effects on production, which is at variance with the effects of temperature. Research with cucumber and tomato has shown that both day and night temperature have similar effects and that the 24-h average temperature is most important in regulating the growth and development of the crop (Slack and Hand, 1983; de Koning, 1985). It may be concluded, therefore, that to optimize the glasshouse environment, humidity should receive a higher priority in momentary control than temperature. For the economic optimization of the glasshouse environment more detailed information is needed on the long- and short-term effects of extreme day and night humidity levels on fruit production and quality.

The authors thank J. Janse for recording keeping quality, and L. van Paassen, Y. Ruyzenaars, I. Schilstra and C. Sonneveld for their assistance and advice.

REFERENCES

Aalbersberg, Y. W. (1984). Growth and production depend on calcium and EC. Tuinderij, 64 (19), 28-31. [Dutch].

Acock, B., Charles-Edwards, D. A. and Hand, D. W. (1976). An analysis of some effects of humidity on photosynthesis by a tomato canopy under winter light conditions and a range of carbon dioxide concentrations. Journal of Experimental Botany, 27, 933-941.

Baër, J., and Smeets, L. (1978). Effect of relative humidity on fruit set and seed set in pepper (*Capsicum annuum* L.). Netherlands Journal of Agricultural Science, 26, 59-63.

Bakker, J. C. (1984). Physiological disorders in cucumber under high humidity conditions and low ventilation rates in greenhouses. Acta Horticulturae, 156, 257-264.

Bunce, J. A. (1984). Effects of humidity on photosynthesis. Journal of Experimental Botany, 35, 1245-1251.

Grierson, W., and Wardowski, W. F. (1975). Humidity in horticulture. HortSience, 10, 356-360.

Hoffman, G. J. (1979). Humidity. In: Controlled Environment Guidelines for Plant Research. (T. W. Tibbits and T. T. Kozlowski, Eds), Academic Press, New York, 141-172.

Janse, J., and Welles, G. W. H. (1984). Effects of energy saving measures on keeping quality of tomato and cucumber fruit. Acta Horticulturae, 163, 261-269.

Koning, A. de (1985). Waste heat research at Naaldwijk. Groenten en Fruit, 40 (37), 52-53. [Dutch].

Lipton, W. J. (1970). Growth of tomato plants and fruit production in high humidity and at high temperatures. Journal of the American Society of Horticultural Science, 95, 674-680.

Palzkill, D. A., Tibbits, T. W., and Struckmeyer, B. E. (1980). High relative humidity promotes tipburn on young cabbage plants. HortScience, 15, 659-660.

Slack, G., and Hand, D. W. (1983). The effect of day and night temperatures on the growth, development and yield of glasshouse cucumbers. Journal of Horticultural Science, 58, 567-573.

Steekelenburg, N. A. M. van and Vooren, J. van de (1980). Influence of the glasshouse climate on development of disease in a cucumber crop with special reference to stem rot caused by *Didymella bryoniae*. Acta Horticulturae, 118, 45-56.

Uffelen, J. A. M. van (1985). Autumn cucumbers in the energy conservative glasshouse. Groenten en Fruit, 41 (8), 34-37. [Dutch].

Vooren, J. van de (1981). Effect of day and night temperatures on earliness and fruitproduction in cucumber. Acta Horticulturae, 118, 187-189.

Vooren, J. van de, Lint, P. J. A. L. de, and Challa, H. (1978). Influence of varying night temperature on a cucumber crop. Acta Horticulturae, 87, 249-255.

Vooren, J. van de, and Strijbosch, T. (1980). Glasshouse ventilation control. Acta Horticulturae, 106, 117-124.

Winspear, K. W., Postlethwaite, J. D., and Cotton, R. F. (1970). The restriction of *Cladosporium fulvum* and *Botrytis cinerea* attacking glasshouse tomatoes, by automatic humidity control. Annals of Applied Biology, 65, 75-83.

5.2 Calcium deficiency of glasshouse cucumber as affected by environmental humidity and mineral nutrition.

Journal of Horticultural Science, 63: 241-246.

SUMMARY

The effects of interactions between environmental humidity, calcium supply and electrical conductivity (EC) of the growing medium on calcium deficiency in cucumber leaves were investigated in two glasshouse experiments. A low or high humidity during the day was combined with either a low or a high humidity during the night. The 24h average vapour pressure deficits achieved over the period from planting until calcium deficiency occurred varied from 0.44 to 0.88 kPa. Visible symptoms and the calcium content of the leaves were closely correlated with 24h average vapour pressure deficit.

The effect of humidity on calcium deficiency increased with increasing EC and decreasing calcium supply. When calcium accounted for more than 47% of all cations in the root environment, the effect of humidity on calcium deficiency was negligible.

It was concluded that deficiency symptoms gradually became apparent when the calcium content of the leaf margins fell below 500 mmol kg^{-1} dry matter. At low vapour pressure deficits, the minimum level of calcium required in the root environment is 40% of all cations, which can be reduced to 25% at high vapour pressure deficits. It is recommended that an EC of 2.0 dS m^{-1} be used to avoid calcium deficiency.

THE limited information available on the effects of high humidity on glasshouse vegetable crops is no doubt a result of the difficulty of controlling humidity in glasshouses. Most of the data on the effects of high humidity, therefore, have been obtained from growth-chamber experiments with small plants (Bunce, 1984; Van de Sanden, 1985), and little information is available from experiments with mature crops (Baër and Smeets, 1978; Bakker *et al.*, 1987).

Generally, vegetative growth and production of glasshouse cucumbers is enhanced by high humidity (Bakker *et al.*, 1987). However, some adverse effects are associated with extremely high humidity like heat damage and calcium deficiency (Bakker, 1985; Bakker *et al.*, 1987). Calcium deficiency in leaves may reduce leaf area and thereby the potential productive capacity of the crop. Besides humidity, calcium deficiency in leaves is closely correlated to nutrition (Adams, 1985; Ward, 1973). However, no information is available on interactions between humidity and nutrition. This information is needed to optimize vegetative growth and production and can be used to develop control procedures in which root environment and greenhouse conditions are controlled interdependently.

The effects of humidity and nutrition on calcium deficiency in leaves were investigated in two experiments in spring 1984 and 1986.

MATERIALS AND METHODS

The experiments were done in eight double-glazed compartments of a Venlo-type glasshouse. In both experiments four combinations of day and night humidity were applied in duplicate. These were continuously high (h/h) or low (l/l) humidities and alternating low and high humidities (h/l and l/h). The different humidities were obtained by applying minimum ventilation and pipe temperature settings, a thermal screen and artificial humidification. Temperatures were kept the same in all humidity treatments in both experiments. A detailed description of the environmental treatments is given by Bakker *et al.* (1987). Plants at the fifth-leaf stage were planted on 20 December, 1983 and 14 January, 1986 for Experiments 1 and 2, respectively. The plants were grown on rockwool slabs placed in a gutter and irrigated with a nutrient solution with the aid of a trickle irrigation system. The nutrient solution was recirculated. Root temperature was controlled at 20-21 °C. The plants were grown as vertical cordons and were trained by the "umbrella" method. Plant density was 1.5 plants m^{-2}. To guarantee sufficient water supply and to prevent accumulation of nutrients in the rockwool, the irrigation frequency was high and related to the total water uptake of the crop.

In Experiment 1, three electrical conductivity (EC) regimes were combined with four calcium levels at constant K/Mg ratio. In Experiment 2, eight EC levels were applied. The nutrient solutions were applied in duplicate in both experiments. The ratios of the ions not under investigation were kept the same in all treatments as applied in commercial practice (Sonneveld and de Krey, 1986).

The EC values required in the root-environment and the cation ratios used in the experiments are listed in Table I. The pH varied between 5.6 and 5.9 in the root environment in both experiments.

Assessments of the extent of calcium deficiency in leaves were made according to the scale described by Bakker (1984). Samples of young leaves (length < 7 cm) were gathered 6-7 weeks after planting from several treatments. The samples were dried at 80 °C, ground, digested according to Schaumlöffel (1960) and analysed for K, Ca and Mg as described by De Bes (1986). In Experiment 1, samples were also gathered from leaves with calcium deficiency symptoms. From these samples the leaf margin and centre were analyzed separately.

RESULTS

Greenhouse environment.- The average vapour pressure deficits (VPD) at day, night and 24h, measured over the period from planting until the leaf samples were gathered, are listed in Table II. Differences in 24h-average temperature

TABLE I.
EC regimes and cation mol-ratios in the two experiments.

Experiment	EC regime	cation ratios K : Ca : Mg
1 (spring 1984)	2, 6(4)2, 6(8)2 *	73 : 13 : 14
		65 : 23 : 12
		55 : 35 : 10
		43 : 49 : 8
2 (spring 1986)	1.5, 2.0, 2.5, 3.0	59 : 31 : 10
	3.5, 4.0, 4.5, 5.0	

* - 6(4)2 means: EC at start 6dS m^{-1}, after 4 weeks reduced to 2 dS m^{-1}

TABLE II.
Average vapour pressure deficit (kPa) for the first 7 weeks. d = 10.00-16.00 h, n = 22.00-04.00 h, 24h = 00.00-24.00 h.

Treatment	Experiment 1			Experiment 2		
	d	n	24h	d	n	24h
1/1	0.86	0.75	0.78	0.91	0.89	0.90
h/1	0.69	0.76	0.72	0.75	0.79	0.76
1/h	0.69	0.38	0.54	0.79	0.35	0.54
h/h	0.54	0.37	0.44	0.66	0.34	0.46

between the environmental treatments were less than 0.5 °C (Bakker *et al.*, 1987).

Root environment.- The EC levels obtained in the root-environment, and the cation ratios in the recirculation water are presented in Table III. Comparison of Tables I and III shows that the EC levels obtained were close to the levels required. Cation ratios in the recirculation water differed from the ratios supplied, due to accumulation. The EC values and cation ratios referred to in the remainder of the text are those presented in Table III.

Calcium deficiency.- The relationship between VPD (day, night and 24h average) and the assessments of calcium deficiency, at different rates of calcium supply or EC level, were examined by linear regression analysis. The highest correlation coefficients were obtained with 24h average VPD. The relationship between VPD and calcium deficiency is presented for four cation ratios in Figure 1 (Experiment 1). The effect of VPD decreased with increasing calcium supply. When more than 47% of the cations in the root environment were present as Ca, almost no calcium deficiency occurred. No interactions between calcium and EC were observed. In Figure 2, the relationship between

VPD and calcium deficiency is presented at four levels of EC (Experiment 2). Calcium deficiency in this experiment was slightly less than in Experiment 1 due to the higher calcium content of the nutrient solution. Calcium deficiency was least at an EC of 2.1 dS m^{-1} and the effect of VPD increased with increasing EC.

TABLE III.
EC levels obtained in the rockwool and cation ratios in the recirculation water for the two experiments.

Experiment	EC treatments	cation ratios K : Ca : Mg
1 (spring 1984)	2.3, 5.1, 5.2	69 : 16 : 15
		54 : 28 : 18
		38 : 47 : 15
		26 : 64 : 10
2 (spring 1986)	1.6, 2.1, 2.7, 3.2	37 : 46 : 17
	3.7, 4.1, 4.5, 5.1	

TABLE IV.
Calcium content (mmol kg^{-1} dry matter) of leaf margin (m) and centre (c) at two calcium levels and two vapour pressure deficits.

		VPD (kPa)		
calcium		0.75 (l/l)	0.43 (h/h)	mean
16%	m	367	277	322
	c	429	390	410
64%	m	783	689	736
	c	941	920	931
mean	m	575	483	529
	c	685	655	670

TABLE V.
Calcium content (mmol kg^{-1} dry matter) at two EC levels and two vapour pressure deficits.

	VPD (kPa)		
EC	0.88 (l/l)	0.44 (h/h)	mean
1.6	328	243	285
4.5	214	189	202
mean	271	215	

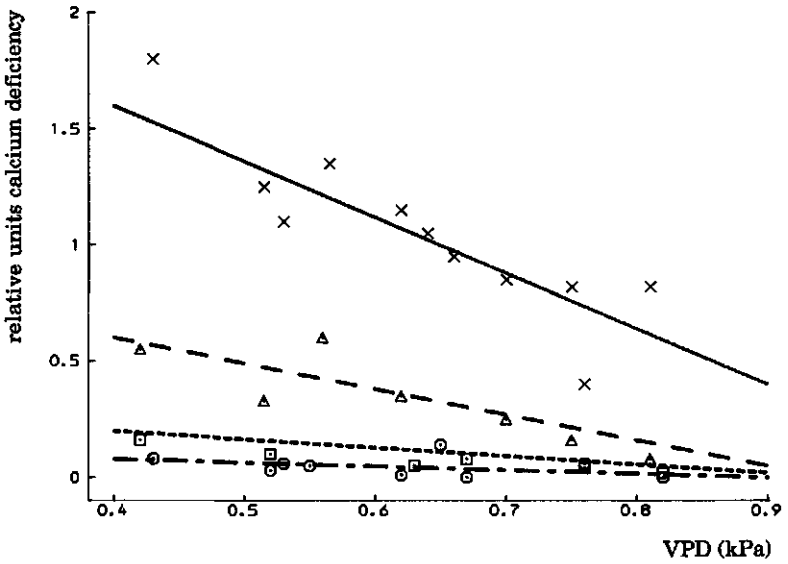

Fig. 1. Relationship between mean 24h vapour pressure deficit and calcium deficiency symptoms in leaves at four levels of calcium in the root environment. ×—×:Ca 16%, r=-0.84; △--△:Ca 28%, r=-0.90; □···□:Ca 47%, r=-0.48; ○-·-·○:Ca 64%, r=-0.51.

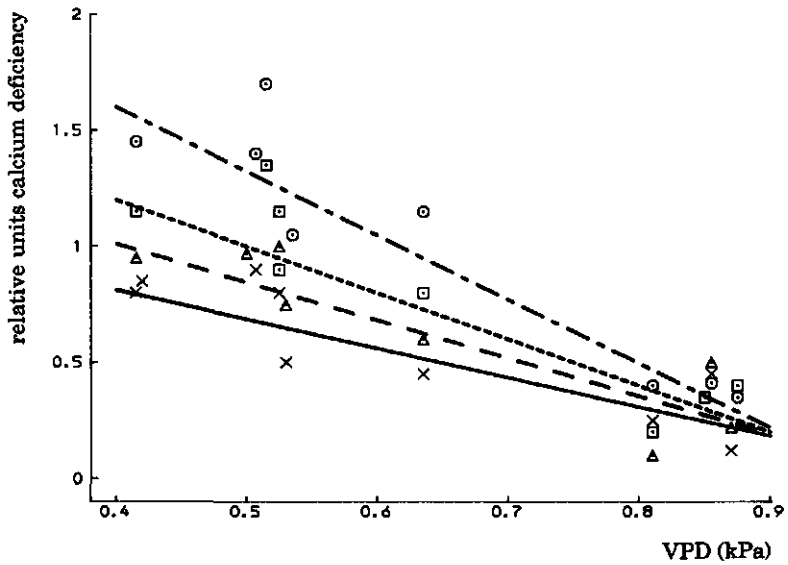

Fig. 2. Relationship between mean 24h vapour pressure deficit and calcium deficiency symptoms in leaves at four levels of EC in the root environment. ×—× :EC 2.1, r=-0.42; △--△ :EC 3.2, r=-0.43; □···□ :EC 4.1, r=-0.46; ○-·-·○ :EC 5.1, r=-0.51.

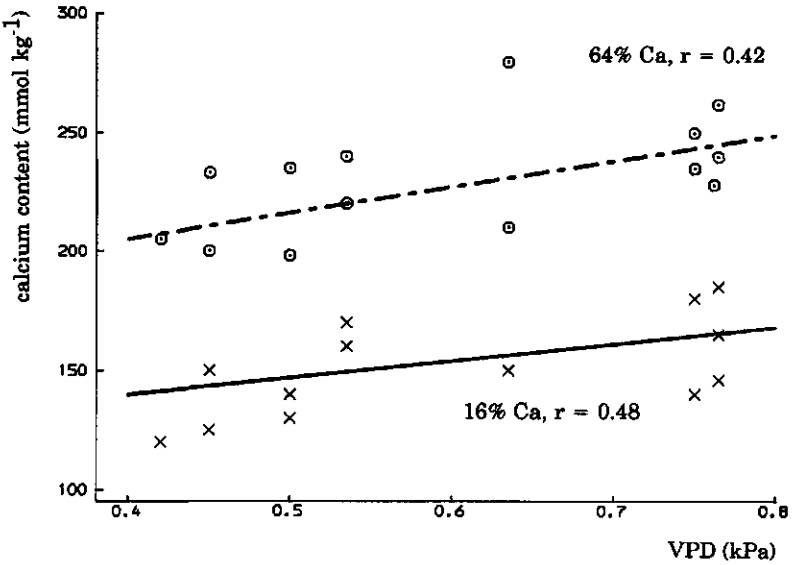

Fig. 3. Effect of mean 24h vapour pressure deficit on the calcium content of young leaves at two levels of calcium in the root environment.

Tissue analysis.- In Experiment 1, the calcium content of the young leaves decreased with decreasing calcium supply and decreasing VPD (Figure 3). For both the levels of calcium in the root environment shown (16% and 64%), the relationship between VPD and calcium content was significant at P=0.05. The calcium content of the leaves for the EC regimes 2 and 6(8)2 in Experiment 1 was 197 and 182 mmol kg^{-1} dry matter, respectively (significant at P=0.01). The calcium contents of the margins and centres of leaves with calcium deficiency symptoms for two calcium supply levels and the extreme environment treatments (l/l and h/h) are listed in Table IV. The calcium content of the leaf margin was more affected by humidity than that of the leaf centre. The average calcium contents of the leaf margin and centre at high humidity were 16% and 4% less, respectively, than at low humidity. The difference in calcium content of the leaf margin and leaf centre was 21%. The effect of humidity was less at high calcium supply than at low.

In Experiment 2, the leaf samples were taken from the extreme environmental treatments and the EC levels 1.6 and 4.5 dS m^{-1}. The results are listed in Table V. Although the differences were not significant, the tendency is for calcium content to be reduced with decreasing VPD and increasing EC. The relative contributions (in moles) of potassium, calcium and magnesium in the leaf samples were 75.4: 13.7: 10.9 % and 80.2: 9.5: 10.3 %

respectively for EC 1.6 and 4.5. At low humidity and high humidity the relative contributions were 78.8: 10.7: 10.4 and 76.9: 12.4: 10.7. The average calcium content of the leaves in Experiment 2 was lower than in Experiment 1, despite the higher calcium supply, which can be explained by differences in leaf age and the time of sampling.

DISCUSSION

The results of Experiment 1 show an interaction between VPD and calcium supply with respect to calcium deficiency (Figure 1). When more than 47% of cations are present as calcium, the effect of humidity on visible symptoms is negligible, but there is still an effect on the calcium content of the leaves (Figure 3). At low calcium supply however, humidity has a significant effect on both the visible symptoms and the calcium content of the leaves. Since calcium transport is affected by transpiration, the symptoms usually occur on slowly transpiring organs, such as young leaves, and are enhanced by high growth rates (Wiebe, 1981).

Vegetative growth of cucumber is enhanced by either high day or night humidity (Bakker *et al.*, 1987) so the occurrence of calcium deficiency can be explained by the combined effect of reduced transpiration and high growth rate under the high humidity conditions.

From the results of tissue analysis in Experiment 1, it can be concluded that the symptoms occur in leaves with a low calcium content at their margins (Table IV). At low calcium supply, the calcium content of the leaf margins is about 320 mmol kg^{-1} which is comparable with the deficiency level found by Adams (1985) in complete leaves. Severe symptoms occur at a level of 50 mmol kg^{-1} but the onset of symptoms was not found to be associated with any specific level of calcium in the leaves (Ward, 1973). Considering the calcium content of the leaf margins at the highest calcium supply (Table IV), it seems that visual symptoms (Figure 1) gradually become apparent below a calcium level in the leaf margins of around 500 mmol kg^{-1} dry matter.

The effect of VPD on visual symptoms increases with increasing EC (Figure 2). At EC 1.6 the level of calcium in the leaves is 41% greater than at EC 4.5 (Table V). This can be explained by the higher ion activity of calcium and a higher root pressure and transpiration at low EC.

Calcium deficiency in leaves can be avoided by increasing the calcium level of the nutrient solution or by reducing its EC. The optimum level, however, depends on the greenhouse environment. When more than 47% of the cations in the root environment are calcium, fruit production is reduced while a low EC results in a reduction of their keeping quality (Aalbersberg, 1984).

From the results obtained, it can be concluded that at low VPD the minimum percentage of calcium required in the root environment is about 40% of all cations. At high VPD, the calcium supply can be reduced to about 25% of

all cations. An EC of 2.0 dS m^{-1} seems desirable to avoid calcium deficiency and also from the point of view of production.

The authors wish to thank J. A. M. van Uffelen and G. W. H. Welles for their assistance and advice.

REFERENCES

Aalbersberg, Y. W. (1984). Growth and production depend on calcium and EC. Tuinderij, 64 (19), 28-31. [Dutch].

Adams, P. (1985). Nutritional disorders of cucumbers. Acta Horticulturae, 156, 251-256.

Bakker, J. C. (1985). Physiological disorders in cucumber under high humidity conditions and low ventilation rates in greenhouses. Acta Horticulturae, 156, 257-264.

Bakker, J. C., Welles, G. W. H. and Uffelen, J. A. M. van (1987). The effects of day and night humidity on yield and quality of glasshouse cucumbers. The Journal of Horticultural Science, 62 (3), 361-368.

Baër, J. and Smeets, L. (1978). Effect of relative humidity on fruit set and seed set in pepper (*Capsicum annuum* L.). Netherlands Journal of Agricultural Science, 26, 59-63.

Bes, S. S. de (1986). A summary of methods for analysing glasshouse crops. Publication Glasshouse Crops Research Station, Naaldwijk, The Netherlands, 5pp.

Bunce, J. A. (1984). Effects of humidity on photosynthesis. Journal of Experimental Botany, 35, 1245-1251.

Sanden, P. A. C. M. van de (1985). Effect of air humidity on growth and water exchange of cucumber seedlings. Acta Horticulturae, 174, 256-268.

Schaumlöffel, E. (1960). Uber die Kolorimetrische Bestimmung der Mikronährstoffe Kupfer, Zink, Kobalt, Mangan, Eisen und Molybdän aus einer Aschenlösung durch fraktionierte Extraktion. Landwirtschaft Forschung XIII, 278-286.

Sonneveld, C. and Krey, C. de (1986). Nutrient solutions for vegetables and flowers grown in water or substrates, Publication Glasshouse Crops Research Station No. 8, Naaldwijk, The Netherlands. 30pp.

Ward, G. M. (1973). Calcium deficiency symptoms in greenhouse cucumber. Canadian Journal of Plant Science, 53, 849-856.

Wiebe, H. J. (1981). Effect of water quantity on physiological disorders and quality of plants. Acta Horticulturae, 119, 67-76.

5.3 The effects of air humidity on growth and fruit production of sweet pepper (*Capsicum annuum* L.).

Journal of Horticultural Science, 64: 41-46.

SUMMARY

The effects of day and night humidity levels on autumn- and spring grown sweet pepper (*Capsicum annuum* L.) were investigated in two glasshouse experiments. In the autumn experiment four different humidity levels during the night were compared. In the spring experiment a high or low humidity by day was combined with either a high or low humidity during the night. The vapour pressure deficits achieved over the period in which the treatments were applied, varied from 0.33 to 0.79 kPa by day, from 0.27 to 0.86 kPa by night and the 24-h mean varied from 0.30 to 0.78 kPa. Temperature differences between the treatments were not more than 0.5 °C. No detrimental effects of humidity on growth were observed. Neither vegetative growth nor early or final yields were significantly correlated with humidity by day, night or 24-h mean but the mean fruit weight was increased by high humidity by night.

HUMIDITY has become more important as an environmental factor since the introduction of energy-saving measures in glasshouses. Reduced ventilation and increased insulation of glasshouses have led to restricted air exchange and a concomitant increase in humidity. High humidity can adversely affect crop yield by increasing disease incidence (Van Steekelenburg, 1986) and physiological disorders (Ehret and Ho, 1986). On the other hand, high humidity may enhance vegetative growth and improve production (Bakker *et al.*, 1987).

Although humidity is one of the main glasshouse environmental factors, information on its effects on glasshouse crops is limited. Grange and Hand (1987) reviewed the effects of humidity on growth of horticulture crops but very little information is available on its effects on yield and quality, presumably because most results have been obtained from growth chamber experiments. The effects on production of tomato were studied by Lipton (1970), and of cucumber by Bakker *et al.* (1987). With sweet pepper, however, information is restricted to the effects of 24-h mean humidity on fruit and seed set (Baër and Smeets, 1978).

The development of environmental control procedures to optimize crop production is one of the central issues in glasshouse climate research in the Netherlands (Kooistra, 1986), and requires information on the effects of humidity on vegetative growth, yield and quality. The responses of sweet pepper to different humidities have been studied in two experiments at the Glasshouse Crops Research Station (GCRS). The object of these experiments was to investigate if there were any significant effects of night and day humidity on growth and yield.

MATERIALS AND METHODS

The experiments were done in eight double-glazed compartments of a Venlo type glasshouse. The details of the technical equipment and control devices have been described by Bakker *et al.* (1987). In Experiment 1 (autumn 1986), four different night humidities, with one constant humidity by day, were applied from 28 August until final harvest on 25 October using cv. Bolero. The treatments were: a moderate humidity by day combined with either a very low (m/ll), a low (m/l), a moderate (m/m) or a high humidity by night (m/h). In Experiment 2 (spring 1987), four combinations of day and night humidity were used from 2 December 1986 until four weeks from the start of harvesting in the most advanced treatment (14 April 1987) using cv. Delphin. The humidity regimes were either continuously high (h/h) or low (l/l) or alternating low and high humidities by day and by night (l/h and h/l). In both experiments the humidity treatments were duplicated in separate compartments.

Different humidities were obtained by using combinations of a thermal screen, a humidification system and minimum ventilation (Bakker *et al.*, 1987). To increase the humidity, the screen was kept closed and the humidification system turned on. To reduce humidity in Experiment 1, the screen was opened and different minimum ventilation levels were applied. In Experiment 2, humidity was reduced by opening the thermal screen. It was not possible to continue the humidity treatments beyond 14 April in Experiment 2 because of increasing solar heat gain and rising outdoor ambient temperatures. The average daily radiation integrals (400-700 nm) inside the glasshouse, from planting until 25 October in Experiment 1 and until 14 April in Experiment 2, were 6.81 MJ m^{-2} day^{-1} and 1.35 MJ m^{-2} day^{-1}, respectively. The details of the environmental treatments, planting dates and cultivars are listed in Table I.

Temperature differences between the different treatments were minimized by a special heating procedure. The setpoints for heating in compartments with a low humidity treatment were adjusted to the temperature achieved in the compartment with the high humidity treatment (i.e. the compartment with the highest temperature because of the extra heat gain from the humidification system). CO_2 was controlled at 350 vpm and 600 vpm by day in Experiment 1 and 2 respectively. In Experiment 1 no additional root heating was applied, but in Experiment 2 the root temperature was controlled at 21-22 °C.

The plants were grown on rockwool slabs and irrigated with a complete nutrient solution; the excess solution was recirculated. Within each compartment, 11 sub-treatments were applied using solutions of different electrical conductivity (EC) but no significant interactions between environment and sub-treatment on fruit production and quality were found. Therefore, only the effects of humidity are presented. In Experiment 2, the total water uptake was measured on 14 plants per compartment grown at an EC of 3.0 dS m^{-1} and a pH of 5.5. At this EC level, the composition of the nutrient solution was: NO_3^-, 12.25; $H_2PO_4^-$, 1.25; SO_4^{2-}, 1.25; NH_4^+, 0.25; K^+,

TABLE I.
Details of the planting dates, cultivars and treatments for two experiments with sweet pepper.

Experiment number	Planting date	Cultivar	Day/night treatments					
			Symbol	Air temperature Heating °C	Air temperature Ventilation °C	Minimum Ventilation rate (*)	Screen % closed	Humidification + = on
1	15/07/86	Bolero	m/ll	20/16	20.5/16.5	0/6	-/-	-/-
			m/l			0/3	-/-	-/-
			m/m			0/0	-/-	-/-
			m/h			0/0	-/100	-/+
2	02/12/86	Delphin	l/l	23/18	24/19	0/0	85/85	-/-
			h/l			0/0	100/85	+/-
			l/h			0/0	85/100	-/+
			h/h			0/0	100/100	+/+

* ventilation rate expressed as times per hour

6.0; Ca^{2+}, 3.75; Mg^{2+}, 1.125 mmol l^{-1} and Fe, 10; Mn, 10; Zn, 4; B, 25; Cu, 0.5; Mo, 0.5 μmol l^{-1}.

The plants (*Capsicum annuum* L.) were planted at the 10th leaf stage at a density of 2.9 plants m^{-2}. The plants were trained with two stems; flowers were removed from the first 10 leaf nodes with no artificial pollination. Red fruits were harvested once a week, and their number, weight and market grade were recorded. Fruits with a fruit weight below 100 g or with blossom-end rot were graded as Class 2. In the last two weeks of the harvesting period, green as well as red fruits were harvested.

In Experiment 2 the keeping quality of the fruits was regularly assessed. The average plant length and total leaf area were recorded in Experiment 2; leaf area was estimated from measurements of the leaf dimensions of the individual leaves (Robbins and Pharr, 1987). Various relations between leaf area, leaf length and leaf width were tested and the best correlation was obtained between leaf area and leaf width using the following equation for leaves wider than 5 cm:

$$A = 16.6\ W - 51.4 \quad (r=0.825)$$

where: A = leaf area in cm^2, and W = the leaf width in cm. This relation did not differ significantly between the environmental treatments.

RESULTS

Environment.- The vapour pressure deficits (VPD) measured during the period in which the treatments were applied, and measured over the total period are presented in Table II. The range of VPD observed in Experiment 1 was relatively small compared to that in Experiment 2. In Experiment 1, humidities during the night were not as high as in Experiment 2 because high ventilation rates were necessary to control glasshouse temperature. In both experiments, the range of VPD during the night was greater than during the day.

Differences in 24-h mean temperature were not more than 0.5 °C in Experiment 1, and not more than 0.2 °C in Experiment 2 (Table II). The relative water uptake until 14 April 1987, using the l/l treatment as a reference, was 79.5, 77.5 and 74 % for the h/l, l/h and h/h treatment, respectively.

Vegetative growth.- No detrimental effects were observed of high humidities on vegetative growth and development. The plants grew well in all treatments. Plant length and total leaf area did not differ significantly between treatments (Table III) but the total leaf number and average area per leaf in l/h and h/h treatments were significantly different (P=0.05). Linear regression analysis showed that only the relation between vapour pressure deficit by day and the average area per leaf was significant (P=0.05).

Fruit production.- The treatments had no significant effect on the early and final yield of total fruit (Class 1 + Class 2) in either experiment (Table IV). The % Class 1 of early yield differed significantly between the l/l and h/h treatment in Experiment 2 (Table IV). Mean fruit weight of early yield was reduced significantly by low humidity by night in Experiment 2. No differences in % Class 1 and mean fruit weight of final yield were observed in either experiment.

The relations between VPD, early yield, final yield and mean fruit weight were examined by linear regression analysis. Final yields were negatively correlated with VPD measured over the period in which the treatments were applied (from 28 August until 25 October 1986 in Experiment 1 and from 2 December 1986 until 14 April 1987 in Experiment 2), as well as with the VPD measured over the period from planting until final harvest but no significant effects of VPD by day, night or 24-h mean on early or final yields were found in either Experiment. Also a 2×2 factorial analysis of variance showed no significant effects of day or night humidity on early and final yield (Experiment 2).

TABLE II

Day, night and 24-h mean temperature and vapour pressure deficit at different day/night humidity treatments for two cropping periods of sweet pepper in Experiments 1 and 2.

Experiment 1

	period 28/8/86-25/10/86						total period (15/7/86-5/10/86)					
	Temperature (°C)			VPD (kPa)			Temperature (°C)			VPD (kPA)		
	day	night	24h	day	night	24h	day	night	24h	day	night	24h
m/ll	23.0	19.2	20.5	0.76	0.79	0.78	24.2	19.0	21.0	0.86	0.70	0.74
m/l	23.5	19.4	21.0	0.75	0.72	0.72	24.5	19.2	21.3	0.84	0.66	0.72
m/m	22.8	19.2	20.5	0.64	0.60	0.64	24.0	18.9	21.0	0.79	0.57	0.64
m/h	23.1	19.4	20.7	0.79	0.53	0.61	24.3	19.1	21.2	0.86	0.51	0.61

Experiment 2

	period 02/12/86-14/4/87						total period (02/12/86-21/7/87)					
	Temperature (°C)			VPD (kPa)			Temperature (°C)			VPD (kPA)		
	day	night	24h	day	night	24h	day	night	24h	day	night	24h
l/l	24.4	20.2	21.7	0.66	0.86	0.75	24.8	19.9	22.0	0.78	0.67	0.71
h/l	24.7	20.1	21.8	0.41	0.72	0.56	24.8	19.8	22.0	0.62	0.58	0.59
l/h	24.3	20.5	21.9	0.63	0.42	0.50	24.7	20.1	22.1	0.72	0.44	0.59
h/h	24.9	20.0	21.9	0.33	0.27	0.30	25.1	19.9	22.2	0.59	0.31	0.44

TABLE III.

Measures of vegetative growth (per plant) of sweet pepper at 14 April 1987, at different day/night humidity regimes (Experiment 2).

Treatment day/night	Length cm	Leaf number	Leaf area m^2	Average leaf per leaf cm^2
1/1	158.0	300.8	1.59	52.9
h/1	144.0	304.0	1.54	50.8
1/h	147.8	278.6	1.52	54.9
h/h	154.8	312.6	1.54	49.7
LSD (P=0.05)	n.s.	25.5	n.s.	3.9

* - reduced leaf area as a consequence of leaf necrosis

TABLE IV.

Total (Class 1 + Class 2) fruit yield, %Class 1 fruit yield and mean fruit weight (MFW) of total fruit of sweet pepper grown at different humidity regimes for two production periods in Experiments 1 and 2.

Experiment 1

Treatment day/night	Early yield (to 9/10/86)			Final yield (to 25/10/86)		
	Total $kg\ m^{-2}$	Class 1 %	MFW g	Total $kg\ m^{-2}$	Class 1 %	MFW g
m/11	1.49	44.7	114.3	3.61	72.2	136.8
m/1	1.74	46.2	116.5	3.62	68.9	138.0
m/m	1.53	44.2	119.5	3.66	70.2	140.1
m/h	1.20	41.3	113.0	3.75	73.0	143.1
LSD (P=0.05)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Experiment 2

	Early yield (to 14/4/87)			Final yield (to 21/7/87)		
	Total $kg\ m^{-2}$	Class 1 %	MFW g	Total $kg\ m^{-2}$	Class 1 %	MFW g
1/1	0.97	95.2	112.5	10.81	84.6	145.5
h/1	1.20	96.2	119.1	11.37	85.7	147.9
1/h	1.03	96.9	130.7	11.08	86.2	148.5
h/h	1.02	97.5	132.3	11.91	86.1	146.2
LSD (P=0.05)	n.s.	2.3	9.9	n.s.	n.s.	n.s.

Mean fruit weight of total yield in Experiment 1 and of early yield in Experiment 2 were inversely correlated with VPD by night at P=0.05. The relations between mean fruit weight and VPD by night for both experiments are presented in Figure 1.

Fruit quality.- Keeping quality did not differ significantly between treatments and no significant relationships were found between keeping quality and humidity by day, night or 24-h mean (Janse, 1989).

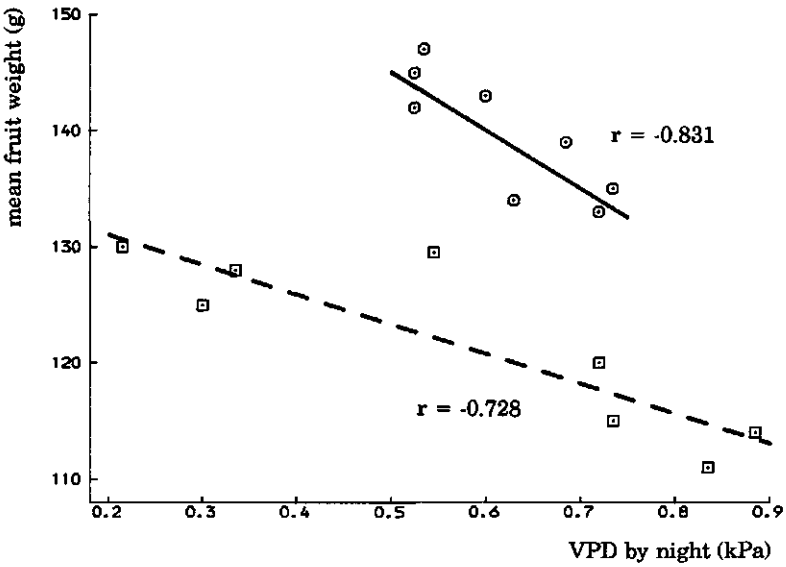

Fig. 1. Relation between mean fruit weight and vapour pressure deficit by night for Experiment 1 (total yield, o—o) and Experiment 2 (early yield, □-–□).

DISCUSSION

With sweet pepper, vegetative growth and yield are closely correlated with the 24-h mean temperature as well as with the day/night temperature amplitude (Bakker and Van Uffelen, 1988). The effect of the day/night temperature amplitude, however, is small compared to the effect of 24-h mean temperature. Since the 24-h mean temperature and the differences between day and night temperature were almost equal in all treatments in the present experiments (Table II), it was assumed that they did not produce any differences in vegetative growth and yield between treatments.

Vegetative growth of sweet pepper (expressed as length and total leaf area) was not affected by environmental humidity in the range investigated (Table III). This concurs with the results of Baër and Smeets (1978) who found no

effects in the range of 50 to 80% relative humidity (r.h.). Grange and Hand (1987) state that in the range 1.0 to 0.2 kPa VPD (i.e. 55 to 90% r.h. at 20 °C) no significant effects on physiology and development of horticultural crops are to be expected. However, the response of vegetative growth to humidity does vary between species; cucumber, for example, showed an increase in growth in the range of 0.75 to 0.4 kPa VPD (Bakker *et al.*, 1987).

From the vegetative development (Table III) one might expect an equal potential (dry matter) production capacity since the total dry matter production of a crop depends on light interception which, in turn, depends on leaf area (Fitter and Hay, 1981). With fruit vegetable crops, of course the major goal is a high fruit (fresh weight) production rather than dry matter production or vegetative growth. Differences in processes like dry matter distribution (dry matter content of the fruits), flowering, fruit set and fruit growth may account for variations in final fruit yield.

The dry matter content of sweet pepper fruits is not affected by humidity (Bakker, 1989), however, the mean fruit weight (fresh) was significantly higher at high nighttime humidity (Figure 1), but not by day. According to Bradfield and Guttridge (1984), this is due to the transport of water into fruits by root pressure, stimulated by high humidity by night. Since the dry matter content of the sweet pepper fruits is not affected (Bakker, 1989), these results suggest that at high humidity by night, the fruits account for a larger fraction of total dry matter than at low humidity by night.

Besides mean fruit weight, fruit set is also affected by humidity. Under normal growing conditions, without artificial pollination, fruit set of sweet pepper is improved by high humidity by day (Bakker, 1989). Since mean fruit weight is related to night-time humidity (Figure 1) and not humidity by day, the increase in number of fruits due to improved fruit set at high humidity by day, did not lead to a reduction in mean fruit weight. This response might be due to an increase in the assimilation rate of plants carrying fruits (Hall and Milthorpe, 1978).

As high humidity does not have significant detrimental effects on yield of sweet pepper or keeping quality (Janse, 1988), it may be concluded that, with respect to these parameters, it is unnecessary to control humidity within the range investigated.

This study was partly financed by the energy fund of the Ministry of Agriculture and Fisheries.

The author thanks G.W.H Welles and J.A.M van Uffelen for their assistance and advice during the experiments, and W.A. van Winden and H. Challa for their encouragement and assistance in preparing this paper.

REFERENCES

Baër, J., and Smeets, L. (1978). Effect of relative humidity on fruit set and seed set in pepper (*Capsicum annuum* L.). Netherlands Journal of Agricultural Science, 26, 59-63.

Bakker, J.C. (1989). The effects of environmental humidity on flowering, fruit set and fruit growth of sweet pepper. Scientia Horticulturae, 40, 1-8.

Bakker, J.C. and Van Uffelen, J.A.M. (1988). The effects of diurnal temperature regimes on growth and yield of sweet pepper. Netherlands Journal of Agricultural Science, 36, 201-208.

Bakker, J.C., Welles, G.W.H., and Van Uffelen, J.A.M. (1987). The effects of day and night humidity on yield and quality of glasshouse cucumbers. Journal of Horticultural Science 62, 361-368.

Bradfield, E.G. and Guttridge, C.G. (1984). Effects of night-time humidity and nutrient solution concentration on the calcium content of tomato fruit. Scientia Horticulturae, 22, 207-217.

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

Fitter, A.H. and Hay, R.K.M. (1981). Environmental Physiology of Plants. Academic Press, London, New York, 355pp.

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

Hall, A.J. and Milthorpe, F.L. (1978). Assimilate source-sink relationships in *Capsicum annuum* L. III. The effects of fruit excision on photosynthesis and leaf and stem carbohydrates. Australian Journal of Plant Physiology, 5, 1-13.

Janse, J. (1989). Effects of humidity, temperature and concentration of the nutrient solution on firmness, shelf life and flavour of sweet pepper fruits (*Capsicum Annuum* L.). Acta Horticulturae, 244, 123-131.

Kooistra, E. (1986). Developments in the control of growing conditions in Dutch glasshouse horticulture. Netherlands Journal of Agricultural Science 34, 381-385.

Lipton, W. J. (1970). Growth of tomato plants and fruit production in high humidity and at high temperatures. Journal of the American Society of Horticultural Science, 95, 674-680.

Robbins, N.Z. and Pharr, D.M. (1987). Leaf area prediction models for cucumber from linear measurements. HortScience, 22, 1264-1266.

Rylski, I. and Spigelman, M. (1982). Effects of different diurnal temperature combinations on fruit set of sweet pepper. Scientia Horticulturae 17, 101-106.

Van Steekelenburg, N.A.M. (1986). *Didymella bryoniae* on glasshouse cucumbers. Thesis, Agricultural University, Wageningen, The Netherlands, 105pp.

5.4 Effects of day and night humidity on yield and fruit quality of glasshouse tomatoes (*Lycopersicon esculentum* Mill.).

Journal of Horticultural Science, 65: 323-331.

SUMMARY

Two spring crops and one autumn crop of tomato (*Lycopersicon esculentum* Mill.) were grown under natural light conditions in a glasshouse at different day and night humidity levels. A high or low humidity by day was combined with either a high or low humidity by night. Vapour pressure deficits (VPD), achieved over the period in which the treatments were applied, ranged from 0.35 to 1.0 kPa by day, from 0.21 to 0.71 kPa by night, and the 24-h mean from 0.2 to 0.8 kPa. Temperature differences between treatments were restricted to less than 0.7 °C. Calcium deficiency and concomitant leaf area reduction was most severe under continuously high humidity. Stomatal conductance was significantly increased by high humidity. Early yield was higher at high humidity by day, but final yield was reduced by either a high humidity by day or night. Mean fruit weight and keeping quality were reduced under high humidity. Final yield and mean fruit weight were significantly related to 24-h mean VPD. It is concluded that yield losses under high humidity are due to restricted fruit growth. Humidity control with tomato should concentrate on the avoidance of long periods with high environmental humidity.

PROFITABILITY of glasshouse crops has been markedly improved over the last decade by the application of energy saving techniques which reduced the total energy input. Since ventilation and condensation are of major importance in the total vapour balance of glasshouses (Bakker, 1986), the reduced air exchange and higher inner surface temperatures in energy conserving greenhouses lead to an increase in humidity and consequently to a reduction of the transpiration (Stanghellini, 1987). It is obvious that final yield and quality of fruit vegetable crops may respond significantly to an increase in humidity (Lipton, 1970; Bakker *et al.*, 1987), although Grange and Hand (1987) state that, in the range of 1.0 to 0.2 kPa, the effect of humidity on physiology and development of horticultural crops is expected to be small. Final yield is the overall result of various processes like vegetative growth, flowering, fruit set and fruit growth, each to a greater or lesser extent affected by humidity. With tomato, yield may be significantly reduced by blossom-end rot which is closely related to humidity (Bradfield and Guttridge, 1984; Ehret and Ho, 1986). The production potential may be reduced by leaf area reduction resulting from calcium deficiency in leaves (Armstrong and Kirkby, 1979; Holder and Cockshull, 1988).

On the other hand however, owing to increased stomatal conductance, photosynthesis may be increased by high humidity (Acock *et al.*, 1976; Bunce, 1984). This leads to the hypothesis that day and night humidity differ in their effect, which is validated by results with cucumber (Bakker *et al.*, 1987). In this field information concerning tomato is lacking, as most results have been

obtained from experiments with continuously high and low humidity levels. A distinguishing feature of today's environmental control is the possibility of maintaining different day and night levels and to use integration routines to maintain long-term averages (de Koning, 1988). Although the technical facilities are available, the knowledge of crop responses is still insufficient to optimize the utilization of these techniques.

This work attempts to contribute to the knowledge of responses of growth and yield of tomato to day and night humidity levels. It is part of a research project of the Glasshouse Crops Research Station (GCRS) focusing on the effects of humidity on fruit vegetable crops. The results of three experiments conducted with tomato in spring and autumn 1985 and spring 1989 are presented in this paper.

MATERIALS AND METHODS

The experiments were performed in eight double glazed compartments of a Venlo type greenhouse, especially designed for research on the effects of glasshouse and root environment. Each compartment (dimensions 15.0 × 12.8 m^2) is equipped with a mobile polythene screen and a humidification system of water baths with a total area of 7 m^2. More details of the control devices and technical equipment are described by Bakker *et al.* (1987). Within each compartment 12 different root environment treatments (nutrient concentration, composition of nutrient solution, root temperature) can be applied in duplicate. Since no significant interactions between humidity levels and root environment were found with respect to growth and yield in either experiment, only the climate effects are described here, based on the results with a K:Ca ratio of 2 and an EC level of 3.0-3.5 dS m^{-1} (25 °C). The composition of the nutrient solution was: NO_3^-, 13.5; $H_2PO_4^-$, 2.0; SO_4^{2-}, 3.5; NH_4^+, 0.5; K^+, 9.5; Ca^{2+}, 4.75; Mg^{2+}, 1.5 mmol l^{-1} and Fe, 15; Mn, 10, ; Zn, 5; B, 25; Cu, 0.75 and Mo, 0.5 μmol l^{-1}. The solution was applied with the aid of a trickle irrigation system. Excess solution was recirculated and the irrigation frequency was relative to transpiration. The required conductivity was kept constant throughout, by weekly adjustments. Tomato seedlings were planted on rockwool slabs (dimensions 10×7.5 cm) placed in a gutter, when the inflorescences of the first truss were visible. Crop density was 2.5 plants m^{-2}. The plants were trained over the wire (height 2.5 m) and stopped at 0.5 m above the ground level.

In all experiments four day/night humidity regimes were duplicated in separate compartments. A high or low relative humidity by day (sunrise to sunset) was combined with either a high or low relative humidity by night (sunset to sunrise). The treatment symbols used are h/h and l/l for the continuously high and low humidities and h/l and l/h for the alternating low and high humidities. Different levels of day and night humidity were obtained

TABLE I.
Details of planting dates, cultivars and day/night environmental treatments for three experiments with tomato.

Experiment number	Planting date	Cultivar	Day/night treatments						
			Symbol	Air temperature Heating °C	Air temperature Ventilation °C	Minimum Ventilation %	Screen % closed	Humidification + = on - = off	Periods of treatments from
1	13/12/84	Calypso (round)	l/l	21/16	22/17	50/50	0/0	-/-	Planting until 15/04/85
			h/l			0/50	0/0	+/-	
			l/h			50/ 0	0/100	-/+	
			h/h			0/ 0	0/100	+/+	
2	18/07/85	Vision (beefsteak)	l/l	18/18	19/19	50/ 0	0/0	-/-	Planting until 12/11/85
			h/l			0/50	0/0	+/-	
			l/h			50/ 0	0/100	-/+	
			h/h			0/0	0/100	+/+	
3	21/12/88	Spectra (round)	l/l	17/17	17.5/17.5	0/ 0	90/90	-/-	Planting until 20/03/89
			h/l			0/ 0	100/90	-/-	
			l/h			0/ 0	90/100	-/+	
			h/h			0/ 0	100/100	-/+	

* day/night humidity treatment, l=low, h= high

by using the polythene screen and the humidification system and by adjusting minimum ventilation. In Experiment 1 and 2, to increase humidity, the humidification system was set on, and in addition at night the thermal screen was closed if the outside temperature fell below 12 °C. To reduce humidity the screen was opened and (day and night) a minimum ventilation setting, proportional to ambient temperature and windvelocity was maintained (Van de Vooren and Strijbosch, 1980). Pure supplementary CO_2 was given by day and controlled by conductometric devices at a level of 340 vpm, irrespective of the ventilator opening. In Experiment 3 the polythene screen was also used by day to increase the humidity. To reduce humidity, the screen was partly opened (day or night) thus restricting light differences between the treatments to less than 2% (measured difference of overall light transmission). The setpoint for the screen was independent of ambient and glasshouse environmental conditions. In this experiment a special heating procedure (Bakker, 1989) was used to prevent temperature differences. The glasshouse atmosphere was enriched with CO_2 to 800 vpm until the humidity treatments were stopped, subsequently CO_2 was controlled at 400 vpm, irrespective of the ventilator opening. Details of the planting dates, cultivars and environmental treatments are listed in Table I.

Calcium deficiency in the leaves was assessed visually according to a scale from 0 (no symptoms) to 3 (severe symptoms, yellow/necrotic leaf margins on more than 5 leaves per plant) in Experiment 1 and 3. In these experiments length, number of flowering and kinked trusses were also recorded at the end of the humidity treatments. Leaf area measurements were made on 8 plants per treatment in Experiment 3. In this experiment stomatal conductance was measured during three days in March with a Li-Cor steady state porometer LI-1600. Measurements were done on the first leaf above the fourth truss, in compartments with a high or low humidity. Three times a week fruits were harvested and their number and weight were recorded. Shelf-life of fruits from the h/h and l/l treatment was determined several times in each experiment according to the method described by Janse and Welles (1984).

RESULTS

Environments.- In Table II the temperatures and vapour pressure deficits achieved are presented for two cropping periods to indicate the environmental conditions until early (2-3 kg m^{-2}) and final yield. In the following, only the environmental conditions during the periods of treatment are used for analysis, so comments here are restricted to those periods.

Temperature differences (24-h mean) between the treatments were less than 0.7 °C, 0.4 °C and 0.1 °C in Experiments 1, 2 and 3, respectively (Table II). In Experiment 1, the vapour pressure deficits varied from 0.35 to 0.45 kPa by day, from 0.21 to 0.52 kPa by night and the 24-h mean varied from 0.23 to

TABLE II

Day, night and 24-h mean temperature and vapour pressure deficit at different day/night humidity treatments for two cropping periods* of tomato in Experiments 1, 2 and 3.

Treatment	First period						Total period					
	Temperature (°C)			VPD (kPa)			Temperature (°C)			VPD (kPA)		
	day	night	24h	day	night	24h	day	night	24h	day	night	24h
Experiment 1												
l/l	21.1	16.4	18.3	0.45	0.52	0.47	22.4	16.9	19.3	0.57	0.50	0.52
h/l	21.6	16.4	18.5	0.36	0.43	0.38	22.6	17.0	19.4	0.46	0.44	0.45
l/h	20.9	17.2	18.6	0.46	0.27	0.33	22.2	17.5	19.5	0.61	0.35	0.50
h/h	21.7	17.3	19.0	0.35	0.21	0.23	23.0	17.6	20.0	0.50	0.27	0.35
Experiment 2												
l/l	25.4	17.9	20.3	0.83	0.47	0.54	23.7	17.9	20.2	0.72	0.57	0.60
h/l	25.3	18.6	20.7	0.85	0.50	0.60	23.6	18.8	20.6	0.70	0.53	0.58
l/h	25.5	18.1	20.6	0.80	0.30	0.47	23.8	18.1	20.3	0.68	0.26	0.43
h/h	25.2	18.6	20.8	0.77	0.31	0.48	23.6	18.7	20.6	0.62	0.25	0.38
Experiment 3												
l/l	20.5	17.6	18.6	1.01	0.71	0.80	21.2	17.4	18.9	0.92	0.55	0.68
h/l	20.6	17.6	18.6	0.54	0.63	0.62	21.2	17.4	18.9	0.62	0.49	0.54
l/h	20.5	17.6	18.7	0.93	0.38	0.39	21.1	17.4	18.9	0.80	0.33	0.51
h/h	20.6	17.6	18.6	0.51	0.27	0.35	21.2	17.4	18.9	0.64	0.29	0.43

* The cropping periods were:
Experiment 1: first: 13/12/84 - 15/04/85, total period 13/12/84 - 24/06/85
Experiment 2: first: 18/07/85 - 26/09/85, total period 18/07/85 - 12/11/85
Experiment 3: first: 22/12/88 - 20/03/89, total period 22/12/88 - 01/06/89

0.47 kPa. In Experiment 2, night-time humidity was similar to that in Experiment 1, but humidity by day was lower because more ventilation was necessary to control temperature. Vapour pressure deficit by day varied from 0.62 to 0.72 kPa, by night from 0.25 to 0.57 kPa and the 24-h mean varied from 0.38 to 0.60 kPa (Table II). In Experiment 3 humidity was generally lower than in Experiment 1 and 2. Vapour pressure deficit by day varied from 0.51 to 1.01 kPa, from 0.27 to 0.71 by night and the 24-h mean from 0.35 to 0.80 kPa.

Vegetative growth and development.- No significant differences in length and rate of flowering were observed (Table III). In the h/h treatment in Experiment 1, the percentage of kinked trusses was significantly higher than in the other treatments (Table III). Relative units calcium deficiency in leaves was higher in the h/h treatment than in the other treatments in Experiment 1 and 3 (Table III). The h/h treatment also significantly reduced the leaf area between truss four and seven and of total leaf area until truss eight in Experiment 3 (Table IV). In Experiment 2 there were no signs of calcium deficiency.

TABLE III.
Length, number of flowering trusses, % kinked trusses (of truss 4 to 6 in Experiment 1 and of truss 1 to 8 in Experiment 3) and calcium deficiency of tomato plants grown at different day/night humidity regimes (l=low, h=high).

Treatment day/night	Exp.	Length (cm) 1	Length (cm) 3	Flowering truses 1	Flowering truses 3	% Kinked truses 1	% Kinked truses 3	Calcium deficiency 1	Calcium deficiency 3
l/l		180.1	220.7	8.6	7.5	60.4	40.0	1.1	0.0
h/l		181.0	229.2	8.8	7.7	64.6	54.5	1.1	0.0
l/h		180.0	226.0	8.7	7.4	69.2	48.2	1.4	0.0
h/h		184.6	226.3	8.8	7.5	80.8	44.5	2.6	1.5
LSD (P=0.05)		n.s.	n.s.	n.s.	n.s.	9.6	n.s.	1.3	0.1

TABLE IV.
Leaf area (cm^2) between individual trusses at four day/night humidity treatments (l=low, h=high) (Experiment 3).

trusses	h/h	l/h	h/l	l/l	LSD 5%
9-10	1427	1395	1396	1381	n.s.
8-9	1398	1551	1500	1520	n.s.
7-8	1118	1513	1427	1703	n.s.
6-7	809	1656	1414	1600	286
5-6	897	1599	1425	1590	391
4-5	1124	2018	1797	1902	442
3-4	1524	2146	1907	1931	617
2-3	1775	2095	1875	1860	n.s.
1-2	1984	1870	2084	1973	n.s.
0-1	1769	1586	1441	1731	n.s.
0-8	11000	14483	13370	14290	2612

Stomatal conductance.- A high humidity increased the stomatal conductance significantly under both low and high radiation conditions. Leaf temperature did not differ between the high and low humidity treatments.

On 2 and 13 March 1989 (dull weather, maximum global radiation outside 200 and 220 Wm^{-2}, respectively) the average conductance at high humidity was 0.93 and 0.84 cm s^{-1}, at low humidity 0.63 and 0.71 cm s^{-1}, respectively, both differences significant at $P<0.05$. Under brighter weather conditions (8 March 1989, maximum global radiation outside 590 Wm^{-2}), the difference was even more pronounced (Figure 1). Average conductance at low and high humidity was 0.47 and 1.14 cm s^{-1}, respectively (significant difference at $P<0.01$).

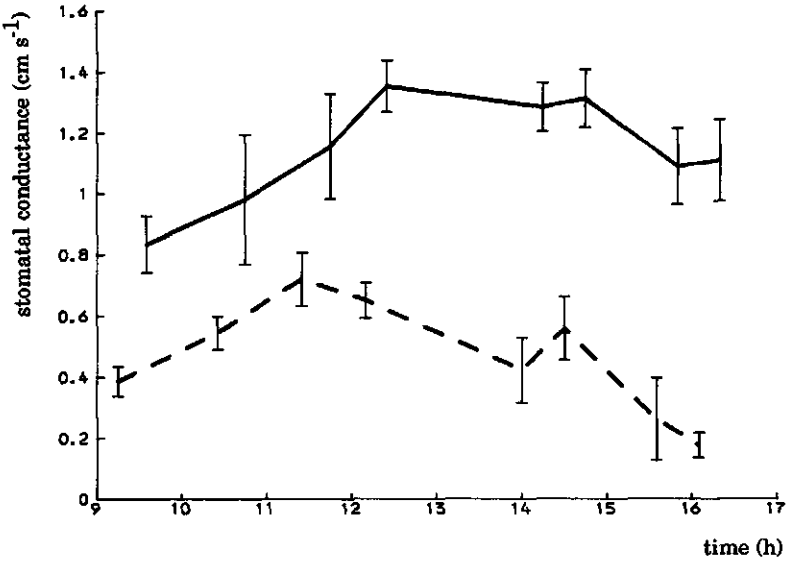

Fig. 1. Stomatal conductance of the first leaf above the fourth truss at two humidity levels by day, high: ——— (0.2 to 0.7 kPA); low: – – – – (0.7 to 1.6 kPa). Bars indicate the 95% confidence levels. Observations on a single day, 8 March 1989.

Fruit production and quality.- Fruit production was generally of good quality. The percentage of fruits with blossom-end rot was negligible in all experiments (less than 0.5%).

Analysis of the fruit production results of the three individual experiments showed that in none of the experiments early yield (kg m^{-2}) was significantly affected by humidity (Table V). However, the tendency in all experiments is a higher early yield at high day time humidity, which is confirmed by the two by two analysis of variance including all experiments (see below). The number of fruits differed significantly only in the early production period of Experiment 1, between the h/h and l/h treatment ($P=0.05$). Mean fruit weight (g $fruit^{-1}$) of early yield differed significantly in Experiment 3 (Table V). Final yield was significantly lower at the h/h than at the h/l and l/l treatments in Experiment 1. In Experiment 2 only the difference between the h/h and l/l treatments was significant. In Experiment 3 treatments did not differ significantly but the tendency was the same as in Experiments 1 and 2 (Table V). A significant difference in mean fruit weight of final yield was found between the h/h and l/l treatments in Experiment 1, and between the h/h and h/l and l/l treatments in Experiment 3. In Experiment 2 no significant differences were found (Table V).

The residual variance of each production parameter (yield, number of fruits and mean fruit weight) was examined by a standard analysis of variance procedure for the three individual experiments. For all production parameters, the three residual variances did not differ significantly at P=0.01 (Hartley's test for three variances at 3 degrees of freedom; Hartley, 1950). This enables the use of the three successive experiments as blocks. From a two by two analysis of variance of the pooled data it was concluded that there were no significant interactions between experiments and day or night humidity so in the latter only the main effects of day and night humidity and their interaction (also not significant) are discussed.

The major result is a significant increase of early yield by high humidity by day. Final yield is decreased by a high humidity either by day or by night without an interaction between day and night (Table VI). Mean fruit weight of final yield responded in a comparable way to day and night humidity. Number of fruits of final yield was slightly (3-4%) higher at low humidity by night, $P<0.05$. (Means of mean fruit weight and number of fruits are not presented because of the difference between round and beefsteak tomato).

From the final yields presented in Table VI, humidity by night seems to have a greater effect than humidity by day. However, this difference can be explained from the differences in VPD range by day and night in the various experiments (Table II) and the fact that humidity treatments were related to the astronomical day and night (average night length is equal to or greater than the day length). The former, combined with the absence of any interaction between day and night humidity (Table VI) indicates that final yield of tomato responds to the 24-h mean humidity.

TABLE V.

Fruit yield (kg m^{-2}) and mean fruit weight (MFW, g) of tomato grown at different day/night humidity regimes (l=low, h=high) for two production periods in Experiments 1, 2 and 3.

Treatment	Early yield						Total yield					
	Exp. 1 to 15/4/85		Exp. 2 to 1/10/85		Exp. 3 to 28/4/89		Exp. 1 to 24/6/85		Exp. 2 to 12/11/85		Exp. 3 to 2/6/89	
	Yield	MFW	Yield	MWF	Yield	MFW	Yield	MFW	Yield	MFW	Yield	MFW
l/l	2.54	51	3.20	239	2.25	62	13.11	58	9.75	173	9.30	66
h/l	2.88	52	3.45	239	2.35	65	12.36	55	9.59	171	9.21	65
h/h	2.39	51	3.35	232	2.01	64	11.96	55	9.14	168	8.73	63
h/h	3.06	52	3.50	230	2.44	71	10.60	50	9.05	165	8.06	60
LSD 5%	n.s.	n.s.	n.s.	n.s.	n.s.	1.4	1.72	4.2	0.63	n.s.	n.s.	4.5

TABLE VI.
Effects of day and night humidity on early and total yield (kg m^{-2}) of tomato (two-by-two analysis of variance including both experiments).

Day	high		low		Significance		
					main effects		interaction
Night	high	low	high	low	day	night	day × night
Early yield	3.00	2.89	2.58	2.60	<0.05	n.s.	n.s.
Total yield	9.25	10.38	9.42	10.71	<0.01	<0.01	n.s.

TABLE VII.
Coefficients for linear relations between final yield (kg m^{-2}), and mean fruit weight (MFW, g) of tomato, and 24-h mean vapour pressure deficit (VPD) measured over the period in which the treatments were applied. Y = a VPD + b.

Experiment		a	b	% variance accounted for	VPD range
1	yield	11.01	8.12	91.4	0.20 - 0.50 kPa
	MFW	35.95	41.83	92.0	
2	yield	3.03	7.90	61.7	0.45 - 0.61 kPa
	MFW	29.3	154.82	35.1	
3	yield	2.69	7.30	52.9	0.35 - 0.80 kPa
	MFW	17.14	52.22	55.8	

Coefficients a and b are significantly different from zero at P<0.05

Therefore relations between final yield (kg m^{-2}), mean fruit weight (g $fruit^{-1}$) and 24-h mean vapour pressure deficit were examined by regression analysis. Final yields and mean fruit weight were significantly related to the VPD, measured over the period in which the treatments were applied, in all experiments (Table VII).

Keeping quality.- In Experiment 1, shelf life was 20% shorter at the h/h treatment than at the l/l treatment (significant at P=0.05). In Experiment 2 no differences in shelf life between the treatments were observed. In Experiment 3, shelf life of fruits harvested from the first trusses was not significantly affected, fruits harvested of trusses 5 and 6 showed a reduction in shelf life of 15% when grown under continuously high humidity compared to the other treatments (significant at P=0.05).

DISCUSSION

In Experiment 3, temperature differences between the treatments were within the accuracy of temperature measurement. In Experiments 1 and 2, however, differences of 0.7 °C and 0.5 °C were observed (Table II), although attempts were made to minimize temperature differences between the treatments. With tomato, stem elongation and rate of flowering and fruit growth are correlated with temperature (Van de Vooren, 1986; de Koning, 1987). The effect of temperature on fruit growth decreases with increasing mean temperature and is most pronounced on early yields and at temperatures below 17-18 °C (van Holsteijn, 1987). According to the results of de Koning (1987), effects of the temperature differences achieved in these experiments on early yield (2-3 kg m^{-2}) are of minor importance. At a 0.7 °C higher temperature the gain in number of fruits of early yield is estimated to be 2 fruits m^{-2} (de Koning, 1987) which equals a benefit of 0.1 kg m^{-2}, or about 20% of the difference in early yield between the l/l and h/h treatment in Experiment 1 (Table V). The effect of the small temperature differences on final yield is even smaller and may be considered to be negligible (de Koning, 1987). From the former, and the absence of significant differences in length and rate of flowering (Table III), it is concluded to be unlikely that the small differences in temperature influence the observed effects on final yields. Low humidity, combined with low calcium supply or high salinity, may reduce yield by the incidence of blossom-end rot (Bradfield and Guttridge, 1984; Ehret and Ho, 1986). In these experiments however, the incidence of blossom-end rot was prevented by a low salinity level and a calcium concentration (190 mg l^{-1}) well over the deficiency level for blossom-end rot of 70 mg l^{-1} (Massey, Hayward and Winsor, 1984).

Humidity in the range investigated has no effect on stem elongation and rate of flowering (Table III), which concurs with Lipton (1970). Hurd (1973) also found very little effect of humidity on vegetative growth of tomato under low light conditions. Our results confirm the conclusions of Grange and Hand (1987), who state that in the humidity range of 0.2 to 1.0 kPa, no significant effects on vegetative growth, expressed as length, may be expected. Leaf area, however, was significantly reduced (Table IV), corroborating the results of Burrage, (1988). This is an effect of calcium which is closely correlated to high 24-h average humidity (Bakker *et al.*, 1987). At high humidity and low electrical conductivity less calcium is transported to young expanding leaves (Ehret and Ho, 1986).

Fruit growth of individual trusses is associated to assimilate import from nearby leaves, of which the three subtended are the most important source (Shishido and Hori, 1977). As the lower leaves (up to truss 3) were not suffering from calcium deficiency and subsequent growth reduction (Table IV), the positive effect of high humidity by day on early yield (Table VI) is considered the effect of increased stomatal conductance, which favours the carbon dioxide exchange and photosynthesis of the crop (Ward and Bunce,

1986). Similar results were obtained with cucumber (Bakker *et al.*, 1987) and chrysanthemum (Gislerød and Nelson, 1989). As discussed before, a part (up to one-fifth) of the beneficial effect of humidity by day may have been the result of temperature affecting the fruit number.

Higher up the plant, leaves between truss three and seven, which developed entirely during the treatment period, showed significant growth reduction (Table IV), resulting in less fruit growth in corresponding trusses, and consequently a reduced mean fruit weight of total yield (Table V). After the treatments were stopped, leaves developed normally and an equal fruit production of corresponding trusses could be expected. However, as no fruits were harvested of these trusses in Experiment 3, it is not possible to verify this expectation.

High humidity also promoted kinked trusses in Experiment 1 (Table III) which restricts the phloem sap flow into the fruits. As the latter is the main source for fruit growth of tomato (Ehret and Ho, 1986), it may further reduce fruit growth. The relative reduction of mean fruit weight in Experiment 1 is indeed greater than in Experiment 3, as can be seen in Table V. The reduced mean fruit weight of total yield at high humidity in Experiment 1 is therefore considered to be a combined effect of reduced leaf area and kinked trusses, in Experiment 3 it is ascribed to leaf area reduction only. In the long run, day and night humidities both decrease yield (Table VI), the assumed positive effect of higher stomatal conductance is then counteracted by the severe leaf area reduction (Table IV) and kinked trusses. If such counteraction is absent, a high humidity by day may improve yield.

Furthermore, from the coefficients in Table VII and the lower and upper levels of VPD in all experiments, it can be calculated that reducing the VPD from the highest to the lowest level reduces yield by 24, 5 and 13% in Experiments 1, 2 and 3, respectively. Associated mean fruit weight reductions are 18, 3 and 12%, respectively. So it is concluded that in all experiments yield reduction must be ascribed mainly to reductions in mean fruit weight, in keeping with the results of Lipton (1970).

For tomato long-term high humidity is detrimental, yield and keeping quality are reduced. Comparing the effects and ranges of VPD investigated in the various experiments, it seems obvious that yield responses are most pronounced at very low VPD levels. Within environmental control, humidity control with tomato should therefore receive a high priority and concentrate on avoiding long term high humidity levels, to optimize fruit production and quality.

The author thanks G.W.H. Welles and K. Buitelaar for their assistance and advice during the experiments, and W.A. van Winden for his encouragement and assistance in preparing this paper.

REFERENCES

Acock, B., Charles-Edwards, D.A., and Hand, D.W. (1976). An analysis of some effects of humidity on photosynthesis by a tomato canopy under winter light conditions and a range of carbon dioxide concentrations. Journal of Experimental Botany, 27, 933-941.

Armstrong, M.J., and Kirkby, E.A. (1979). The influence of humidity on the mineral composition of tomato plants with special reference to calcium distribution. Plant and Soil, 52, 427-435.

Bakker, J.C. (1986). Measurement of canopy transpiration or evapotranspiration in greenhouses by means of a simple vapour balance model. Agricultural and Forest Meteorology, 37, 133-141.

Bakker, J.C. (1989). The effects of air humidity on growth and fruit production of sweet pepper (*Capsicum annuum* L.). Journal of Horticultural Science, 64, 41-46.

Bakker, J.C., Welles, G.W.H., and Van Uffelen, J.A.M. (1987). The effects of day and night humidity on yield and quality of glasshouse cucumbers. Journal of Horticultural Science 62, 361-368.

Bradfield, E.G., and Guttridge, C.G. (1984). Effects of night-time humidity and nutrient solution concentration on the calcium content of tomato fruit. Scientia Horticulturae, 22, 207-217.

Bunce, J.A. (1984). Effects of humidity on photosynthesis. Journal of Experimental Botany, 35, 1245-1251.

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

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

Gislerød, H.R., and Nelson, P.V. (1989). The interaction of relative air humidity and carbon dioxide enrichment in the growth of *Chrysanthemum* x *morifolium* Ramat. Scientia Horticulturae, 38: 305-313.

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

Hartley, H.O. (1950). The maximum F ratio as a short-cut test for heterogeneity of variance. Biometrika, 37, 308-312.

Holder, R., and Cockshull, K.E. (1988). The effect of humidity and nutrition on the development of calcium deficiency symptoms in tomato leaves. In: The Effects of High Humidity on Plant Growth in Energy Saving Greenhouses, (Cockshull, K.E., Ed.)., Report EUR 11261, Office for Official Publications of the European Communities, Luxembourg, 53-60.

Holsteijn, G.P.A. van (1987). Small differences in temperature, great differences in yield. Groenten en Fruit, 42 (30), 42-43. [Dutch].

Hurd, R.G. (1973). Long-day effects on growth and flower initiation of tomato plants in low light. Annals of Applied Biology, 73, 221-228.

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

Koning, A.N.M. de (1987). Temperature in the heated tomato crop (3). For maximum yield ease up in time. Groenten en Fruit, 43 (23), 45-48. [Dutch].

Koning, A.N.M. de (1988). An algorithm for controlling the average 24-hour temperature in glasshouses. Journal of Horticultural Science, 63, 473-477.

Lipton, W. J. (1970). Growth of tomato plants and fruit production in high humidity and at high temperature. Journal of the American Society for Horticultural Science, 95, 674-680.

Massey, D.M., Hayward, A.C. and Winsor, G.W. (1984). Some responses of tomatoes to calcium concentration. Annual Report for 1983 of the Glasshouse Crop Research Institute, Littlehampton, 54-56.

Shishido, Y., and Hori, Y. (1977). Studies on translocation and distribution of photosynthetic assimilates in tomato plants. II. Distribution patterns as affected by phyllotaxis. Tohoku Journal of Agricultural Research, 30, 87-94.

Stanghellini, C. (1987). Transpiration of greenhouse crops, an aid to climate management. Thesis Agricultural University, Wageningen, The Netherlands, 150pp.

Vooren, J. van de, and Strijbosch, T. (1980). Glasshouse ventilation control. Acta Horticulturae, 106, 117-124.

Vooren, J. van de, Welles, G.W.H., and Hayman, G. (1986). Glasshouse crop production. In: The tomato crop, (Atherton J.G. and Rudich, J., Eds.). Chapman and Hall, London, New York, pp 581-624.

Ward, D.A., and Bunce, J.A. (1986). Responses of net photosynthesis and conductance to independent changes in the humidity environments of the upper and lower surfaces of leaves of sunflower and soybean. Journal of Experimental Botany, 37, 1842-1853.

5.5 Effects of day and night humidity on yield and fruit quality of glasshouse eggplant (*Solanum melongena* L.).

Journal of Horticultural Science, 65: 747-753.

SUMMARY

A spring and autumn crop of eggplant (*Solanum melongena*) were grown under natural light conditions in a glasshouse at different day and night humidities. A high or low humidity by day was combined with either a high or low humidity by night. Vapour pressure deficits (VPD) achieved over the period in which the treatments were applied, ranged from 0.44 to 1.18 kPa by day, from 0.24 to 0.91 kPa by night, with a 24-h mean from 0.34 to 0.99 kPa. The rate of plant development was unaffected by humidity. Fruit yields were reduced by continuously low VPD compared with the other treatments. The yield reduction could be attributed to less fruits picked. Mean fruit weight was higher at high humidity by day. Continuously high VPD increased calyx withering, low VPD had no detrimental quality effects but promoted the incidence of *Botrytis cinerea*.

ENVIRONMENTAL control will be more cost effective if more is known about the effects of the various environmental factors on crop productivity (yield and quality). The deficiency in knowledge of crop productivity to day and night humidity is one of the constraints on optimising the utilization of modern environmental control techniques.

The reported responses of vegetative growth (expressed as length, leaf area, fresh and dry weight) of various crops to environmental humidity are variable. Depending on the humidity range most results indicate an improvement of growth at high humidity (e.g. Hoffmann, 1979; Papenhagen, 1986). However, the majority of these results have been obtained with seedlings under continuously high or low humidities in growth chamber experiments. When grown under glasshouse conditions for longer periods of time, the same crop may show a different response compared to those in growth chamber experiments (e.g. Grange and Hand, 1987 and Gislerød and Nelson, 1989, for Chrysanthemum; Swalls and O'Leary, 1975 and 1976, for tomato). Moreover, within the humidity range glasshouse crops are generally exposed to (i.e. 0.2-1.0 kPa), yield responses differ significantly between species. Elevated environmental humidity increased final yield of cucumber whereas yield of tomato decreased (Bakker *et al.*, 1987; Bakker, 1990; Holder and Cockshull, 1990), while sweet pepper did not respond significantly in the range investigated (Bakker, 1989).

In most humidity studies it is impossible to distinguish the effects of humidity by day from those of night-time humidity. The importance of making a distinction between both effects has been indicated by recent research with cucumber and tomato (Bakker *et al.*, 1987; Bakker, 1990). Besides yield,

quality of the product (external quality, keeping quality) significantly affects the short- and long-term return for growers. Information on humidity effects on this aspect is limited although it is necessary to optimize environmental control.

Certain quality aspects (disorders) are related to calcium and can be attributed both to local shortage of calcium (deficiency in leaves: Holder and Cockshull, 1990; or in fruits: Bradfield and Guttridge, 1984) or to excess (gold specks in tomato fruits: den Outer and van Veenendaal, 1989). Humidity affects transpiration and thereby the uptake, transport and distribution of calcium (Ho, 1989). Low humidity promotes the transport of calcium to transpiring organs (leaves, calyx) whilst the transport to fruits is reduced. High humidity reduces calcium uptake suppressing transpiration but by night it favours calcium transport to fruits, reducing the incidence of blossom end rot (Bradfield and Guttridge, 1984).

The major fruit quality problem of eggplant in commercial practice is calyx withering (Maaswinkel, 1988) which reduces the market price, and promotes fruit rot during storage (Eindhoven, 1989). The main objective of this investigation was to study the fruit yield and quality responses (calyx withering and fruit rot) of eggplant to day and night humidity. The results of two experiments (spring and autumn crop) are described.

MATERIALS AND METHODS

Eight double-glazed compartments of a Venlo-type glasshouse for research on the effects of glasshouse and root environment were used in this study. Details of glasshouse dimensions, control devices, technical equipment and heating procedure to prevent temperature differences have been described in several previous papers (Bakker *et al.*, 1987; Bakker, 1989; Bakker, 1990).

Within each compartment different nutritional sub-treatments were applied. In Experiment 1 (spring crop) these comprised K/Ca, NO_3/SO_4 and NO_3/NH_4 ratios (for details: Maaswinkel, 1988). In Experiment 2, (autumn crop) nine Ca/Mg/P ratios were applied: Ca: 9, Mg: 1 mmol l^{-1}, Ca: 6, Mg: 4 mmoll $^{-1}$ and Ca: 2, Mg: 8 mmol l^{-1}, each combined with a P level of 0.5, 1.0 or 2.0 mmol l^{-1}. The nutrient solution was applied with a trickle irrigation system, excess solution was recirculated. No significant interactions between environment and sub-treatments on fruit yield and quality were observed in either experiment. Hence this paper is restricted to humidity effects. In both experiments four day/night humidity regimes were replicated in two compartments. A high or low relative humidity by day (sunrise to sunset) was combined with either a high or low relative humidity by night (sunset to sunrise). Continuously high and low humidities are indicated with the symbols h/h and l/l whilst h/l and l/h are used for the alternating low and high day/night humidities.

To increase humidity, a polythene screen was closed (day or night) and a humidification system switched on, both independent of ambient and glasshouse environmental conditions. To lower humidity, the screen was partly opened (day or night) and the humidification system switched off. Light differences between the low and high daytime humidity treatments were less than 2% (measured difference of overall light transmission).

In Experiment 1 (spring 1988) the treatments were applied from planting until end of March. In Experiment 2 (autumn 1989) the treatments were applied in the latter part of the cropping period. It was not possible to continue the treatments after 1 April in Experiment 1, or to start the treatments before 1 September in Experiment 2 because of high solar heat gain and elevated outdoor ambient temperatures.

Pure CO_2 was used to enrich the glasshouse atmosphere to 700 and 400 vpm, from dawn to dusk in Experiment 1 and 2, respectively, independently of the ventilator opening. Sowing dates, planting dates and environmental treatments are listed in Table I. Average daily photosynthetically active radiation (400-700 nm) in the glasshouses were 0.40, 0.43, 1.10, and 1.59 MJ m^{-2} day^{-1} for December 1987, January, February and March 1988, respectively (Experiment 1), and 4.27, 3.49, 2.35 and 1.34 MJ m^{-2} day^{-1} for July, August, September and October 1989, respectively (Experiment 2).

Seeds (*Solanum melongena*, cv. 'Dobrix') were sown in perlite. Seedlings were propagated on rockwool under standard conditions (day/night temperature 20/19 °C, nutrient solution: Ca: 6, Mg: 4, P: 1 mmol l^{-1}). At the 6-8 leaf stage the plants were transferred to their final cropping location and planted on rockwool slabs (dimensions 10×7.5 cm). Plants were arranged in N-S rows with a crop density of 2.5 plants per m^2 and were trained with two stems.

Increase in plant length during the periods of treatment was recorded in both experiments of plants grown at the standard nutrient solution Ca: 9, Mg: 4, P: 1 mmol l^{-1}. In Experiment 1 the leaf area was measured on eight plants per treatment at the end of the period of treatment. The leaf area of leaves removed during the cropping period was added to the measured values to give total leaf area production. Total number of flowers was counted on ten plants in each compartment in Experiment 1. Fruits were harvested once a week and records kept of their number, weight, presence of disorders (calyx withering and calcium deficiency) and occasionally their keeping quality at 20 °C and 90 % r.h.

RESULTS

Environments.- In Table II the average temperatures and vapour pressure deficits achieved during the periods of treatment are presented. Temperature differences (24-h mean) between the treatments were less than 0.2 °C and 0.5 °C in Experiment 1 and 2, respectively. In Experiment 1, average vapour

TABLE I.
Sowing and planting dates and details of environmental treatments for two experiments with eggplant.

Experiment	Sowing and planting dates	Treatment	Air temperature day/night Heating °C	Air temperature day/night Ventilation °C	Screen % closed	Humidification + = on - = off	Periods of treatments from
1	s: 8/10/87	1/1	21/18	22/19	90/90	-/-	planting
	p: 7/12/87	h/1			100/90	+/-	until
		1/h			90/100	-/+	30/3/88
		h/h			100/100	+/+	
2	s: 25/05/89	1/1	21/18	22/19	90/90	-/-	01/09/89
	p: 27/06/89	h/1			100/90	+/-	until
		1/h			90/100	-/+	19/10/89
		h/h			100/100	+/+	

pressure deficit achieved in the treatments ranged from 0.44 (h) to 1.04 kPa (l) by day and from 0.42 (h) to 0.91 kPa (l) by night. In Experiment 2, night-time humidity was higher than in Experiment 1 as a consequence of crop size and ambient conditions. Humidity by day was lower because more ventilation was necessary to control temperature. Average vapour pressure deficit by day achieved in the treatments ranged from 0.51 (h) to 1.18 kPa (l), and from 0.24 (h) to 0.85 kPa (l) by night. In both experiments humidity by day in the h/h treatment was higher than in the h/l treatment whereas in the l/l treatment it was lower than in the l/h treatment. At night the humidity was higher in the h/h than in the l/h treatment whereas it was lower in the l/l than in the h/l treatment.

Vegetative growth and development.- The crops showed normal development under the different environmental conditions. No visual detrimental effects were observed. Vegetative growth, expressed as plant length and leaf area, and the total number of flowers did not differ significantly between treatments (Table III). At the end of treatments in Experiment 1 the leaf area of removed leaves was 1.3 m^2 (average of all treatments, no significant differences).

Diseases.- At the end of the treatment period in Experiment 1 fruits were infected by *Botrytis cinerea*. On 30 March 1988, 30% of fruits (length >2 cm) were infected at the h/h treatment, whilst in the other treatments no infection was observed. In Experiment 2 first symptoms of *Botrytis* were observed at the continuously high humidity on young fruits (length <2 cm) at time of final harvest but no data were collected.

TABLE II

Day, night and 24-h mean temperatures and vapour pressure deficits at different day/night humidity treatments in Experiments 1 and 2.

Treatment	Experiment 1						Experiment 2					
	Temperature (°C)			VPD (kPa)			Temperature (°C)			VPD (kPA)		
	day	night	24h	day	night	24h	day	night	24h	day	night	24h
l/l	22.8	19.5	20.8	1.04	0.91	0.97	24.7	21.3	22.6	1.18	0.85	0.99
h/l	23.1	19.5	20.9	0.50	0.77	0.64	25.2	21.2	23.0	0.67	0.74	0.69
l/h	22.8	19.6	20.9	1.00	0.56	0.75	24.9	21.7	22.9	1.02	0.32	0.63
h/h	23.1	19.6	21.0	0.44	0.42	0.42	25.3	21.4	23.1	0.46	0.24	0.34

TABLE III.
Vegetative growth and flowering during treatment periods.

Treatment day/night	Experiment 1			Experiment 2
	Height cm	Leaf area m^2	Flower numbers	Height cm
1/1	85.3	2.41	46.5	59.7
h/1	86.2	2.51	48.8	64.0
1/h	83.8	2.41	48.0	62.1
h/h	86.5	2.40	47.3	55.9
LSD (P=0.05)	n.s.	n.s.	n.s.	n.s.

Fruit production.- Fruit production was analysed with a standard analysis of variance procedure for both experiments. In Experiment 1 the yield up to two weeks after the treatments were stopped was used in the analysis. In Experiment 2 yield from 14 September (two weeks after the start of the treatments) until final harvest was analysed, thus restricting results to fruits which grew for more than 50% of their maturation period under the various humidity treatments. (Average fruit maturation rate in autumn was 4 weeks, which is about one week shorter than during spring due to higher temperatures; Bakker, 1988).

Results show that neither yield (kg m^{-2}), number of fruits, nor the mean fruit weight were significantly affected by humidity (Table IV). However, the tendency is a lower yield at continuously high humidity. For all production variates (yield, number of fruits and mean fruit weight) the residual variances of both experiments did not differ significantly at P=0.01 (Hartley's test for two variances at 3 degrees of freedom; Hartley, 1950). The data of both experiments were pooled in a two by two analysis of variance in which the experiments were used as blocks. From this two by two analysis of variance it was concluded that there were no significant interactions between experiments and humidity treatments. Concerning yield and number of fruits, the interaction between day and night humidity was significant. At high humidity by night, increasing day-time humidity decreased yield and number of fruits. At low humidity by night, increasing day-time humidity had no significant effect. From Table V it can be seen that the interaction follows from the fact that the h/h treatment differs significantly in number of fruits and yield from the other treatments. Concerning mean fruit weight no significant interactions were observed, so main day and night effects were investigated. Mean fruit weight was significantly higher at high humidity by day, while mean fruit weight did not differ significantly between high and low humidity by night.

TABLE IV.
Number of fruits (number m^{-2}), fruit yield (kg m^{-2}) and mean fruit weight (MFW, g) of total fruit of eggplants grown at different humidity regimes.

Treatment day/night	Experiment 1			Experiment 2		
	number m^{-2}	kg m^{-2}	MFW g	number m^{-2}	kg m^{-2}	MFW g
l/l	12.5	2.85	228	7.5	1.73	231
h/l	13.1	3.09	235	7.1	1.70	239
h/h	13.9	3.06	220	7.2	1.62	228
h/h	12.1	2.71	224	5.7	1.46	255
LSD (P=0.05)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

TABLE V.
Effects of day and night humidity on number of fruits (number m^{-2}), yield (kg m^{-2}) and mean fruit weight (MFW, g) during periods of treatment of eggplant (two-by-two analysis of variance including both experiments).

Day	low		high		Significance (LSD 5%) main effects		interaction
Night	low	high	low	high	day	night	day × night
Number	9.99	10.55	10.10	8.91	-	-*	0.95
Yield	2.29	2.34	2.40	2.09	-	-	0.20
MFW	230	223	237	240	10.5	n.s.	n.s.

* - main effects not analysed as interaction is significant

Fruit quality.- In Experiment 1 calyx withering was significantly affected by humidity. The percentage of calyx withering did not differ significantly between the h/h, h/l and l/h treatment (average 6.5% of fruits) but the l/l treatment showed significantly more fruits with calyx withering (40% of fruits) than the other humidity treatments (Maaswinkel, 1988). In Experiment 2 no calyx withering was observed on fruits harvested during the period of treatment.

The percentage of fruits suffering from calcium deficiency was less than 2% in each treatment in both experiments. This was considered too low to be of any statistical interest. In neither experiment significant differences between treatments were found with respect to fruit rot during storage.

DISCUSSION

In Experiment 1, temperature differences between the treatments were almost within the accuracy of temperature measurement. In Experiment 2, however, differences of 0.5 °C were observed (Table II), although attempts were made to minimize temperature differences between the treatments. For most vegetable crops vegetative growth and rate of flowering are highly correlated with temperature (e.g. cucumber: Slack and Hand, 1983; tomato: de Koning, 1988; sweet pepper: Bakker and van Uffelen, 1988; eggplant: Takahashi *et al.*, 1974). As no significant differences between the treatments were observed with respect to plant length and rate of flowering (Table III), it seems unlikely that the small differences in temperature interfered with the observed effects of humidity.

Humidity in the range investigated has no effect on stem elongation and rate of flowering (Table III), which corresponds with the response of other fruit vegetable crops sweet pepper and tomato (Bakker, 1989; Bakker, 1990). Since leaf area was not significantly affected either (Table III), it is concluded that humidity in the range from 0.3 to 1.0 kPa has no significant effect on vegetative growth and development of eggplant.

The number of fruits was lower at the h/h treatment than at the other treatments (Table V). As flowering was not affected (Table III) and no significant differences in fruit maturation rate were observed (Bakker, 1988) this leads to the conclusion that at continuously high humidity, fruit set was lower than in the other treatments. This, combined with the environmental conditions (Table II), indicates reduced fruit set below VPD levels of 0.5 kPa.

Generally, mean fruit weight of fruit vegetable crops increases when the number of fruits is being restricted, however, the gain in mean fruit weight is not always sufficient to compensate for the loss of number of fruits (Stenvers and Staden, 1976; Hurd *et al.*, 1979). The results here support this as the loss in number of fruits at continuously high humidity is not compensated for by the small increase in mean fruit weight at high humidity by day (Table V). The decreasing yield at the h/h treatment can therefore be attributed to less fruits (Table V).

An additional detrimental effect of high humidity is the incidence of fungal diseases, in this case *Botrytis*, on fruits, after long term exposure to low vapour pressure deficits. Similar results have been reported by Winspear, *et al.* (1970) for *Botrytis* in tomato, and by van Steekelenburg and Welles (1988) for *Didymella bryoniae* in cucumber. However, due to the time of incidence it is concluded to be unlikely that the production results used in the analysis are affected by this fungal disease. Due to *Botrytis* infection, fruit and calyx may become detached (Eindhoven, 1989), so it seems plausible to argue that yield and quality at the continuously high humidity would have been decreased as result of *Botrytis*, if the periods of treatment could have been expanded.

This leads to the conclusion that with eggplants long periods of high

humidity (VPD below 0.5 kPa) should be avoided to prevent yield losses by low fruit set and the incidence of fungal diseases. Low humidities (in this case VPD above 0.7 kPa), however, reduce external fruit quality due to calyx withering and thereby lower the market price significantly. Consequently an intermediate humidity level (between 0.5 and 0.7 kPa VPD) meets both requirements of yield and quality and can be recommended.

The author thanks R.H.M. Maaswinkel, G.W.H. Welles, S.J. Paternotte for their assistance during the experiments and discussing the results, and W.A. van Winden for encouragement and assistance in preparing this paper.

REFERENCES

Bakker, J.C. (1988). Onderzoek luchtvochtigheid bij aubergine: gematigd niveau optimaal voor produktie en kwaliteit. Tuinderij, 69 (24), 48-49.

Bakker, J.C. (1989). The effects of air humidity on growth and fruit production of sweet pepper (*Capsicum annuum* L.). Journal of Horticultural Science, 64, 41-46.

Bakker, J.C. (1990). Effects of day and night humidity on yield and fruit quality of glasshouse tomatoes (*Lycopersicon esculentum* Mill.). Journal of Horticultural Science, 65, in press.

Bakker, J.C., and Van Uffelen J.A.M. (1988). The effects of diurnal temperature regimes on growth and yield of glasshouse sweet pepper. Netherlands Journal of Agricultural Science, 36, 201-208.

Bakker, J.C., Welles, G.W.H., and Van Uffelen, J.A.M. (1987). The effects of day and night humidity on yield and quality of glasshouse cucumbers. Journal of Horticultural Science, 62, 361-368.

Bradfield, E.G., and Guttridge, C.G. (1984). Effects of night-time humidity and nutrient solution concentration on the calcium content of tomato fruit. Scientia Horticulturae, 22, 207-217.

Eindhoven, W. (1989). Herfstteelt aubergine: Klimaatregeling vraagt extra aandacht. Tuinderij, 69 (19), 17.

Gislerød, H.R., and Nelson, P.V. (1989). The interaction of relative air humidity and carbon dioxide enrichment in the growth of *Chrysanthemum* × *morifolium* Ramat. Scientia Horticulturae, 38, 305-313.

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

Hartley, H.O. (1950). The maximum F ratio as a short-cut test for heterogeneity of variance. Biometrika, 37, 308-312.

Ho, L.C. (1989). Environmental effects on the diurnal accumulations of 45Ca by young fruit and leaves of tomato plants. Annals of Botany, 63, 281-288.

Hoffman, G. J. (1979). Humidity. In: Controlled Environment Guidelines for Plant Research. (T. W. Tibbits and T. T. Kozlowski, Eds), Academic Press, New York, 141-72.

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

Hurd, R.G., Gay, A.P., and Mountifield, A.C. (1979). The effect of partial flower removal on the relation between root, shoot and fruit growth in the indeterminate tomato. Annals of Applied Biology, 93, 77-89.

Koning, A.N.M. de (1988). The effect of different day/night temperature regimes on growth, development and yield of glasshouse tomatoes. Journal of Horticultural Science, 63, 459-463.

Maaswinkel, R.H.M. (1988). Aubergine: geringe verdamping beperkt kans op kelkverdroging. Groenten en Fruit 44 (22): 39.

Outer, R.W. den, and Veenendaal, W.L.H. van (1989). Gold speckles and crystals in tomato fruits (*Lycopersicon esculentum* Mill.) Journal of Horticultural Science, 63, 645-649.

Papenhagen, A. (1986). Hohe Luftfeuchte hat auf Planzen begrenzten Einfluss. Gartnerbörse und Gartenwelt, 36, 1343-1346.

Slack, G. and Hand, D.W. (1983). The effect of day and night temperatures on the growth, development and yield of glasshouse cucumbers. Journal of Horticultural Science, 58, 567-573.

Steekelenburg, N.A.M. van and Welles, G.W.H. (1988). Influence of day/night humidity and cation ratios and concentration in the nutrient solution on incidence of *Didymella bryoniae* in glasshouse cucumbers. Netherlands Journal of Agricultural Science, 36, 225-230.

Stenvers, N, and Staden, O.L. (1976). Growth, ripening and storage of tomato fruits (*Lycopersicon esculentum* Mill.) III. Influence of vegetative plant parts and effects of fruit competition and seed number on growth and ripening of tomato fruits. Gartenbauwissenschaft, 41 (6), 253-259.

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

Swalls, A.A., and O'Leary, J.W. (1976). Growth, water consumption and salt uptake of tomato plants in high humidity-high carbon dioxide greenhouse environments. Journal of the Arizona Academy of Science, 11, 23-26.

Takahashi, B., Eguchi, T., and Yoneda, K. (1974). Studies on the flower formation in tomatoes and eggplants. IV. Effects of temperature regimes and fertilizer levels on the flower bud differentiation in tomatoes and eggplants. Journal of the Japanese Society for Horticultural Science, 43, 237-246.

Winspear, K.W., Postlethwaite, J.D. and Cotton, R.F. (1970) The restriction of *Cladosporium fulvum* and *Botrytis cinerea*, attacking glasshouse tomatoes, by automatic humidity control. Annals of Applied Biology, 65, 75-83.

6. General discussion

It was clearly shown that the yields of the four crops respond differently to humidity. High humidity improved fruit yields of cucumber whilst the highest yields with tomato were obtained at the lowest humidity levels. Yield of eggplant was only slightly lower at high humidity while with sweet pepper no significant difference could be demonstrated (Table 6.1). A comparison with reports in the literature could only be made for tomato where the results are in accordance with those of Suto and Ando (1975) and Holder and Cockshull (1990).

Table 6.1 summarizes the major results of this study. Despite the significant effects of humidity on final yield of cucumber and tomato, the effect on the different production processes was not always clearly demonstrated. However, in some cases the measured responses tended to be in accordance with expected or estimated effects (e.g. dry matter production) and the lack of statistical significance is probably caused by the limited number of replications (Chapter 1) and the humidity range achieved in the various experiments. From other research it was concluded that, (despite a limited number of replications), significant effects were mostly observed when VPD differed by 1 kPa (Hoffman, 1979). Although attempts were made to make the variations in humidity as large as possible, actual differences in the various experiments were generally less than 1 kPa.

High humidities, though improving photosynthesis do not necessarily favour production because not all production processes respond to humidity in the same way. The influence of the various processes on final yield and the differences and similarities between the four crops will be discussed against the background of the relational diagram presented in Chapter 1.

Dry matter production

Crop photosynthesis and associated dry matter production depend on the total light interception and the light response curve of individual leaves. The effect of humidity on light interception is mediated through the slowly responding morphological component LAI as a result of effects on leaf formation and leaf expansion. The momentary effect of humidity on the rate of leaf photosynthesis operates through its effect on stomatal conductance.

Photosynthesis rate. Humidity has a significant effect on leaf conductance, both during the daytime and at night (section 2.3). In addition to the response of stomata to humidity that of the cuticular conductance may also explain the response of leaf conductance to humidity, especially at night (section 2.3).

Variations in leaf and crop photosynthesis due to variations in daytime humidity are limited to about 10 and 3% respectively (section 2.4). This effect is of the order of magnitude of actual observations with tomato (section 3.3; Acock et al., 1976). It was concluded that from differences in photosynthesis only small effects on yield (i.e. of the order of 3%) could be anticipated (Chapter 3).

Table 6.1
Major effects of humidity as observed with the four crops.

	cucumber	eggplant	sweet pepper	tomato	Chapter
final yield	+	0-	0	-	5
leaf conductance	+	+	+	+	2
photosynthesis (estimated)	+	+	+	+	2
leaf area	+	0	0	-	3 and 5
calcium deficiency	+	0	0	+	5
total dry matter	?	0	0	0+ (1)	
dry matter distribution	?	0	?	0	3
number of fruits	+	-	0	0	4 and 5
pollination	?	-	+	-	4
seed set	?	?	+	-	4
mean fruit weight	+	+	0+	-	4 and 5
external quality	-	+	0-	-	5
keeping quality	-	0	-	-	5

+ = more or higher at increased humidity, - = lower or less,
0 = unaffected, ? = not investigated
(1) = young plants

Leaf area. Total leaf area is determined by leaf number and size. With cucumber, the rate of leaf formation was greater at high humidity, especially on the side shoots. This is probably caused by improved lateral branching induced by high humidity (McIntyre, 1977). Also with tomato and pepper the number of leaves tended to be higher at high humidity (sections 3.3 and 5.3), results which are confirmed by Holder and Cockshull (1990), and Mortensen (1986). That the effect was only significant with cucumber is most likely caused by the way the crops are cultivated. With cucumber only two or three lateral branches are allowed to grow after removal of the main growing point. With the other crops under investigation, all lateral branches are removed or restricted to several leaves throughout the growth period, so these crops cannot benefit from more leaves through increased lateral branching.

Leaf expansion is improved by a high turgor pressure which is favoured by a suppressed transpiration rate (Gandar and Tanner, 1976; Bunce, 1978; Brown and Tanner, 1983). With both cucumber and tomato leaf area was indeed

improved by high humidity but the effect on leaf expansion was small (section 3.3), in accordance with results of van de Sanden and Veen (1991). The exception to this rule was the occurrence of visible calcium deficiency which caused reductions in leaf area. Humidity affects transpiration to a large extent (Stanghellini, 1987; Ho, 1988), not only through the effect on the vapour pressure gradient between the leaf and surrounding air but also due to the response of leaf conductance. Although nighttime transpiration rate is generally much lower than during the day, due to the long night length in winter/spring, elevated humidity at night in this study also significantly contributed to the reduction of the transpiration integral (section 5.3). This may explain why no clear difference between day and night humidity on leaf area was observed (sections 3.3 and 5.1). Especially in the early growth stage, better light interception may give rise to higher crop photosynthesis, resulting in a higher RGR at high humidity (van de Sanden and Veen, 1991).

In the long run, however, high humidity may cause calcium deficiencies (Bakker, 1985; Ehret and Ho, 1986; section 5.2) which may lead to leaf area reductions of up to 50% (Holder and Cockshull, 1990; section 5.5). These detrimental effects may overrule the increase in number of leaves and the slightly improved leaf expansion at high humidity.

Humidity and calcium

The effect of humidity on transpiration is much greater than on calcium uptake (Armstrong and Kirkby, 1979). However, relatively less calcium is transported to the apex and young expanding leaves at high humidity possibly by a change of calcium movement along the stem (Ehret and Ho, 1986).

Calcium is an important component in the determination of the mechanical properties of the cell wall such as wall plastic extensibility (Taiz, 1984; Baydoun and Brett, 1984) and the membrane permeability (van Goor, 1968; Pomeroy and Andrews, 1985). The threshold values of calcium content associated with visible symptoms and leaf area reduction are not well known for the various crops. With tomato the symptoms became apparent at a calcium level below 250 mmol kg^{-1} dry matter (Holder and Cockshull, 1990) and with cucumber at a level below 500 mmol kg^{-1} dry matter (section 5.2). Severe deficiency symptoms occur with tomato below 50 to 100 mmol kg^{-1} (Adams, 1988; de Krey et al., 1990) and for cucumber below 300 mmol kg^{-1} (Adams, 1985; section 5.2). The close correlation between calcium deficiency and 24-h average Vapour Pressure Deficit (section 5.2; Holder and Cockshull, 1990) suggests that the negative effects of reduced transpiration by day may be compensated for by a higher transpiration at night. With cucumber calcium deficiency symptoms were less pronounced than with tomato, while pepper and eggplant showed no visible symptoms or leaf area reduction at all. The reason for this difference is unclear and requires further research.

Although calcium deficiency may lead to smaller leaves due to deficiencies, at low humidity the calcium level in leaves increases thus probably reducing cell wall extensibility. It is suggested that at low humidity, besides the low turgor pressure due to the high transpiration rate, also the high calcium level attributes to a reduced leaf expansion.

As leaf area is an important determinant of crop photosynthesis, the relations between humidity, calcium and leaf area should be analysed in a more quantitative way to provide information on the optimal humidity for total leaf growth.

Dry matter distribution and content

Humidity had no significant effect on dry matter distribution between leaves, stem and fruits (section 3.3). At continuously elevated humidity the shoot/root ratio tended to increase, or in other words, shoot growth was enhanced at the expense of root growth, in accordance with several other observations (Swalls and O'Leary, 1975; Gislerød and Nelson, 1989). However, the gain in shoot dry weight was only marginal so that no substantial contribution to fruit dry weight is to be anticipated. As dry matter content of leaves, fruits and stems were also unaffected by humidity (section 3.3), differences in (fresh) fruit yield did not arise from a changed distribution or from a higher water content.

Humidity treatments were continued for long periods. Consequently both the availability of assimilates (through effects on stomata and leaf area) and the total sink strength (effects on fruit and seed set) were influenced. Assuming partitioning to be regulated by sink activity (Schapendonk and Brouwer, 1984; Marcelis *et al.*, 1989) it could well be that extreme humidity conditions over short periods of time may induce changes in dry matter partitioning by affecting pollination and seed set. Besides this possibility humidity may also influence dry matter distribution through a secondary effect. For example with eggplant, except for the direct effect on fruit set, at the end of the experimental period part of the fruits were infected by *Botrytis* causing fruit abortion. It seems plausible that this had an impact on dry matter distribution due to a decrease of total sink activity of fruits.

As dry matter distribution and content were unaffected by humidity it is concluded that the major effect of high humidity on yield is mediated through its impact on the light interception resulting from either the enlargement (through the number of leaves and leaf expansion) or the decrease of the LAI (through calcium deficiency) and the (marginal) effect on photosynthesis as such.

Specific day/night effects

It is well known that humidity by day has a specific effect on photosynthesis and pollination. Beneficial effects on photosynthesis have been discussed previously, the effects of high humidity on pollination are negative (except for pepper). However, their impact on final yield is generally limited (largest effects with tomato). Only with cucumber a significant effect of day time humidity on yield could be demonstrated (section 5.1). With pepper fruit weight was specifically related to humidity by night (sections 4.3 and 5.4). It was suggested that this positive effect of night-time humidity is possibly caused by a higher root pressure which favours the water transport into the fruits (Bradfield and Guttridge, 1984). However, a positive pressure can only build up when canopy transpiration is below the rate of active water uptake. With cucumber, rate of active water uptake was estimated to be about 15 g $m^{-2}h^{-1}$ (Welles *et al.*, 1984), which is relatively low compared to the normal night-time transpiration rates which may be up to 40-60 g $m^{-2}h^{-1}$ for cucumber (de Graaf and van den Ende, 1981) and 30-40 g $m^{-2}h^{-1}$ for tomato (de Graaf, 1983; Stanghellini, 1987). Only under conditions with extreme high humidity crop transpiration will be suppressed below 15 g $m^{-2}h^{-1}$, e.g. for tomato below a VPD of about 0.15 kPa (Stanghellini, 1987). Consequently periods with a positive water potential will generally be not so common. Crops which have a relatively low leaf conductance at night, e.g. pepper and eggplant (section 2.3) and a consequently low nighttime transpiration (Seginer *et al.*, 1990) have probably an advantage over cucumber which has a relatively high leaf conductance and nighttime transpiration. Yet with eggplant this effect of nighttime humidity was not observed and more knowledge on the actual root pressure and influences of the root environment is required to support this suggestion.

Discrepancies with results obtained in controlled environments

Humidity affects processes involved in production with largely different response times and this is most likely one of the major causes for differences found between controlled environment and long term glasshouse experiments (Swalls and O'Leary, 1975; 1976). When plants are grown in controlled environments (e.g. growth chambers), due to space-limitations and the costs of operation, the period of exposure is relatively short. The effects observed will reflect mainly the beneficial influence on processes with a short response time (e.g. photosynthesis and leaf expansion) since the period of exposure is not long enough to induce the detrimental effects described in this study. Such time dependent crop responses were observed with tomato where high humidity had a positive effect on early yield whilst in the long run strongly negative effects were demonstrated (section 5.4). It is obvious that this implies a danger of

extrapolating results from short term growth chamber experiments only, to practical glasshouse cultures.

Consequences

In commercial practice it is commonly accepted that plants grown under a high humidity level are "weak" or "soft" and are more sensitive to sudden changes in the glasshouse environment. There are indeed reasons to believe that high humidity affects plant and fruit quality in a negative way. For instance tomato fruits grown at high humidity generally have a shorter shelf life because they become soft more quickly (Janse and Welles, 1984), which may be ascribed to a faster loss of water. Also the reduced root growth after exposure to high humidity possibly contributes to leaf damage observed after a sudden increase of transpiration (Bakker, 1984). Finally it is possible that adaptations of stomatal density may be at least partly responsible for the "weaker" plants with respect to disease resistance (section 2.2).

With tomato it is normal practice to encourage the plants to enter the reproductive phase by restricting their water supply, resulting in "hard" plants with a higher percentage of dry matter as opposed to "soft" plants grown at abundant water supply (de Koning and Hurd, 1983). This is probably caused by a combined effect of limited water supply and concomitant high EC level. The effects of EC on dry matter content and leaf water potential are more pronounced than the effects of humidity in the range investigated here (van de Sanden and Veen, 1991). It can be concluded that to avoid "soft" plants the manipulation of the root environment seems a more effective and less costly method than reducing the humidity.

For cucumber it was estimated that, at the current energy prices, the energy costs of measures to prevent condensation during the early morning hours, are equal to or even higher than the yield losses due to infected fruits by *Mycosphaerella* (Bakker *at al.*, 1990). Yet, in commercial practice it is generally argued that the potential beneficial effects of high humidity do not compensate for the lower quality and the (long term) risks associated to high humidity (e.g. Welles, 1985; Jarvis, 1989). Especially when energy prices are relatively low, reducing the humidity by heating and ventilating simultaneously is considered an acceptable "insurance premium" to prevent diseases and to maintain a healthy crop and a good fruit quality. In fact nowadays growers seem to revert to the control strategies of the 1960s when it was common practice to prevent high humidity by simultaneously heating and ventilating (van de Vooren *et al.*, 1986). Simulations with a greenhouse/crop model (Houter *et al.*, 1989) indicated that these measures require a considerable amount of energy, being of the order of 15-25% of total annual energy costs. However, bearing the results of this study in mind, it is questionable whether this control strategy is necessary (and economic) for extended periods of time, at least for cucumber, pepper and

eggplant. However, due to the significant spatial variation in greenhouse environment (Bakker and Van Holsteijn, 1989) in fact the coldest spots, with consequently highest (relative) humidity and most risk of condensation (Strijbosch, 1976) primarily determine the growers humidity control strategy (Zandbelt, 1984). As a consequence the humidity control strategies used, require more energy than theoretically necessary. Reduction of horizontal temperature variations will not only contribute to a better energy efficiency (Bakker and Jacobs, 1986) but also to a more uniform and higher yield (Bakker and van Holsteijn, 1989). Furthermore a higher humidity setpoint will be acceptable due to the reduced risk of condensation and this in turn will also contribute to a more efficient use of energy.

As yield and quality of the various crops respond entirely differently to humidity, the humidity control strategy is different for each crop (Chapter 5).

In general the response of an organism to an environmental factor may depend on the point of time (day, night, growth stage), duration of the exposure and on the level of that factor (Levitt, 1980) in which the level×duration integral is generally referred to as dose. Besides the more gradual response of plants to different doses, effects of environmental factors sometimes can be characterized by actual threshold values (e.g. in the case of temperature: direct cold or heat damage; for humidity: condensation on leaves). When comparing the effects of humidity with those of other environmental factors it is obvious that especially temperature and light are far more important (e.g. Slack and Hand, 1983, de Koning, 1990) within the normal range in commercial glasshouse cultivation. The response of growth and yield to humidity shows a certain similarity with the response to temperature, i.e. a close relationship with the average level of either temperature or humidity. The crop apparently is capable of compensating for a period with a low level by a period with a high level if certain level×time integrals (doses) are not exceeded (de Koning, 1990).

The ability of processes with a long response time to compensate for deviations from an average level offers a way to optimize environmental control. The acceptable deviations from the average level define the room for optimization of processes with a short response time.

For environmental factors the acceptable range is generally smaller at longer periods of exposure (Figure 6.1). This research mainly concentrated on continuous exposure to humidity (right of line B, Figure 6.1).

The detrimental effects of high humidity on yield are generally a consequence of calcium related disorders and leaf area reduction. The idea suggested by Aikman and Houter (1990) to use knowledge on calcium uptake and distribution as affected by environmental humidity and transpiration, together with better defined threshold values for calcium deficiency within environmental control strategies, should therefore receive attention in future research. This might lead to the definition of a minimum transpiration level

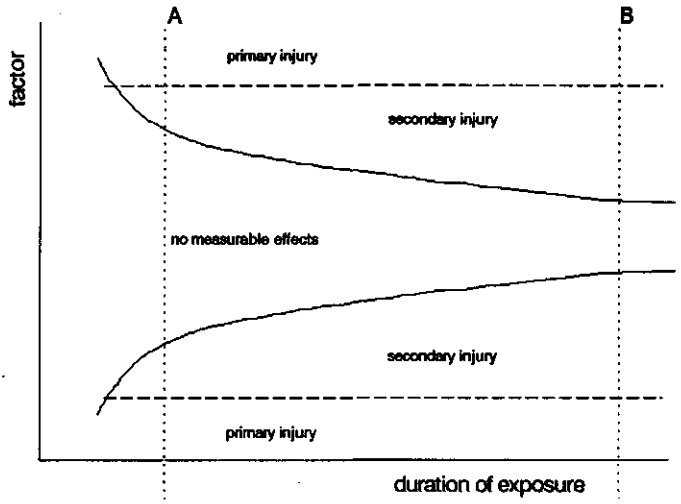

Figure 6.1
Schematic relation between dose (level×duration of exposure) of an environmental factor and crop response. Left of line A: very short period of exposure, right of line B: continuous exposure.

(i.e. lower boundary value in Figure 6.1) as a criterion instead of a long term maximum humidity level.

For optimization of crop growth and production it is necessary to keep the average temperature and humidity levels within a given range and at the same time gain maximum profit of the momentary conditions as light and CO_2. The use of more sophisticated control strategies may improve (economic) production, but more information is necessary, especially due to interactions between the various processes. The development of growth and production models based on processes like photosynthesis and dry matter distribution seems a promising way to represent this information. In these models knowledge on the source/sink relations is a major bottleneck (Spitters and van Keulen, 1990), especially for crops which grow indeterminately. To simulate the dynamic changes of dry matter partitioning, the influence of humidity on seed set could be included within the sink/source regulation of dry matter of tomato, using the quantitative response of pollen release and adhesion to the stigma. With cucumber, having parthenocarpic fruit set, dry matter distribution remains fairly constant within the humidity range investigated (0.2 to 0.7 kPa VPD). The implementation of the results obtained in this study with respect to stomatal behaviour (section 2.3) is another step in the direction of including humidity effects in the short term control strategy.

References

Acock, B., Charles-Edwards, D.A. and Hand, D.W., 1976. An analysis of some effects of humidity on photosynthesis by a tomato canopy under winter light conditions and a range of carbon dioxide concentrations. J. Exp. Bot., 27: 933-941.

Adams, P., 1988. Some effects of environment on the calcium status of tomato leaves. In: K.E. Cockshull, Ed., The effects of high humidity on plant growth in energy-saving greenhouses. Report EUR 11261, Office for Official publications of the European Communities, Luxembourg: 61-70.

Aikman, D.P. and Houter, G., 1990. Influence of radiation and humidity on transpiration: Implications for calcium levels in tomato leaves. J. Hort. Sci., 65: 245-253.

Armstrong, M.J. and Kirkby, E.A., 1979. The influence of humidity on the mineral composition of tomato plants with special reference to calcium distribution. Plant and Soil, 52: 427-435.

Arny, C.J. and Rowe, R.C., 1991. Effects of temperature and duration of surface wetness on spore production and infection of cucumbers by *Didymella bryoniae*. Phytopathology, 81: 206-209.

Bakker, J.C., 1984. Effects of changes in ventilation on cucumber. Acta Hort., 148: 519-524.

Bakker, J.C., 1985. Physiological disorders in cucumber under high humidity conditions and low ventilation rates in greenhouses. Acta Hort., 156: 257-264.

Bakker, J.C. and Jacobs, A.F.A., 1986. Met thermografie naar betere temperatuurverdeling. Groenten en Fruit, 41 (35): 34-35.

Bakker, J.C. and Holsteijn, G.P.A. van, 1989. Horizontal temperature distribution in heated glasshouses: causes and effects. Acta Hort., 245: 226-231.

Bakker, J.C., Nienhuis, J.K., Steekelenburg, N.A.M. van, and Welles, G.W.H., 1990. Korte notitie berekeningen aan gasverbruik bij komkommer in relatie tot het voorkomen van *Mycophaerella*, PTG, Naaldwijk, 6pp.

Baydoun, E.A.H. and Brett, C.T., 1984. The effect of pH on the binding of calcium to pea epicotyl cell walls and its implications for the control of cell extension. J. Exp. Bot., 35: 1820-1831.

Bradfield, E.G. and Guttridge, C.G., 1984. Effects of night-time humidity and nutrient solution concentration on the calcium content of tomato fruit. Scientia Hort., 22: 207-217.

Brown, P.W. and Tanner, C.B., 1983. Alfalfa stem and leaf growth during water stress. Agronomy Journal, 75 (5): 799-805.

Bunce, J.A., 1978. Effects of water stress on leaf expansion, net photosynthesis, and vegetative growth of soybeans and cotton. Can. J. Bot., 56: 1492-1498.

Challa, H., 1990. Crop growth models for greenhouse climate control. In: R.Rabbinge, J. Goudriaan, H. van Keulen, F.W.T. Penning de Vries and H.H. van Laar, Eds., Theoretical production ecology: reflections and prospects. Simulation monographs 34, Pudoc, Wageningen: 125-145.

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

Gandar, P.W. and Tanner, C.B., 1976. Leaf growth, tuber growth and water potential in potatoes. Crop Science, 16 (4): 534-538.

Gislerød, H.R. and Nelson, P.V., 1989. The interaction of relative air humidity and carbon dioxide enrichment in the growth of *Chrysanthemum* × *morifolium* Ramat. Scientia Hort., 38: 305-313.

Goor, B.J. van, 1968. The role of calcium and cell permeability in the disease blossom-end rot of tomatoes. Physiologia Plantarum, 21: 1110-1121.

Graaf, R. de, 1983. Verdamping van tomaat. Invloed van schermen gedurende de nacht. Groenten en Fruit, 39 (21): 26-27.

Graaf, R. de and van den Ende, J., 1981. Transpiration and evapotranspiration of the glasshouse crops. Acta Hort., 119: 147-158.

Ho, L.C., 1988. Effects of high humidity and high salinity on calcium distribution in tomato plants. In: K.E. Cockshull, Ed., The effects of high humidity on plant growth in energy saving greenhouses. Report EUR 11261, Office for Official publications of the European Communities, Luxembourg: 71-80.

Ho, L.C. and Hewitt, J.D., 1986. Fruit development. In: J.G. Atherton and J. Rudich, Eds., The tomato crop. Chapman and Hall, London, 201-240.

Hoffman, G.J., 1979. Humidity. In: T.W. Tibbits and T.T. Kozlowski, Eds., Controlled environment guidelines for plant research. Academic Press, New York: 141-172.

Holder, R. and Cockshull, K.E., 1990. Effects of humidity on the growth and yield of glasshouse tomatoes. J. Hort. Sci., 65: 31-39.

Houter, G., Gijzen, H., Nederhoff, E.M. and Vermeulen, P.C.M., 1989. Simulation of CO_2 consumption in greenhouses. Acta Hort., 248: 315-320.

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

Jarvis, B., 1989. Dewpoint from the speaking plant. Grower, 112 (7): 14-17.

Koning, A.N.M. de, 1990. Long term temperature integration of tomato. Growth and development under alternating temperature regimes. Scientia Hort. 45, 117-127.

Koning, A.N.M. and Hurd, R.G., 1983. A comparison of winter-sown tomato plants grown with restricted and unlimited water supply. J. Hort. Sci., 58: 575-581.

Krey, C. de, Welles, G.W.H., Bakker, J.C., Buitelaar, K. and Janse, J., 1990. Luchtvochtigheid en calcium/kalium bij tomaat; een proef uitgevoerd in de Energiekas in het voorjaar van 1989. Intern verslag PTG, 49, 23pp.

Levitt, J., 1980. Responses of plants to environmental stresses. Volume II: Water, radiation, salt and other stresses. Academic Press, New York, 607 pp.

Marcelis, L.F.M., Heuvelink, E. and Koning, A.N.M. de, 1989. Dynamic simulation of dry matter distribution in greenhouse crops. Acta Hort., 248: 269-276.

McIntyre, G.I., 1977. Environmental control of lateral budgrowth in sunflower (*Helianthus annuus*). Can. J. Bot., 55: 2673-2678.

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

Pomeroy, M.K. and Andrews, C.J., 1985. Effect of low temperature and calcium on survival and membrane properties of isolated winter wheat cells. Plant Physiol., 78: 484-488.

Sanden, P.A.C.M. van de, and Veen, B.W., 1991. Effects of air humidity and nutrient solution concentration on growth, water potential and stomatal conductance of cucumber seedlings. Submitted to Scientia Hort.

Schapendonk, A.H.M.C. and Brouwer, P., 1984. Fruit growth of cucumber in relation to assimilate supply and sink activity. Scientia Hort., 23: 21-33.

Seginer, I., Kantz, D., Levav, N. and Peiper, U.M., 1990. Night-time transpiration in greenhouses. Scientia Hort., 41: 265-276.

Slack, G. and Hand, D.W., 1983. The effect of day and night temperatures on the growth, development and yield of glasshouse cucumbers. J. Hort. Sci., 58: 567-573.

Spitters, C.J.T. and Keulen, H. van, 1990. Toepassing van simulatie en systeemanalyse: stand van zaken en knelpunten. CABO-Verslag nr. 128, Wageningen, 34pp.

Stacey, D.L., 1983. The effect of artificial defoliation on the yield of tomato plants and its relevance to pest damage. J. Hort. Sci., 58: 117-120.

Stanghellini, C., 1987. Transpiration of greenhouse crops. An aid to climate management. Dissertation Agricultural University, Wageningen, 150 pp.

Strijbosch, Th., 1976. Langdurige nat-perioden bij de heteluchtteelt zijn te voorkomen. Tuinderij, 16 (5): 22-23.

Suto, K., and Ando, T., 1975. The effect of atmospheric humidity and soil moisture contents on plant water status and on the growth of sweet pepper and tomato plants. Bul. Veg. and Orn. Crop Res. Sta., A (Ishinden-Ogoso, Tsu), 2: 49-63.

Swalls, A.A. and O'Leary, J.W., 1975. The effect of relative humidity on growth, water consumption and calcium uptake in tomato plants. J. Ariz. Acad. Sci., 10: 87-89.

Swalls, A.A. and O'Leary, J.W., 1976. Growth, water consumption and salt uptake of tomato plants in high humidity-high carbon dioxide greenhouse environments. J. Ariz. Acad. Sci., 11: 23-26.

Taiz, L., 1984. Plant cell expansion: Regulation of cell wall mechanical properties. Ann. Rev. Plant Physiol., 35: 585-657.

Vooren, J. van de, Welles, G.W.H. and Hayman, G., 1986. Glasshouse crop production. In: J.G. Atherton and J. Rudich, Eds., The tomato crop. Chapman and Hall, London, 201-240.

Welles, G.W.H., 1985. Ventileren een kwestie van afwegen. Tuinderij, 65 (5): 30-31.

Welles, G.W.H., Uffelen, J.A.M. van, Bakker, J.C. and Veelen, I. van, 1984. Onderzoek naar de invloed van het kasklimaat in combinatie met de voedingsconcentratie en -samenstelling op de produktie, kwaliteit en het optreden van fysiogene afwijkingen bij herftskomkommers. Intern Jaarverslag PTG, Naaldwijk: 120-122.

Zandbelt, A.J., 1984. Vochtregelen met de klimaatcomputer. Tuinderij, 64 (30): 22-25.

Summary

Climate control is an important tool for influencing the production of glasshouse crops. During the last decades environmental control has developed into a fully automatic system. The optimization of environmental control requires the development of new control strategies. Therefore knowledge of the effects of various environmental factors on short and long term responses of growth, production and quality is necessary.

Energy saving was the motive for the research described in this thesis. Under pressure of increasing energy prices at the end of the seventies, energy saving techniques were introduced on a broad scale in glasshouse industry. One of the consequences of these measures was an increasing humidity in greenhouses and crop responses to this environmental factor gained interest.

This study concentrates on long term responses of growth, flowering, production and quality of the four major Dutch fruit vegetable crops (cucumber, tomato, sweet pepper and eggplant) under greenhouse conditions. Within this framework, besides the long term responses, two processes with short relaxation times, being important in the determination of growth and production, were also investigated (stomatal conductance and pollination).
The fruit production (fresh weight) largely depends on crop photosynthesis, dry matter distribution within the plant and the dry matter content of the fruits. Crop photosynthesis depends on the total light interception and the photosynthetic light response curve of individual leaves. The influence of humidity on the light interception is mediated through the slowly responding morphological component LAI. The momentary effect of humidity on the rate of leaf photosynthesis operates through its effect on stomatal conductance. Besides the production and distribution of dry matter among leaves, stem, roots and fruits, the formation of fruits is also essential for fruit vegetable production. The related processes are flowering, pollination, fruit set, seed set and fruit growth.

Humidity affects stomatal conductance and crop photosynthesis. The leaf conductance depends on the momentary response of stomata to humidity (Chapter 2). The relative response of leaf conductance to humidity was equal for the four crops. An increase of VPD by 1 kPa decreased leaf conductance of the four crops by about 50%. At night also a clear effect of humidity on leaf conductance was observed which is possibly related to a response of cuticular conductance to momentary humidity.

The adaptation of the leaf (long term response) was analysed by determining the effect of humidity on stomatal density and size. Stomatal density of tomato, eggplant and sweet pepper was higher at high humidity. The length of the pore increased at high humidity with cucumber, tomato and sweet pepper. However,

within the humidity range from 0.2 to 1.6 kPa VPD, the differences in pore area had no significant effect on leaf conductance at equal environmental conditions.

The effect of humidity on leaf- and crop photosynthesis was estimated by simulation. It was concluded that under normal growing conditions this effect is limited to about 10 and 3%, respectively.

The effects of humidity on dry matter production and partitioning and on the dry matter content of fruits are described in Chapter 3. With tomato a higher RGR was observed at high humidity by day. This was ascribed to a higher Net Assimilation Rate. The increase in NAR was of the order of the estimated increase of leaf photosynthesis.

Tomato showed a slight increase of the stem dry weight fraction at high humidity. With both tomato and eggplant the long term dry matter distribution between leaves, stem and fruits was unaffected by humidity but the shoot/root ratio tended to be higher. With cucumber a higher Specific Leaf Area was observed at high humidity, with tomato and eggplant the SLA was unaffected.

Humidity had no effect on the dry matter content of the fruits with either crop. Therefore the effect of humidity on (fresh) fruit production are not related to dry matter distribution or water content of the fruits.

With fruit vegetable crops flowering, fruit set and fruit growth are of major importance. The effect of humidity on these processes is described in Chapter 4. The rate of flowering was unaffected by humidity. The number of flowers per axil (eggplant, sweet pepper) or per truss (tomato) was also unaffected. With cucumber the rate of flowering is possibly higher at high humidity because of a higher rate of leaf formation.

With tomato the number of seeds per fruit was determined by the (short term) effects of humidity on pollen dehiscence and adhesion to the stigma. High humidity decreased the number of seeds with tomato whilst with sweet pepper a slight increase of seeds at high humidity by day was found. Fruit set (non-aborted fruits) of tomato and cucumber was unaffected by humidity, with sweet pepper it was higher at high humidity whilst with eggplant it was lower. Mean fruit weight of cucumber and eggplant was higher at high humidity by day whilst with sweet pepper fruit weight was increased by high humidity by night. Mean fruit weight of tomato was lower at high humidity, either by day or by night. Humidity had no effect on fruit maturation rate of either crop. With tomato humidity affects final yield only through the mean fruit weight whilst with the other three crops also the effect on the number of fruits is important.

The effects of day-, night- and 24h average humidity (between 0.3 and 0.9 kPa VPD) on crop growth, production and fruit quality of the four crops is described in Chapter 5. Long term exposure to high humidity caused severe calcium deficiency in tomato, and, to a slightly lesser extent, in cucumber leaves. With tomato this led to a leaf area reduction of as much as up to 50%. With eggplant and sweet pepper no calcium deficiency was observed.

Total yield of cucumber was positively correlated to humidity by day. Fruit colour and keeping quality were lower at high humidity. Calcium deficiency was closely related to 24h average humidity and was higher at high EC and a low calcium level of the nutrient solution.

Production and keeping quality of sweet pepper did not clearly respond to humidity in the range investigated.

Early yield of tomato was slightly higher at high humidity by day but final yield was significantly reduced by high humidity due to a reduced mean fruit weight. This was caused by the reduction of leaf area due to calcium deficiency. Keeping quality of tomato was lower at high humidity.

Continuously high humidity decreased the number of fruits with eggplant which reduced final yield. External fruit quality was better at high humidity because of a lower incidence of calyx withering. Based on the results for each crop practical guidelines were deduced to improve production and quality.

In the last chapter (Chapter 6) the effects of humidity on the various processes and their mutual relations are discussed. It is concluded that the overall effect of humidity on yield of the four fruit vegetable crops consists of the positive (higher rate of leaf formation and expansion) or negative (calcium deficiency) effects on leaf area and the small effect on photosynthesis.

Discrepancies with results obtained in controlled environments are most likely caused by the generally short periods of exposure in growth chambers so that mainly short term responses are observed.

On the basis of the results from this study the measures taken in commercial glasshouse horticulture to influence the humidity are evaluated. In this light, the frequently used techniques of heating and ventilating simultaneously to lower humidity are, from production point of view, debatable, especially with cucumber, eggplant and sweet pepper.

Finally some suggestions are presented to use the effects of humidity on stomatal conductance and seed set within simulation models. Considering the effect of humidity on leaf area, more research is required in the field of relationships between humidity, calcium uptake and distribution and leaf area.

Samenvatting

De regeling van het kasklimaat is een belangrijk instrument om het produktieproces in de glastuinbouw te sturen. In de afgelopen decennia heeft de kasklimaatregeling zich ontwikkeld van handmatig ingrijpen tot een geautomatiseerd systeem. Een belangrijke voorwaarde voor een optimale inzet van deze systemen is het formuleren van regelstrategieen. Hiervoor is onder andere kennis over de invloed van verschillende kasklimaatfactoren op reacties van groei, produktie en kwaliteit op de korte- en lange termijn noodzakelijk.

De "energiebesparingsproblematiek" vormde de aanleiding tot het onderzoek van dit proefschrift. Onder druk van de stijgende energieprijzen werden aan het einde van de jaren '70 in de tuinbouw op grote schaal energiebesparende maatregelen ingevoerd. Als gevolg van deze maatregelen steeg de gemiddelde luchtvochtigheid in de kassen. Dit leidde tot een toenemende interesse in de reaktie van gewassen op deze klimaatfactor.

Het onderzoek in dit proefschrift concentreert zich met name op reakties op de lange termijn van groei, bloei, produktie en kwaliteit van de belangrijkste vruchtgroentegewassen (komkommer, tomaat, paprika en aubergine) onder kasomstandigheden. Daarnaast zijn een tweetal snel reagerende processen onderzocht die in dit verband een belangrijke rol bleken te spelen bij de beïnvloeding van de uiteindelijke groei en produktie (stomataire geleiding en bestuiving).

De vruchtproduktie (versgewicht) hangt in hoge mate af van de gewasfotosynthese, de verdeling van droge stof binnen de plant en het droge stof gehalte van het geoogste produkt. De gewasfotosynthese wordt bepaald door de totale lichtonderschepping door het gewas en de fotosynthese-licht response curve van individuele bladeren. De invloed van luchtvochtigheid op de lichtonderschepping hangt samen met de beinvloeding van de morfologische component LAI (langzaam proces). De invloed op de bladfotosynthesesnelheid hangt samen met de reaktie van de stomataire geleidbaarheid (momentane reaktie). Naast de produktie en verdeling van droge stof over blad, stengel, wortels en vruchten als geheel, speelt bij vruchtgroentegewassen de aanleg van vruchten een essentiële rol. De processen die hierbij invloed hebben zijn bloei, bestuiving, vrucht- en zaadzetting en vruchtgroei.

De luchtvochtigheid beïnvloedt de stomataire geleidbaarheid en daarmee de gewasfotosynthese. De bladgeleidbaarheid hangt af van de momentane reaktie van stomata op de luchtvochtigheid (Hoofdstuk 2). De relatieve invloed van luchtvochtigheid op de bladgeleidbaarheid was bij alle gewassen gelijk. Een verhoging van het vochtdeficit met 1 kPa leidde bij alle gewassen tot een halvering van de bladgeleidbaarheid. Ook 's nachts werd een duidelijk effect

van luchtvochtigheid op de bladgeleidbaarheid aangetoond wat mogelijk gedeeltelijk het gevolg is van een veranderde cuticulaire geleidbaarheid onder invloed van momentane luchtvochtigheid.

De morfologische aanpassing van het blad (lange termijn reaktie) is geanalyseerd door de invloed van lange termijn blootstelling aan luchtvochtigheid op de stomataire dichtheid te bepalen. Hoge luchtvochtigheidsniveau's verhoogden de stomataire dichtheid van tomaat, aubergine en paprika terwijl ook de lengte van de stomata toenam. Deze morfologische aanpassing had (binnen het luchtvochtigheidstraject 0.2 tot 1.6 kPa vochtdeficit) echter geen meetbare invloed op de bladgeleidbaarheid onder gelijke klimaatomstandigheden.

Door simulatieberekeningen werd het effect van de luchtvochtigheid op de blad- en gewasfotosynthese ingeschat. Op basis daarvan werd geconcludeerd dat in praktijksituaties de invloed van luchtvochtigheidsfluctuaties in kassen op de blad- en gewasfotosynthese beperkt is tot respectievelijk ongeveer 10 en 3%.

De invloed van luchtvochtigheid op de produktie en verdeling van droge stof en op het droge stof gehalte in het oogstbare produkt wordt beschreven in Hoofdstuk 3. Verhoging van de dagluchtvochtigheid leidde bij het onderzochte tomatengewas tot een verhoging van de relatieve groeisnelheid. Dit werd toegeschreven aan een verhoging van de netto assimilatie snelheid. De gemeten verhoging was van dezelfde orde grootte als de geschatte invloed op de (blad)fotosynthese.

Bij tomaat was de fractie droge stof in de stengel in een vroeg stadium iets hoger bij hoge luchtvochtigheid. De over langere tijd waargenomen verdeling van droge stof tussen blad, stengel en vruchten, werd, zowel bij tomaat als bij aubergine, niet beïnvloed door de luchtvochtigheid. Bij beide gewassen werd wel een tendens waargenomen van een iets hogere spruit/wortel verhouding bij hoge luchtvochtigheid. Bij komkommer leidde hoge luchtvochtigheid daarnaast tot een verhoging van de Specific Leaf Area, bij tomaat en aubergine werd deze reaktie niet gevonden.

Bij geen van de vier onderzochte gewassen werd een invloed van luchtvochtigheid op het droge stof gehalte van de vruchten waargenomen. De invloed van luchtvochtigheid op de uiteindelijke vruchtproduktie (versgewicht) werd dus niet veroorzaakt door een andere verdeling van de geproduceerde droge stof over blad, stengel, wortels en vruchten, of het watergehalte van de vruchten.

Bij de produktie van vruchtgewassen spelen de processen bloei, vruchtzetting en vruchtgroei een belangrijke rol. De invloed van de luchtvochtigheid op deze processen wordt beschreven in Hoofdstuk 4. De bloeisnelheid wordt niet beïnvloed door de luchtvochtigheid. Het aantal bloemen per oksel (aubergine,

paprika) en per tros (tomaat) bleef eveneens gelijk. Alleen bij komkommer werd de vorming van bloemen waarschijnlijk enigszins versneld als gevolg van een snellere afsplitsing/ontvouwing van bladeren bij hoge luchtvochtigheid.

Het aantal zaden per vrucht werd bij tomaat in hoge mate bepaald door de (korte termijn) invloed van de luchtvochtigheid op het vrijkomen van het stuifmeel uit de meeldraden en de hechting aan de stempel. Een hoge luchtvochtigheid verlaagde het aantal zaden bij tomaat terwijl bij paprika het aantal zaden iets hoger was bij hogere luchtvochtigheid overdag. De vruchtzetting (aantal niet geaborteerde vruchten) van tomaat en komkommer werd niet beïnvloed, bij paprika was de zetting iets hoger en bij aubergine iets lager bij hoge luchtvochtigheid. Het vruchtgewicht van komkommer en aubergine was hoger bij hoge dagluchtvochtigheid terwijl bij paprika de vruchten zwaarder waren bij een hoge luchtvochtigheid tijdens de nacht. Het vruchtgewicht van tomaat daalde bij een stijging van de luchtvochtigheid, zowel overdag als 's nachts. Bij geen van de gewassen werd een invloed van de luchtvochtigheid op de uitgroeiduur van de vruchten waargenomen. Bij tomaat beïnvloedde de luchtvochtigheid de uiteindelijke produktie alleen via het vruchtgewicht terwijl bij de andere drie gewassen zowel aantal als vruchtgewicht een rol bleken te spelen.

De invloed van de dag- nacht en etmaal luchtvochtigheid (range op etmaalbasis ongeveer 0.3 tot 0.9 kPa VPD) op gewasontwikkeling, produktie en kwaliteit van het geoogste produkt is voor de vier gewassen beschreven in Hoofdstuk 5. Langdurige blootstelling aan hoge (etmaal) luchtvochtigheidsniveau's leidde bij tomaat, en in iets mindere mate bij komkommer, tot calciumgebrek in de bladeren. Hierdoor traden bij tomaat bladoppervlaktereductie op tot 50%. Bij aubergine en paprika werden geen visuele symptomen waargenomen.

De totale produktie van komkommer was positief gecorreleerd met de luchtvochtigheid overdag. De vruchtkleur en houdbaarheid werden daarentegen negatief beïnvloed door hoge luchtvochtigheid. Het calciumgebrek in de bladeren was gecorreleerd met de etmaal luchtvochtigheid, en trad sterker op bij een hoge EC en een laag Ca aanbod in de voeding.

Paprika vertoonde geen duidelijke reaktie op luchtvochtigheid zowel ten aanzien van de produktie (gewicht) als de houdbaarheid van de vruchten.

De vroege produktie van tomaat was iets hoger onder hoge (dag) luchtvochtigheid maar de totale produktie was veel lager als gevolg van een sterke daling van het gemiddeld vruchtgewicht. De belangrijkste oorzaak hiervoor was de sterke bladoppervlaktereductie als gevolg van ernstig calcium gebrek. Ook de houdbaarheid van de vruchten daalde bij hogere luchtvochtigheid.

Continu hoge luchtvochtigheid verlaagde het aantal geoogste vruchten van aubergine en daarmee de totale produktie. De externe vruchtkwaliteit nam bij dit gewas toe bij hoge luchtvochtigheid als gevolg van een verminderde aantasting door kelkverdroging. Mede op grond van dit onderzoek konden voor

elk gewas praktische richtlijnen worden geschetst voor de regeling van luchtvochtigheid die moeten leiden tot een kwantitatief en kwalitatief goede produktie.

In het laatste hoofdstuk (Hoofdstuk 6) worden de deel-resultaten in hun onderlinge samenhang nogmaals belicht. De conclusie is dat de luchtvochtigheid de produktie van de onderzochte vruchtgroenten met name beïnvloedt door de positieve (versnelde bladaanleg en betere uitgroei) of negatieve effecten (inductie van Calciumgebrek) op het bladoppervlak en slechts een gering effect op de fotosynthese.

Discrepanties met klimaatkameronderzoek hangen zeer waarschijnlijk samen met de relatief korte periode van blootstelling aan luchtvochtigheid in klimaatkamers waardoor met name de korte termijn effecten zichtbaar gemaakt worden.

De in de tuinbouw praktijk genomen maatregelen ter beïnvloeding van de luchtvochtigheid worden geplaatst naast de gevonden resultaten. Bij de in de praktijk veelvuldig toegepaste maatregelen ter verlaging van de luchtvochtigheid kunnen, vanuit produktieoogpunt, een aantal vraagtekens geplaatst worden, met name bij komkommer, paprika en aubergine.

Tenslotte worden suggesties gedaan om de gevonden invloed van luchtvochtigheid op de stomataire geleidbaarheid en zaadzetting op te nemen in simulatiemodellen. Gezien het effect van luchtvochtigheid op het bladoppervlak is meer aandacht nodig voor de onderlinge relaties tussen luchtvochtigheid, calcium opname en -verdeling en het bladoppervlak.

Curriculum vitae

Jacobus Cornelis Bakker werd geboren op 6 maart 1957 te Rotterdam. Na het behalen van het atheneum-B diploma aan de Scholengemeenschap Johannes Calvijn te Rotterdam begon hij in 1976 de studie Tuinbouwplantenteelt aan de Landbouwhogeschool (thans Landbouwuniversiteit) Wageningen. De kandidaatsfase werd in januari 1980 afgesloten en in 1982 werd de studie afgerond (met lof). Het vakkenpakket bestond uit het hoofdvak Tuinbouwplantenteelt (gewaskundig) en de bijvakken landbouwbedrijfsgebouwen en meet- regel- en systeemtechniek.

In 1982 volgde de aanstelling als wetenschappelijk onderzoeker kasklimaat bij het Proefstation voor Tuinbouw onder Glas (PTG). Naast het onderwerp van dit proefschrift waren fysische- en regeltechnische aspecten van het kasklimaat en kwaliteitsproblemen bij tomaat en paprika belangrijke onderzoeksterreinen. Sinds 1991 is hij hoofd van de sectie kasklimaat binnen de afdeling Teelt en Kasklimaat.