BENCH HEATING FOR POTPLANT CULTIVATION:
analysis of effects of root - and air temperature on growth, development and production

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

J.V.M. VOGELEZANG

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Proefschrift

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Stellingen

1. De toleranties voor hoge worteltemperatuur zijn bij potplanten ruimer voor de groei- dan voor de ontwikkelingsreacties.

   (dit proefschrift)

2. Verhoging van de worteltemperatuur beïnvloedt de bloei van potplanten voornamelijk via effecten op de temperatuur van het (laaggelegen) groeipunt.

   (dit proefschrift)

3. Bij het interpreteren van gewasreacties op klimaatfactoren moet meer aandacht geschonken worden aan de interactie tussen microklimaat en gewasarchitectuur.

   (dit proefschrift)

4. De onjuiste veronderstelling dat bij de teelt van potplanten de worteltemperatuur niet hoger mag zijn dan de luchttemperatuur heeft investering in - en doelmatig gebruik van tablet- en vloerverwarming ten minste tien jaar vertraagd.

5. Het vasthouden aan vermeende teeltkundige 'wetmatigheden' frustreert vernieuwingen in de teelt.

6. De veronderstelling dat een omvangrijk wortelstelsel een voorwaarde is voor maximale bovengrondse groei ('the more roots the better shoot growth') is, bij de huidige stand van de techniek, ook voor potplanten achterhaald.

   M. van Noordwijk and P. de Willigen, 1987. Agricultural concepts of roots: from morphogenetic to functional equilibrium between root and shoot growth. Neth. J. Agri. Sci., 35: 487-496

7. De acquisitie van extern gefinancierde projecten binnen het landbouwkundig onderzoek vereist een aangepaste organisatie die toegesneden is op projectmatig werken.

8. De structureel achterblijvende ontwikkeling van de akkerbouw ten opzichte van de tuinbouw rechtvaardigt een wijziging in de huidige verdeling van onderzoekcapaciteit in de plantaardige produktie.

9. Het zou niet vanzelfsprekend moeten zijn dat vaders full-time blijven werken.

10. De variatie in temperatuur-aanwijzing langs wegen zegt meer over de kwaliteit van de metingen dan over lokale temperatuurverschillen.

11. Het beeld dat ouders hebben van de tijd vlak na de geboorte van hun kinderen wordt rooskleuriger naarmate het langer geleden is.

Stellingen behorende bij het proefschrift "Bench heating for potplant cultivation: analysis of effects of root - and air temperature on growth, development and production" door J.V.M Vogelezang.

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ABSTRACT

VOGELEZANG, J.V.M., 1993. **Bench heating for potplant cultivation: analysis of effects of root - and air temperature on growth, development and production.** Dissertation, Agricultural University, Wageningen, The Netherlands, 115 pp; 19 figs; 33 tables; English and Dutch summaries.

This thesis deals with the application of bench heating systems for potplant cultivation, which were developed for application of low temperature heating water from flue gas condensers and external waste heat sources. Compared to the traditional way of heating, a 'reversed' temperature gradient is created on heated benches, with a high root-zone temperature compared to the air temperature. Knowledge of root-zone temperature requirements and - tolerances is necessary in order to fully exploit the potentials of bench heating systems.

The influence of bench heating on microclimate was established for an aluminium bench heating system, which was mainly used in this study. It provided a uniform horizontal temperature distribution, and a rather constant vertical temperature gradient up to 45 cm crop height. Humidity did not detoriate with increasing root-zone temperatures.

Growth and flowering of *Saintpaulia* were enhanced by increased root-zone temperature (23-26°C). Flowering of *Begonia* showed narrow tolerances for the air temperature, whereas the root-zone temperature was of minor importance in the range 18-26°C. Elevated root-zone (19-30°C) and/or air temperatures (19-24°C) affected growth rate of *Ficus benjamina* and *Schefflera* positively during the first three weeks of growth, but in later stages of growth no effect of root temperature could be detected. Flowering and growth of *Spathiphyllum* were largely influenced by the air temperature, whereas root-zone temperature was of less importance for flowering in the range 20-26°C. Increasing root-zone (19-26°C) and air temperatures (19-22°C) promoted flowering of *Guzmania* without negative effects on size of inflorescences. Plant quality and keepability were not unfavourably affected in the crops under investigation. For *Saintpaulia* and *Spathiphyllum*, the number of lateral shoots was reduced at increased root temperatures.

Response patterns of plant processes affected by root temperature were analysed with respect to optimal range and tolerances. There is no evidence that water and nutrient uptake were limiting growth of most potplants in the investigated root temperature range. Growth was influenced more by the air temperature than the root-zone temperature. The growth response of *Saintpaulia* was an exception, where a lower plant dry matter percentage was observed at increased root-zone temperature (resulting in increased plant fresh weight), which might have been due to a reduced resistance for water uptake at these temperatures. Effects of the root temperature were most pronounced on development processes (flowering, shoot formation). For crops with a shoot meristem situated close to the root-zone, effects of increased root-zone temperature on earliness of flowering were most likely due to the locally increased temperature of the shoot apex. Consequences for the use of bench heating systems in commercial practice are discussed with respect to bench construction, climate control, crop management and economical perspectives.

Key words: bench heating, air temperature, root temperature, glasshouse climate, root growth, dry matter production, growth, flowering, quality, keepability, potplant, *Saintpaulia*, *Begonia*, *Ficus benjamina*, *Schefflera*, *Spathiphyllum*, *Guzmania*.

CONTENTS

1. GENERAL INTRODUCTION

1.1 Scope of the investigation

In The Netherlands, most of the greenhouses are heated with high temperature water circulating through a pipe heating system. Supply temperature of the heating water is about 90°C and return temperature of the water is 70-75°C. High temperature heating water is usually derived from boilers heated with natural gas. In the period from 1973, the first year of the energy crisis, to 1984, gas prices increased from 5.9 to 44.5 ct.m^{-3}. This resulted in a rise of energy costs as part of total production costs in greenhouse cultivation from 13.7% in 1973 to 22.6% in 1984, despite energy saving techniques (Sonneveld, 1983; Van Nieuwkerk, 1988). Growers reduced energy costs per m^2 greenhouse by improving the insulation of greenhouses with screens and increasing the boiler efficiency with flue gas condensers. At the same time, production per m^2 greenhouse was increased by using improved cultivation methods and highly productive cultivars.

In the early eighties, bench heating systems were developed for potplant cultivation. The availability of low temperature heating water from flue gas condensers, stimulated the idea to enlarge the heating surface by using the whole bench bottom as heating element (Van Weel, 1984). Furthermore, other (external) sources of low temperature heating water were also introduced as an alternative energy source for greenhouse cultivation, such as electricity generating stations and industries (Sonneveld, 1983; Van Nieuwkerk, 1988). Compared to traditional heating systems for potplants, which are placed overhead and under benches, bench heating systems improve energy utilization and control of microclimate. The heating efficiency is increased by bringing the heat source nearer to the crop. This is certainly valid in situations where root-zone temperatures are limiting crop growth. Furthermore, it offers the possibility to control the root-zone temperature more directly, whereas in traditional heating systems only the air temperature is controlled. Finally, a uniformly heated bench bottom provides an equal temperature distribution among the plants, which will improve homogeneity of the crop.

It is clear, that the introduction of bench heating systems might be an important step forwards in the cultivation of potplants. However, it causes at the same time a dramatic change in microclimate. By placing the potplants directly on the heated surface, the temperature difference between root-zone and air is increased. Since their introduction in the early eighties, growers did install these new heating systems, but the temperature was kept relatively low. This strategy was based on the assumption that root-zone and air temperature should not differ too much (Meeuwissen, 1984). In order to fully exploit the potentials of bench heating systems, it is therefore necessary to know root-zone temperature tolerances and - requirements in relation to surrounding air temperature. Bench heating systems may also cause other microclimatic changes, which have to be investigated and evaluated. These facts allows us to ascertain the best control strategy for heating, and establish the economical value of this heating system. This may not only contribute to a more efficient production of potplants for individual growers, but also to energy saving and hence to a reduction of CO_2-release into the air, and a reduction of thermal pollution by industries.

The application of bench heating systems as a new cultivation method for potplants causes a change in microclimate (see above). Compared to the traditional method of heating, the most dramatic change is the higher temperature of the roots compared to that of the shoot. Aim of this study is, therefore, to investigate responses of potplants to (increased) root temperature in order to optimize the use of bench heating systems. Empirical research is, however, less suitable as the only research method, due to the diversity of the assortment of potplants and possible interactions with other environmental factors. Knowledge about underlying plant physiological processes facilitates extrapolation to other crops. By integration of knowledge at crop level and at process level, a more general overview and understanding of the effects of root temperature is provided, which will be the basis for extrapolation.

In the next sections a literature review is presented to define the starting-point of this study. It provides a picture of the present-day state of controlling root temperature in protected cultivation (section 1.2), and the responses to root temperature at crop level (section 1.3) and at process level (section 1.4).

1.2 History of controlling root temperature

In agriculture, interest in controlling root temperature has been limited, since control of soil temperature in the open field is difficult. The most intensive control is found in the heated glasshouse industry. Early studies with several ornamentals were performed with electric heating cables buried in the soil (Allen, 1934; Cathey, 1954; Emsweller and Tavernetti, 1931; Kohl et al., 1949; Seeley and Steiner 1965; Shanks and Laurie, 1949a; 1949b). Introduction of alternative substrates for greenhouse crops and the Nutrient Film Technique raised the interest for the role of root temperature on plant growth, due to the ability to control the root-zone layer more directly without affecting the air temperature to a great extent (Cooper and Thornley, 1976; Moss, 1983; Orchard, 1980; Rudd-Jones and Winsor, 1978). At the same time, the rise in energy costs, due to the oil crisis, brought up the question whether and to what extent a rise in root temperature could compensate for a lower greenhouse air temperature; this research was done mainly for tomatoes, cut roses, cut chrysanthemums and gerbera (Brown and Omrod, 1980; Devonald and Tapp, 1987; Hurd and Graves, 1985; Jones et al., 1978; Hurewitz et al., 1984; Maher, 1978; Moss, 1983; Moustafa and Morgan, 1982; Takano, 1988; Tesi, 1977; Tsujita et al., 1981; Tsujita and Dutton; 1983; Tsujita and Dutton, 1987). For bedding - and potplants, root-zone warming was introduced as means to heat the crop more efficiently (Henly and Bonadruk, 1983; Janes et al., 1981; Van Weel, 1984; White, 1982).

1.3 Effects of root temperature on crop responses

The effects of root temperature on plant growth was reviewed extensively by Cooper in 1973. He concluded, that there is in general an optimum temperature for dry weight of the whole plant; responses to root temperature differ between genera, species and cultivars. Since then, a great deal of research has been dedicated to effects of root-zone heating on greenhouse crops. These which will now be discussed briefly.

At usual air temperature, production of roses in response to increased root temperature differed, varying from negative (Kohl et al., 1949; Shanks and Laurie, 1949a; 1949b), to positive (Moss and Dalgliesh, 1984; Schaupmeyer, 1984) or none (De Dood, 1989; Orchard, 1989); at a lower air temperature, root-zone warming did increase flower production (Brown and Omrod, 1980a; Moss and Dalgleish, 1984; Tsujita and Dutton, 1983; Zeroni and Gale, 1982; 1987). Similar interactions between root and air temperature have been found for chrysanthemum (Brown and Omrod, 1980b; Morgan and Moustafa, 1986) and with some exceptions for tomato (Gosselin and Trudel, 1983a; Maher, 1978; 1980; Maletta and Janes, 1987; Moss, 1983). Several reports on potplants, such as poinsettia, foliage - and bedding plants, showed equal or more favourable growth of plants with soil heating in combination with a reduced air temperature compared to an unheated control under a more favourable air temperature (Bonadruk et al., 1981; Conover and Poole, 1987; Janes and McAvoy, 1983; Shedlosky and White, 1987). In the afore-mentioned reports, it is, however, not always clear whether high root temperatures can substitute high aerial temperatures.

An interaction between root temperature and light level has been found for tomatoes and *Cucurbitaceae* (Gosselin and Trudel, 1984; 1985; Kleinendorst and Veen, 1983; Risser et al., 1982; Trudel and Gosselin, 1982). An increase in root temperature was more effective on growth and fruit production with ample light levels. Flower production of carnation was not influenced much by soil temperature in a wide temperature range (Johnson and Haun, 1972; Ferry and Hanan, 1978; Holley, 1954; Seeley and Steiner, 1965), but quality of flower stems were influenced positively by soil heating under long-day conditions (Johnson and Haun, 1972). Cyclamen sown in October responded positively to increased root-zone temperature, but not when sown in August, due to differences in daylength, radiation flux densities and natural temperatures (interpreted as temperatures due to solar radiation) during early growth (Fick and Widmer, 1989).

Generally, the optimum root temperature for growth becomes lower with advancing maturity (Brouwer, 1962; 1964; Nielsen, 1974). Higher root than air temperatures is commonly used for the rooting of several flowering and foliage plants, because propagation is accelerated (Bonadruk et al., 1981; Poole and Waters, 1971; Von Hentig and Fischer, 1987). An interaction between soil heating and development stage has been found for chrysanthemum (Barett et al., 1978; Brown and Omrod, 1980b; Cairol, 1982); growth and flower quality were affected positively by soil heating during the long-day period, but negatively during the short-day period.

Root-zone temperatures investigated did not exceed 30°C in most studies. Temporary high root-zone temperatures were investigated in Florida for container-grown trees and foliage plants, where root temperatures during daytime may exceed 40°C during 2-6 hours in summer. Responses to root temperature differed with plant genera, although temperatures above 32-34°C appeared to be supra-optimal for growth (Foster et al., 1991; Ingram et al., 1986; Johnson and Ingram, 1984).

The majority of these results show a positive effect of root-zone heating on crop production, but it appears that crop responses to root temperature may also depend on above ground factors, such as the air temperature, light level and daylength. These findings, however, do not indicate which limitation(s) of root function occurred in response to root temperature. Predictions of feasibilities of root-zone heating for other crops and/or other environmental conditions require more insight in physiological mechanisms underlying the root temperature responses.

1.4 Effects of root temperature on plant processes

Major functions of the roots are the uptake of water, the absorption of nutrients, and the synthesis of plant growth regulators. Furthermore, the root system requires carbohydrates produced in the shoot. These processes in the roots, and the transport functions to (and from) the shoot are sensitive to temperature. In literature most knowledge is available on the effects of suboptimal and low root temperatures on agricultural field crops. These will now be discussed briefly.

Water uptake. - Temperature has an instantaneous effect on water uptake related to the influence on the viscosity of water, and water permeability of the cellular membranes. In general, two temperature ranges could be distinguished, one with a high, and one with a low Q_{10}-value. Above a certain 'critical temperature' only the effect of viscosity of water could be observed as limiting water uptake, whereas below this critical temperature decreased permeability of the roots strongly adds to decreased water uptake at these temperatures. The critical temperature decreased after adaptation to lower root temperature within 36 hours (Kuiper, 1964). Other factors involved in reduced uptake at low soil temperatures are decreased metabolic activity (reducing nutrient accumulation, which is important for active water uptake), decreased availability of soil water (more water is retained in cold soil) and decreased root growth (Kramer, 1983). Root temperature induced differences in growth of leaves, which appeared to be related to effects of root temperature on water balance in the plant (Abdelhafeez et al., 1971; Adams, 1988; Brouwer, 1962; Brouwer and Hoogland, 1964). This influence of root temperature on leaf area could be fully attributed to an influence on cell elongation (Brouwer, 1962; Brouwer and Hoogland, 1964). Abdelhafeez et al. (1971) suggested that reduced transpiration per unit leaf area at low root temperatures was most likely due to increased resistance for water uptake at these temperatures, but he also found temporary stomatal closure at high transpiration in plants at low soil temperature.

Nutrient uptake. - The effect of root temperature on nutrient uptake depends on concentration in the soil, the form in which it is present (organic or inorganic) and the mobility (Nielsen, 1974). Reduced nutrient uptake at low soil temperatures is primarily caused by inhibited root growth, and to a much lesser degree by a direct effect on uptake kinetics of nutrients such as phosphorus (Marschner, 1986). Crops grown in nutrient solution generally showed increased (water and) nutrient uptake with prolonged exposure to increasing root temperatures up to 28°C, which appeared to be related to (temperature induced) differences in growth. The uptake of particular nutrient differed, however, in temperature response (Adams, 1988; Chong and Ito, 1982; Moorby and Graves, 1980; Rudd-Jones and Winsor, 1978). There is some evidence, that fertilization should be adapted to air and root temperature (Brown and Omrod, 1980a; Cornillon and Kung, 1982; Gosselin and Trudel, 1983b).

Plant growth regulators. - Root temperature may also interfere with the hormone status of the plant. Water - or temperature stress, not only act upon water uptake and nutrient uptake, but also on the hormone supply from root to shoot and vice versa (Torrey, 1976). Hormone supply to the shoot might be altered by root temperature in two ways, either by effects on the synthesis of hormones and/or by alterations in the transport of the hormones. At low root temperatures cytokinin concentrations were decreased in both roots and exudate of cucumber, suggesting inhibition of cytokinin synthesis within the roots (Tachibana, 1988). Skene and Kerridge (1967) showed an effect of root temperature on relative levels of two chromatografic fractions showing cytokinin activity in the root exudate of *Vitis vinifera*. In maize, Atkin et al. (1973) found an increase in all fractions with cytokinin activity with increasing temperature, with an optimum at 28°C root temperature, and a sharp decline of cytokinin activity at 33°C. Low root temperatures reduced gibberellin activity in maize and tomato (Atkin et al., 1973; Menhenett and Wareing, 1975). Abscisic acid activity was greatest at low root temperatures (Atkin et al., 1973). Effects of root temperature on transport from roots to shoot was observed by Smith and Dale (1988), who found that blockage of abscisic acid export from the leaves could not account for the increased concentration in root-cooled plants. Most studies were aimed at one or two hormones, but there is evidence that the regulation of either a specific developmental process or an adaptive process (to the environment) is usually influenced by more than one plant growth regulator. In a recent review of Itai and Birnbaum (1991), interactions between plant growth regulators in the root were analysed, and it was concluded that (1) the level of one growth regulator influences the level of others; (2) simultaneous changes occur in a number of hormones as a result of one environmental factor (e.g. root temperature, Atkin et al., 1973) and (3) simultaneous changes occur in a number of hormones during a specific developmental process. Furthermore it was stated, that roots are capable of synthesizing all known, natural plant growth regulators.

Photosynthesis and respiration. - Various investigators have reported effects of root temperature on photosynthetic rate, but results are variable. No significant effect of root temperature on leaf photosynthesis was found for tomato plants grown in greenhouses (Gosselin and Trudel, 1984), but leaf photosynthesis of sweet pepper was highest at 36°C root-zone temperature (Gosselin and Trudel, 1985). Harssema (1977) found no differences in net assimilation rate for young tomato plants grown under natural glasshouse conditions in the range of 12 to 35°C root temperature. However, Hurewitz and Janes (1983) found for tomato seedlings in controlled environmental chambers, that exposure to increased root temperature for a 2-week period increased net photosynthetic rates on leaf, leaf area and dry weight base up to 30°C, as did net photosynthetic rate per leaf on short term basis (up to 48-h). They suggested, that increased sink strength at 30°C led to high rates of translocation of assimilates from the leaves, which correlated well with rates of photosynthesis and growth. There is also evidence, that temperature induced changes in water balance through stomatal conductance (Abdelhafeez et al., 1971) (see above) or changes in hormonal balance may contribute to differences in photosynthesis (Guinn and Mauny, 1980). Hickleton (1988) reported for chrysanthemum lower leaf net CO_2 exchange rates for 28°C root temperature at 16°C night temperature compared to 12 and 20°C root temperature, but not at 12°C night temperature. Lowering the soil from 18 to 6°C did not affect net photosynthetic rate of pot chrysanthemum (Mortensen, 1982).

There is little known about respiration rate of roots (and shoots) in response to root temperature of intact plants. Increasing root-zone temperatures from 28 to 40°C increased root respiration of *Ilex crenata* 'Rotundifolia' (Foster et al., 1991). Szaniawski and Kielkiewicz (1982) found with sunflower plants, that increasing root temperature (10 to 30°C) enhanced both root and shoot maintenance respiration rate, whereas no effect of the root temperature on growth respiration rate was observed. The latter is in agreement with Penning de Vries (1972), who concluded that the conversion efficiency of assimilates to structural dry weight is independent of temperature in the normal range investigated. However, an increased shoot maintenance respiration rate in response to root temperature contradicts general knowledge on maintenance processes (Penning de Vries, 1975). The conversion efficiency of the roots is quite often rather low, while that of the shoots and other above ground organs tends to be higher (Lambers, 1985).

Conclusions.- A great deal of research has been dedicated to crop responses to increasing root temperatures (section 1.3). Responses to root temperature differed between crops (e.g. carnation showing a much weaker response than other crops), and responses to root temperature may interfere with other environmental factors, such as air temperature, light level and daylength (section 1.3). Interpretation of underlying plant physiological processes remains difficult. It is likely, that several plant processes determine the integrated crop response to root temperature. However, the extent to which individual processes contribute to overall shoot growth, in response to changes in root temperature, may differ. Effects of the root temperature on resistance to water uptake, and as a result on leaf area, may particularly affect growth at (early) developmental stages when the Leaf Area Index is low. Nutrient uptake appears not to affect growth rate if availability in the soil is sufficient, but supply of nutrients has to be adapted to uptake potential of the roots at different temperatures (Marschner, 1986). There is no clear picture of how root temperature affect the hormonal balance of plants; it may influence developmental processes (e.g. growth of lateral buds and flower initiation in response to cytokinins, Skene, 1976). Effects of root temperature on the rate of gross photosynthesis and maintenance respiration, and as a result on net carbon gain, remain unclear on the basis of this literature overview.

1.5 Aim and outline of this study

Most research on root temperature in protected cultivation has focussed on vegetable crops and cut flower production, and relatively few reports are available on potplant cultivation. Consequently, the first objective of this study was to investigate how far results of root-zone heating with potplants are generally in agreement and can be explained with the preliminary picture presented in the literature review. Effects of root temperature on crops were therefore analysed in relation to aerial conditions (e.g. air temperature, section 1.3). Furthermore, it should be noted that a high root-zone temperature may result in a high (local) aerial temperature, due to the technical design of bench heating systems. A quantitative description of microclimate with bench heating was therefore necessary. The second objective of this study was to infer which physiological processes may explain the overall crop response of potplants to root-zone heating. Fundamental studies on root temperature were, however, mostly aimed at growth processes (section 1.4), and information on development processes, an important aspect for potplants, is limited. Special attention was therefore paid to this aspect of cultivation (e.g. flowering, shoot formation).

This work was part of a larger project investigating the possibilities of waste and reject heat application for the glasshouse industry (Germing, 1984; Post et al., 1986), and was therefore combined with practical research. Experiments were carried out with commercial bench heating systems in greenhouses, under practice-based conditions. The range of root-zone temperatures investigated, was based on temperatures which can be obtained with bench heating systems using low temperature heating water (40-50°C maximum). Furthermore, from data presented by Cooper (1973) and Brouwer (1962) it was concluded, that prolonged exposure to root-zone temperatures higher than 30°C is supra-optimal for growth of most crops. Therefore, the maximum root-zone temperature investigated was 30°C.

The scope of the research was potplants in general. However, there are numerous crops with 190 species and many more cultivars cultivated on commercial scale in The Netherlands (Stichting Vakinformatie Siergewassen, 1990). To be able to generalize among potplants, the following research strategy was chosen: (1) selection of a limited number of species, based on origin and architecture of the crop (see further); (2) identification of relevant plant processes affected by increasing root-zone and/or air temperature in the selected crops; (3) infer the general response patterns of plant processes to temperature with respect to optimal range and tolerances. From this knowledge, extrapolation to other crops is facilitated. A preliminary inventory among experienced growers with bench or floor heating was used for the crop selection (Vogelezang, 1985). The position of the shoot apex is important with respect to local temperature rise of plant tissue due to root-zone heating, and was the basis for the selection of *Saintpaulia* and *Begonia* as main crops (respectively low and high shoot apex). Other evaluated crops were *Ficus benjamina*, *Schefflera arboricola*, two foliage plants, and *Spathiphyllum* and *Guzmania empire*, two monocotyledons. In this way, a diversity of crop characteristics was obtained in this study, which may help to extrapolate to a wider group of potplants. An overview of the characteristics of the six selected crops is given in table 1.1.

Crop production is the resultant of a complex system of interacting plant processes. A simple relational diagram, based on Penning de Vries (1982) and De Wit (1978) is presented in figure 1.1. It includes the processes which might influence crop growth in response to root temperature (section 1.4). Crop photosynthesis depends on light interception of the canopy and the efficiency of light utilization. Root temperature, through its effect on leaf area, may influence crop photosynthesis, as long as the leaf area index is not at saturation point for light interception. Root temperature may affect photosynthesis also through water balance mediated effects on stomatal conductance. Carbohydrates, produced in photosynthesis, are converted to structural dry matter, but a significant portion is respired. Maintenance respiration of the roots will increase at increasing root temperatures at the expense of crop growth. Effects of root temperature on shoot/root-ratio (Brouwer, 1963; 1983) may improve crop growth by an increase of (light intercepting) leaf area and by a reduction of respiration losses (see above). The flowering response depends on the rate of flower initiation and the rate of flower development, but the effects of the root temperature vary among species (section 1.3).

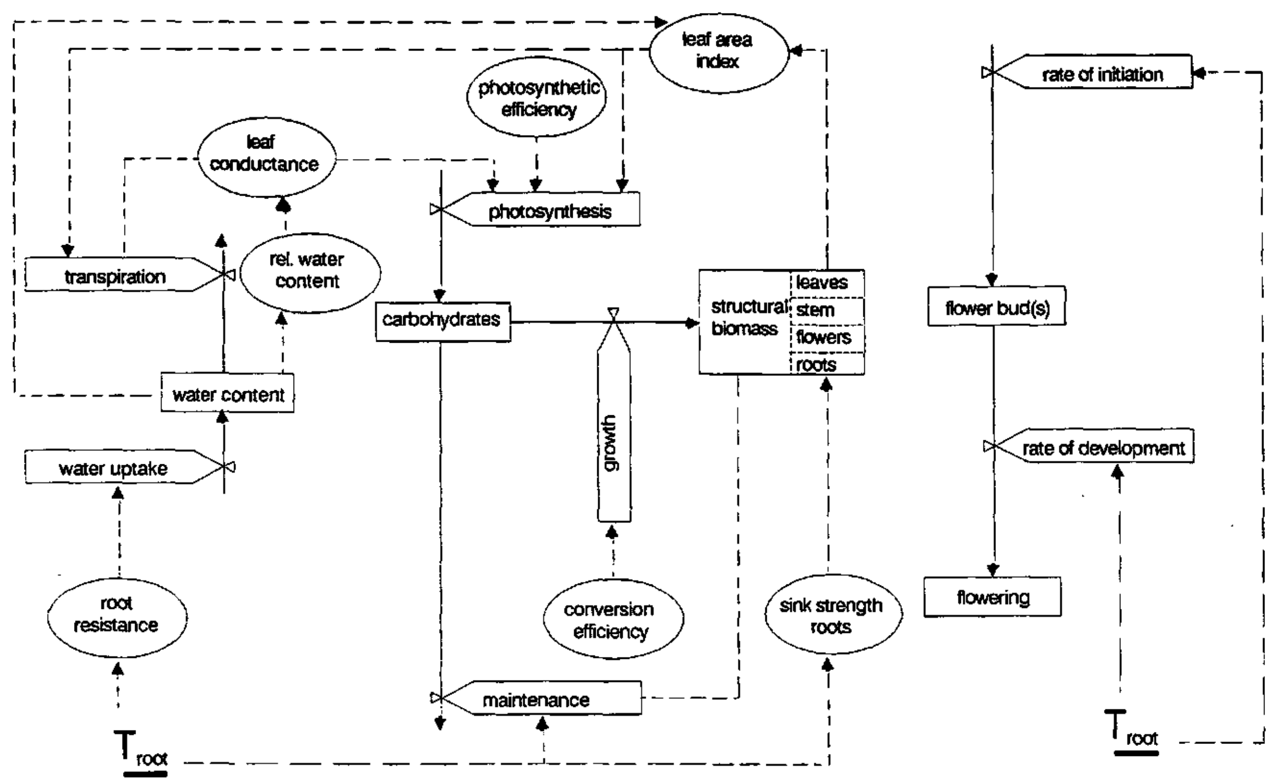

Figure 1.1. Simple relational diagram of the production system. Rectangles represent state variables, valve symbols represent flows and circles represents intermediate variables (after Penning de Vries, 1982).

TABLE 1.1

Some characteristics of the six selected crops.

Botanical name	Cultivar	Family name	Class	Region of origin
Saintpaulia ionantha	'No. 19' and 'No. 49'	*Gesneriaceae*	Dicotyledon	Tropical East Africa
Begonia x hiemalis	'Toran'	*Begoniaceae*	Dicotyledon	Tropical and subtropical
Ficus benjamina		*Moraceae*	Dicotyledon	Tropical and subtropical
Schefflera arboricola	'Compacta'	*Araliaceae*	Dicotyledon	Tropical (Asia)
Spathiphyllum	'Mauna Loa' and 'Luna'	*Araceae*	Monocotyledon	Tropical
Guzmania minor	'Empire'	*Bromeliaceae*	Monocotyledon	American tropics

1.6 Introduction to the chapters

After the general introduction, a description of microclimate on heated aluminium benches, the bench heating system mainly used in this study, is given in Chapter 2. For the six selected potplants, effects of root-zone and air temperature on crop responses and relevant plant processes is presented in Chapter 3, 4, 5 and 6. For the main crops, *Saintpaulia* and *Begonia*, additional experiments were performed under controlled environmental conditions (section 3.2 and 4.2 respectively). A general discussion is given in Chapter 7, where plant processes are analysed in their temperature tolerances and - requirements. In the last chapter, conclusions for commercial practice are presented.

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2. MICROCLIMATE

EFFECT OF AN ALUMINIUM BENCH HEATING SYSTEM ON MICROCLIMATE IN POTPLANT CULTIVATION

ABSTRACT

Influence of an aluminium bench heating system on microclimate was evaluated in glasshouse compartments with potplants. Root-zone temperatures up to 30°C were used on heated benches combined with an average greenhouse air temperature between 17 and 20°C. An aluminium bench heating system provided a uniform horizontal temperature distribution. Until 45 cm crop height, a rather constant vertical temperature gradient among the plants was observed on a heated bench: an increase in bench bottom temperature of 2°C led to an increase in root-zone temperature of 1°C and an increase of air and leaf temperature of 0.4°C in the investigated temperature range. The vertical temperature gradient above a heated bench surface was increased slightly if the horizontal screen was not used. Humidity conditions among plants were more influenced by the air temperature among the plants than by the root-zone temperature.

Abbreviation: LAI = leaf area index.

INTRODUCTION

By placing the potplants directly on a heated surface, the temperature difference between root-zone and air will be larger than with traditional heating systems for potplants. The air temperature among the plants may also differ considerably from the greenhouse air temperature, which is traditionally controlled at some distance above crop height. Other aspects of microclimate might also change due to bench heating, such as the incidence and development of fungal diseases in relation to relative humidity and surface wetness of the foliage, or changes in vapour pressure deficit affecting plant transpiration (Grange and Hand, 1987). Determination of the physical environment above heated benches is therefore necessary.

The research with bench heating, described in this thesis, was mainly carried out with aluminium benches. Influences of this heating system on microclimate is evaluated in this chapter. Vertical temperature distribution and humidity among the plants were measured in relation to the bench surface temperature and surrounding factors, such as the greenhouse air temperature and the presence of an internal screen. The horizontal bench bottom and root-zone temperature distribution was also examined. The results have a descriptive character.

MATERIAL AND METHODS

The experiments took place in glasshouse compartments (8.0 m x 12.8 m) with six 1.8 m x 4.8 m aluminium benches in each compartment. The benches were constructed with eight winged aluminium pipes connected with nails to the bench top (Fig. 2.1). Plants were cultivated in an ebb and flood system. The gully for the supply and return of water was situated in the middle of each bench; the bench bottom was

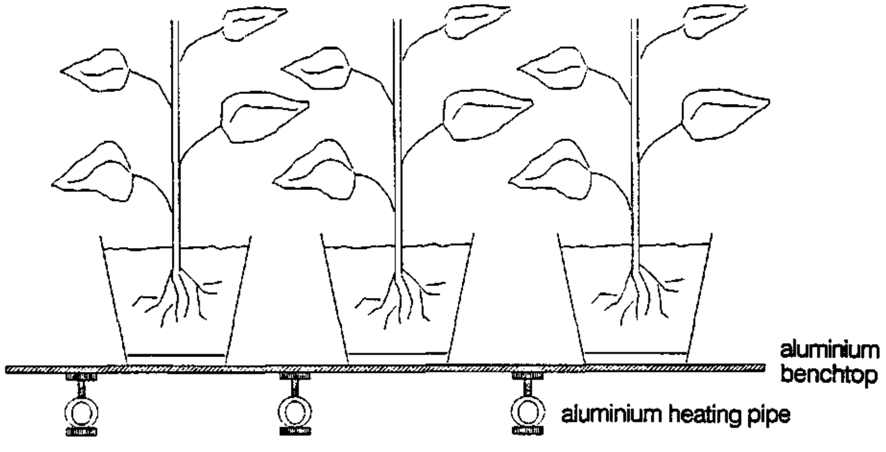

Fig. 2.1. Construction of the aluminium bench heating system.

constructed with a slope of 0.5%. The bench heating was controlled by the actual root-zone temperature measured with a Pt-100 sensor located 1 cm from the pot bottom, in the central pot above the second loop of the heating system after inlet of the heating water. An aluminium pipe heating system was installed overhead to provide additional heating. The overhead heating system was controlled by the greenhouse air temperature, measured with a ventilated psychrometer in the mid-path of the greenhouse compartment 40 cm above bench height. An internal horizontal moveable screen (Ludwig Svensson 56) was installed.

All microclimate measurements were carried out with a data-acquisition system (Hewlett-Packerd 3497A). Bench bottom -, root-zone - and unshielded air temperatures at different crop heights were measured with Pt-100 sensors. Root-zone temperatures were measured 1 cm from the pot bottom. Dry - and wet bulb temperatures were measured 25 cm above the bench surface with ventilated psychrometers containing Pt-100 sensors; to achieve minimal air disturbance psychrometer type 2 was chosen (Stichting Technische en Fysische Dienst voor de Landbouw, 1979). Leaf temperatures were measured with fine copper-constantan thermocouples (type T), which were put in the bottom mesophyl layer of the leaf. Data were sampled every 5 minutes. All results are given as mean during night time (22:00 - 4:00 h).

Horizontal temperature gradient. - Root-zone - and bench bottom temperatures were measured just above heating tubes at several locations which were spread over the whole surface of one heated bench bottom. Root-zone temperatures were measured in 11-cm pots filled with humid potting soil. Setpoints for root-zone and greenhouse air temperature were 30 and 17°C respectively.

Vertical temperature gradient. - The effect of bench heating on vertical temperature distribution was studied during an experiment with *Schefflera arboricola* 'Compacta' in 13-cm plastic pots. Microclimate measurements were carried out on two benches in the same glasshouse compartment: one bench was an unheated control, the other bench was controlled by a root-zone temperature of 30°C. The greenhouse air temperature was controlled by an average 24-hour temperature related to solar radiation, as described by De Koning (1988). The horizontal screen was closed during night time. Measurements were carried out during different stages of crop growth.

The effect of screening on vertical temperature distribution was studied during an experiment with *Spathiphyllum* 'Luna' in 14-cm plastic pots, with the same experimental design as mentioned above. Measurements were carried out during two successive periods of four nights with and without horizontal screen.

Humidity. - The effect of root-zone - and greenhouse air temperature on humidity among the plants was studied in six glasshouse compartments with different setpoints in each glasshouse compartment for the bench heating - and the overhead heating system. Three root-zone temperatures were applied, ambient, 23 and 26°C at two levels of greenhouse air temperature (17 and 20°C). The horizontal screen was closed during night time. Measurements were carried out during five nights in a fully grown Spathiphyllum crop in 14-cm plastic pots.

RESULTS

Horizontal temperature gradient. - The root-zone - and bench bottom temperatures above heating tubes varied from 29.4 to 31.4°C (n=11 locations) and 38.7 to 40.0°C (n=4 locations) respectively, with a supply and return water temperature of 43.0 and 40.0°C. Variation in root-zone temperature among pots (2.0°C) was larger than variation in bench bottom temperature (1.3°C). Temperature variation in time was +/- 0.1°C for the root-zone temperature and +/- 0.7°C for the bench bottom temperature.

Vertical temperature gradient. - In all four measurement periods, the greenhouse air temperature was well above the night temperature setpoint (Table 2.1), and therefore the overhead system was not used in that period. On the unheated bench, bench bottom -, root-zone -, air - and leaf temperature did not vary much from each other. A rise of the bench bottom temperature of 20°C led to a rise of the root-zone temperature of 11 to 12°C in all four measuring periods. The air temperature at the top of the crop was influenced to a lesser extent by bench heating than the air temperature halfway the crop, due to mixing with colder greenhouse air. In the first three periods, where crop heights stayed below 45 cm, bench heating increased air and leaf temperature 3 to 4°C compared to the unheated control. A lower rise of the air and leaf temperature was found in period four, which is probably due to a decreasing effect of bench heating on temperature at high crop height, 75 cm above bench surface. In all four measuring periods, the leaf temperature above the unheated control was lower than the air temperature (air-low and air-high, Table 2.1), whereas the leaf temperature was in between - or higher than both air temperatures above the

TABLE 2.1

Influence of bench heating on vertical temperature distribution in a Schefflera crop during different stages of growth, characterized by plant density (plants.m^{-2}) and Leaf Area Index (LAI). Temperatures are given as mean during night time (°C, 22:00-4:00 h; n=4).

	Period 1		Period 2		Period 3		Period 4	
	Unheated control	Heated bench	Unheated control	Heated bench	Unheated control	Heated bench	Unheated control	Heated bench
Plants.m^{-2}	51	51	29	29	19	19	19	19
LAI	0.3	0.5	0.7	1.1	2.1	2.8	3.7	4.2
Temperature:								
Bench bottom	15.5	36.1	16.7	37.5	17.7	38.1	17.4	36.9
Root-zone	16.4	27.9	17.7	29.8	18.7	30.1	18.5	29.7
Air-low[1]	16.2	19.9	17.3	20.5	18.5	22.3	17.8	19.4
Air-high[2]	16.6	18.9	17.9	19.7	18.9	20.7	17.7	18.4
Leaf	15.6	20.0	16.6	20.6	17.6	21.0	16.8	18.8
Crop height (cm)	20		30		45		75	
Air-gr.house[4]	17.2 (14.1)		17.8 (14.0)		20.0 (14.0)		18.8 (14.4)	
Air-outdoor[5]	1.8		4.7		5.1		11.9	

[1] = non-ventilated air temperature, halfway crop height
[2] = non-ventilated air temperature, at the top of the crop
[3] = mean of 4 leaf temperatures spread over the plant
[4] = ventilated air temperature, in the mid-path of the greenhouse 40 cm above bench surface; setpoint between parenthesis
[5] = weather station, 8.5 m above ground surface.

TABLE 2.2

Effect of a horizontal screen on vertical temperature gradient above a heated bench in a Spathiphyllum crop (25 plants.m^{-2}, Leaf Area Index of 2.1). Temperatures are given as mean during night time (°C, 22:00-4:00 h; n=4 days).

	Open screen	Closed screen
Temperature:		
Bench bottom	26.4	26.1
Root-zone	23.0	23.3
Air-low[1]	19.9	19.8
Air-high[2]	17.3	18.2
Leaf[3]	16.6	17.4
Air-greenhouse[4]	17.7 (17.7)	17.2 (17.1)
Air-outdoor[5]	4.9	3.7

[1] = non-ventilated air temperature, 5 cm above the bench bottom
[2] = non-ventilated air temperature, 25 cm above the bench bottom halfway crop height
[3] = mean of 4 leaf temperatures spread over the plant
[4] = ventilated air temperature, in the mid-path of the greenhouse 40 cm above bench surface; setpoint between parenthesis
[5] = weather station, 8.5 m above ground surface.

TABLE 2.3

Effect of different settings of root-zone and greenhouse air temperature on specific humidity (g.kg^{-1}), vapour pressure deficit - air (g.kg^{-1}) and relative humidity (%) in a Spathiphyllum crop (20 plants.m^{-2}, Leaf Area Index of 7.0). Data are given as mean during night time (22:00 - 4:00 h, n=5 days).

Temperature setpoint		Specific humidity	Vapour pressure deficit	Relative humidity	Air temperature
Root-zone	Greenh. air				
17	17	10.2	2.0	83	17.0
23	17	10.5	4.4	70	20.2
26	17	10.4	6.6	61	22.3
20	20	11.0	4.0	73	20.3
23	20	10.8	4.2	72	20.3
26	20	10.9	6.4	63	22.6

heated bench.

The presence of a horizontal screen reduced the vertical temperature gradient among the plants to some extent (Table 2.2). Despite a lower greenhouse air temperature, the air temperature halfway the crop and the leaf temperature were higher if the screen was used.

Humidity. - Differences in specific humidity were small between different settings of the root-zone temperature (Table 2.3), whereas a higher setting of the greenhouse air temperature led to a higher specific humidity. Increased vapour pressure deficit and decreased relative humidity among the plants on heated benches, were due to the increased air temperature.

DISCUSSION

This study shows that an aluminium bench heating system may provide a uniform horizontal heat distribution within given physical possibilities. Some temperature gradient in a heated bench bottom is inevitable, due to the temperature difference between supply and return temperature, but apparently heat transmitted well from heating tube to bench bottom in this bench construction. Variation among pots in root-zone temperature (2.0°C) was larger than variation in bench bottom temperatures (1.3°C), which might be due to differences in humidity of the potting soil. Yang and Albright (1985) showed, that temperature profiles within a container depend on soil thermal conductivity, which increases with rising water content of the soil. They suggested to keep the root-zone close to saturation for better temperature uniformity and higher root-zone temperatures. A variation in root-zone temperature among pots more than 3°C is not desirable for crops sensitive to root-zone temperatures, such as *Saintpaulia* (Chapter 3). This will lead to undesirable heterogeneity among plants.

Until a crop height of 45 cm, a rather constant vertical temperature gradient was measured on a heated aluminium bench in a Schefflera crop. An increase in bench bottom temperature of 2°C led to an increase in root-zone temperature of 1°C and an increase of air - and leaf temperature of 0.4°C in the investigated temperature range. This coherence between temperature changes was established during night time. Continuous 24-h measurements of air temperatures among the plants showed, that the effect of bench heating on air temperature is less during day time, owing to the effect of sun radiation on temperature (Table 4.1). However, 24-h root-zone and air temperatures measured during several crop experiments - described in Chapters 4, 5, and 6 - showed a comparable ratio between increase in root-zone and air temperature of 1 : 0.3-0.4°C. The ratio between increases in bench bottom, root-zone, air and leaf temperature, mentioned above, seems therefore useful to characterize heat transmission for this aluminium bench construction.

Above unheated benches the leaf temperature was lower than the air temperature, whereas above heated benches the leaf temperature was in between or higher than the air temperature halfway - or at canopy level. Since the overhead heating system was not used during the night period, difference in leaf temperature may be explained by radiative heat exchange with the bench heating system. Differences in crop densities (LAI), which was higher on heated than on unheated benches, might have attributed to higher radiation losses to the greenhouse cover on unheated benches.

The vertical temperature gradient above a heated bench was decreased slightly if the horizontal screen was used. This may be explained by a decreased radiation to a (warmer) greenhouse cover with screening. A former microclimate experiment with *Begonia x hiemalis* showed an even greater effect of screening on the vertical temperature distribution (Vogelezang and Van Weel, 1990): in the situation without a screen, air - and plant temperatures were 3 to 5°C lower, despite a higher bench bottom temperature.

A lower specific humidity was found if bench heating was used at a lower greenhouse air temperature (to reach a certain air temperature among the plants), indicating that an increase of evaporation from the potting soil at higher root-zone temperatures was compensated by condensation on the inner glassroof at the lower greenhouse air temperature. Humidity conditions, which are important for plant transpiration and fungal disease control, were therefore not deteriorated by increased root-zone temperatures. It should be noted, that this situation of microclimate was established for aluminium benches with ebb/flood watering, through which excessive evaporation from the bench bottom was avoided. Influences of increased root-zone temperatures on humidity might be less favourable when bench heating is combined with a humid bottom surface.

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3. SAINTPAULIA

3.1 EFFECT OF ROOT-ZONE HEATING ON GROWTH, FLOWERING AND KEEPING QUALITY OF *SAINTPAULIA*

Scientia Horticulturae, 34: 101-113.

ABSTRACT

Two cultivars of *Saintpaulia* ('Rhapsody' Nos. 19 and 49) were subjected to three levels of root-zone temperatures, ranging from 17 to 25°C. High root-zone temperatures accelerated flowering as a result of an enhanced rate of plant growth and a promoted flower development; growth analysis showed an increased LAR, resulting in higher growth rates. The percentage plant dry matter decreased compared to the unheated control. Root-zone heating increased the air temperature around the plant and therefore the leaf temperature and growing-point temperature were also increased. Elevated root-zone temperatures reduced cultivation time by 10-15% without unfavourable effects on plant quality and keepability.

Keywords: greenhouse; keepability; root-zone; *Saintpaulia*; temperature.

Abbreviations: LAR=leaf area ratio; LSD=least significant difference; NAR=net assimilation rate; RGR=relative growth rate.

INTRODUCTION

In The Netherlands about 50% of the potplants are grown on benches. As a result of the rapid rise in energy prices, bench-heating systems were developed to use low-temperature water from flue gas condensers for heating purposes (Van Weel, 1984). Bench-heating also offers the possibility of controlling the plant-zone temperatures more efficiently. Since its introduction, about 25% of the nurseries with potplants have installed bench-heating. A newer development is the installation of heated concrete floors. Both heating systems have great impact on the root-zone temperature. Knowledge about the plant responses to root-zone heating offers the possibility of optimizing crop production and maximizing heat output.

The root temperature affects a number of growth processes in the plant. The uptake and translocation of nutrients (Nielsen, 1974), plant growth (Cooper, 1973; Mortensen, 1982), dry matter distribution (Shishido and Hori, 1979) and flower production (Brown and Omrod, 1980; Merritt and Kohl, 1982) are all influenced by root temperature. Root-zone warming has been shown to improve crop productivity (Nisen et al., 1977; Trudel and Gosselin, 1982) and to reduce energy costs (Jones et al., 1977; Moss, 1984). Most studies on root temperature have been done with vegetable crops and cut flowers, especially since the introduction of the nutrient film technique.

This study was undertaken in order to investigate the response to root-zone heating of *Saintpaulia*, a commercially important potplant with a year-round production.

MATERIAL AND METHODS

Experiments. - The research took place from November 1984 until August 1985, and included three successive experiments which were carried out in one greenhouse with several control units for bench-heating in order to create different levels of root-zone

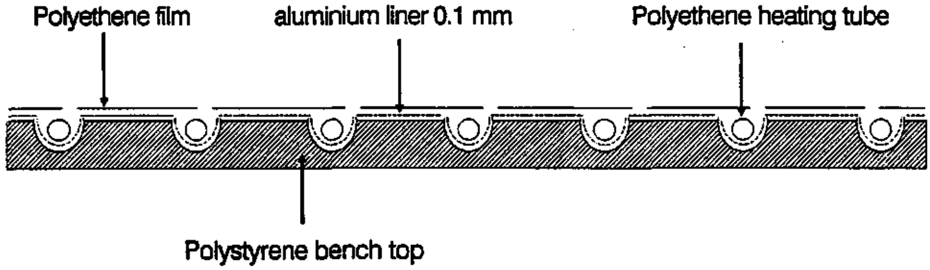

Fig. 3.1 Construction of the bench-heating system.

temperatures. The benches were constructed with a polystyrene foam base with slots for the 20-mm polythene heating tubes. An even distribution of heat was obtained by using a 0.1 mm aluminium liner under the tubes and a spacing of 0.15 m (Fig. 3.1). The watering system consisted of capillary mats in combination with a drip irrigation system under the mats. A plastic liner covering the capillary mat prevented excessive evaporation. The bench-heating system was controlled by the actual root-zone temperature, measured with a thermistor sensor in the pot 1 cm from the bottom. The temperature of the water running through the bench-heating system was limited to 50°C in order to prevent damage to the polythene heating tubes.

Two *Saintpaulia* cultivars were used ('Rhapsody' Nos. 19 and 49). Rooted cuttings were potted in 7.5-cm plastic pots in a mix of 50% black peat and 50% white peat. Seven kg lime, 0.75 kg 14N-7P-14.9K, 0.1 kg 18.7P and micro elements were added per m^3 potting medium. During the first weeks of the experiments the plants were placed in trays on the benches 100 plants m^{-2} and watering was done by hand with plain water. After 4 weeks all plants were fertilized regularly with 0.75 $g.l^{-1}$ 13N-4.4P-22.4K. Soil samples were taken twice to check electrical conductivity (guide value 0.5 $mS.cm^{-1}$), Ph (guide value 6.0) and nutrient composition. Mean ambient CO_2 level was 800-1000 $ml.m^{-3}$ during the experiments when window ventilators were closed. In the middle of the experimental period the plant density was reduced to 43 $plants.m^{-2}$ by taking the plants out of the trays and placing them separately on the benches.

All three experiments were carried out with three levels of root-zone temperature ranging from 17° to 25°C, every treatment replicated once. For Experiments 1 and 2, 12 plants were sampled from each experimental unit (plot) at 2-week intervals, beginning at the start of the experiment. Experiment 3 was a simplification of the previous ones with measurements every two weeks on the same plants ($n = 15$ for each plot).

TABLE 3.1

Average root-zone temperature (°C), air temperature (°C) and relative humidity (%) recorded during the experiments. s_{max} = maximum standard deviation of the 24-h means

	No heating			Moderate heating			High heating		
	Root	Air	RH	Root	Air	RH	Root	Air	RH
Experiment 1									
Weeks from planting on 1 Nov. 1984									
0-6	17.9	18.3	78	21.4	18.8	78	25.2	19.5	76
7-12	16.5	17.0	68	20.6	18.1	66	23.0	18.6	68
Experiment 2									
Weeks from planting on 1 Febr. 1985									
0-6	16.9	17.5	77	21.9	18.4	76	23.8	18.3	75
7-12	19.2	19.4	76	21.5	20.1	73	24.0	20.3	72
Experiment 3									
Weeks from planting on 14 May 1985									
0-5	19.2	19.8	76	22.2	20.5	75	24.0	20.6	76
6-10	20.0	20.1	76	22.2	21.0	73	23.5	20.8	74
s_{max}	1.3	1.4	7	1.0	1.2	7	1.2	1.2	7

The root-zone temperatures (measured with thermocouple wires 1 cm from the pot base), the air temperatures and relative humidity (measured with ventilated psychrometer units holding thermocouple wires) were monitored continuously with a data-collection system, Kaye type III (Table 3.1).

Statistical analysis. - Measurements were recorded at 2-week intervals. This resulted in a time function for each plot-mean of every observed variable. A least-square polynomial was fitted to these functions; the corresponding three orthogonal polynomial coefficients were calculated per plot for each observed variable. These coefficients summarize the main characteristics of growth in the plot considered of the observed variable during the experiment; they represent the mean, the mean growth rate and mean increase of growth rate of the variable observed. The observed variables were dry and fresh weight of stem, leaves and inflorescences, leaf area, leaf thickness, number of leaves and inflorescences, percentage plant dry matter, and the logarithms of the total dry weight and the total leaf area.

The orthogonal polynomial coefficients were submitted to univariate analysis of variance. Tests were performed for a linear temperature trend. Since the effect of temperature often could not be adequately described by a linear trend only, also (non-simultaneous) tests for pair-wise difference were also done (Fisher's LSD). All tests were performed at the 5% level. Subsequently, the polynomial fits to the log dry weight and the log leaf area were used to estimate the relative growth rate (RGR), the net assimilation rate (NAR) and the leaf area ratio (LAR) (Hunt, 1978). This part of the analysis is a descriptive sequel to the formal analysis of variance; the estimates from the analysis of variance are summarised in plots of the RGR, LAR and NAR.

Microclimatic responses. - To investigate the effect of bench-heating on microclimate, plant temperatures were measured in two identical greenhouses, one of which was heated with a bench-heating system and the other with a traditional heating system. The bench-heating system was constructed of an aluminium base and aluminium pipes, which were connected to the base with a glue. Water with a temperature of 40-42°C was permanently running through the bench-heating system. Watering of the plants was done with a flooded watering system.

Root-zone temperature (2 cm from the pot bottom), air temperature and plant temperatures were measured with thermocouple wires connected to a data-collection system (Kaye type III).

Experiment to test keeping quality. - This experiment was a continuation of Experiment 2. All three root-zone temperature treatments and both cultivars were included. After the production phase, half of the plant material was placed in dark storage for 7 days with a temperature of 17°C and a relative humidity of 70%. After the dark storage period these plants were transferred to a simulated interior environment, together with the control plants (no storage), with a light intensity at plant level of about 4000 lux natural daylight, a temperature of 22 ± 4°C and a relative humidity of 60 ± 10%. There was one replication for every treatment, with 5 plants as an experimental unit. The number of open and wilted flowers were counted twice a week. The same statistical methods were used as described before, with the starting number of flowers as covariant.

RESULTS

Effects on flowering. - During the first two experiments fresh and dry weight of inflorescences and the number of inflorescences appearing were recorded. Analysis of variance showed a significant increase for all three variables by increasing root-zone temperature; bench-heating improved flowering significantly compared to the unheated benches. As an example, the fresh weight of inflorescences of one cultivar is given in Figure 3.2. The more rapid increase in fresh weight during the second experiment can be explained by the better light conditions during that growing season. During the third experiment, only the numbers of inflorescences appearing were counted, and again a significant positive effect of root-zone temperature was found.

Dry matter distribution and plant development.- During the first weeks after planting, root formation will take most of the plant's energy. During all three experiments the fastest rooting was observed on the heated benches.

As shown in Figure 3.2, root-zone heating induced earlier flowering. By the time flowering started on the heated benches, plant dry weight was significant smaller compared with the unheated treatment (Table 3.2). A correlation with the stage of plant development - expressed as number of leaves formed - was found, but cannot entirely explain the effect of root-zone heating on flower formation.

A stereo-microscopic study showed initiation of adventitious buds in every leaf axil of *Saintpaulia* plants. The first buds initiated did not develop, but some adventitious shoots were formed by 'No. 19'. Formation of adventitious shoots after formation of a number of fully developed inflorescences was observed, mainly in 'No. 19'.

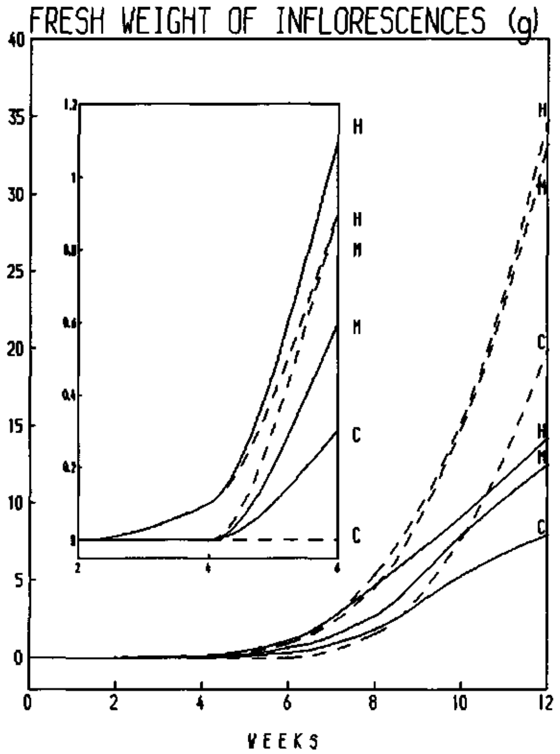

Fig. 3.2. Effect of root-zone heating on fresh weight of inflorescences; ' No. 49'. Inset: the period from 2 to 6 weeks enlarged. ——, Experiment 1; - - -, Experiment 2; C, unheated control; M, moderate heating; H, high heating.

TABLE 3.2

Plant dry weight (g) at the moment that the first inflorescences appeared. Moment of appearance = 0.5 g fresh weight of inflorescences per plot. Different letters mean a significant difference at the 5% level for each separate experiment

	Experiment 1			Experiment 2		
	'No. 49'	'No. 19'	Mean	'No. 49'	'No. 19'	Mean
No heating	0.93	1.21	1.07 (a)	1.28	1.53	1.40 (a)
Moderate heating	0.81	1.09	0.95 (ab)	1.00	1.37	1.18 (b)
High heating	0.71	0.89	0.80 (b)	1.01	1.26	1.13 (b)
Mean	0.82 (a)	1.06 (b)		1.09 (a)	1.39 (b)	

A significant interaction between root-zone temperature and cultivar was found on the number of leaves formed. Both cultivars showed a more rapid formation of leaves on the heated benches, but 'No. 19' also tended to form more adventitious shoots instead of inflorescences at the lowest root-zone temperature. These results show that the rapid flower formation on heated benches was not only caused by a faster plant development, but also by a mechanism independent from plant development and the amount of dry weight.

Plant growth analysis. - Data in Figure 3.3 show the effect of root-zone temperature on RGR,NAR and LAR for 'No. 49'; qualitatively the same effects were observed for the other cultivar. In both experiments LAR was obviously increased by root-zone heating. During the first experiment the NAR was hardly affected by root-zone temperature, but the second experiment showed a negative response for the heated treatments. As the effect of root-zone heating on LAR counterbalanced the effect on NAR during the second experiment, both experiments have resulted in higher growth rates for plants growing on heated benches.

Plants grown on heated benches had a significantly lower dry matter percentage and thinner leaves than plants grown on unheated benches (Table 3.3), due to the effect of root-zone temperature on LAR (Fig. 3.3). These effects on plant growth are positive as long as the plant quality and keepability are not unfavourably influenced.

TABLE 3.3

Effect of root-zone temperature on plant dry matter (%) and leaf-thickness (mg.cm^{-2}) at the end of the experiment. Different letters mean a significant difference at the 5% level for each separate experiment

	Experiment 1			Experiment 2		
	'No.49'	'No.19'	Mean	'No.49'	'No.19'	Mean
Percentage dry matter						
No heating	3.91	4.17	4.04 (a)	4.96	5.16	5.06 (a)
Moderate heating	3.45	3.56	3.50 (b)	4.25	4.67	4.47 (b)
High heating	3.40	3.57	3.48 (b)	4.33	4.47	4.41 (b)
Mean	3.58 (a)	3.77 (b)		4.52	4.77	
Leaf thickness						
No heating	0.031	0.038	0.035 (a)	0.050	0.056	0.053 (a)
Moderate heating	0.027	0.032	0.029 (b)	0.041	0.048	0.045 (b)
High heating	0.027	0.031	0.029 (b)	0.039	0.047	0.043 (b)
Mean	0.028 (a)	0.034 (b)		0.044 (a)	0.050 (b)	

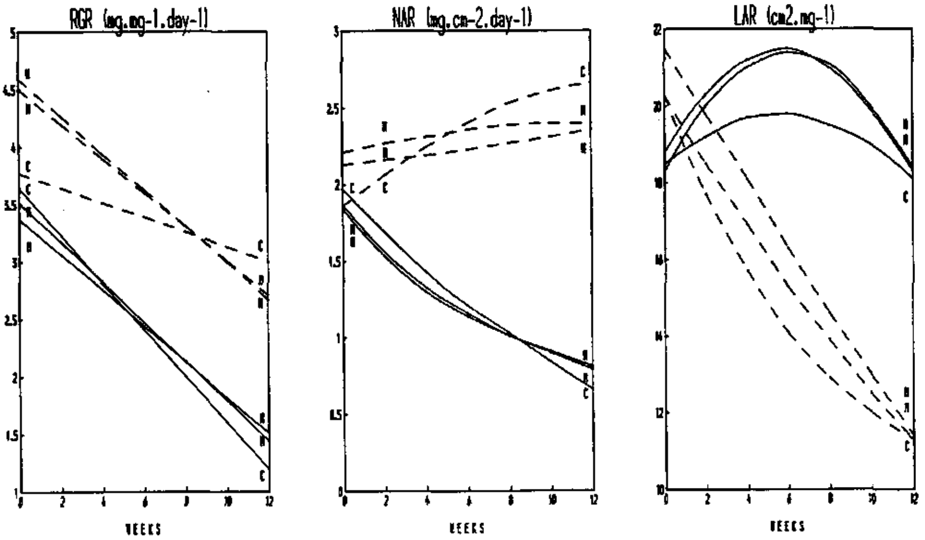

Fig. 3.3. Effect of root-zone temperature on RGR ($mg.mg^{-1}.day^{-1} * 10^{-2}$), NAR ($mg.cm^{-2}.day^{-1} * 10^{-3}$) and LAR ($cm^2.mg^{-1}$); No. '49'.——, Experiment 1; - - -, Experiment 2; C, unheated control; M, moderate heating; H, high heating.

TABLE 3.4

Numbers of weeks required to form equal numbers of inflorescences (x). Different letters mean a significant difference at the 5% level for each separate experiment

	Experiment 1 (x=5.25)	Experiment 2 (x=7.70)	Experiment 3 (x=5.20)
No heating	10.6 (a)	10.8 (a)	9.2 (a)
Moderate heating	8.8 (b)	9.9 (ab)	8.2 (b)
High heating	8.3 (b)	9.6 (b)	7.9 (b)

Cultivation time and plant quality. - The effect of root-zone heating on flowering and growth has resulted in a shorter cultivation time for the plants grown on heated benches (Fig. 3.4). The amount of acceleration has been calculated for each experiment, using the number of visible inflorescences as observed variable (Table 3.4). The calculated acceleration of cultivation time is in agreement with the results presented in Figure 3.2. Bench-heating had the most influence on cultivation time during the winter season, but was also effective during other seasons. All experiments have shown a longer cultivation time for plants grown on unheated benches than on heated ones.

At the end of Experiment 2, the plant qualities of the root-zone treatments were evaluated by growers and inspectors of a flower auction. No influence of bench-heating on plant quality could be found. A difference in plant colour due to the effect of root-zone temperature on dry-matter percentage could not be detected either.

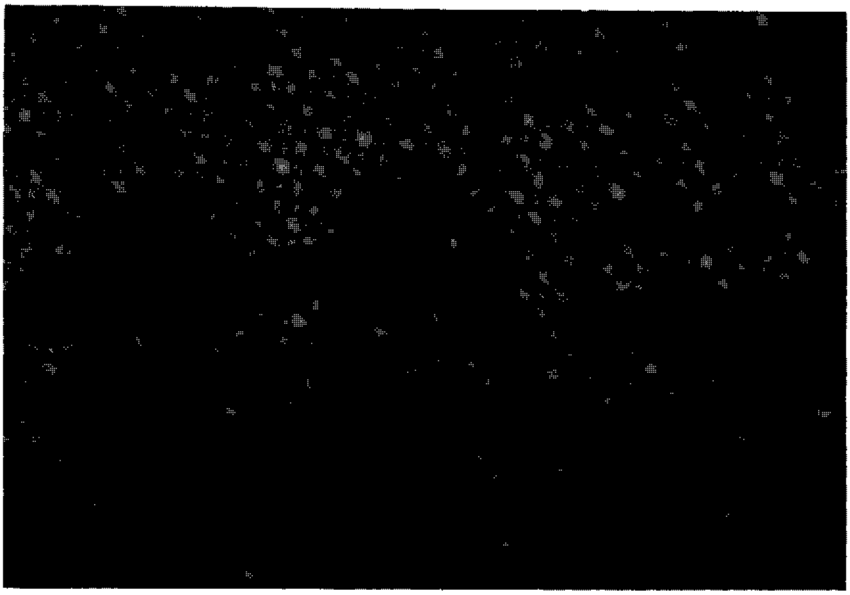

Fig. 3.4. Elevated root-zone temperatures (plant in the middle, 22°C; plant on the right, 24°C) reduced cultivation time compared to the unheated control (plant on the left, 17-19°C) without unfavourable effects on plant quality.

Microclimate responses. - The effect of root-zone heating on plant temperatures is presented in Figure 3.5. Bench-heating not only affected the air temperature around the plant (see Table 3.1), but also influenced the growing-point and leaf temperature to an even higher extent. The growing-point temperature was much more related to the root-zone temperature than to the air temperature in both heating situations, while the leaf temperature responded more rapidly to changes in air temperature compared to the response of the growing-point temperature.

Keeping quality. - Figure 3.6 indicates that the keepability was affected by root-zone temperature during the production phase. Analysis of variance showed a significant effect of root-zone heating on the number of open flowers and the rate of senescence for both cultivars. The total numbers of flowers formed are presented in Table 3.5. Starting from the remaining number of open flowers at the end of the experiment, the difference in keepability of plants grown on heated or unheated benches was about 3 weeks. Analysis of variance showed a significant effect of dark storage on the rate of senescence but not on the number of flowers formed. These results indicate that the initiation of the flowers produced had already taken place during the production phase.

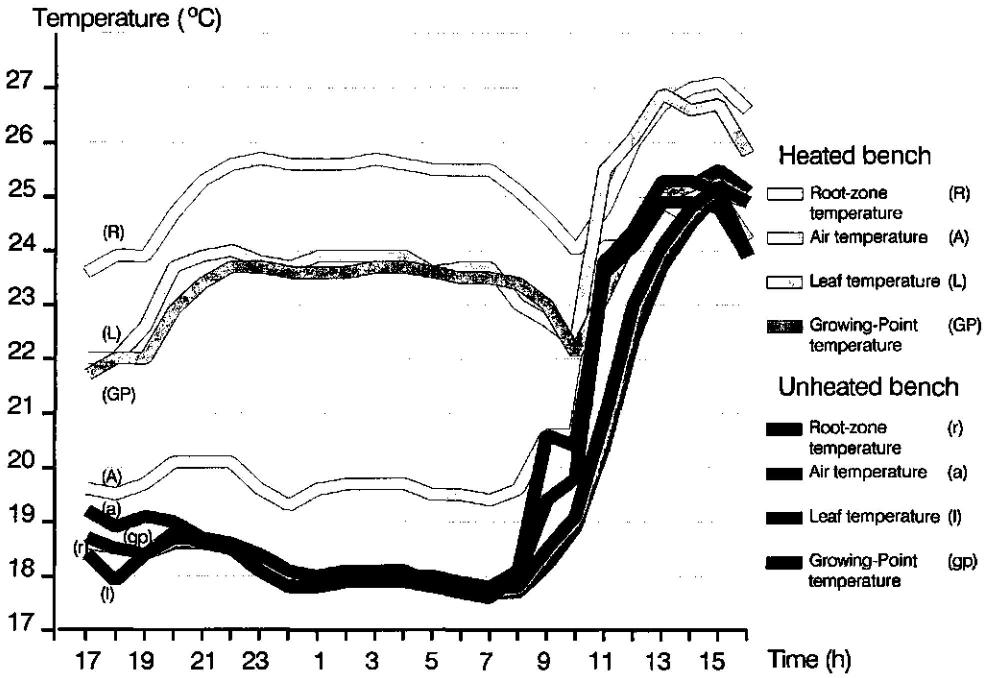

Fig. 3.5. Responses of root-zone temperature (2 cm from pot base), air temperature (around the crop), leaf temperature and growing-point temperature on unheated and heated benches.

TABLE 3.5

The effect of root-zone temperature on the total numbers of flowers during post-harvest life. Different letters mean a significant difference at the 5% level.

	No dark storage		Dark storage		Mean
	'No.49'	'No.19'	'No.49'	'No.19'	
No heating	115	99	113	85	103 (a)
Moderate heating	147	122	149	121	135 (b)
High heating	151	122	154	121	137 (b)
Mean	138 (a)	112 (b)			

An unexpected phenomenon was the formation of double flowers by 'No. 19', which is a negative quality aspect. After the first observation of double flowers, this number was counted regularly. Analysis of variance showed a significant effect of root-zone temperature on this variable, because plants grown on unheated benches yielded more double flowers than plants grown on heated benches.

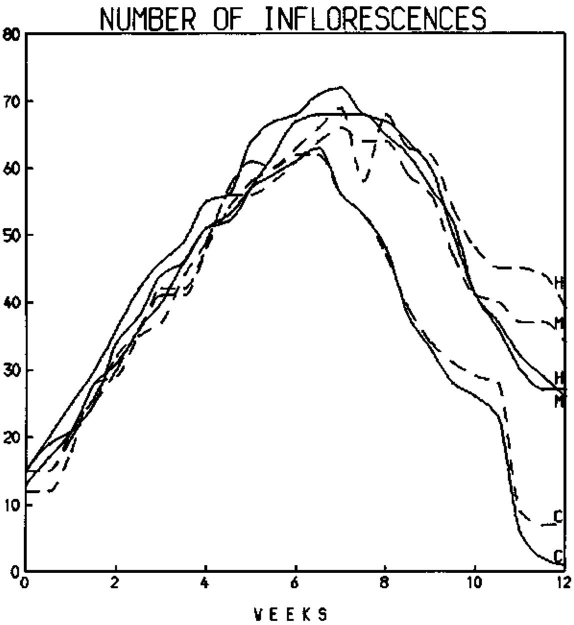

Fig. 3.6. Effect of root-zone heating on the number of open flowers during post-harvest life; 'No. 49'. ——, no storage; - - -, dark storage; C, unheated control; M, moderate heating; H, high heating.

DISCUSSION

This study has demonstrated that root-zone heating altered several aspects in the growth and development of two cultivars of *Saintpaulia* plants. Fast root development was observed on the heated benches. Hendriks (1984) reported high rates of root development as a result of a rise in air temperature, but this effect is probably more related to the rise in root-zone temperature. The direct influence of high root development rates on plant development and growth is not clear, but it might contribute to the fast cropping observed.

Initiation of flowering is not related to day length (Post, 1942) and started gradually during the cultivation period. Light intensity is an important controlling factor for flower initiation in *Saintpaulia* (Stinson and Laurie, 1954; Hildrum and Kristoffersen, 1969). Low air temperatures (14-15°C) have been shown to inhibit flowering (Herklotz, 1964; Papenhagen and Sprau, 1984). Went (1957) stated that both vegetative growth and flowering occur optimally with much higher night-temperatures than day-temperatures.

Flower formation was accelerated by an increase of root-zone temperature, whereby two effects of root-zone temperature can be distinguished; (1) Cultivation on heated benches enhanced the rate of plant development. This effect can be related to the root-zone temperature, but plant temperatures can also be involved. An effect of bench-heating on air temperature was measured (Table 3.1), but the influence on the growing-point temperature was more evident (Fig. 3.5). (2) The experiments demonstrated not only an effect on plant development, but also that root-zone heating affected the formation of vegetative or generative plant organs in the leaf axils ('No. 19'), indicating that growth regulators may be involved.

It is obvious that the small differences in air temperature between the unheated and heated treatments cannot be responsible for the difference in flowering response, but a direct influence from growing-point and/or root temperature is more likely. The extension of the post-harvest life of *Saintpaulia* emphasizes the effect of root-zone heating on flowering. It is a reasonable hypothesis that root-zone heating promoted an earlier initiation of flowering or more rapid development of flowerbuds already initiated. This was reported before by Janes and McAvoy (1982). The methods used in the present study were insufficient to differentiate between flower initiation and faster development after initiation. The initiation of the flowering process seemed to be related to the plant growth rate rather than plant weight, according to the results presented in Table 3.2.

The effect of root-zone temperature on the LAR has been reported previously (Janes et al., 1981). Brouwer and Hoogland (1964) stated that the influence of root temperature on LAR was a result of an extended cell elongation. The negative response of the NAR during the second experiment cannot be explained and awaits further study.

Root-zone heating has been demonstrated to have great influence on the growth and flowering of *Saintpaulia* plants. Cultivation time could be reduced without unfavourable effects on plant quality and keepability. Some of the observed responses to an increased root-zone temperature may be attributed to changes in the balance of growth regulators. Effects of altered translocation of growth regulators were reported (Atkin et al., 1973), as well as promotion of plant growth as a result of hormone application (Brouwer and Kleinendorst, 1967). For *Saintpaulia* plants with a growing-point very close to the pot medium, not only the root temperature but also other plant temperatures may have been involved in those processes.

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APPENDIX 3.1

In this appendix, some additional results are given of the experiments described in section 3.1, which are relevant for a better understanding. Furthermore, an additional statistical analysis has been carried out for the growth analysis (Fig. 3.3).

Growth analysis. - In the growth analysis presented in section 3.1, polynomes were fit to the time course of log dry weight and of log leaf area. These functions estimate the time course of relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) (Fig. 3.3). An additional analysis was made on the mean RGR, NAR and LAR over the period from week 2 to 12 according to Garretsen and Keuls (1986) to investigate the significance of differences observed.

There was no significant effect (p=5%) of root-zone heating on mean RGR (Table 3.6). Significant differences were observed for LAR in both experiments. A significant lower NAR was found for the highest temperature treatment in the second experiment. In the first experiment, final dry weight was not significantly affected, whereas in the second experiment a slight increase in dry weight was found on heated benches compared to the unheated control (data not shown). However, effects on plant fresh weight were significant in both experiments. Plants grown on heated benches had a significantly higher final fresh weight than plants grown on unheated benches (Table 3.7), due to a much lower percentage dry matter on heated benches (Table 3.3). Plants grown on heated benches flowered earlier and cultivation time was therefore reduced (Table 3.4), but plant fresh weight at the marketable stage was similar to plants grown on unheated benches (Table 3.8). Root-zone heating did not influence plant quality and keepability unfavourably (section 3.1).

TABLE 3.6

Effect of root-zone heating on mean RGR ($mg.mg.day^{-1}$), NAR ($mg.cm^{-2}.day^{-1}$) and LAR ($cm^2.mg^{-1}$) over the period from week 2 to 12. Different letters mean a significant difference at the 5% level for each separate experiment.

	Exp. 1			Exp. 2		
	'No. 49'	'No. 19'	Mean	'No.49'	'No. 19'	Mean
RGR $*10^{-2}$						
No heating	2.411	2.229	2.320 (a)	3.386	3.712	3.549 (a)
Mod. heat.	2.441	2.303	2.372 (a)	3.608	3.729	3.668 (a)
High heat.	2.476	2.227	2.351 (a)	3.632	3.813	3.723 (a)
Mean	2.443 (b)	2.253 (a)		3.542 (a)	3.751 (b)	
NAR $*10^{-3}$						
No heating	1.219	1.407	1.313 (a)	2.267	2.961	2.614 (b)
Mod. heat.	1.138	1.366	1.252 (a)	2.329	2.688	2.508 (ab)
High heat.	1.153	1.240	1.196 (a)	2.201	2.619	2.410 (a)
Mean	1.170 (a)	1.337 (b)		2.266 (a)	2.756 (b)	
LAR						
No heating	19.8	15.8	17.8 (a)	15.0	12.5	13.8 (a)
Mod. heat.	21.5	16.9	19.2 (b)	15.5	13.9	14.7 (b)
High heat.	21.5	17.7	19.6 (b)	16.5	14.6	15.5 (c)
Mean	20.9 (b)	16.8 (a)		15.7 (b)	13.7 (a)	

TABLE 3.7

Effect of root-zone temperature on plant fresh weight at the end of the experiment. Different letters mean a significant difference at the 5% level for each separate experiment.

	Exp. 1			Exp. 2		
	'No. 49'	'No. 19'	Mean	'No. 49'	'No. 19'	Mean
No heating	44.8	50.2	47.5 (a)	75.2	73.9	74.6 (a)
Mod. heat	52.8	60.8	56.8 (ab)	105.0	82.8	93.9 (b)
High heat.	58.7	57.5	58.1 (b)	103.9	87.9	95.9 (b)
Mean	52.1	56.1		94.7 (b)	81.5 (a)	

TABLE 3.8

Dry matter distribution (%) over stem, leaves and inflorescences and plant fresh weight (g) of the marketable product of *Saintpaulia* for the unheated control and moderately heated treatment. The difference in development stage (flowering) was 2 weeks and 1 week for respectively Experiment 1 and 2 (Table 3.4). In both experiments there were no significant temperature effects at the 5% level.

	Control			Heated		
	'No. 49'	'No. 19'	Mean	'No. 49'	'No. 19	Mean
Experiment 1						
Stem (%)						
Leaves (%)	23.4	26.8	25.1	24.2	25.9	25.0
Infloresc. (%)	55.1	58.2	56.6	53.8	56.1	55.0
	21.2	14.9	18.0	21.8	18.0	19.9
Fresh weight(g)	50.2	44.8	47.5	46.7	46.0	46.3
Experiment 2						
Stem (%)	16.6	19.8	18.2	18.1	19.0	18.5
Leaves (%)	55.8	61.4	58.6	52.5	57.4	54.9
Infloresc. (%)	27.8	18.8	23.3	29.7	23.0	26.3
Fresh weight(g)	74.0	75.2	74.6	71.9	86.7	79.3

Dry matter distribution. - The distribution over stem, leaves and inflorescences in time is presented in Figure 3.7 for cultivar 'No. 49'; qualitatively the same response was observed for 'No. 19'. Flowering started two weeks earlier on heated benches in the second experiment, whereas flowering on heated benches was promoted more gradually in the first experiment. When the dry matter distribution at the end of the experiments is compared at the same developmental stage (marketable stage), there were no significant differences between the unheated and heated treatment (Table 3.8). In 'No. 19', the distribution on heated benches was in both experiments slightly in favour of inflorescences at the expense of leaves, compared to the distribution on unheated control, but this is most likely due to decreased side shoot formation on heated benches in this cultivar.

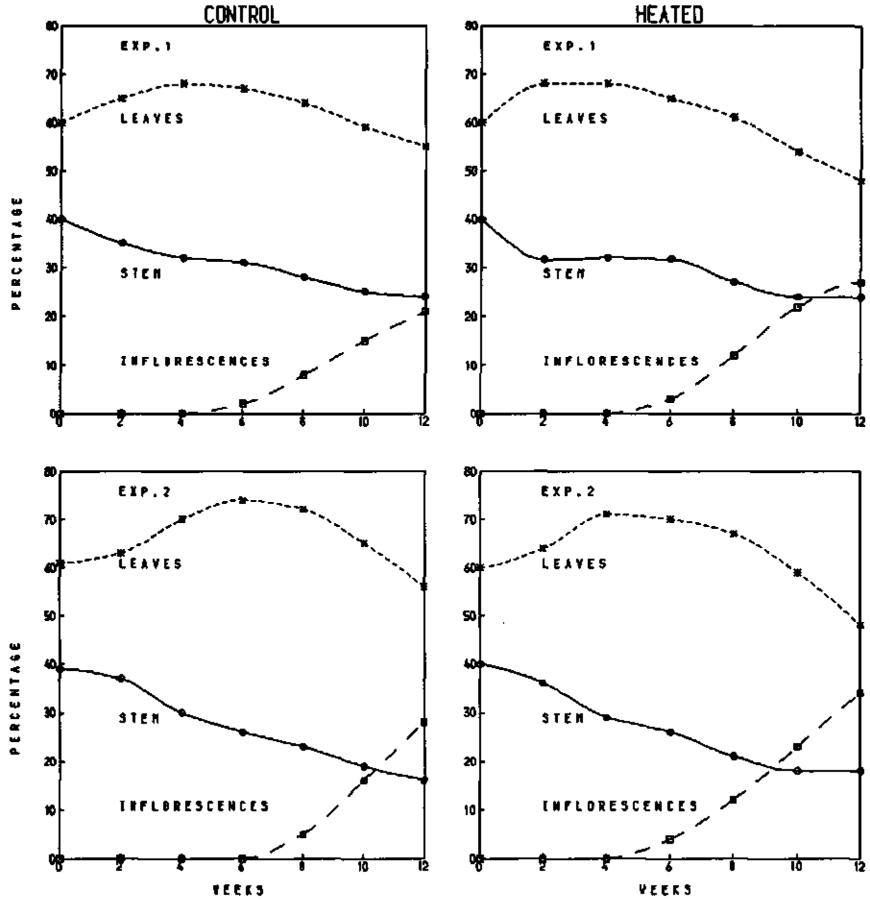

Figure 3.7. Dry matter distribution (%) in time over stem, leaves and inflorescences of *Saintpaulia* cultivar 'No. 49' for the unheated control and moderately heated treatment.

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3.2 ADDITIONAL EXPERIMENTS

ABSTRACT

The effect of a wide range of root-zone temperatures (13-26°C) on growth and flowering of *Saintpaulia* 'Rhapsody' Nos. 19 and 49 was studied at a fixed greenhouse air temperature of 19°C. This experiment was carried out with Wisconsin tanks, in which root-zone temperatures can be controlled independently of air temperature. Rate of flowering and growth were positively affected by increasing root-zone temperatures up to 23°C. No significant differences were found between 23 and 26°C root-zone temperature. These results indicate, that the root-zone temperature was the main factor influencing growth on heated benches and not the air temperature among the plants (section 3.1). Effects of bench heating on flower initiation were investigated in a separate experiment. Plants grown on heated aluminium benches (root-zone temperature 22°C) did not show earlier flower initiation compared to the unheated control (root-zone temperature 18°C). An enhanced rate of flowering at increased root-zone temperatures seems therefore mainly caused by an enhanced rate of plant and flower development.

INTRODUCTION

Experiments described in the previous section showed responses of *Saintpaulia* to increased root-zone temperatures on a commercially used bench heating system. From these experiments it was concluded, that root-zone heating promoted plant growth as well as flowering of *Saintpaulia* in the investigated temperature range. The interpretation of these experiments gave rise to some questions (discussion, section 3.1). Since the experiments with root-zone heating were carried out with a commercially used bench heating system, root-zone and air temperature were increased simultaneously. Therefore, it was not possible to attribute the observed effects to root temperature only. To clarify this point, an additional experiment was set up in order to study the separate effects of root-zone temperature at one level of air temperature among the plants.

Another question concerned the flowering response of *Saintpaulia* to root-zone heating. Root-zone heating induced earlier flowering, which was partly explained by the rate of plant development, expressed as number of leaves formed (section 3.1). Effects on flower initiation and/or flower development could not be distinguished in these experiments. In order to clarify this point, flower initiation with plants cultivated on heated or unheated benches was investigated.

MATERIAL AND METHODS

Experiment 1. - The experiment took place from November 1984 until February 1985 in a greenhouse filled with a *Saintpaulia* crop. Eight Wisconsin tanks (0.69 x 0.69 x 0.28 m) were placed at random in the middle of the greenhouse compartment. Nine water-tight plastic pots (16 cm diameter) with adequate drainage were inserted in the lid of the metal tank. Root-zone temperatures were 13, 18, 23 and 26°C with one replication for each treatment. Root-zone temperatures at 1 cm from the pot bottom were monitored continuously with Pt-100 elements connected to a Kipp-recorder (type BD301). Root-zone temperatures could be controlled with an accuracy of +/-

1°C. The air temperature just above the crop was measured with shielded thermocouples connected to a separate data-collection system (Kaye type III). The air temperature was not influenced by the root-zone temperature. Average day (10:00-16:00), night (22:00-4:00) and mean air temperature were 20.3, 18.8 and 19.2°C respectively. After 9 weeks of cultivation, two Wisconsin tanks had to be removed, due to technical problems (a 13 and 23°C temperature treatment).

Rooted cuttings of *Saintpaulia* 'No. 19' and 'No. 49' were placed in 7.5 cm plastic pots in a mix consisting of 50% black peat, 50% white peat, fertilized with 7 kg lime, 0.75 kg 14N-7P-14.9K, 0.1 kg 18.7P and microelements as stock fertilization m^{-3}. Each 16-cm pot of the Wisconsin tank was filled with humid soil in which three 7.5-cm pots with plants were placed. Standard cultural procedures were followed. Watering and fertilization were adapted to the root-zone temperature treatment. Guide values for electrical conductivity and pH were 0.5 $Ms.cm^{-1}$ and 6.0 respectively. From each 16-cm pot one plant was harvested and examined after 6 weeks of cultivation. The second and third plant were harvested after 9 and 12 weeks respectively. The observed variables were fresh and dry weight of stem, leaves and inflorescences, number of leaves and inflorescences and leaf area. Leaf thickness was calculated as leaf dry weight per unit leaf area. Data were analysed as mean over the three harvest periods with analysis of variance at the 5% confidence level.

Experiment 2. - Plant material was described by Mathijssen (1987). The experiment started in October 1985 and lasted 12 weeks. Rooted cuttings of seven cultivars of *Saintpaulia*, under which 'No. 19' ('Maria') and 'No. 49' ('Bertina') were planted and cultivated on unheated or heated aluminium benches. Root-zone temperatures 2 cm from the pot bottom were 18 and 22°C, whereas the air temperature above the crop was increased 0.5-1°C due to bench heating. Plants of cultivars 'No. 19' and 'No. 49' were examined after 0, 1, 2, 4, 6 and 10 weeks of cultivation. The description of Stinson and Laurie (1954) was used for classification of axillary buds. Three stages of bud development were distinguished: development of axillary buds into rounded forms (stage I), axillary buds having two bracts (stage II) and floral meristems (stage III). When the stem of the floral bud elongated, it was classified as visible inflorescence.

RESULTS

Experiment 1. - Plants grown at 13°C root-zone temperature showed poor rooting until the end of the experiment. Root growth of the other temperature treatments was sufficient. Fresh weight of inflorescences increased significantly at higher root-zone temperatures up to 23°C in both cultivars (Fig. 3.8, Table 3.9). Flowering was almost inhibited at a root-zone temperature of 13°C and stem elongation of flowering inflorescences was strongly reduced. The root-zone temperature affected growth of both cultivars in the same way. Plants grown at 13°C root-zone temperature formed smaller, thicker leaves when compared to the other temperature treatments. Number of leaves per plant and plant dry weight increased when the temperature was raised from 13 to 23°C. No significant differences in flowering and growth were found at 23 and 26°C root-zone temperature.

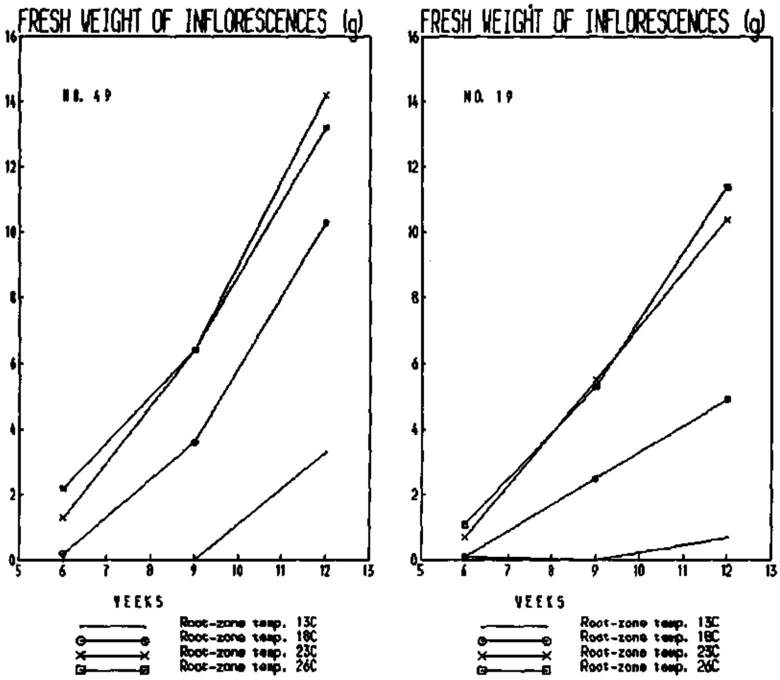

Fig. 3.8. *Experiment 1.* Effect of root-zone temperature on fresh weight of inflorescences in both cultivars.

TABLE 3.9

Experiment 1. Effect of root-zone temperature on fresh weight of inflorescences, leaf thickness, number of leaves and plant dry weight of *Saintpaulia* (as mean over 3 harvest periods in week 6, 9 and 12 of the cultivation period). Different letters show a significant difference at the 5% confidence level.

Treatment root-zone	Fresh weight Infloresc. (g)	Leaf thickness (mg.cm $^{-2}$)	Number of leaves.plant $^{-1}$	Plant dry weight(g)
13	0.6 (a)	0.049 (c)	14.3 (a)	1.27 (a)
18	3.7 (b)	0.037 (b)	17.0 (b)	1.44 (ab)
23	6.5 (c)	0.033 (a)	18.0 (b)	1.62 (bc)
26	6.7 (c)	0.034 (a)	16.9 (b)	1.58 (bc)

TABLE 3.10

Experiment 2. Effect of bench heating (18 and 22°C root-zone temperature) on rate of flower initiation in *Saintpaulia* Nos. 49 and 19 after 6 and 10 weeks of cultivation. Flower initiation is expressed as leaf number with first visible inflorescence (the leaf number counted from base to shoot tip). Standard deviation is given between parenthesis ($n=10$).

Bench heating	Week 6		Week 10	
	'No. 49'	'No. 19'	'No. 49'	'No. 19'
Unheated (18°C)	7.4 (1.2)	8.4 (1.3)	6.1 (1.5)	9.0 (1.5)
Heated (22°C)	6.6 (1.9)	8.3 (2.3)	6.0 (1.4)	9.6 (2.7)

Experiment 2. - At the start of the experiment (Week 0) buds were in stage I and II. In this primordial condition, it is not possible to distinguish floral primordia from leaf primordia (Stinson and Laurie, 1954). The first clear signs of floral initiation was observed in Week 1 (stage III) in both cultivars and temperature treatments. No abortion of floral meristems was observed in both temperature treatments in later stages of growth. Since all floral meristems developed into full-grown inflorescences, the leaf number with first visible inflorescence was taken as variable for first flower initiation (Table 3.10). Heterogeneity among plants made interpretation of results difficult. Inflorescences were initiated in an earlier stage of plant development in 'No. 49' than in 'No. 19'. The first inflorescence was formed in leaf number 6-7 in 'No. 49', and in leaf number 8-9 in cultivar 'No. 19'. Plants grown on heated benches did not show earlier flower initiation compared to the unheated control. A few axillary shoots were formed after inflorescences were full-grown, mainly in 'No. 19' on heated benches.

DISCUSSION

In the first experiment, growth and flowering of *Saintpaulia* was enhanced by raising the root-zone temperatures in the range from 13 to 23°C. A further root-zone temperature increase till 26°C, however, did not further enhance growth and flowering. These results conform well with the experiments with bench heating presented in section 3.1. It is therefore likely, that the results obtained in those experiments can be entirely ascribed to effect of root-zone temperature. The role of the temperature of the growing-point remains uncertain. Because *Saintpaulia* is a rosette plant, its growing-point will have a temperature somewhere in between root-zone and air temperature (Fig. 3.5, section 3.1). Research with maize demonstrated the importance of growing-point temperature in relation to root and air temperature (Brouwer et al., 1973). The rate of leaf appearance of maize was determined by the temperature of the root medium up to the 8th leaf. In these early stages of development the temperature of the growing-point was the same as the root temperature. In later stages of growth the air temperature gradually took over the control of this process, when the growing-point emerged from the root environment into the air. Growth activities of *Saintpaulia*, such as leaf and flower initiation, might also be mainly dependent on the temperature of the growing region.

No effect of root-zone heating on earliness of flower initiation was found in the second experiment in both cultivars. This indicates that earlier flowering on heated benches is due to faster plant and flower development only and not to earlier initiation (discussion section 3.1). The effect of root-zone heating on axillary shoot formation in cultivar 'No. 19' is not clear. In this experiment, formation of axillary shoots was enhanced slightly at the highest root-zone temperature (22°C) on heated benches, while in former experiments it occurred mostly on unheated benches at lower root-zone temperatures (17-20°C). The numbers of axillary shoots per plant differed among the experiments. In the present experiment it concerned a few buds in each plant, whereas in previous experiments (section 3.1) flowering was interrupted every few flowers by the formation of axillary shoots.

Lowering the root-zone temperature from 18 to 13°C strongly reduced elongation of leaves and stems of inflorescences. Above 18°C, plants grew normal, although leaf thickness decreased up to 23°C root-zone temperature. This is in agreement with former experiments, where an increased leaf area ratio (LAR) and decreased leaf thickness were found if root-zone heating was applied (Tables 3.3, 3.6). A reduced elongation of stems and leaves could be a result of a reduced water uptake at low root temperatures, leading to lower area/weight - and fresh/dry weight ratios (Abdelhafeez et. al., 1971; Janes et. al., 1981). Atkin et al. (1973) suggested, that poor maize shoot growth during prolonged low root temperature of 8 and 13°C might be related to an altered balance between growth promoters and inhibitors that are exported to the shoots from the roots.

It can be concluded, that enhanced flowering and growth of *Saintpaulia* on heated benches can be ascribed to effects of root-zone and/or growing-point temperature, and not to the air temperature among the plants. Earlier flowering is due to faster plant and flower development only and not to earlier initiation.

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4. BEGONIA

4.1 EFFECT OF ROOT-ZONE AND AIR TEMPERATURE ON FLOWERING, GROWTH AND KEEPING QUALITY OF *BEGONIA X HIEMALIS* 'TORAN'

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ABSTRACT

Begonia x hiemalis 'Toran' was subjected to different root-zone temperatures up to 29°C on heated aluminum benches combined with a general greenhouse air temperature of 19-20°C or less. The aluminium bench increased the temperature among the plants to 5°C above the air temperature during the night, depending on the root-zone temperature setting, growing season and greenhouse air temperature. Narrow air temperature tolerances were found for flowering, with an optimal value of 18-19°C in the winter season, whereas the root-zone temperature was of less importance in the range between 18 and 26°C. Lowering the root-zone temperature during the generative stage of growth did not improve the flowering response, compared with a continuous high root-zone temperature of 29°C. Root-zone and air temperature were more critical for flowering than for growth rate or specific leaf area in the temperature range investigated. The post-harvest experiments demonstrated similar tolerances for air and root-zone temperature. Flowering was severely affected by a long period of drought in darkness during transport simulation, but nog if light was supplied during this simulation.

Keywords: air temperature; *Begonia x hiemalis*; greenhouse; keepability; root-zone temperature.

Abbreviations: LSD=least significant difference; SLA=specific leaf area.

INTRODUCTION

Potplant cultures in greenhouse are traditionally heated by two separate steel pipe systems which are placed overhead and under the benches. A disadvantage of this lay-out is the fact that heat transfer from the lower heating system to the plants is blocked, especially in situations where moveable benches are used. In order to save energy, floor and bench heating systems have been developed (Van Weel, 1984). In this case the potplants are placed directly on the heated surface, and because of this the temperature difference between the root-zone and the air is higher than in traditional heating systems. In order to optimize the design and the use of these new heating systems, the crop response to root-zone and air temperatures has to be investigated. Experiments with *Saintpaulia* showed that elevated root-zone temperatures reduced cultivation time without unfavourable effects on plant quality and keeping potential (Vogelezang, 1988). This species reacted very well to the application of bench heating, both flowering and growth rate being enhanced in the temperature range investigated. In order to generalize the knowledge of plant responses to either root-zone or air temperature, more crops have to be investigated. This will also provide guidance for application of these new heating systems for commercial practice.

In the present study the effect of root-zone heating was investigated for a *Begonia* crop, a different type of flowering pot plant with higher growing points than *Saintpaulia*. It is important to get insight into the separate effects of root-zone and air temperature and their interactions to get a better understanding of the temperature tolerances and requirements of different plant processes. This research was performed with a bench heating system, a cultivation system which is in commercial use. However, in a bench heating system both root-zone and air temperature are influenced at the same time. Therefore, the greenhouse air temperature was included in the experimental design in order tot create different combinations of air and root-zone temperatures. This strategy provided the opportunity to separate air temperature effects and root-zone temperature effects.

No information is available about optimal ranges of root-zone temperature for potplants. Most studies on root-zone heating have been made on vegetable and cut flower crops (Vogelezang, 1988). Therefore, root-zone temperatures up to 29°C were investigated in the first experiment to get general information about the reactions to a wide range of root-zone and air temperatures. In the second experiment the root-zone temperature was lowered during the generative stage of growth to study the effects of root-zone temperature on flowering in more detail. More information is available in the literature about the optimal air temperature for *Begonia x hiemalis*. Negative effects on flowering are reported for several cultivars with air temperatures above 20°C under long-day conditions (Sandveg, 1969; 1971). After 6 weeks of treatment with a relatively low light intensity, flowering was prevented at 24°C by 16-h photoperiod. On the other hand, vegetative growth and plant development were stimulated by long days and high air temperature (Sandveg, 1971; Powell and Bunt, 1978). However, cultivars of *Begonia x hiemalis* can differ considerably in physiological response (Heide and Rünger, 1985). This makes comparison and generalisation of results difficult.

MATERIAL AND METHODS

The experiments took place in six identical glasshouse compartments (8.0 x 12.8 m) with six 1.8 x 4.8 m aluminium benches in each compartment. The benches were constructed with eight aluminium pipes connected to the bench top (Fig. 4.1). Each group of three benches was controlled by the actual root-zone temperature measured with a sensor placed in the pot 1 cm from the pot bottom with an accuracy of ±1°C. An aluminium overhead pipe system was installed to provide additional heating. The water temperature of the overhead heating system was controlled by the air temperature 40 cm above the bench surface. The effect of bench heating on air temperature between the crop was measured separately with ventilated psychrometers containing Pt-100 elements. In the first experiment the climate measurements were collected during the whole growing period. In later experiments the measurements with the separate data-collection system were limited to samples during the growing period which could sufficiently describe the effects.

Three experiments were performed in different growing seasons in 1986 and 1987 with 'Toran' , one of the few double-flower cultivars which can be grown year-round and needs only a few applications of growth regulators. Rooted leaf cuttings were potted in 13-cm plastic pots in an ebb and flood mix with 25% perlite, 3.5 kg lime,

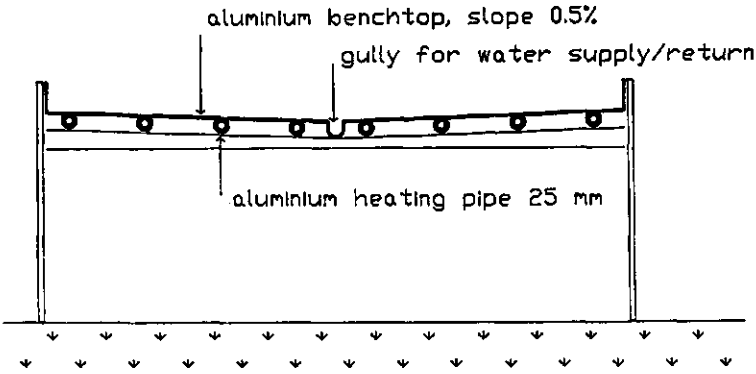

Fig. 4.1. Construction of the aluminium bench heating system.

0.75kg 14N-16P-18K and 6.4 g micro-elements as stock fertilisation m^{-3}. Watering was done with an ebb and flood system for each group of three benches. At each time of watering additional fertilisation was given. Soil samples were taken every 4 weeks to check electrical conductivity (guide value 0.9 $mS.cm^{-1}$), pH (guide value 6.0) and nutrient composition. Mean ambient CO_2 level was 300-350 $ml.m^{-3}$ during the experiments. Plant densities depended on the stages of growth as 56, 30 or 19 $plants.m^{-2}$. Previous research with 'Toran' had shown that this cultivar does not need special daylength conditions to induce flowering (Westerhof, 1980). Additional illumination with incandescent light (8 $W.m^{-2}$ installed) was given up to 13-14 h day^{-1} to stimulate vegetative growth (Boonstra, 1984). In all experiments the energy screen was closed during the day, when global radiation outside the greenhouse was higher than 350 $W.m^{-2}$.

Plant measurements were recorded at 2-week intervals on 12 plants from each experimental unit. The observed variables were fresh and dry weight of stem, leaves and inflorescences, numbers of leaves and leaf area. Specific leaf area (SLA), percentage dry matter and leaf thickness (leaf fresh weight per unit leaf area) were calculated. As the plant material showed a great heterogeneity in the first experiment, additional samples were taken in the next experiments to measure the flowering response ($n=60$). For the variable percentage non-flowering plants the arcsin transformation was used to overcome differences in variance (Sokal and Rohlf, 1981). All experiments were carried out with one replication for each temperature treatment.

Experiment 1. - This experiment started in April 1986 and lasted 10 weeks. Three root-zone temperatures were applied, ambient, 23 and 29°C, to find an indication of the optimal one. As it is known that an aluminium bench heating system increases the air temperature among the plants, a normal greenhouse air temperature of 19-20°C and a lower one were given. The design of this experiment was a split-plot scheme. This means that the main effect of air temperature could not be tested, because it was confounded with greenhouse effects. It is assumed therefore, with good reason (see below), that the variance of greenhouse effects, such as light transmission and crop handling, is equal to the variance within a greenhouse. The air temperature between the crop acts as regressor, which implies that the variance in air temperature is already taken into account. Therefore, the split-plot design is omitted in the analysis.

Separate linear regression models were fitted to a number of response variates, stemming from observations during the experiment. The potential set of explanatory variables consisted of: a constant; root-zone temperature; air temperature; (root-zone temperature)^2; (air temperature)^2; interaction between the effects of root-zone and air temperature. The fact that these terms are interdependent renders the selection of variables and the interpretation of regression coefficients difficult. For each variate a model was selected in accordance with three criteria. Namely, explanatory variables were included in the final model that were both marginally and conditionally significant at a 5% level, and the model as a whole was tested at the same level (Montgomery and Peck, 1982).

Experiment 2. - The effect of root-zone temperature on flowering was studied in more detail in Experiment 2, which started at the end of November 1986. Its aim was to avoid the negative effects of bench heating by lowering the root-zone temperature during the generative stage of growth. Six treatments were carried out, whereby the root-zone temperature during the generative stage was equal to or lower than that during the vegetative stage. The root-zone temperature was lowered half-way through the experiment, after 8 weeks of vegetative growth and before flowering occurred. This experiment could be analysed sufficiently with analysis of variance.

Experiments to test keeping quality.- The first test was a continuation of Experiment 1. All temperature treatments were included and 12 plants of each experimental unit were directly placed in a conditional room (20°C day and 15°C night temperature, 60% relative humidity and a light level of 12 $W.m^{-2}$ with SON-T lamps). The numbers of open and wilted flowers were recorded over 9 weeks. At the end of the experimental period all visible buds were counted. As the greenhouse experiments showed an effect of root-zone temperature on root structure, other aspects were studied in the second test, such as soil moisture and light conditions during a transport simulation. The soil of all pots was saturated with plain water and different periods of drought were tested in dark- and light-conditioned rooms (20°C day and 15°C night temperature, 60% relative humidity and light level of 4.5 $W.m^{-2}$ with TL 58W). The flowering response was followed in these conditioned rooms for 6 weeks, with two groups of six plants in each treatment.

RESULTS

Effects of microclimate.- Bench heating increased the temperature among the plants up to 5°C above the greenhouse air temperature during the night, depending on root-zone temperature setting, growing season and greenhouse air temperature (Table 4.1). The differences during the day were less owing to the effect of radiation on temperature. More detailed research showed that a different vertical temperature distribution is created by bench heating compared with a situation where only an overhead pipe system is used. Other factors interacted with this influence on microclimate, such as outdoor climate, energy screen and density of the crop (Vogelezang and Van Weel,

TABLE 4.1

Root-zone (°C, 1 cm from pot bottom) and air temperatures among the plants 25 cm above the benchtop (°C, day: 10:00-16:00 h; night: 22:00-4:00 h) at different temperature regimes for three experiments[1]

Experiment	Treatment air/root	Root 24-h	Air day	Air night	Air 24-h
1 (*n*=70)	17/17 (e=2)	19.2	22.7	16.7	19.1
	17/23 (e=2)	23.2	22.8	17.8	19.8
	17/29 (e=2)	28.6	24.4	19.9	21.3
	20/20 (e=2)	21.5	23.9	19.9	21.3
	20/23 (e=2)	23.1	24.2	20.8	21.9
	20/29 (e=2)	28.6	25.2	22.8	23.4
2 (*n*=38)	16/16 (e=2)	16.3	16.8	15.6	15.9
	16/23 (e=4)	23.0	17.9	17.1	17.2
	16/29 (e=6)	28.8	19.6	18.8	19.0
	16/16 (e=6)	17.1	18.1	15.2	16.2
	16/23 (e=4)	23.1	19.5	17.8	18.3
	16/29 (e=2)	29.0	22.5	20.5	21.2
3 (*n*=22)	16/16 (e=2)	16.7	17.3	16.2	16.4
	16/23 (e=2)	23.0	19.2	18.8	18.8
	16/26 (e=2)	25.9	20.1	19.9	19.8
	19/19 (e=2)	18.7	19.5	18.6	18.8
	19/23 (e=2)	23.1	20.5	20.0	20.1
	19/26 (e=2)	26.0	21.5	20.6	20.9

[1]*n*=number of sampling days during the experimental period; e=number of experimental units.

1989).

Effects on flowering.-Table 4.2 presents the effects of root-zone and air temperature on the flowering response at the end of the experimental period. The amount of fresh weight of inflorescences at the end of the first experiment, where root-zone temperatures up to 29°C were applied, was negatively correlated with the root-zone temperature (Table 4.3). The total number of flowers and buds during post-harvest life was not only negatively correlated with the root-zone temperature, but also with the air temperature (significant *F*-test). The positive correlation between number of flowers and buds during post-harvest life and the amount of fresh weight of inflorescences at the end of the cultivation period is considerable. It was remarkable that during post-harvest life some of the plants grown in 29°C root-zone and normal greenhouse air temperature had only a few flower buds. Also, the formation of leaf-shaped flowers was enhanced by a high root-zone temperature of 29°C.

During the second experiment an attempt was made to avoid negative effects of bench heating on flowering by lowering the root-zone temperature during the generative stage of growth. A relatively low greenhouse air temperature was chosen

TABLE 4.2

Effect of root-zone temperature and air temperature among the plants on flowering response at the end of the growing period for three experiments. The total number of flowers and buds during post-harvest life is also presented for Experiment 1. Experiment 2 was analysed with analysis of variance (LSD at 5%).

Experiment 1						
Setp. air/root	17/17	17/23	17/29	20/20	20/23	20/29
24-h mean air/root	19.1/19.2	19.8/23.2	21.3/28.6	21.3/21.5	21.9/23.1	23.4/28.6
Fresh weight (g) inflorescences	37.5	41.5	29.0	40.8	36.6	30.9
Post harvest, flowers and buds	234	246	200	237	231	170
Experiment 2						
Setp. root/root	29/29	29/23	29/16	23/23	23/16	16/16
% non-flowering plants	66 (c)	58 (c)	65 (c)	34 (a)	47 (b)	33 (a)
Open flowers per plant	2.6 (a)	3.3 (a)	2.2 (a)	6.3 (b)	4.3 (ab)	5.6 (b)
Experiment 3						
Setp. air/root	16/16	16/23	16/26	19/19	19/23	19/26
24-h mean air/root	16.4/16.7	18.8/23.0	19.8/25.9	18.8/18.7	20.1/23.1	20.9/26.0
% non-flowering plants	10.4	5.5	14.8	7.4	14.0	21.5
Open flowers per plant	4.3	8.0	6.6	9.4	7.6	7.0

to compensate for the increase of air temperature among the plants due to bench heating. This strategy was not successful, as the results showed that the percentage flowering plants and the amount of open flowers at the end of the experimental period were significantly reduced if a 29°C root-zone temperature was used (Table 4.2). This experiment demonstrated that flowering was affected by bench heating during the vegetative stage. It is remarkable that a root-zone temperature of 23°C followed by 16°C also reduced flowering compared with continuous 16°C.

Flowering was delayed by a root-zone and air temperature of 16°C in the third experiment. This temperature treatment was therefore omitted in the statistical analysis, as the development stage of these plants at the moment of data sampling differed from the other temperature treatments. Evaluation of the different combinations of root-zone and air temperature on percentage non-flowering plants (Table 4.3) showed that the air temperature among the plant was responsible for this negative flowering response. The number of open flowers was affected by the root-zone temperature (Table 4.3), but differences between temperature treatments were relatively small compared with the effect on percentage non-flowering plants. The number of open flowers was positively correlated with the amount of plant fresh weight. The air temperature among the plants seemed to be the main controlling factor for the

TABLE 4.3

Correlation matrices for Experiments 1 and 3. Only significant correlation coefficients are given at the 5% level ($r \geq 0.576$). Regression coefficients and Student's *t*-values (in parentheses) for the relation between response and explanatory variates are also given

Term	1	2	3	4	5	6	7	Root-zone temperature	Air temperature
Experiment 1									
1 Root-zone temperature	1.000								
2 Air temperature	0.742	1.000							
3 Fresh weight inflorescences	-0.602	-	1.000						
4 Number of flowers and buds									
(post harvest)	-0.780	-0.715	0.645	1.000				-4.45 (-1.89)	-5.90 (-1.02)
5 SLA	0.719	0.856	-	-	1.000			0.06 (0.75)	0.75 (2.88)*
6 % dry matter	-0.764	-0.730	-	-	-0.933	1.000		-0.02 (-1.67)	-0.04 (-1.22)
7 Plant fresh weight	-	-	-	-	-	-	1.000		
Experiment 3									
1 Root-zone temperature	1.000								
2 Air temperature	0.696	1.000							
3 % non-flowering plants	-	0.885	1.000						
4 Open flowers/plant	-0.874	-0.633	-0.680	1.000				-0.33 (-3.29)*	-0.06 (-0.19)
5 SLA	-	0.634	-	-	1.000				
6 % dry matter	-	-0.833	-0.756	-	-0.832	1.000			
7 Plant fresh weight	-	-	-	0.752	-	-	1.000		

*Significant at the 5% level.

flowering response, with an optimal value of 18-19°C in the winter season, whereas the root-zone temperature was of less importance in the range between 18 and 26°C. Definite conclusions about causality of flowering response by a root-zone or air temperature of 16°C cannot be drawn.

Dry matter distribution and growth.- Bench heating affected the distribution and structure of the roots in the pot soil. Roots grown at 23 and 29°C root-zone temperature had a fine branched structure compared with roots at other temperatures; roots grown at 29°C did not grow fully to the bottom of the pot. The fine structure of the roots of *Begonia* and the presence of peat in the pot soil prevented a quantitative evaluation of shoot/root ratios at different temperatures. The growth of leaves and stem was not much affected by the different temperature regimes; only the flowering process was severely affected by temperature (see above). The average course of the dry matter distribution over stem, leaves and inflorescences in time is shown in Fig. 4.2. The formation of leaves and inflorescences was competitive at the end of the growing period. The effect of root-zone and air temperature on vegetative growth are shown in Table 4.4 for Experiments 1 and 3. Higher values for SLA were found at higher air temperatures, but the differences between the temperature treatments were small in the first experiment. The effect of air temperature on SLA was also reflected

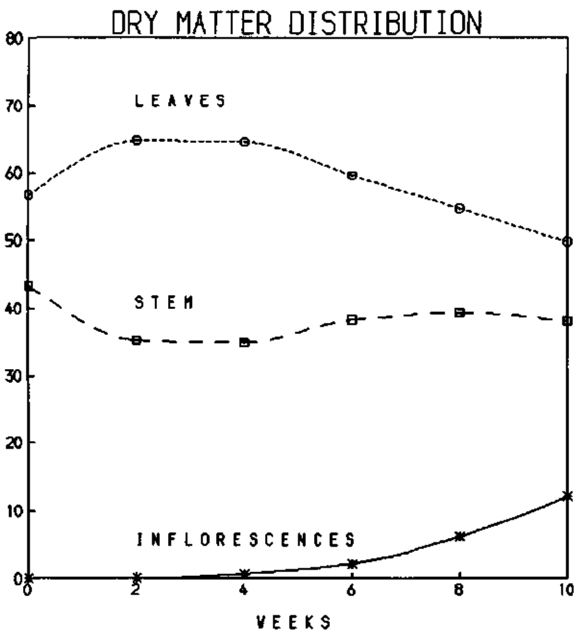

Fig. 4.2. Dry matter distribution (%) over stem, leaves and inflorescences as means for all temperature treatments (Experiment 1).

TABLE 4.4

Effect of root-zone temperature and air temperature among the plants on vegetative growth for two experiments. Specific area (SLA) and percentage dry matter are expressed as means during the growing period, while plant fresh weight is given at the end of the experimental period

Experiment	Setpoint air/root	24-h mean air/root	SLA ($cm^2 mg^{-1}$)	Dry matter (%)	Plant fresh weight (g)
1	17/17	19.1/19.2	36.9	5.18	251.1
	17/23	19.8/23.2	39.2	4.84	273.6
	17/29	21.3/28.6	39.1	4.86	248.5
	20/20	21.3/21.5	38.9	4.94	239.3
	20/23	21.9/23.1	39.7	4.90	256.1
	20/29	23.4/28.6	40.4	4.73	254.8
3	16/16	16.4/16.7	49.8	4.29	121.8
	16/23	18.8/23.0	53.4	3.93	147.0
	16/26	19.8/25.9	53.9	3.85	126.9
	19/19	18.8/18.7	55.3	3.84	150.4
	19/23	20.1/23.1	55.4	3.81	148.4
	19/26	20.9/26.0	56.2	3.70	128.9

in the mean dry-matter percentages, which were highly correlated (see Table 4.3). The effect of bench heating on these morphological aspects did not reduce plant quality. A significant effect on leaf thickness could not be detected in the marketable crop. The negative correlation between dry-matter percentage and percentage non-flowering plants in Experiment 3 is not clear. Results of Experiments 1 and 3 did not show a significant effect of root-zone and air temperature on plant fresh weight (Table 4.3). A low final plant fresh weight was observed in the third experiment compared with the first, which was caused by the lower light conditions during that growing season (Table 4.4).

Keeping quality.- In comparison with the first test, relatively low numbers of flowers were counted owing to the lower light intensity in Experiment 3. Plants grown with a low root-zone and air temperature of 16°C yielded more flowers than plants grown with higher temperatures (Table 4.5), but more than 50% of these flowers had only a few petals. This phenomenon was reduced to 0-30% per plant at higher temperatures. Therefore, the ornamental value of plants grown on heated benches was better compared with the unheated controls (16°C).

Flowering was severely affected by a long period of drought in darkness (Table 4.5). A higher rate of senescence of flowers present was observed under these conditions as well as a slow rate of opening of flower buds. No significant effect on drought tolerance was found when light was supplied during the transport simulation. A treatment where plants were watered during the transport simulation was not included, so definite conclusions about causality cannot be drawn from this experiment. It is clear that transport under dark conditions could have dramatic effects for *Begonia*.

TABLE 4.5

Effect of temperature (A) and different periods of drought during the transport simulation (B) on the total number of open flowers during post-harvest life (Experiment 3)

(A) Temperature

Setpoint air/root	24-h mean air/root	Control	Transport simulation: 4 and 10 days dry	
			Light	Dark
16/16	16.4/16.7	50.5 (c)[1]	46.0 (c)	36.6 (b)
16/23	18.8/23.0	32.9 (b)	30.0 (ab)	23.3 (a)
16/26	19.8/25.9	29.3 (ab)	30.0 (ab)	22.0 (a)

(B) Drought tolerance

Drought	Transport in:	
	Light	Dark
Control	37.6 (b)[1]	37.6 (b)
4 days	33.6 (b)	30.1 (ab)
10 days	37.1 (b)	24.5 (a)

[1]Different letters mean significant differences at the 5% level (LSD)

DISCUSSION

Both root-zone and air temperature influenced the flowering response in *Begonia x hiemalis* 'Toran'. Narrow limitations were found for the air temperature among the plants in the third experiment, which took place in the winter season, with an optimal value of 18-19°C. The air temperature among the plants seemed to be the main controlling factor for the flowering response, whereas the root-zone temperature was of less importance in the range between 18 and 26°C. As Bernier et al. (1981) have stressed, all environmental factors, such as daylength, temperature and light intensity, may interact on flowering, such that each factor may change the threshold of the others. For several *Begonia* cultivars an interaction between daylength and air temperature was reported by Sandveg (1969, 1971). A strong negative effect was found on flowering if high air temperatures were combined with a 13- or 16-h daylength. As the experiments in the present study were carried out with continuous daylength of 13-14 h, the results are in agreement with reported responses. Short-day conditions may change the tolerances of the air temperature for the flowering process, but it would retard vegetative growth to a great extent (Powell and Bunt, 1978; Steib, 1981). The present results indicate that there might also be an interaction between air temperature and light intensity. During the first experiment in the spring, higher air temperatures between the crops reduced the flowering response compared with the experiment in the winter. Therefore air temperature limitations seemed to be related to the light intensity during growth. High irradiances might shift the optimal air temperature upwards, as the availability of carbohydrates for growth and flowering is less limiting under those circumstances. Final plant weight was also much higher within a shorter cultivation time if growth took place in the spring compared with growth in the winter (Table 4.4).

Lowering the root-zone temperature during the generative stage of growth did not improve the flowering response compared with a continuous high root-zone temperature of 29°C. The root-zone temperature had already affected flower induction, whereas the root-zone temperature during flower realisation seemed to be of minor importance. A root-zone temperature of 29°C appeared too high for flowering, regardless of the air temperature between the crops, as was found in the first experiment. *Begonia x hiemalis* 'Toran' had rather strict air-temperature requirements for flowering, whereas the root-zone temperature seemed to be of less importance. Additional experiments where root-zone and air temperature are separated, should bring more insight into these effects on plant development and flowering.

Root-zone temperatures above 23°C clearly affected the distribution and structure of root growth compared with lower root-zone temperatures. A fine branched structure was observed at higher root-zone temperatures, whereas roots grown at 29°C did not grow fully to the bottom of the pot. The same effects of root temperature on diameter and branching of the roots was found in tomato and rose plants (Shanks and Laurie, 1949; Abdelhafeez et al., 1971; Moorby and Graves, 1980). Moorby and Graves suggested that the resistance to water and mineral transport was reduced at higher root temperatures.

Root-zone and air temperatures were more critical for flowering than for growth rate or morphological aspects. Relatively high value for SLA were found in the winter season, whereby effects of the air temperature were also more evident. Differences in SLA and percentage dry matter can lead to plant quality differences in the marketable crop, but an effect on leaf thickness could not be detected at the end of the growth period. Undesired internode and inflorescence elongation could be regulated with growth retardants. Therefore a good quality product can be grown on heated benches.

The present experiments showed that bench heating has only restricted use, as the air temperature among the plants has relatively low limits during the heating season. The root-zone temperature might be varied in a broader temperature range between 18 and 26°C, but high settings of the root-zone temperature will lead to suboptimal levels of the air temperature among the plants on heated benches. A reduction of inflorescences was also observed for 'Rosalie' and 'Schwabenland' when bench heating was applied with a root-zone temperature of 23°C at a usual greenhouse air temperature of 20°C (Verberkt, 1988). These results are in agreement with the present study and indicate that the reaction of *Begonia x hiemalis* to root-zone and air temperature described here might have some general validity.

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4.2 ADDITIONAL EXPERIMENT

J.V.M. Vogelezang and J.G.F. Lieshout[1]

ABSTRACT

The effect of a wide range of root-zone temperatures (18-28°C) on flowering and growth of *Begonia x hiemalis* 'Toran' was studied at two air temperatures (18, 21°C) in conditioned growth chambers. Wisconsin tanks were used to control root-zone temperature. An air temperature of 21°C reduced flowering, whereas increasing root-zone temperatures had a slight negative effect on flowering in the investigated range. Growth was not affected significantly by the root-zone temperature. At an air temperature of 18°C specific leaf area was reduced and plant dry weight increased, compared to 21°C air temperature. Results of this experiment confirm those obtained with bench heating.

Abbreviation: SLA = specific leaf area.

INTRODUCTION

Experiments described in the previous paragraph showed responses of *Begonia x hiemalis* 'Toran' to root-zone and air temperatures on a commercially used aluminium bench heating system. In a bench heating system root-zone and air temperature are increased at the same time. In order to separate effects of root-zone and air temperature to a certain extent, the greenhouse air temperature was included in the experimental design. From these experiments it was concluded, that root-zone and air temperature were more critical for flowering than for the growth of *Begonia*. Narrow air temperature limitations were found for optimal flowering (optimum 18-19°C), whereas the root-zone temperature was of less importance in the range between 18 and 26°C. A root-zone temperature of 29°C appeared too high for flowering, regardless the air temperature among the plants. These conclusions were investigated in an additional experiment under controlled environmental conditions of root-zone and air temperature. Two preliminary conclusions were tested in this experiment: 1) an air temperature of 21°C is too high for optimal flowering, regardless the root-zone temperature in the range between 18 and 28°C and 2) a root-zone temperature of 28°C is too high for optimal flowering, whereas root-zone temperatures in the range between 18 and 26°C will not give negative flowering responses. Although in this experiment emphasis was laid on flowering response, effects of root-zone and air temperature on growth were also studied.

MATERIAL AND METHODS

The experiment was carried out in two identical phytotron chambers with a constant air temperature of 18 and 21°C. In these chambers, Wisconsin tanks (0.69 x 0.69 x 0.28 m) were used to create a range of root-zone temperatures. Nine water-tight plastic

[1]Dept. of Horticulture, Wageningen Agricultural University, The Netherlands

TABLE 4.6

Experimental design with setpoints for air and root-zone temperatures and number of replications.

Temperature (°C) air	root-zone	Number of replications
18	18	2
18	21	1
18	26	2
18	28	2
21	18	2
21	21	2
21	26	2
21	28	1

pots (16 cm diameter) with adequate drainage were inserted in the lid of the metal tank. Equal root-zone and air temperatures were obtained on a grid similar in size to the Wisconsin tank, but without temperature control. The experimental design is presented in Table 4.6. Since only a limited number of Wisconsin tanks were available for this experiment, it was not possible to replicate each root-zone temperature treatment. At 18°C air temperature the 21°C root-zone temperature, and at 21°C air temperature the 28°C root-zone temperature treatment was not replicated. Root-zone temperatures could be controlled with an accuracy of +/- 1°C. An insulating layer of 1 cm expanded clay granules covered the potting medium to reduce the vertical temperature gradient in the potting soil. The gradient was reduced from 5 to 2°C at 18°C air - and 28°C root-zone temperature. Average mean air temperatures in the phytotron chambers were 18.4 and 21.4°C; relative humidities were respectively 73 and 68%.

Rooted cuttings of *Begonia x hiemalis* 'Toran' were potted on the 1st June 1989 and were grown to a marketable crop in 12 weeks. Cuttings were selected on height, number and diameter of the shoots according to results reported by Verberkt and Overbeeke (1989). In each pot one cutting was placed in a mix consisting of 25% perlite, 75% white peat, 3.5 kg lime, 0.75 kg 14N-16P-18K and microelements as stock fertilization m^{-3}. Watering and fertilization were done by hand and were adapted to the temperature treatment. Soil samples - from extra standard carts in each phytotron chamber - were taken every four weeks to check electrical conductivity (guide value 0.9 $mS.cm^{-1}$), pH (guide value 6.0) and nutrient composition. CO_2 was not supplied. Light intensity was 28-30 $W.m^{-2}$ at plant height (TL 50W/84F). Daylength was 14 hours during the whole experimental period; at the end of each day 1 hour incandescent light (1 $W.m^{-2}$) was supplied to obtain normal stem elongation.

Some plants were lost during the experiment due to stem rot (*Phytophtora*) or leaf curl. Open spaces were filled with plants of the same size. Destructive plant measurements were carried out at the end of the experimental period.

Heterogeneity among plants was large, despite selection of the cuttings at the start of the experiment. To reduce variation in the plant data, a selection was carried out: plants were not taken into account if the standard deviation of observed variables was more or less than twice the standard deviation of the experimental unit (one Wisconsin tank) or of the temperature treatment (two replicates). This resulted in an average of 7 plants per experimental unit (out of 9). The experiment was analysed by regression analysis at the 5% confidence level. Since there was no replication of the air temperature, it was assumed that the variance of growth chambers effects, such as light distribution, was equal to the variance within a growth chamber. In this way, effects of the air temperature could be tested, but conclusion should be looked at with care. Main effects of air and root-zone temperatures were tested first. In case of a significant effect of the root-zone temperature, linear and quadratic effects were also tested with orthogonal polynomes at the 5% confidence level (Montgomery and Peck, 1982).

RESULTS

Effects on flowering. - First flowering was observed after six weeks of cultivation at both air temperatures. At all root-zone temperatures flowering started at that date at

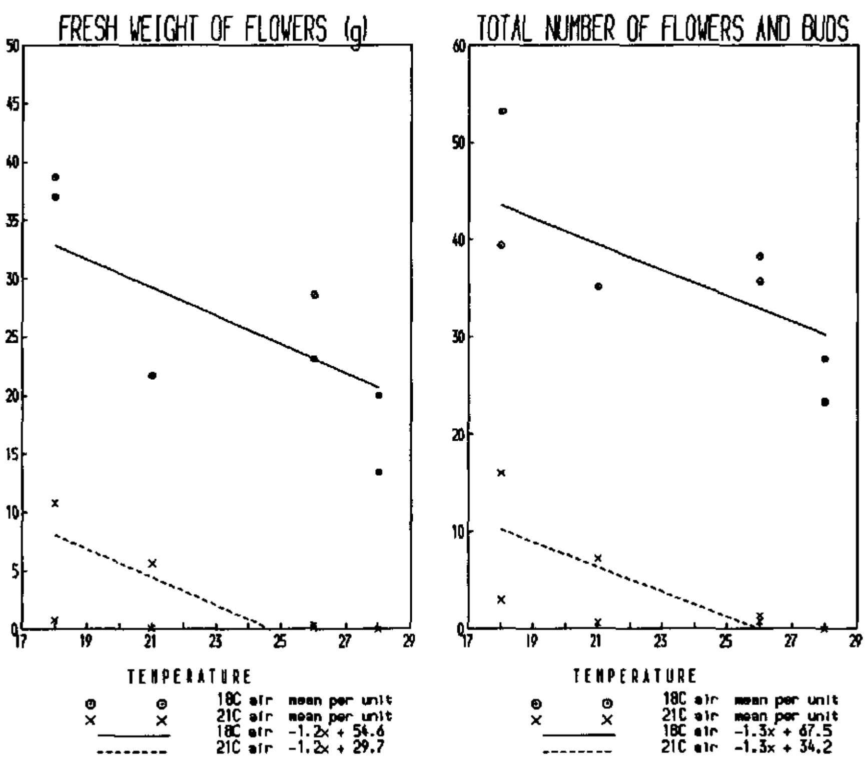

Fig. 4.3. Effect of root-zone and air temperature on flowering response at the end of the experimental period.

18°C air temperature, while at 21°C air temperature it took nine weeks before flowering occurred at 26 and 28°C root-zone temperature. Regression analysis showed decreasing linear responses to increasing root-zone temperatures in the investigated range for most variables concerning flowering. As an example, the fresh weight of flowering parts and total number of flowers and buds are presented in Figure 4.3. It is clear that 18°C air temperature favoured flowering compared to 21°C. Increasing root-zone temperatures had a slightly negative effect at both air temperatures. At the end of the experiment, only one or two plants flowered poorly at 28°C root-zone - and 21°C air temperature. No temperature effects were found on the formation of leaf-shaped flowers.

Effects on growth. - Distribution and structure of the roots was affected by the air and root-zone temperature. Roots grown at 18°C air temperature showed higher root densities in the potting soil than roots grown at 21°C air temperature. A reduced amount of roots was also observed at 26 and 28°C root-zone temperature; at these temperatures, the roots were finer branched compared to the lower root-zone temperatures.

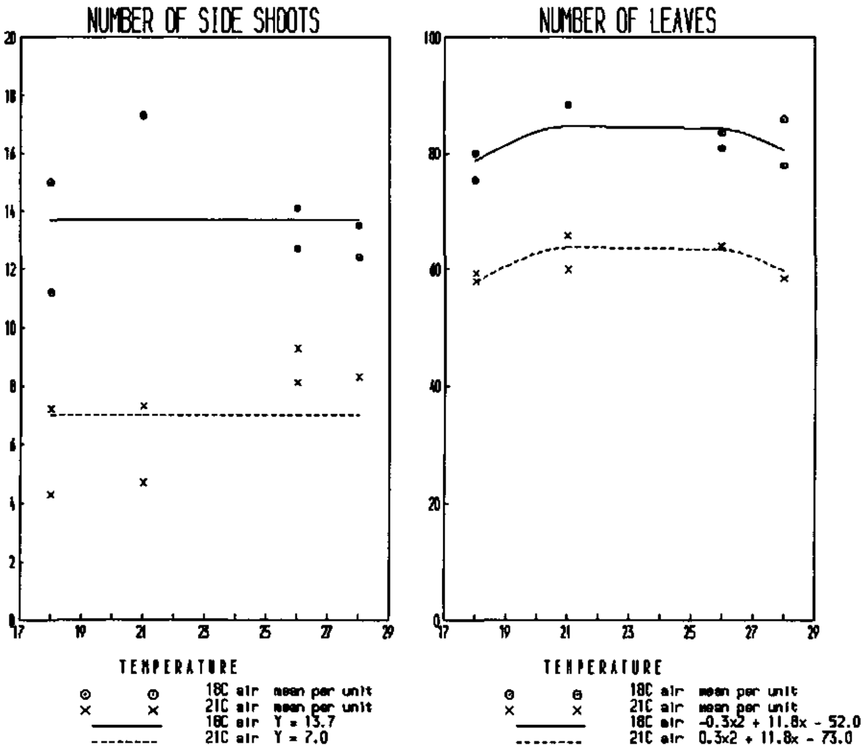

Fig. 4.4. Effect of root-zone and air temperature on number of side shoots and number of leaves at the end of the experimental period.

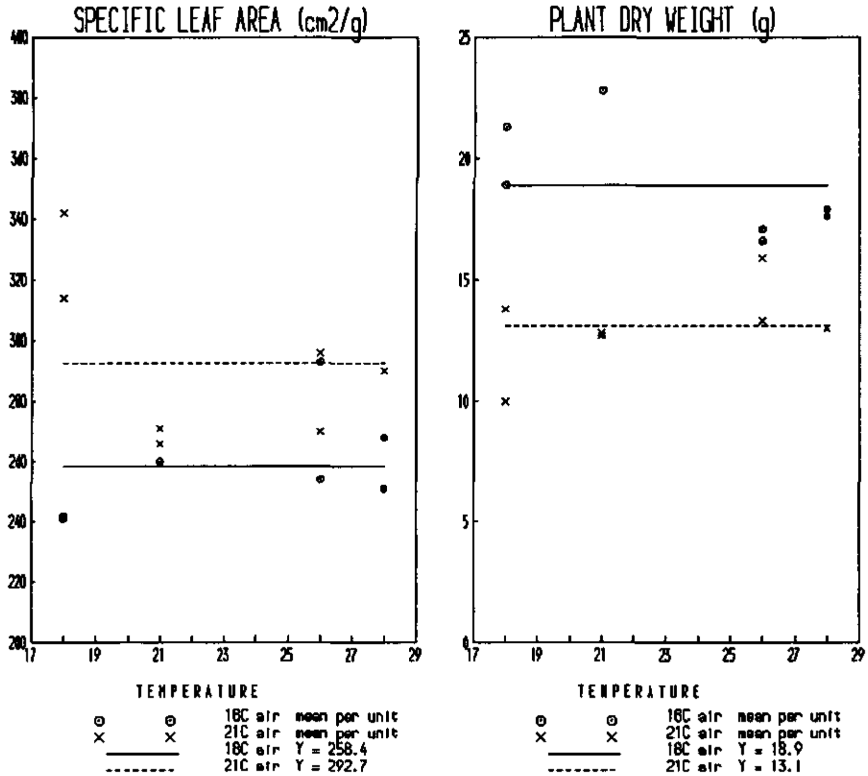

Fig. 4.5. Effect of root-zone and air temperature on specific leaf area and plant dry weight at the end of the experimental period.

In comparison with the flowering responses, most growth parameters showed a constant relation to increasing root-zone temperatures. In most cases a significant effect of the air temperature was observed. Number of leaves and number of side shoots were reduced at 21°C air temperature (Fig. 4.4), while the root-zone temperature had only a slight effect on the number of leaves. Higher values for SLA were found at 21°C air temperature compared to 18°C air temperature (Fig. 4.5). A reduced leaf thickness - on fresh weight base - was also found at 21°C air temperature. Plant dry weight was increased at 21°C air temperature (Fig. 4.5). Plant length and number of basal shoots were not affected significantly by the air or root-zone temperature. Plants grown at 18°C air temperature had a better ornamental value than plants grown at 21°C, due to higher numbers of leaves and side shoots.

DISCUSSION

At 21°C air temperature flowering of *Begonia x hiemalis* 'Toran' was reduced compared to 18°C air temperature, whereas increasing root-zone temperatures had a slightly negative effect on flowering up to 28°C. This result is in general agreement with former results (section 4.1), showing narrow tolerances for the air temperature

(18-19°C at low light levels in winter season) and a minor importance of the root-zone temperature up to 26°C. A sharp decline in flowering response by increasing the root-zone temperature from 26 to 28°C was not found in this experiment, as expected beforehand. At 21°C, flowering was almost prevented at root-zone temperatures of 26 and 28°C, whereas an equal decrease was found at 18°C air temperature. The question arises whether flowering at high root-zone and air temperatures is delayed or suppressed permanently. An indication is derived from the post-harvest experiment after experiment 1 in section 4.1, which showed no flowering of some plants grown at 29°C root-zone and normal greenhouse air temperature of 20°C. It seems therefore likely, that flowering can be suppressed permanently at root-zone temperatures of 26°C or higher in combination with too high air temperatures. In this experiment, which was carried out at relatively low light levels, an air temperature of 21°C was already too high, whereas the greenhouse experiments showed higher optimal values for the air temperature at higher irradiances (discussion section 4.1).

The root-zone temperature was of no importance for vegetative growth of *Begonia x hiemalis* 'Toran', which is in agreement with former experiments (section 4.1). In contrast to these greenhouse experiments, plant dry weight was influenced significantly by the air temperature in the phytotron experiment. Effects of the air temperature on SLA were similar, although an effect on final leaf thickness could not be detected at the end of the greenhouse experiments. Final plant dry weight was higher in the phytotron experiment compared to plants grown at higher irradiances in the greenhouse experiment (Experiment 1, section 4.1). Differences in growth responses between the greenhouse experiments and the phytotron experiment were most likely due to experimental conditions. Plants grown in Wisconsin tanks in the phytotron chambers might have benefitted longer from the effects on SLA, due to less mutual shading compared to the greenhouse experiments. The 3 x 3 design of pots in the Wisconsin tank has also led to differences in light utilization among individual plants. Root growth was also much less restricted in the Wisconsin tanks, due to a larger pot size. On the other hand, watering was less optimal in the phytotron experiment. It is therefore to certain extent difficult to compare growth in greenhouses with that in the phytotron experiment.

It can be concluded, that the air temperature has more effect on flowering of *Begonia* than the root-zone temperature in the investigated range. A sharp decrease in flowering response by increasing the root-zone temperature from 26 to 28°C has not been found; the effect of high root-zone temperatures appears dependent on the level of the air temperature.

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5. FOLIAGE PLANTS

EFFECT OF ROOT-ZONE AND AIR TEMPERATURE ON GROWTH, ORNAMENTAL VALUE AND KEEPABILITY OF *FICUS BENJAMINA* AND *SCHEFFLERA ARBORICOLA* 'COMPACTA'

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ABSTRACT

Two species of foliage plants were subjected to different root-zone temperatures up to 30°C on heated aluminium benches with a usual greenhouse temperature of 20°C or lower. Elevated root-zone and air temperatures had a promoting effect on growth rates in the beginning of the cultivation period. In the later stages of growth, no effect of the root-zone temperature on growth could be detected. Bench heating with a root-zone temperature of 30°C and an air temperature among the plants of 23-24°C reduced cultivation time for *Schefflera arboricola* 'Compacta' and *Ficus benjamina* by 2.5 weeks compared with the lowest temperature of 19°C, while the ornamental value was not unfavourably affected. A large part of the total heating demand can be supplied by bench heating systems as relatively high root-zone temperatures up to 30°C can be used during the whole cultivation period. Bench heating increased the accumulation of salts in the 4-cm top layer of the potting soil. Both crops tolerated high electrical conductivity levels in the top layer, even if salts were rinsed back to the roots by watering on top of the potting soil during post-harvest life.

Keywords: air temperature; *Ficus benjamina*; growth; keepability; root-zone temperature; salinity of potting soil; *Schefflera arboricola*.

Abbreviations: EC = electrical conductivity; LAI = leaf area index; LAR = leaf area ratio; NAR = net assimilation rate; RGR = relative growth rate.

INTRODUCTION

As heating costs are important, a lot of research has been carried out to reduce the energy losses of greenhouses and to provide heat more efficiently to the crop. The control of (micro)climate is still an important issue and the environmental aspects also urge the reduction of energy consumption. For potplant cultures, bench and floor heating systems have been developed to supply heat more efficiently to the crop. Since their introduction in The Netherlands in 1980, growers have installed these new heating systems, but the temperature has been kept relatively low. This strategy was based on the assumption that root-zone and air temperature should not differ too much. More knowledge about the effects of root-zone and air temperature on crop responses is needed to optimize the use of these heating systems.

Saintpaulia showed a positive response to bench heating on growth rate and flowering (Vogelezang, 1988). For *Begonia x hiemalis* grown on heated benches, the air temperature among the plants should be kept relatively low (Vogelezang, 1990). In this study, the results of two species of foliage plants are presented. *Ficus benjamina* is a branching, woody type of foliage plant, while *Schefflera arboricola* is a more herbaceous species with one growing point. Both crops are economically important in The Netherlands.

Information about optimum temperatures during growth in greenhouses indicates that night temperatures should not exceed 18-20°C for *Ficus* species and 18°C for *Schefflera* species (Van Adrichem et al., 1979; Von Hentig, 1981, 1982). These greenhouse temperatures are still recommended to the growers in the Netherlands and were used as starting point in this study. The aim of the present study was to investigate the separate effects of root-zone and air temperature, and their interactions, and to get a better understanding of the temperature tolerances and requirements of different plant growth processes.

Strong salinization of the top layer is primarily caused by the use of ebb and flood watering systems, and is not affected much by the potting soil mixture or watering frequency (De Kreij and Straver, 1988a). The first experiment of this study showed that the accumulation of salt in the top layer was also enhanced by bench heating. As the watering method changes from upwards (ebb and flood) to downwards (hand watering) in the consumers phase, the flow of salts downwards could be a problem during post-harvest life. Therefore, an experiment was set up to study the effect of different salt distributions in the potting soil on the keepability of *F. benjamina* and *S. arboricola* cultivar 'Compacta'.

MATERIAL AND METHODS

Experiments. - Two experiments were performed in greenhouses at Aalsmeer (The Netherlands), one in spring 1987 and the second in spring 1988. The average outside global radiation was 1583 $J.cm^{-2}.day^{-1}$ during the first experiment and 1177 $J.cm^{-2}.day^{-1}$ during the second one (Meteorological data, Naaldwijk, The Netherlands). Rooted leaf cuttings of *F. benjamina* and *S. arboricola* 'Compacta' were potted in 13-cm plastic pots in an "ebb and flood mix" consisting of 25% perlite, 75% white peat, 3.0 kg lime, 0.75 kg 14N-16P-18K and 0.64 g micro elements as stock fertilization per m^3. Watering was carried out with an ebb and flood system with additional fertilization at each watering time. Soil samples were taken every 3 weeks to check electrical conductivity (EC) (guide value for *Schefflera* 0.9 $mS.cm^{-1}$), pH (guide value 6.0) and nutrient composition. *Ficus* was additionally fertilized by hand to achieve higher EC levels in the potting soil (guide value 1.1 $mS.cm^{-1}$). Mean ambient CO_2 level was 300-350 $ml.m^{-3}$ during the experiments. Plant densities were 51, 29 and 19 plants per m^{-2}, depending on the stage of growth; spacing took place if the leaf area ratio (LAI) was ~3-4. An internal screen (transmission 40-45%) was closed during the day if global radiation outside the greenhouse was > 500 $W.m^{-2}$ during the first 2 weeks and > 700 $W.m^{-2}$ during the remainder of the cultivation period.

In the first experiment, three root-zone temperatures were applied on aluminium benches, namely ambient, 25 and 30°C at one level of greenhouse air temperature (18°C) to find an indication for the optimum one. The control of root-zone and air temperature was carried out by means of equipment described by Vogelezang (1990). As it is known that an aluminium bench heating system also increases the air temperature among the plants, two greenhouse air temperatures were included in the second experiment, namely 17 and 20°C. This set-up made it possible to separate, to a certain extent, the effects of root-zone and air temperature on crop responses. The effect of bench heating on the air temperature between the crop was measured separately with ventilated psychrometers 25 cm above the bench surface.

Statistical analysis. - Plants were observed at 3-week intervals, eight plants from each experimental unit. The variables recorded were fresh and dry weight of stem and leaves, leaf area, plant length to determine the cultivation time, number of leaves and number of side shoots (*Ficus*) to determine ornamental value.

The dry weight records were used to calculate the increase in dry weight by the equation

$$Y = a \times T^{b} \quad (1)$$

where Y = dry weight (g); T = time (in weeks from Week 3); a and b are constants. For the growth analysis, the following equation was used

$$RGR = LAR \times NAR \quad (2)$$

whereby the relative growth rate (RGR) was based on the assumption of exponential growth in the investigated period and leaf area ration (LAR) was calculated as total plant leaf area divided by total dry weight of the areal parts of the plant.

The cultivation time is expressed as the number of weeks required to produce a certain plant length; the final plant length of the slowest growing plot is used to calculate the reduction of cultivation time of the other plots.

For *Ficus*, the leaf density, which is calculated as the number of leaves per cm plant length, and the number of side shoots are used as characteristics of ornamental value. For *Schefflera*, the internode length is used as a quality aspect. Differences in final leaf thickness, which is calculated as fresh weight of leaves per cm^2 leaf area, and percentage dry matter can lead to noticeable differences in leaf colour and firmness, and were therefore also examined.

All experiments were carried out with one replication for each temperature treatment. Experiment 1 could be analysed sufficiently with analysis of variance. The second experiment was analysed by regression analysis, with the same assumptions as described by Vogelezang (1990). Separate linear regression models were fitted to a number of response variables. The potential set of explanatory variables considered was a constant, root-zone, air, root-zone^2, air^2, and the interaction between the effects of root-zone and air temperature. The fact, that these terms are interdependent renders the selection of variables and the interpretation of regression coefficients difficult. For each variable, a model was selected in accordance with three criteria. Namely, explanatory variables were included in the final model that were both marginally and conditionally significant at the 5% level, and the model as a whole was tested at the same level (Montgomery and Peck, 1982).

Experiment to test keeping quality. - Before post-harvest life was evaluated, different salt distributions in the potting soil were created by rinsing half of the experimental material of three root-zone temperature pre-treatments (20, 25 and 30°C) with 1 l of tap water (see Table 5.5). To all treatments, a transport simulation of 0 or 7 days was given in darkness at 17°C and 70% relative humidity. During post-harvest life, watering was done by hand on top of the potting soil or with an ebb and flood system to create differences in water and salt movement through the potting soil. Tap water, without fertilizers, was used for watering. Two groups of four plants were placed in a conditioned room (20°C day and night temperature, 60% relative humidity and a light level of 4.5 $W.m^{-2}$ photosynthetically active radiation with fluorescent lamps TL 58W, colour 84). Post-harvest life was evaluated during 10 weeks.

RESULTS

Rooting. - Good roots were formed in all temperature treatments and in both experiments. In the second experiment, the amount and distribution of roots was examined visually after 3 weeks of growth. No differences were found for *Ficus*, but the root density on the outside surface of the potting soil of *Schefflera* was slightly promoted by higher root-zone temperatures. Also, the structure of the roots was affected by the root-zone temperature. Roots of *Schefflera* grown at 25 or 30°C had a finer branched structure compared with the unheated controls. In all temperature treatments, the roots grew to the pot bottom. The fine structure of the roots and the presence of peat in the potting soil prevented a quantitative evaluation of shoot/root ratios at different temperatures.

Growth and dry matter distribution. - The first experiment showed a significant effect of bench heating on final plant fresh weight and cultivation time for *Ficus* (Table 5.1). As bench heating increased both root-zone and air temperature at the same time, conclusions about causality cannot be drawn from this experiment. No significant effects were found in the first experiment for *Schefflera*, which is probably due to the heterogeneity of the plant material.

In the second experiment, both crops were affected by bench heating. It was found that the function $Y = a \times T^b$ (Y=dry weight; T=time in weeks from Week 3; a and b are constants) provided a good description of the time course of dry weight with very high percentages of accounted variances (≥95%). This means there is a linear relationship between logY and logT, with b as the regression coefficient for the slope and log$a$ as an estimate for the intercept. Parameters a and b were highly negatively correlated with each other. As parameter b was less correlated with the explanatory variables than parameter a, parameter b was fixed in the final model (Table 5.1). This means that differences between temperature treatments mainly developed during the beginning of the cultivation period, because parameter a has most influence at low T. Therefore, the dry matter distribution and growth rate were studied in more detail during this period.

The dry matter distribution over stem and leaves is not constant in time (Fig. 5.1). When the rooted cuttings of *Schefflera* were potted, they had only a few very small leaves, which led to a very low percentage of leaves of the new shoot at the start of the experiment. Leaves expanded rapidly during the first period of growth (Fig. 5.1). RGR was significantly enhanced by higher air temperatures in the first 3 weeks (Table 5.2); a significant effect of the air temperature on LAR was found, but variance within treatments was too large to find any significance on net assimilation rate (NAR). For *Ficus*, a gradual decrease in percentage leaf dry matter and an

TABLE 5.1

Effect of air temperature and root-zone temperature on the increase in dry weight (equation: $Y = a \times T^b$, where Y=dry weight in g; T=time in weeks from Week 3; a and b are constants), cultivation time, final fresh weight and ornamental value at the end of the experimental period (12 weeks for *Ficus*, 15 weeks for *Schefflera*) for the two experiments. Cultivation time is expressed as the number of weeks required to reach equal plant length (l, in cm). Leaf density is expressed as the number of leaves per cm plant length. Different letters indicate significant difference at the 5% level for each crop (Experiment 1). Correlation matrices and regression analysis for Experiment 2 are presented in Tables 5.3 and 5.4. ns=no significant temperature effects.

	Crop	Setpoint air/root	24-h mean air/root	Parameter a (*10^{-2})	Cultivation time	Plant fresh weight (g)	Number of shoots	Leaf density	Percent dry matter	Leaf thickness ($mg.cm^{-2}$)
				for b=1.8	for l=66.7					
1	*Ficus*	18/18	21.7/21.7	15.61 (a)	11.7 (b)	58.9 (a)	14.5 (a)	1.40 (a)	22.8 (a)	0.240 (a)
		18/25	22.2/25.8	16.73 (a)	11.2 (b)	66.6 (b)	15.6 (a)	1.57 (ab)	22.5 (a)	0.230 (a)
		18/30	23.9/30.2	19.49 (b)	10.6 (a)	75.2 (c)	15.6 (a)	1.59 (b)	22.8 (a)	0.241 (a)
				for b=1.9	for l=61.9		Internode length (cm)			
	Schefflera	18/18	21.7/22.0	14.53 (a)	13.9 (a)	164.9 (a)	4.1 (b)		16.1 (a)	0.431 (a)
		18/25	23.2/25.8	15.40 (a)	14.1 (a)	155.7 (a)	3.7 (a)		15.9 (a)	0.437 (a)
		18/30	24.8/30.2	14.68 (a)	14.0 (a)	159.6 (a)	3.7 (a)		15.7 (a)	0.421 (a)
				for b=2.0	for l=47.4		Number of shoots	Leaf density		
2	*Ficus*	17/17	19.5/19.2	4.12	11.2	27.9	14.4	0.92	21.8	0.250
		17/25	20.9/25.3	6.11	9.9	42.6	23.7	1.18	21.2	0.245
		17/30	22.5/30.0	6.80	9.0	46.4	28.0	1.31	21.1	0.232
		20/20	21.1/20.8	6.08	9.8	43.7	26.1	1.35	20.7	0.240
		20/25	22.1/25.2	6.62	9.2	46.2	27.0	1.23	21.0	0.234
		20/30	23.3/30.0	6.55	8.7	44.8	26.3	1.32	20.9	0.236
				for b=2.7	for l=56.0		Internode length (cm)			
	Schefflera	17/17	19.2/19.7	1.36	14.6	142.4	4.0 (ns)		14.6	0.441 (ns)
		17/25	21.3/25.6	1.70	13.6	176.7	4.0 (ns)		14.8	0.449 (ns)
		17/30	22.9/30.0	1.67	13.2	161.9	4.0 (ns)		15.2	0.436 (ns)
		20/20	20.9/21.3	1.79	13.1	177.2	4.2 (ns)		15.2	0.451 (ns)
		20/25	22.2/25.5	1.65	13.5	163.3	4.1 (ns)		15.2	0.450 (ns)
		20/30	23.8/30.1	1.96	12.2	188.5	4.1 (ns)		15.4	0.453 (ns)

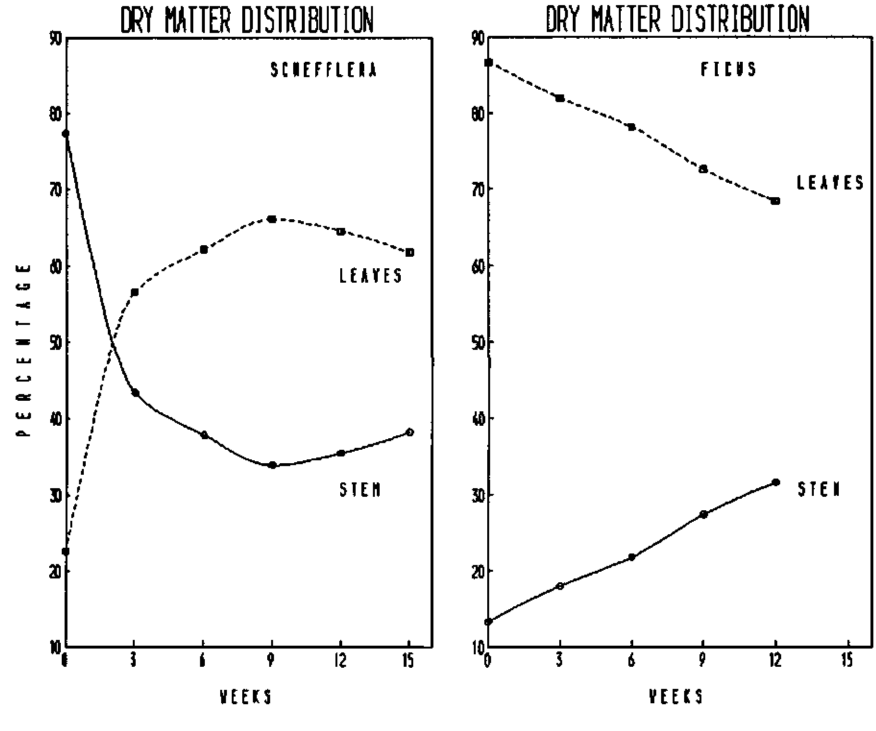

Fig. 5.1. Experiment 2. Dry matter distribution (%) over stem and leaves as a mean for all temperature treatments.

increase in percentage stem dry matter was observed (Fig. 5.1). The combination of higher root-zone and air temperatures influenced RGR positively in the first 3 weeks of growth (significant *F*-test, Table 5.2); both NAR and LAR were affected by root-zone and/or air temperature. In both crops, RGR was no longer significantly affected by root-zone and air temperature in the following cultivation weeks (Table 5.2).

A lead in growth gained at the beginning of the cultivation period persisted until the end, resulting in a reduction of cultivation time. In the second experiment, cultivation times for *Schefflera* and *Ficus* were reduced by 2.5 weeks compared with the cultivation time at the lowest actual air and root-zone temperature of 19°C (Table 5.1). Differences in plant fresh weight were less pronounced, caused by larger variances within treatments. The regression analysis on the final plant data showed that the air temperature was the most important factor and that the root-zone temperature was of minor importance in both crops (Tables 5.3 and 5.4).

TABLE 5.2

Experiment 2. Effect of air and root-zone temperature on RGR ($g.g.day^{-1}$), NAR ($g.cm^{-2}.day^{-1} * 10^{-4}$) and LAR in Weeks 0-3 and on RGR in Weeks 3-6. The level of significance in the regression analysis is 5%. ns = not significant

Crop			Weeks 0-3			Weeks 3-6
	Setpoint air/root	24-h mean air/root	RGR	NAR	LAR	RGR
Ficus	17/17	16.6/17.3	0.012	0.97	127	0.022
	17/25	18.6/25.0	0.017	1.10	152	0.031
	17/30	19.8/30.0	0.022	1.35	160	0.028
	20/20	19.5/19.5	0.017	1.08	156	0.028
	20/25	20.4/25.0	0.021	1.30	164	0.029
	20/30	21.2/30.0	0.023	1.31	172	0.029
Regression analysis						
Root-zone temperature			Significant	Significant	ns	ns
Air temperature			*F*-test	*F*-test	Significant	ns
Schefflera	17/17	16.3/17.1	0.073	5.85	125	0.063
	17/25	18.9/25.0	0.074	5.34	139	0.069
	17/30	19.6/30.0	0.094	5.80	162	0.061
	20/20	19.3/19.5	0.091	5.81	157	0.056
	20/25	20.1/25.0	0.095	5.73	166	0.061
	20/30	21.7/30.0	0.102	6.12	168	0.056
Regression analysis						
Root-zone temperature			ns	ns	ns	ns
Air temperature			Significant	ns	Significant	ns

Ornamental value. - The effect of root-zone and air temperature on ornamental value is presented in Table 5.1 for both experiments. The number of side shoots and the leaf density of *Ficus* were positively influenced by the air temperature among the plants (Table 5.4). Both the leaf density and number of lateral shoots are related to the development of the lower situated growing points and are highly correlated with each other (Table 5.3). The internode length of *Schefflera* was only slightly affected in the first experiment. In the second experiment, leaf thickness and percentage dry matter were influenced by the air temperature, but differences between temperature treatments could not be detected visually in both crops. All investigated variables for *Ficus* were highly correlated with each other. There was a remarkable difference in the number of lateral shoots between Experiments 1 and 2 (Table 5.1). Although the final plant fresh weight was higher in the first experiment, the number of lateral shoots was much lower compared with the second experiment. Recent experiments at the Research Station for Floriculture in Aalsmeer (The Netherlands) have shown that vegetatively propagated cuttings have a much lower number of lateral shoots compared with cuttings from tissue culture stockplants. This effect on side shoot formation decreased with the age of the tissue culture stockplants (Kromwijk and van Mourik, 1990).

TABLE 5.3

Experiment 2. Correlation matrix for *Ficus benjamina* and *Schefflera arboricola* 'Compacta'. Only significant correlation coefficients are given (5% level, $r \geq 0.468$)

Ficus benjamina

Term	1	2	3	4	5	6	7	8	9	10	11	12[1]
1. Root-zone temp.	1.000											
2. Air temperature	0.873	1.000										
3. Root-zone temp.^{2}	-	-	1.000									
4. Air temperature^2	-	-	0.717	1.000								
5. Air x root-zone	-	-	0.889	0.946	1.000							
6. Parameter a	0.692	0.791	-	-0.626	-0.579	1.000						
7. Cultivation time	-0.774	-0.886	-	0.518	-	-0.882	1.000					
8. Fresh weight	0.602	0.734	-0.475	-0.660	-0.611	0.978	-0.835	1.000				
9. Nr. lateral shoots	0.587	0.731	-	0.642	-0.569	0.958	-0.826	0.973	1.000			
10. Leaf density	0.550	0.726	-	-0.551	-	0.829	-0.685	0.864	0.854	1.000		
11. Pct. dry matter	-	-0.473	-	0.586	0.479	-0.484	0.605	-0.581	-0.565	-0.621	1.000	
12. Leaf thickness	-0.619	-0.779	-	0.538	-	-0.603	0.695	-0.595	-0.565	-0.578	0.593	1.000

Schefflera arboricola 'Compacta'

Term	1	2	3	4	5	6	7	8	9[1]
1. Root-zone temp.	1.000								
2. Air temperature	0.935	1.000							
3. Root-zone temp.^{2}	-	-	1.000						
4. Air temperature^2	-	-	0.811	1.000					
5. Air x root-zone	-	-	0.922	0.973	1.000				
6. Parameter a	0.559	0.733	-	-	-	1.000			
7. Cultivation time	-0.706	-0.844	-	-	-	-0.933	1.000		
8. Fresh weight	-	0.622	-	-	-	0.953	-0.809	1.000	
9. Pct. dry matter	-	0.560	-	-	-	0.721	-0.685	0.617	1.000

1 Numbers correspond with those in the column.

TABLE 5.4

Experiment 2. Regression coefficients and Student's *t*-values (in parentheses) for the relationships between response and explanatory variates

Crop	Response variable	Root-zone temperature	Air temperature	Air temperature²	Air x root-zone temp.
Ficus	Parameter a (* 10^{-2})	0.037 (0.52)	0.455 (1.75)	0.029 (0.11)	-0.096 (-1.00)
	Cult. time	-0.024 (-0.43)	-0.545 (-2.77)[1]	0.113 (1.62)	
	Fresh weight	0.018 (0.03)	3.600 (1.69)	-0.240 (-0.11)	-0.615 (-0.79)
	Nr. of shoots	-0.038 (-0.09)	2.650 (1.65)	-0.840 (-0.50)	-0.162 (-0.27)
	Leaf density	-0.008 (-0.62)	0.102 (2.17)[1]	-0.025 (-1.50)	
	Pct. dry matter	-0.089 (-0.99)	0.277 (1.46)	-0.055 (-0.81)	
	Leaf thickness	0.0002 (0.42)	-0.005 (-2.31)[1]	-0.001 (1.45)	
Schefflera	Parameter a (* 10^{-2})	-0.052 (-2.38)[1]	0.226 (3.97)[1]		
	Cult.time	0.130 (1.91)	-0.740 (-4.20)[1]		

[1] Significantly different at the 5 % level.

TABLE 5.5

Effect of root-zone heating during cultivation and effect of different watering methods just before transport and during post-harvest life on EC (mS.cm^{-1}, 25°C) of the top soil layer (one-third) and the rest of the potting soil for *Schefflera arboricola* 'Compacta' in 13-cm pot size (n=8)

Setpoint air/root	24-h mean air/root	Pot layer	Rinsing with tap water		Watering strategy	
			Before	After	Ebb/flood	By hand
20/20	20.9/21.3	Top	6.5		5.9	2.6
		Rest	1.1		0.9	2.0
		Top		2.4	4.9	2.2
		Rest		1.2	0.9	1.4
20/25	22.2/25.5	Top	6.4		8.2	3.6
		Rest	1.0		0.9	1.9
		Top		3.3	6.1	2.3
		Rest		1.3	0.7	2.0
20/30	23.8/30.1	Top	9.7		9.3	4.7
		Rest	1.3		1.0	2.9
		Top		4.0	6.4	2.5
		Rest		1.7	0.9	1.7

Keeping quality. - The effect of root-zone heating and different watering methods on the distribution of salts in the potting soil is presented for *Schefflera* 'Compacta' in Table 5.5. The results for *Ficus* are similar, but EC values are in general somewhat lower in the top layer and higher in the rest of the potting soil. A statistical analysis cannot be given as the soil samples from the two replica had to be combined to provide enough material for the soil analysis. The results have therefore a descriptive character. During the experiment, a range of EC levels from 6.5 up to 9.7 was created in the top layer of the potting soil due to the different root-zone temperature treatments. Rinsing the potting soil with 1 l tap water decreased the EC in the 4-cm top layer by ~50%. The EC levels in the lower two-thirds of the potting soil did not change much by rinsing with tap water and were about equal for the three root-zone temperatures. Hand watering on top of the potting soil during post-harvest life did not decrease the EC in the top layer much further if the potting soil had already been rinsed with 1 l tap water. Non-rinsed potting soils showed a decrease in salt content in the top layer and an increase in EC in the lower two-thirds layer if the plants were watered by hand. Watering with an ebb and flood system during post-harvest life increased the EC of the top layer in most of the treatments. Any effect on leaf drop or leaf colour could not be detected in the *Schefflera* crop. *Ficus* plants which were subjected to 7 days transport simulation in the dark showed leaf yellowing 1 week after the transport simulation, which disappeared in the following 3 weeks. Poole and Conover (1979) reported a decrease in the chlorophyll content of *F. benjamina* if the time in dark storage increased, which can explain the observed leaf yellowing. Some leaf drop of matured (yellow) leaves at the base of the stem was observed, but this effect was not related to any treatment. Both crops tolerated high EC levels in the top layer of the potting soil, even if salts are rinsed back to the roots by watering on top of the potting soil during post-harvest life.

DISCUSSION

This study showed that the first growth phase was most sensitive for the investigated environmental influences. During the first 3 weeks of growth, differences in growth rates between the temperature treatments were built up, which persisted during later stages of growth. A couple of plant processes could have been involved in this early phase of growth, such as root formation and/or efficiency of the root system, an enhanced rate of assimilation and an improved dry matter utilization. The root density on the outside surface of the potting soil of *Schefflera* was slightly promoted by higher root-zone temperatures in the first 3 weeks of growth, but this effect could not be found in the RGR during this period. In this crop, the air temperature seemed to be the most important factor, whereby differences in RGR in the first cultivation weeks were mainly caused by differences in LAR. For *Ficus*, the root-zone and/or air temperature were affecting both NAR and LAR positively in the first 3 weeks of growth. However, effects of the root-zone temperature could no longer be detected in the regression analysis on the final plant data. In later stages of growth, the variances between the root-zone temperature treatments were most likely overshadowed by the influence of the air temperature and increased variation among older plants.

In both crops, the air temperature seemed to be far more important in obtaining a certain marketable product than the root-zone temperature in the investigated range. Mortensen and Larsen (1989) also found that the recommended air temperatures are suboptimal for obtaining maximum growth. They showed that the optimum temperatures for six foliage plants varied considerably between the species, ranging from 21 to 32°C. *F. benjamina* had a high temperature optimum of 32°C, *S. arboricola* was not included in their research. However, their study was performed under high light conditions and not with a canopy, so optimum temperatures could be lower if light levels and light utilization are less optimal.

Roots of *Schefflera* at a root-zone temperature of 25 or 30°C had a finer branched structure compared with the unheated control. This effect on the structure of roots is also observed in previous experiments with *Begonia*, where roots grown at 23 or 29°C had a finer branched structure compared with lower temperatures (Vogelezang, 1990). Visually, the root structure of *Ficus* was not affected by temperature, but the root structure of this species is very fine and differences are, therefore, very difficult to determine. In contrary to the results with *Begonia*, roots did grow fully to the pot bottom, even at the highest root-zone temperature of 30°C. It indicates that this temperature is well tolerated by both crops, even when there are large differences between root-zone and air temperature during growth.

This study showed that *F. benjamina* and *S. arboricola* 'Compacta' can be successfully grown on heated aluminium benches. If root-zone temperatures > 25°C can be used during cultivation, a large part of the total heating demand can be supplied with this heating system (Van Weel, 1984). Results with *F. benjamina* cultivar 'Exotica' on heated concrete floors were in agreement with those of this study (Van Leeuwen, 1989). Although this experiment was performed under poor light conditions, floor heating promoted growth and plant quality. Nisen et al. (1978) reported that soil temperatures up to 30°C can be used for *Ficus elastica* (with a minimum air temperature of 15°C), which is in agreement with the present results. Conover and Poole (1987) reported variable, but generally adverse effects on plant height and quality grade of *F. benjamina* if root-zone temperatures were increased from 20 to 35°C. They started the experiment with 15-cm old plants and they finished it 4 months later, thus obtaining higher final shoot fresh weight compared with our experiments. However, the present study demonstrated that the effect of root-zone temperature in later stages of growth was of less importance in comparison to the influence of the air temperature. Differences in reported responses to root-zone temperature might be explained by differences in greenhouse air temperature, watering and fertilizer application or stage of growth.

The post-harvest experiment showed that high EC levels in the top layer of the potting soil had no effect on keepability, even if salts are rinsed back to the roots by watering on top of the potting soil during post-harvest life. However, evaporation from the potting soil should be reduced as much as possible in order to reduce excessive use of nutrients and unnecessary heating losses. Covering the top layer with impenetrable loose material could reduce the accumulation of salts in the top layer, but is not sufficient (De Kreij and Straver, 1988b). They suggested to use lower EC concentrations in the watering solution in order to reduce the accumulation of salts.

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6. SPATHIPHYLLUM AND GUZMANIA

EFFECT OF ROOT-ZONE AND AIR TEMPERATURE ON FLOWERING AND GROWTH OF *SPATHIPHYLLUM* AND *GUZMANIA MINOR* 'EMPIRE'

Scientia Horticulturae, 49: 311-322

ABSTRACT

Spathiphyllum and *Guzmania*, two flowering potplants were subjected to different root-zone temperatures up to 30°C on heated aluminium benches with a usual greenhouse temperature of 20°C or lower. The optimal air temperature for flowering of *Spathiphyllum* was 22°C, whereas root-zone temperatures in the range between 20-26°C were of less importance. Growth, development, plant height and leaf size of *Spathiphyllum* were enhanced by higher air temperatures up to 23°C. Elevated root-zone temperatures increased the shoot/root-ratio, decreased the number of side shoots, but the dry weight per shoot was increased. Plant shape of *Spathiphyllum* can therefore largely be influenced by the root-zone and air temperature. Growth and development of *Guzmania* were enhanced by higher air temperatures up to 22°C. Increasing root-zone (19 to 26°C) and air temperatures (19 to 22°C) promoted flowering without negative effects on the quality of inflorescences.

Both crops can successfully be grown on heated benches, but root-zone temperatures above 26°C are not advisable for either crop. In both crops flowering is a temperature sensitive process, which determines the optimal temperature settings of bench heating systems.

Keywords: air temperature; greenhouse; *Guzmania minor*; root-zone temperature; *Spathiphyllum*.

INTRODUCTION

The need for more efficient use of energy has led to the introduction of bench and floor heating systems for potplant cultures in 1980 in the Netherlands. Since then, research has continued to optimize the design and the use of these heating systems (Vogelezang and Van Weel, 1989). In comparison with traditional heating systems, which are placed overhead and under benches, the root-zone temperature is increased to a higher extent than the air temperature with bench and floor heating systems. An important aspect is therefore the response of different crops to an increased root-zone temperature in relation to the air temperature. Former research with *Saintpaulia*, *Begonia* and two foliage plants (Vogelezang, 1988, 1990, 1991) has demonstrated that there were similarities and differences in plant response to root-zone and air temperature, which have consequences for the use of bench and floor heating systems. In this study, the results of two other types of flowering plants are presented: *Spathiphyllum* and *Guzmania minor* cultivar 'Empire'. Both crops are economically important in The Netherlands.

Information about optimal temperatures during growth in greenhouses indicates that temperatures should be 18-20°C for *Spathiphyllum* (Langius, 1985; Von Hentig, 1989) and 19-22°C for most of the Bromeliaceae (De Jong, 1988). These greenhouse temperatures were used as starting point in this study. The aim of this research was to get insight into the separate effects of root-zone and air temperature and their interactions, and to get a better understanding of the temperature tolerances and requirements of different plant processes.

MATERIAL AND METHODS

Experiment 1. - In the first experiment, which started in March 1987, three root-zone temperatures were applied on aluminium benches, namely ambient, 25 and 30°C at one level of greenhouse air temperature (18°C) to find an indication for the optimal one. Each temperature treatment was carried out with one replication. Root-zone and air temperature were controlled as described previously (Vogelezang, 1990). The effect of bench heating on the air temperature between the crops was measured with ventilated psychrometers 25 cm above the bench surface. Rooted seedlings of *Spathiphyllum* cultivar 'Mauna Loa Brilliant' were potted in 11-cm plastic pots in an "ebb and flood mix" consisting of 25% perlite, 75% white peat, 3.0 kg lime, 0.75 kg 14N-16P-18K and 6.4 g micro elements as stock fertilisation per m^3. Plants were watered with an ebb and flood system with fertilisation at each time of watering. Soil was sampled every 6 weeks to check electrical conductivity (guide value 1.1 $mS.cm^{-1}$), pH (guide value 6.0) and nutrient composition. Plant densities were depending on the stage of growth 72, 36, 25 and 15 plants per m^2. Unfortunately only 10% of the *Spathiphyllum* plants were flowering after 7 months. Therefore, it was necessary to transfer all *Spathiphyllum* plants to another greenhouse compartment (root-zone and air temperature 20°C). It took another 3 months before most of the plants flowered.

Plant material of *Guzmania minor* 'Empire' was delivered in 10-cm plastic pots in a mixture of black and white peat, peatmoss and perlite. Watering and fertilisation was done by hand (guide values in the potting soil: 0.6 $mS.cm^{-1}$, pH 6.0). After 3 months of cultivation, acetylene was applied for flower induction of *Guzmania*. Plant densities were 72 and 49 plants per m^2. An internal screen (transmission 40-45%) was closed during the day if global radiation outside the greenhouse was higher than 300 $W.m^{-2}$, with an additional whitewash on the roof during the summer months. Plant measurements were taken after 3 and 6 months of cultivation. The flowering response was recorded weekly. The inflorescences of *Guzmania* plants were visually divided in three classes, namely large, normal and small. The size of the normal and small inflorescences was about 35 and 70% smaller than the large ones. Data were analysed with analysis of variance at a 5% level.

Experiment 2. - This experiment started in September 1988. Following the results of the first experiment, the range of root-zone temperature was lowered in this experiment to ambient, 23 and 26°C. As it is known that an aluminium bench heating system also increases the air temperature among the plants, two greenhouse air temperatures were included in the second experiment, namely 17 and 20°C. This set-up made it possible to separate effects of root-zone and air temperature on crop responses to a certain extent. As the plant material of *Spathiphyllum* showed a great heterogeneity in the first experiment, plants from tissue culture of the cultivar 'Luna' were used in this experiment. To study the crop longer than usual in commercial practice, a 14-cm potsize was used. Plant densities were depending on the stage of growth 49, 25 and 20 plants per m^2. Young plant material of *Guzmania minor* 'Empire' was potted in 10-cm pots. The plant density was reduced once from 100 to 56 plants per m^2. Acetylene was applied after 6 months of cultivation for flower induction of *Guzmania*. Watering, fertilisation and other cultivation methods were similar as in Experiment 1, except for the use of the internal screen at night when temperatures outside dropped below 10°C.

Plants were observed at 8-week intervals, eight plants from each experimental unit. Dry and fresh weight and number of leaves were measured in both crops to study growth and development. For *Spathiphyllum*, plant length (from root base to top of the leaves), number of side shoots, average shoot weight, average leaf size and percentage dry matter were used to describe plant shape and firmness. The flowering response was recorded weekly for the whole plot for both crops ($n=40$). In *Spathi phyllum* plants the first flower bud was taken away, and flowers appearing subsequently in the side shoots were recorded weekly until the end of the experiment. The diameter of inflorescences of *Guzmania* was measured. The experiment was carried out with one replication for each temperature treatment. Data were analyzed statistically by means of regression analysis, with the same assumptions as described previously (Vogelezang 1990). Separate linear regression models were fitted to a number of response variates. The potential set of explanatory variables considered were: a constant, root-zone-, air-, root-zone^2-, air^2- and the interaction between the effects of root-zone and air temperature. The fact, that these terms are aliased, renders the selection of variables and the interpretation of regression coefficients difficult. For each variate a model was selected in accordance with three criteria: namely, explanatory variables were included in the final model, that were both marginally and conditionally significant at a 5% level and the model as a whole was tested at the same level (Montgomery and Peck, 1982). For the variable percentage flowering plants the arcsin transformation was used to overcome differences in variance (Sokal and Rohlf, 1981).

RESULTS

Experiment 1. - Soon after the start of the experiment differences in the structure of the roots on the outside surface of the potting soil of *Spathiphyllum* were visible. Roots grown at 30°C did not grow fully to the pot bottom, while excellent rooting was

TABLE 6.1

Experiment 1. Effect of bench heating on plant length and number of side shoots of *Spathiphyllum* 'Mauna Loa Brilliant' after 6 months of cultivation and percentage flowering at the end of the experiment after 10 months ($n=60$). Different letters mean least significant difference at the 5% level.

Setpoint air/root temp. (°C)	24-h mean air/root temp. (°C)	Plant length (cm)	Number of side shoots per plant	% flowering plants
18/18	21.7/22.0	56.2 (a)	4.4 (b)	80 (b)
18/25	23.0/25.6	62.5 (b)	3.9 (b)	76 (b)
18/30	24.4/30.0	62.0 (b)	3.3 (a)	52 (a)

TABLE 6.2

Experiment 1. Effect of bench heating on flowering and size of inflorescences of *Guzmania minor* 'Empire' ($n = 90$). The size of normal and small inflorescences was about 35 and 70% smaller than the large ones. Different letters mean least significant difference at the 5% level.

Setpoint air/root temp. (°C)	24-h mean air/root temp. (°C)	time till flowering	% non-flowering	Size of inflorescences (% of total)		
				Large	Normal	Small
18/18	21.8/22.2	21 weeks (b)	3.5 (a)	76 (b)	22 (a)	2 (a)
18/25	23.3/25.8	20 weeks (a)	0.4 (a)	82 (b)	18 (a)	0 (a)
18/30	25.3/30.0	20 weeks (a)	6.7 (b)	56 (a)	34 (b)	10 (b)

observed at 25°C and ambient root-zone temperatures. Nevertheless, at 30°C root-zone temperature growth was not reduced significantly after 3 or 6 months of cultivation. Plant shape was significantly changed by cultivation on heated benches (Table 6.1). Plant length was increased by bench heating, while the number of side shoots was reduced. Flowering was significantly reduced by bench heating with a root-zone temperature of 30°C, despite the relatively low root-zone and air temperature during the last cultivation period (Table 6.1).

Growth of *Guzmania minor* was not significantly influenced by different combinations of root-zone and air temperature. Bench heating did influence the time till flowering, the percentage of non-flowering plants and the quality of inflorescences (Table 6.2). The moment of flowering was slightly enhanced by higher temperatures, but the average size of the inflorescences was affected negatively. Whether the increased root-zone or air temperature on heated benches were responsible for the plant responses mentioned cannot be concluded from this experiment. However, a root-zone temperature of 30°C, an air temperature of 24-25°C or the combination of both seems to be too high for both crops.

Experiment 2. - Effects of root-zone and air temperature on different plant processes of *Spathiphyllum* are presented in Table 6.3. None of the investigated variates were significant to one explanatory variable only in the correlation matrices. Therefore, only the results of the supplementary regression analysis are presented in Table 6.4. Flowering was delayed with 9 weeks by the lowest air/root temperature treatment of 17/17°C compared with the 20/20°C treatment (Fig. 6.1). The 17°C treatment was omitted in the statistical analysis, as the development stage of these plants differed from the other treatments. Evaluation of the different temperature combinations on the appearance of the first flower showed (Table 6.4(A)), that both root-zone and air temperature had a slightly promoting effect in the range investigated. The combination of highest root-zone and air temperature enhanced flowering by 2 weeks in comparison with 20/20°C (Fig. 6.1). A significant reduction on next appearing flowers in the side shoots was found if the air temperature raised above 22°C (Tables 6.3(C), 6.4(C), Fig. 6.2), while the root-zone temperature had no significant influence. Definite conclusions about the flowering response to 17/17°C cannot be drawn from this experiment.

TABLE 6.3

Experiment 2. Effect of air and root-zone temperature on flowering and crop properties of the marketable crop (A), dry matter distribution over main shoot, side shoots and roots (B) and flowering response in an older crop of *Spathiphyllum* 'Luna' (C). The regression analysis is presented in Table 6.4

(A) Marketable crop (week 24)

Setpoint air/root temp.(°C)	24-h mean air/root temp (°C)	Flowering % flower 1[1]	Fresh weight (g)	Plant length (cm)	Av. leaf size (cm^2)	Mean % dry matter
17/17	17.7/17.6	0	24.4	28.7	19.2	12.0
17/23	19.6/23.0	0	36.7	31.7	24.7	10.9
17/26	21.1/26.0	23	45.8	31.5	26.1	10.8
20/20	20.5/20.5	0	41.3	32.3	27.0	10.8
20/23	21.4/23.0	17	49.9	33.3	28.3	10.4
20/26	23.2/26.0	33	44.1	32.3	28.5	10.7

(B) Dry matter distribution (week 32)

Setpoint air/root temp. (°C)	24-h mean air/root temp. (°C)	Plant dry wt. (g)	Shoot/ root-ratio	No. of leaves main shoot	No. of leaves side shoots	No. of side shoots	Dry weight per side shoot (g)
17/17	17.7/18.3	7.49	3.6	11.1	19.5	6.0	0.55
17/23	19.6/23.1	9.60	4.0	12.7	27.2	5.4	0.90
17/26	21.4/26.0	10.75	4.5	14.0	29.8	4.3	1.27
20/20	20.2/20.7	9.67	3.8	13.1	29.0	6.7	0.71
20/23	21.2/23.2	12.10	4.2	14.3	30.9	6.0	1.01
20/26	23.1/26.1	12.72	4.8	16.8	28.2	4.2	1.34

(C) Flowering response (week 40)

Setpoint air/root temp. (°C)	24-h mean air/root temp. (°C)	% flowering		
		Flower 2[2]	Flower 3	Flower 4
17/17	18.4/19.6	0	0	0
17/23	20.6/22.9	79	54	29
17/26	22.3/25.8	97	79	51
20/20	20.5/21.1	84	61	36
20/23	21.3/23.4	90	68	39
20/26	23.7/25.8	75	20	5

[1] Flowering in week 25.

[2] No significant temperature effects.

TABLE 6.4

Experiment 2. Regression coefficients and Student *t*-values (between arrows) for the relations between response and explanatory variates (*Spathiphyllum*). Underlined *t*-values are significantly different at the 5% level

Response variate	Root-zone temperature	Air temperature	Root zone temperature^2	Air temperature^2	Air x Root-zone temperature
(A) Marketable crop (week 24)					
% flower 1 week 25	0.072 (3.15)	0.088 (2.32)			
Fresh weight (g)	0.260 (0.45)	2.938 (3.03)	0.322 (1.06)	-0.260 (-0.22)	-0.900 (-0.88)
Plant length (cm)	-0.182 (-1.27)	0.659 (2.75)	0.027 (0.36)	0.296 (1.02)	-0.383 (-1.52)
Av. leaf size (cm^2)	-0.324 (-1.91)	1.857 (6.53)	0.075 (0.85)	0.400 (1.17)	-0.585 (-1.95)
Mean % dry matter	-0.007 (-0.19)	-0.180 (-2.99)	0.016 (0.83)	0.083 (1.14)	-0.015 (-0.24)
(B) Dry matter distribution (week 32)					
Plant dry weight (g)	-0.042 (-0.36)	1.025 (5.27)			
Shoot/root-ratio	0.009 (3.33)	0.009 (2.06)			
No. leaves main shoot	-0.010 (-1.07)	1.143 (7.51)			
No. leaves side shoots	-0.551 (-0.97)	2.140 (2.36)	0.427 (0.85)	1.070 (0.76)	-1.760 (-1.13)
No. of side shoots	-0.417 (-3.25)	0.248 (1.19)			
Dry weight per shoot (g)	0.081 (3.48)	0.036 (0.94)			
(C) Flowering response (week 40)					
% flower 3		0.019 (0.59)		-0.211 (-4.39)	0.085 (2.12)
% flower 4		-0.018 (-0.42)		-0.091 (-2.68)	

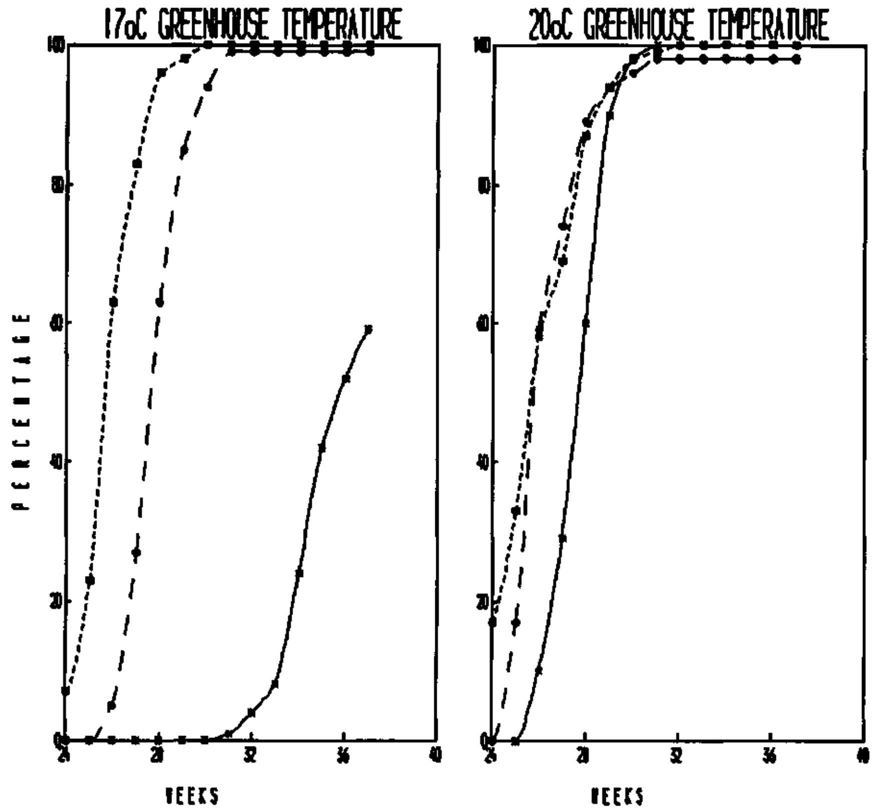

Fig. 6.1. Effect of root-zone and air temperature on appearance of the first flower of *Spathiphyllum* at two greenhouse air temperatures. Low root-zone temperature (ambient,(*——*); Medium root-zone temperature (23°C, o - - - o); High root-zone temperature (26°C,□----□).

Plant fresh weight of *Spathiphyllum* increased significantly by the air temperature (Tables 6.3(A), 6.4(A)) in the investigated range up to 23°C. Also the shape of the plants (like plant length and leaf size) and the percentage dry matter was affected by the air temperature. A higher percentage dry matter has led to noticeable thicker leaves and darker leaf colour in the 17/17°C treatment. In comparison with the first experiment, effects of root-zone temperature on root structure could not be detected visually. The shoot/root-ratio was increased and the number of side shoots decreased by increasing root-zone temperatures (Tables 6.3(B), 6.4(B)). The development of the plants (expressed as number of leaves of main and side shoots) was not influenced by the root-zone temperature, but enhanced by higher air temperatures (Tables 6.3(B), 6.4(B)). Although the number of side shoots was reduced at higher root-zone temperature, the dry weight per side shoot was increased.

During the experimental period two other differences between the temperature treatments were observed in *Spathiphyllum* plants. In December and January 12% of

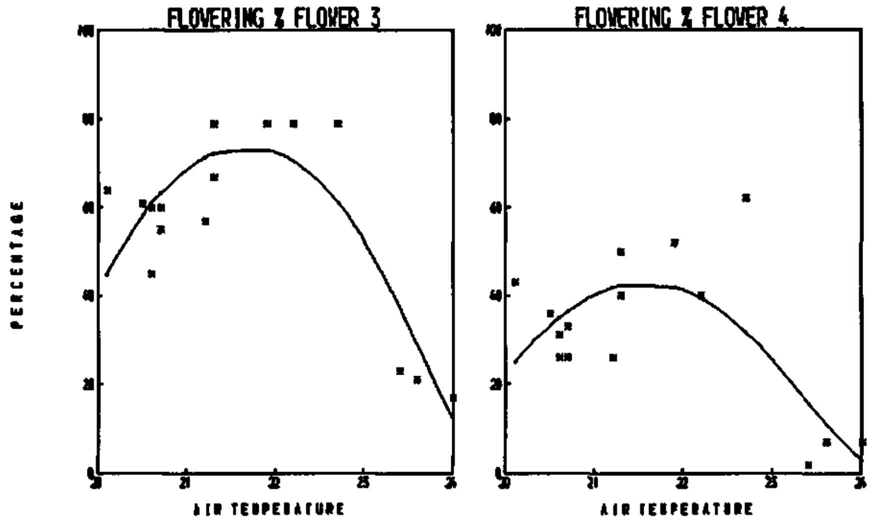

Fig. 6.2. Observed (*) and fitted values (—) of the final regression model for the flowering response of the third and fourth flower for *Spathiphyllum*.

TABLE 6.5

Experiment 2. Effect of air and root-zone temperature on flowering and crop properties of *Guzmania minor* 'Empire' (week 40). The regression analysis is presented in Table 6.6.

Setpoint air/root temp. (°C)	24-h mean air/root temp. (°C)	Time till flowering (weeks)	Fresh weight (g)	No. of leaves	Mean % dry matter
17/17	18.6/20.0	39.7	43.6	25.2	13.4
17/23	19.5/22.6	38.3	47.4	26.1	13.6
17/26	20.5/25.7	36.7	45.6	27.3	13.6
20/20	20.7/21.2	38.0	49.9	27.5	13.4
20/23	20.7/23.7	37.2	53.5	28.4	13.6
20/26	22.1/25.6	35.9	53.5	29.1	13.7

the plants of the 20/26°C treatment were affected by non-infectious variegation (Soraurer, 1924), while all other treatments showed at the most 1.7% infection. In some plants the leaves became totally white during this period. Also the percentage of leaf deformation at the end of the experimental period differed between the treatments, with values ranging from 0.8 to 10.9%. Regression analysis showed, that both phenomena were enhanced by higher air temperatures, and that the root-zone temperature had no effect (data not shown).

The time till flowering of *Guzmania minor* was enhanced by both root-zone and air temperature in the investigated range of temperatures (Tables 6.5, 6.6). In all

TABLE 6.6

Experiment 2. Regression coefficients and Student *t*-values (between arrows) for the relations between response and explanatory variates (*Guzmania*). Underlined Student *t*-values are significantly different at the 5% level.

Response variate	Root-zone temperature	Air temperature	Root-zone temperature^2
Time till flowering	- 0.321 (- 8.73)	- 0.536 (- 7.72)	
Fresh weight	- 0.758 (- 1.56)	3.739 (4.06)	- 0.547 (- 2.98)
No. of leaves	0.022 (0.16)	1.076 (4.21)	
Mean % dry matter	0.048 (3.07)	- 0.003 (- 0.11)	

treatments the flowering response was 100%. The diameter of the inflorescences ranged from 13.2 to 14.1 cm at different temperatures, which were very small differences compared to the first experiment. Both plant fresh weight and number of leaves were affected positively by higher air temperatures up to 22°C, which was the maximum air temperature in this experiment (Tables 6.5, 6.6); the root-zone temperature was of less importance. Differences in percentage dry matter were small.

DISCUSSION

In the first experiment flowering of *Spathiphyllum* showed great heterogeneity, but this is normal for a seedling crop (Langius, 1985). Although the root-zone and air temperature were lowered during the last 3 months of cultivation, there was still an after-effect of bench heating on flowering. This after-effect can be explained, because the time lapse between flower induction and realisation is about 12 weeks for *Spathiphyllum* seedlings (Blacquière and Kuiper, 1989). Uniformity of flowering was much better in the second experiment with 'Luna', obtained from tissue culture. From this experiment it can be concluded, that the optimal air temperature for flowering is 22°C, which is in agreement with Hendriks and Scharpf (1989). They observed best flowering response at constant day/night temperature of 22°C. The root-zone temperature can be varied between 20 to 26°C without negative effects on flowering. The observed negative effect on flowering in the first experiment is most likely caused by too high values of the air temperature between the crop (24-25°C), but a direct negative effect of the root-zone temperature of 30°C cannot be excluded.

In the second experiment growth and development of *Spathiphyllum* was enhanced by higher air temperatures up to 23°C, the highest temperature investigated. Hendriks and Scharpf (1989) reported even higher rates of growth by increasing air temperatures up to 26°C. The root-zone temperature affected side shoot formation and dry matter distribution over shoots and roots. In the second experiment the number of side shoots decreased and the shoot/root-ratio increased by increasing root-zone temperatures up to 26°C. The results of the first experiment with respect to root and side shoot formation are in agreement with mentioned responses, which indicates that the root-zone temperature is affecting these processes up to 30°C. It is clear that both root-zone and air temperature had great influence on growth and shape of *Spathiphyl-*

lum plants; *Spathiphyllum* is a quite temperature-sensitive crop compared to the investigated foliage plants (Vogelezang, 1991). The occurrence of leaf deformation and non-infectious variegation were related to air temperature; the last phenomenon is probably a cultivar dependant problem.

As the first experiment showed differences in root structure of *Spathiphyllum* in relation to root-zone temperature, drought tolerance during transport and ornamental value afterwards were evaluated (Mulderij, 1989). No significant effects were found, even if the crop was cultivated at the highest root-zone temperature of 30°C.

In the first experiment with *Guzmania minor* 'Empire' flowering on heated benches was enhanced, but the size of inflorescences was reduced. From the second experiment it can be concluded, that root-zone temperatures from 19 to 26°C as well as air temperatures from 19 to 22°C promoted flowering without negative effects on the quality of inflorescences. This range of optimal temperatures is in agreement with temperature responses of other *Bromeliaceae* (Zimmer, 1965; 1985a), where optimal air temperatures for flowering are in the range between 22 to 25°C air temperature. Whether the root-zone or the air temperature were responsible for the reduction of size of inflorescences remains uncertain, but a direct negative effect of a root-zone temperature of 30°C is well plausible, since the air temperature among the plants was within the normal range (25°C). In the second experiment maximum growth was obtained at the highest realised air temperature (22°C); in general it is found that temperatures above 20°C are optimal for vegetative growth of *Bromeliaceae* (Zimmer, 1985b).

This study showed that both crops can successfully be grown on heated benches. Results with *Spathiphyllum* 'Adagio' and 'Petite' were in agreement with those of this study: bench heating enhanced flowering, increased plant height and reduced the number of side shoots (Verberkt, 1989). Flowering of *Spathiphyllum* is a temperature sensitive process, which determines the optimal air temperature during cultivation. Root-zone temperatures higher than 26°C are not advisable for both crops.

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7. GENERAL DISCUSSION

7.1 Introduction

The experiments described in Chapters 3, 4, 5 and 6 have shown that an increased root-zone and air temperature, due to bench heating, may have distinct effects on growth, flowering and ornamental value of potplants. An overview of the major results of this study is given in Table 7.1. Similarities and differences in crop response to root-zone and air temperature were found for the six investigated crops. In most crops, growth parameters were affected by the air temperature, except for *Saintpaulia*. Some effects on root growth and structure of the roots were observed at increasing root-zone temperatures (Table 7.2), but they appeared of minor importance for the overall crop response. For developmental processes, such as shoot formation and flowering, both the root-zone and air temperature were important factors.

In this chapter an attempt is made to combine the information of the previous chapters with that from the literature in order to provide, as far as possible, a general overview and explanation of the effects of bench heating on growth and development of the potplant species investigated. Underlying processes will be discussed against the background presented in the general introduction (Chapter 1). There was, however, no clear picture of the effects of root temperature on plant growth regulators (section 1.4), and this part of the discussion, therefore, primarily aims at putting the observations in the context of present general knowledge on the subject. Because it is not only important to know which plant processes were affected, their relative importance will also be considered, and, where possible, insight will be given into the reasons for the differences among species. This information should support extrapolation to other potplants.

7.2 Root growth

In the Netherlands, potplants are usually propagated from cuttings or seeds on specialised nurseries. The cultivation phase starts, therefore, with the process of re-growth of the roots, creating new contact between the root surface and the soil after transplanting in a larger pot. Shoot growth follows re-growth of the roots, establishing another functional equilibrium between shoot and roots (Brouwer, 1963; 1983). Consequently, an increased rate of root development might affect initial shoot growth positively. After this initial phase of root growth, improved functioning of the root system may also affect above ground shoot growth positively (Brouwer, 1963; 1983).

Differences in root development and structure of the roots were observed visually in this study (Table 7.2); quantitative evaluation was, unfortunately, difficult, due to the fine structure of the roots and the presence of peat in the potting soil. The results therefore have a descriptive character.

Re-growth after planting. - During the first weeks of cultivation, an increase of root growth was observed on the outer surface of the potting soil under increasing root-zone temperatures for *Saintpaulia*, *Schefflera* and *Spathiphyllum* (Table 7.2), which is assumed to reflect growth of the entire root system. Root growth might have been

TABLE 7.1

Major effects of bench heating for the six evaluated crops.

Chapter	Saintp. 3	Begonia 4	Ficus 5	Scheffl. 5	Spath. 6	Guzm. 6
Growth						
Final shoot weight	rz	0/a	a	a	a	a
LAR or SLA	rz	a	a	a	a	?
Shoot/root- ratio	?	rz[1]	?	?	rz	?
Distribution stem/ leaves/infloresc.	0	0	0	0	0	-
Flowering						
Time to flower	rz	rz/a	-	-	rz/a	rz/a
Size flowers/ inflorescences	0	0	-	-	0	rz
Ornamental value						
Shoot formation	rz	a	a	-	rz	-
Other aspects[2]	0	0	0	0	rz/a	0
Post-harvest life	rz	rz/a	0	0	0	?

rz = affected by root-zone temperature only
a = affected by air temperature only
rz/a = affected by both root-zone and air temperature
0 = not or slightly affected
? = not investigated
\- = not relevant for that crop
1 = examined visually
2 = variables examined were dependent on crop properties

affected similarly in the other crops, but there were no visible differences in amount and distribution. However, RGR of *Schefflera* was mainly affected by the air temperature and not by the root-zone temperature in that period (Table 5.2), thus fast regrowth of roots (in response to root-zone temperature) appears to be of less importance for initial shoot growth in this crop. This observation is in agreement with Wang (1988), where initial differences in root grade, due to an increased root-zone temperature, did not affect subsequent shoot growth of *Ficus benjamina* and *Codiaeum variegatum*. It is concluded, that root size in the first period of growth does not restrict subsequent shoot growth in the temperature range investigated.

Root distribution. - Increasing root-zone temperatures did not affect root distribution in *Saintpaulia* (investigated up to 26°C), *Ficus*, *Schefflera* and *Guzmania* (investigated up to 30°C) (Table 7.2). Roots of these crops grew normally down to the bottom of the pot, where the highest root densities were found. A different root distribution was found for *Begonia* and *Spathiphyllum*; at the highest root-zone temperature investigated, 29 and 30°C respectively, roots did not grow at the bottom of the pot. Roots of *Begonia* never reached the bottom of the pot during the whole cultivation period, whereas reduced root growth of *Spathiphyllum* in that part was only observed in later

TABLE 7.2

Effects of root-zone temperature on root growth. - = reduced at increased root-zone temperature; + = increased at increased root-zone temperature; 0 = none, or only slightly affected.

	Saintp.	Begonia	Ficus	Scheffl.	Spath.	Guzmania
Initial rooting	+	0	0	+	+	0
Rooting in lowest layer of the potting soil	0	-	0	0	-	0
Root branching	0	+	0	+	+/-*	0

* increased up to 26°C, decreased at 30°C (fig 7.1)

stages (Fig. 7.1). Both crops were cultivated with an ebb and flood watering system with high watering frequencies, which makes it improbable that growth of roots was restricted by availability of soil water. In wet soils, however, soil aeration may be a dominant stress factor (Marschner, 1988). At increasing root-zone temperature, the demand for oxygen may exceed the supply, due to a rise in respiration of the roots and soil micro-organisms, and to a reduced solubility of oxygen in the liquid phase.

Gislerød (1983) showed, that initial rooting of cuttings was better correlated with oxygen diffusion rate (ODR) than with the air content. Guide values for relations between root growth and ODR have been established and an overview was given by Brouwer and Wiersum (1977): roots of several plant species failed to grow when ODR was less than $20\text{-}40.10^{-8}$ $g.cm^{-2}.min^{-1}$. Kowalik (1985) found ODR values < 20.10^{-8} $g.cm^{-2}.min^{-1}$ to be critical and ODR values > 50.10^{-8} $g.cm^{-2}.min^{-1}$ to be optimal for growth of many plants.

In this study, ODR was measured in *Begonia* at 17, 23 and 29°C root-zone temperature according to Kowalik (1985). In the first period of cultivation (week 3-6), ODR was $100\text{-}200.10^{-8}$ $g.cm^{-2}.min^{-1}$ in the central (horizontal) layer, and $60\text{-}140.10^{-8}$ $g.cm^{-2}.min^{-1}$ at the bottom of the pot. Values for ODR decreased in time, and were at the end of cultivation (week 10-11) at the bottom of the pot $30\text{-}40.10^{-8}$ $g.cm^{-2}.min^{-1}$ for all three root-zone temperatures (unpublished data). It is concluded, that it is not likely that oxygen restricted root growth at the bottom of the pot at 29°C. The most plausible cause for poor root growth at the bottom of the pot is local high temperature as such. Bench heating causes a temperature gradient from bottom to rim of the pot (Yang and Albright, 1985), and in heterogeneous soils a root system may allocate its density and activity accordingly to Van Noordwijk (1991). For several environmental factors, such as $[Al^{3+}]$ and low $[O_2]$-sites, 'avoidance' reactions were found if an alternative was offered (Van Noordwijk, 1991). Similar 'avoidance' reactions were found for root temperature in split-root studies. Brouwer (1981) compared the growth rates of root halves at root temperatures in the range from 5 to 40°C in combination with 25°C in the other half (which was supposed to be optimal for maize), and found that increase in root dry matter at 25°C equalled the reduction at other temperatures. Karlsen (1980) concluded from a split-root study with cucumber, that there was only a slight effect on dry matter distribution between root halves at 28 and 14°C compared to 28°C in both halves, and that roots at 28°C appeared to compensate in activity for the reduction in activity at 14°C. Similar adaptations to heterogeneity in root temperature might have occurred in *Begonia* and *Spathiphyllum* at supra-optimal temperatures at the bottom of the pot. This speculation is supported by the observed optimal temperature range for initial rooting for *Begonia* (24-27°C) (Von Hentig and Fisher, 1987). For *Spathiphyllum*, a maximum temperature for initial rooting has not been established yet (fa. Braam, pers. comm.), a temperature of 22°C is generally used after germination (Von Hentig and Wohanke, 1989). For *Spathiphyllum*, growth rate of the roots at high temperature was reduced in later stages of growth; when roots reached the bottom of the pot, further growth in length was restricted (Fig. 7.1). Different temperature optima for initiation and growth of roots have been found (Haissig, 1986), and this may have played a role with this crop.

Root structure. - The root structure was affected visually by the root-zone temperature with *Begonia*, *Schefflera* and *Spathiphyllum*. At increased root-zone temperatures [*Begonia* (23,29°C), *Schefflera* (25,30°C), *Spathiphyllum* (26°C)] roots had a finer structure and were more branched, which is in accordance with other observations (Abdelhafeez, 1971; Barr and Pellett, 1972; Hickleton, 1988; Hurewitz and Janes, 1983; Moorby and Graves, 1980; Shanks and Laurie, 1949). Tomato roots grown at 28°C showed a reduction in the number of cell layers in the cortex and large secondary xylem vessels compared to roots grown at low temperature (Moorby and Graves, 1980). The effects of increased root-zone temperature on root structure, as observed in this study, almost certainly have resulted in a larger surface area of the root sys-

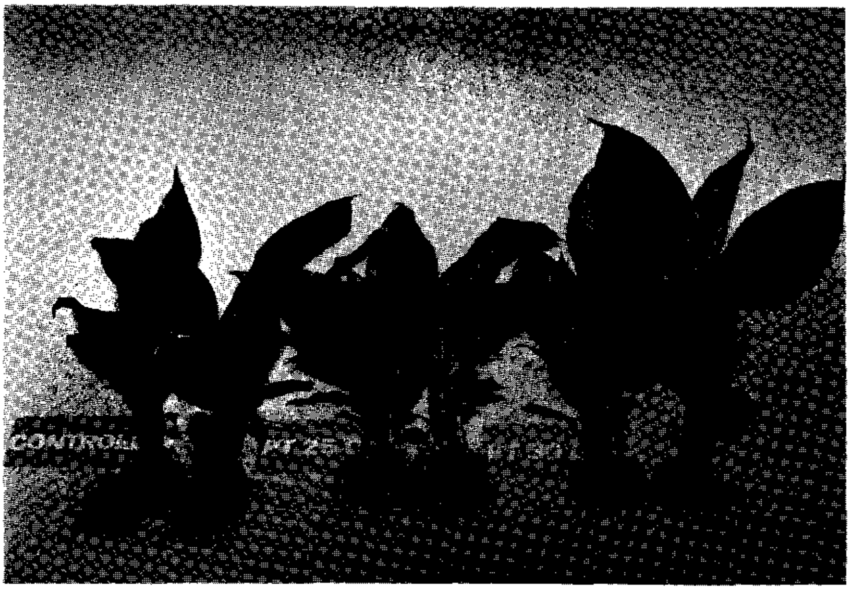

Fig. 7.1. Increased root-zone temperature reduced root growth in later stages of growth at 30°C (plant on the right) compared to 25°C (plant in the middle) and the unheated control (plant on the left, 22°C) (photo was taken after 3 months of cultivation).

tem, which facilitates water and nutrient uptake (Van Noordwijk, 1983). I was not able to get more quantitative information about this morphological response of the roots to temperature. The 'profile wall method' (Van Noordwijk et al., 1985) was evaluated for root systems of *Dieffenbachia*, *Schefflera* and *Spathiphyllum* in 13-cm pots. Estimates of root length varied largely with the actual root length of rinsed roots. Compared to field situations, root growth in pots shows different preferential ways of growth in different soil layers, and it is therefore difficult to make one profile (or more) representative of the entire potting volume (Drost, 1987; Van der Laan, 1986).

For potplants, cultivated with ebb and flood watering systems, water and nutrients are continuously available in the potting soil. Requirements of the root-soil system depend, therefore, more on uptake and transport functions of the roots, than on the ability of the root system to obtain water and nutrients from the root environment. In this study, water and nutrient uptake might have been enhanced at increased root-zone temperatures, due to an increased root surface area, but there is no evidence that these processes were limiting plant growth in the investigated temperature range. *Saintpaulia* might be an exception, where higher area/weight - and fresh/dry weight ratios at increased root-zone temperatures (23-26°C) might have been due to a reduced root resistance for water uptake at these temperatures (section 7.3). From these findings it was concluded, that effects of root-zone temperature on root growth and functioning were in general of minor importance for growth of potplants in the investigated temperature range. Further investigations were therefore aimed at other aspects of crop growth and development.

7.3 Dry matter production

A simple relational diagram of the production system was presented in section 1.5 (Fig. 1.1). It presents the plant processes which might have an influence on crop growth in response to root temperature. For potplants, fresh weight of the finished product was used as main growth parameter in this study. Other evaluated variables were leaf area, shoot/root-ratio and the dry matter distribution between stem, leaves and inflorescences (Table 7.1). The air temperature determined final shoot weight of most evaluated crops, except for *Saintpaulia*, where the root-zone temperature was the determining factor. This difference in growth response to root-zone and air temperature was analysed for *Ficus*, *Schefflera* and *Saintpaulia* by means of growth analysis.

Net assimilation rate. - Both increasing root-zone and air temperature increased NAR in *Ficus benjamina* during the first 3 weeks of growth (Table 5.2). Positive effects of root temperature on NAR were most likely due to an increased rate of photosynthesis (P), since the conversion efficiency is independent of temperature (Penning de Vries, 1972), and the rate of maintenance respiration (R_m) increases at increasing temperature (section 1.4). However, in later stages of growth, no effect of the root-zone temperature on growth could be detected, and here air temperature was the main factor. The question arises why the role of root temperature differed in early and later stages of growth in *Ficus*. As discussed in Chapter 5, in later stages of growth, the differences between the root-zone temperature treatments might have been overshadowed by the influence of the air temperature and increased variation among older plants. It might, however, also be due to the fact that the positive effect of root-zone temperature on P was compensated in a later stage by increasing R_m, which is proportional to the weight to be maintained (Lambers, 1985).

NAR was not correlated to root-zone or air temperature in *Schefflera* (Table 5.2), but this might have been due to large variation within treatments. NAR is ~5 times higher for *Schefflera* than for *Ficus benjamina* in the first period of growth, but this large difference is the result of the starting-material and the way of calculating NAR. For *Schefflera*, the cutting-leaf at the rooted cutting contributes to growth of the new shoot in this early phase of growth, but its area was not taken into account in the growth analysis. This also interfered with the growth simulation of *Schefflera* during the first weeks of growth (Leutscher and Vogelezang, 1990).

Leaf area. - Effect of air temperature on relative growth rate of *Ficus benjamina* and *Schefflera* during the first three weeks of growth was partly or entirely mediated through Leaf Area Ratio (LAR) (Table 5.2). In this early stage of growth, an increased LAR must have contributed to an increase in Leaf Area index (LAI) and hence in light interception, and thus to an increased crop photosynthesis at the relative low LAI (< 1.5). At higher LAI, light interception by the canopy is close to maximum (generally in the range 3 - 6, Gifford and Jenkins, 1981), thus reducing the positive effect of LAR on crop growth rate. Similar morphological effects of air temperature on SLA and LAR (not reported) were found for *Begonia* (Table 4.4, Fig. 4.5) and *Spathiphyllum* (SLA was increased from 30 to 35 $cm^2.mg^{-1}$ by an increase in air temperature from 18 to 23°C). The availability of carbohydrates and water are major determinants of leaf growth (Dale, 1988). It is however not clear, which aspect of leaf growth (cell elongation, synthesis of structural dry matter) is determining the sensitivity of LAR and SLA to air temperature. According to Pieters (1974) high light intensity and low temperature often result in an increase of leaf thickness, which points to competition for carbohydrates; high temperature accelerates leaf area growth, which may act as a sink and compete with the growth in thickness. LAR was also affected in *Saintpaulia* (Fig. 3.3; Table 3.8), where a reduced elongation was found at a low root-zone temperature. This might be related to reduced water uptake at low root-zone temperature or altered balance between growth promoters and inhibitors (section 3.2).

Dry matter distribution. - Dry matter distribution in the shoot was not or only marginally affected by root-zone and air temperature for the evaluated crops (Table 7.1). Also with *Spathiphyllum*, dry matter distribution between stem and leaves was not affected by root-zone and air temperature (data not presented); at the marketable stage (week 24) percentage leaf dry matter varied between 47.9 and 50.4% among the temperature treatments. These findings are in agreement with observations for young tomato plants (Harssema, 1977), cucumber (Marcelis, pers. comm.), sweet pepper (Bhatt and Rao, 1989) and some agricultural crops (Warren Wilson, 1966). Kleinendorst and Veen (1983) reported for young cucumber plants an increasing stem/leaf ratio with increasing shoot temperature from 12 to 24°C. This might, however, be related to (temperature induced) differences in development of the plants. Where differences in dry matter distribution were observed in this study, these were also most likely related to differences in developmental stage (ontogenetic effect). This was demonstrated for *Saintpaulia*, where differences in development were related to the flowering response. Since earliness of flowering (leaf number with first inflorescence) was not affected by root-zone heating (section 3.2), differences in flowering time reflect differences in development in this crop. When marketable saintpaulia plants of the unheated and heated treatments were compared, the former being cultivated over a longer, there were no significant differences in dry matter distribution (Table 3.8).

Shoot/root-ratio clearly increased at increasing root-zone temperature in *Spathiphyllum* (Table 6.3). Although not quantitatively evaluated, increasing root-zone temperature gave rise to decreased root length and root diameter of *Begonia* without affecting shoot weight, thus leading to an increased shoot/root-ratio. Shoot/root-ratio might have been affected similarly in the other crops, but since differences in root density were not visible and root weight could not be measured accurately (section 7.2), this point remains unclear. Similar effects of root temperature on shoot/root-ratio were observed for cucumber and figleaf gourd, except at extremely low root temperature (12°C) (Tachibana, 1982), for tomato in the range 13-30°C (Cooper and Thornley, 1976; Gosselin and Trudel, 1982) and for several woody ornamentals (Barr and Pellet, 1972).

A high shoot/root-ratio is probably related to favourable growth conditions (Klepper, 1991). In the concept of a functional equilibrium between roots and shoot (Brouwer, 1963; 1983) an improved function of the roots results in an increased shoot growth. Increasing root temperature may have a direct positive effect on water uptake (section 1.4), and an indirect influence on uptake functions by effects on root structure (section 7.2). It is probably, however, more meaningful to express the relationship between roots and shoot on an area base (leaf area to root area) than on a weight base (Van Noordwijk, 1983). Thus, an improved functioning of the roots at increased root-zone temperatures might have resulted in a (relatively) smaller root system expressed in weight, but larger root system expressed in area. For *Begonia*, a finer branched structure was indeed observed at increased root-zone temperatures up to 29°C (section 7.2). The growth rate of the root system of *Spathiphyllum* was strongly reduced at 30°C root-zone temperature (Fig. 7.1), whereas final growth was not negatively affected at this temperature. It appears therefore, that water uptake (the most critical root function at restricted root surface area) was not limiting shoot growth at this temperature, which is presumably due to an increased hydraulic conductance per unit surface area at restricted surface area (De Willigen and Van Noordwijk, 1987). An increased shoot/root-ratio at increased root-zone temperature compares well with other situations, where small root systems were sufficient to obtain maximum plant growth if water and nutrients are continuously available (Van Noordwijk and De Willigen, 1987). This condition prevailed in the ebb/flood watering systems, used in this study.

Dry matter production of most evaluated pot plants was influenced more by the air temperature among the plants than by the root-zone temperature in the investigated range. Most pronounced effect of the root-zone temperature was present for *Saintpaulia*, where an increased plant fresh weight was found at increasing root-zone temperatures due to a higher fresh/dry weight ratio (appendix 3.1). A possible explanation for this response might be the warm and humid origin of *Saintpaulia* in East Africa (Hetterscheid, pers. comm.), and related adaptation to low transpiration rates. In this supposition it is plausible that extension growth of *Saintpaulia* is favoured at increased root temperature (affecting the water uptake) and high relative humidity (affecting the transpiration rate). A positive effect was observed by Mortensen (1986) and Papenhagen (1986) up to 90-95% relative humidity. Recently it was found, that fresh weight (and cultivation time) of *Saintpaulia* was reduced at a continuous or daily RH of 60% compared to continuous 90% RH, but not at 60% RH during the night (Schussler, 1992; pers. comm.). These findings support the idea that growth of *Saintpaulia* is very sensitive to internal water status. The diagram of the production system, presented in section 1.5, should, therefore, be extended with a relation to dry matter content and fresh weight.

It is surprising, however, that root-zone temperatures up to 30°C were of minor importance for growth of the other potplants under investigation. It indicates that root activity was not a limiting factor for plant growth in the investigated temperature range under (Dutch) greenhouse conditions. Water and nutrient uptake by the roots seemed adequate at all temperatures (section 7.2), whereas anticipated increased respiratory losses, due to increased root-zone temperatures, did not affect final shoot growth negatively. The latter might be partly explained by adjustment of the root system to root-zone temperature, through improvement of the area/weight-ratio and/or shoot/root-ratio, thus increasing the efficient use of available carbohydrates.

7.4 Lateral shoot formation

For potplants, dry matter distribution is not only an important determinant for growth, but distribution patterns between individual organs may also affect ornamental value. Number and size of leaves, shoots and flowers are important ornamental parameters. Lateral shoot formation in *Saintpaulia*, *Begonia*, *Ficus benjamina* and *Spathiphyllum* was affected by root-zone or air temperature (Table 7.1). The effects, however, have a different background in each crop. For *Saintpaulia* and *Spathiphyllum*, an increased root-zone temperature led to suppressed shoot initiation and/or development. For *Begonia* and *Ficus*, the number of lateral shoots was not affected by the root-zone temperature, but was, however, related to differences in growth at different air temperatures. In *Begonia* the number of side shoots and plant dry weight were reduced at 21°C air temperature compared to 18°C air temperature (section 4.2), whereas for *Ficus benjamina* these parameters were increased when increasing air temperatures from 19 to 23°C (Chapter 5). Apparently, the number of developing shoots correlates with growth at different temperatures, but the optimum for growth is crop-specific (relative low temperature for *Begonia* and high temperature for *Ficus*). The availability of assimilates appears to have an influence on initiation of shoots and subsequent growth. This is in agreement with observations for fruit growth in greenhouse vegetable crops and formation of branches in some cut flowers, where a strong competition for assimilates was observed among fruits c.q. branches, and between fruits c.q. branches and the rest of the plant (Marcelis, 1992).

The number of lateral shoots was reduced in *Spathiphyllum* by increasing root-zone temperatures (Tables 6.1 and 6.3). The same result was obtained with *Saintpaulia* cultivar 'No. 19' (section 3.1). In *Saintpaulia*, increased shoot formation at low temperatures (16-20°C) has also been observed by Götz (1987). Flowering in *Saintpaulia* was interrupted regularly by the formation of lateral shoots at low root-zone temperature (section 3.1). This phenomenon occurred, however, not to the same extent in each experiment (section 3.2). Recent experiments have shown, that lateral shoot formation in *Saintpaulia* increased with decreasing weight of the rooted cuttings (Kromwijk and De Wilde, 1991). There was also a correlation with the growing season. Both factors may explain the difference in lateral shoot formation between different experiments in this study.

In *Spathiphyllum* the decrease in shoot number at increasing root-zone temperatures coincided with increases in plant dry weight (Table 6.3). The availability of assimilates appears, therefore, not to have limited shoot initiation and/or shoot emergence in this crop. In *Saintpaulia* the effect of root-zone temperature on lateral shoot formation appears also unrelated to differences in growth, since the increase in shoot numbers at a low root-zone temperature was accompanied with a reduced plant weight (section 3.1). Effects of temperature on shoot initiation are more likely related to changes in the hormonal balance in these crops.

Exogenously applied synthetic cytokinins increase shoot number in a range of tropical foliage plants, including *Spathiphyllum* and other *Araceae* (Henny, 1991). Cytokinin is also involved in adventitious shoot formation on leaf cuttings *in vivo* (Custers, 1986) and in shoot generation *in vitro* (e.g. *Saintpaulia*, Mølgaard et al., 1991). It is possible that cytokinin synthesis and/or export to the shoot is inhibited at increasing root-zone temperatures. Increased export of cytokinins from the roots has been associated with a larger root system (Skene, 1975), suggesting an increase in the potential number of sites for cytokinin production (root tips). Thus, a decrease in cytokinin export could be a result of a decrease in size of the root system. Indeed, root growth of *Spathiphyllum* was reduced at a root-zone temperature of 30°C (Fig. 7.1). However, the reduction in shoot number also occurred at lower root-zone temperatures in plants with large root systems. Therefore, this hypothesis is probably not valid or too simple. Other hormonal effects could also have occurred in *Saintpaulia* and *Spathiphyllum*, due to the locally increased temperature of the low situated shoot meristem by the increased root-zone temperature. Auxins are mainly produced in the apex, leaf primordia and young leaves (Davies, 1987), and synthesis or turnover may have changed by the increased temperature of the apex. The ability of growing shoot tips to release auxin parallels their ability to inhibit axillary bud growth (Tamas, 1987). However, there is little known about the relation between the amount of endogenous auxins in the tissue and the corresponding plant response (Reinecke and Bandurski, 1987). It has been suggested that basipetal transport of auxin in the stem is necessary to prevent axillary bud growth (Tamas et al., 1989), but the amount of auxin entering the buds after decapitation/removal of the inhibiting apex is more, rather than less, than that moving into the inhibited axillary buds (Tamas and Reimels, 1989). It has also been suggested, that transport to and accumulation of cytokinins in the axillary buds is under apical control and can contribute to the overall controlling influence on bud growth (Tamas, 1987).

Conclusions about causality remain speculative. It is not clear, whether the effects on shoot initiation in *Saintpaulia* and *Spathiphyllum* were the result of similar or different hormonal responses to root-zone or shoot meristem temperature. In *Saintpaulia* 'No. 19', sometimes two primordia were observed instead of one in some leaf axils (unpublished result). Rather than initiation of primordia, hormonal effects could alter growth of the primordia, for instance by altering hormone-directed nutrient transport (Cline, 1991).

7.5 Flowering

Flowering is a complex of processes, which is normally divided into the two major phases of flower initiation and development. In these phases plants react differently to environmental and internal factors (Bernier, 1988). Furthermore, temperatures which promote flower development might result in poor quality of the flowers (Kinet et al., 1981). In this study, flowering was affected by air and/or root-zone temperature in all four investigated flowering potplants (Table 7.1). Flowering of *Saintpaulia* was enhanced at increasing root-zone temperatures. Experiments with *Begonia* showed narrow tolerances for the air temperature and a minor importance of the root-zone temperature. A similar response to root-zone and air temperature was found for *Spathiphyllum*, where tolerances for the air temperature were less than those for the root-zone temperature. For *Guzmania*, effects on the quality of inflorescences were most pronounced. The post-harvest experiments demonstrated similar tolerances for flowering in response to air and/or root temperature as during cultivation, and are therefore not discussed separately.

Earlier flowering at optimum than at ambient root-zone temperature, as found in *Saintpaulia* (23-26°C), *Spathiphyllum* (26°C) and *Guzmania* (26°C), appears to be related to an enhanced rate of flower and plant development, rather than to an earlier flower initiation. This aspect has been investigated in more detail for *Saint paulia* (section 3.2), where it was concluded that earlier flowering was due to faster flower and/or plant development only and not to earlier initiation. All three crops mentioned have a shoot apex close to the root-zone, which will lead to temperatures of the growing-point somewhere inbetween the root-zone and the air, as observed for *Saintpaulia* in this study (Fig. 3.5). A similar local temperature rise in plant tissue has also been found for gerbera by Berninger (pers. comm.): when plants were heated from below, the temperature of flower buds below leaves was 2°C higher than those above. Rate of leaf and flower formation are strongly correlated with the average daily air temperature in many plant species (Bakker and van Uffelen; Van den Berg, 1987; Berghage et al., 1990; Karlsson et al., 1988; 1989; 1990). It is therefore likely, that the effect of root-zone temperature on earliness of flowering is due to the increase of the temperature of the shoot apex resulting from the increased root-zone temperature. This conclusion is supported by the fact, that flowering of *Begonia x hiemalis*, the only investigated potplant with a highly positioned apex, was only slightly affected by the root-zone temperature.

Flowering of *Spathiphyllum* was delayed when grown on heated benches with simultaneous high air (24-25°C) and root-zone temperature (30°C) (Table 6.1). This was most likely caused by too high values of the air temperature (optimum 22°C), but an effect of the root-zone temperature could not be excluded in this study. Inhibitory effects may have been exerted by the roots through root-generated cytokinins or other compounds, such as GAs (Bernier, 1988). Hormonal influences, through an increased temperature of the shoot meristem, may play a role. A suppression of flower initiation seems more plausible than a retarding effect on the emergence of the floral spike, the latter being probably more affected by the surrounding air temperature. Apart from these speculations, information about the regulation of flower initiation in *Spathiphyllum* is still lacking. Exogenous gibberellins are now used commonly in commercial practice in order to control flowering better (Blacquière and De Koster, 1990).

In contrast to most species, flowering in *Bromeliaceae* can be induced with exogenous ethylene (Metzger, 1987), and several ethylene-releasing agents are used commercially (van Dijck et al., 1987; Zimmer, 1985). The shoot apex is the main production site of endogenous ethylene, and production of the shoot apex correlates well with the production per plant (van Dijck et al., 1987). In this study, the percentage of flowering plants decreased at simultaneous high air (25°C) and high root-zone temperature (30°C) (Table 6.2). At the same time, the size of inflorescences was reduced to a large extent, which was most likely caused by a supra-optimal root-zone temperature (> 26°C) (Chapter 6). Kinet et al. (1981) stated, that the size of inflorescences may be reduced due to a shorter period of growth. Since development time was reduced to the same extent at intermediate root-zone and air temperatures without negative effects on the quality of inflorescences (Table 6.2), this explanation does not apply here. Van Dijck et al. (1987) described negative effects on growth and quality of inflorescences in response to the release of ethylene. They also found that increasing temperatures in the range 10-42°C increased the endogenous ethylene production per plant. However, the increase of endogenous ethylene in response to temperature is of a much lower order of magnitude (100 times) than the amounts released by the agents, which makes it less likely that the observed negative effects of bench heating on percentage of success and quality of inflorescences were due to temperature effects on ethylene production. However, temperature might have affected the response to ethylene (Woltering and Harkema, 1987), rather than the production. Other hormones, such as cytokinins (Kinet et al., 1981), also affect size and weight of the reproductive structures.

Root and air temperature requirements for optimal flowering response are crop specific. The optimal range is, however, larger for the root-zone temperature than for the air temperature in all investigated crops. This is in agreement with Kinet et al. (1981), although their conclusion was based on limited experiments. For crops with a low situated shoot meristem, effects of increased root-zone temperature might operate through the locally increased temperature of the shoot apex. It is, however, very difficult to separate effects on root-zone and shoot meristem temperature in such crops, even when experiments are carried out with independent control of root-zone and air temperature (e.g. Wisconsin tanks).

7.6 Overall crop response

The potplants investigated in this study, could be grown successfully on heated benches. With the research strategy, chosen in this study (section 1.5), it was possible to draw conclusions about sensitivity of some plant processes to root-zone and air temperature. Effects of the root temperature were most pronounced on development processes, such as shoot formation and flowering. In all four evaluated flowering crops, a root-zone temperature of 26°C appeared to be the upper limit for flowering, and might be used for other flowering crops as a guide value. Since root-zone and air temperature requirements for flowering are crop specific, they have to be established for each species before practical application; cultivar differences were not observed for *Saintpaulia* (Mathijssen, 1987), *Begonia* (Verberkt, 1988) and *Spathiphyllum* (Verberkt, 1989), and may, therefore, be of minor importance. Growth processes were less dependent on the root-zone temperature, such as NAR, LAR and dry matter distribution within the shoot, or they contributed little to growth over the production cycle as a whole (initial rooting). No limitations of the root-zone temperature for growth became manifest up to 30°C (section 7.3). An exception was *Saintpaulia*, where growth (fresh weight) was positively affected by increased root-zone temperature, which was interpreted as an effect on internal water status (section 7.3). Influence of the air temperature on growth was mainly through effects on LAR at low LAI and low irradiance levels. Relations between temperature, light level and LAI should be analysed in more detail to provide optima for different stages of growth.

Bench heating affects the root-zone temperature, but affects also the aerial environment of the crop, as described in Chapter 2. Accurate measurements of the air temperature among the plants are, however, seldom presented in literature on potplants or bedding plants on heated benches and floors, which renders the interpretation of the results difficult and more case dependent. Reported positive effects of root-zone heating on growth of *Begonia semperflorens* plugs (Graper and Healy, 1990), Petunia (Merritt and Kohl, 1982) and various bedding - and vegetable plants (Shedlosky and White, 1987), may therefore be due to an increased air temperature among the plants rather than just to the root-zone temperature. This may explain the apparent contradictory results of others with bedding plants (Ellis, 1986; Van Leeuwen, 1989), where it was concluded that the air temperature was the most important for plant growth. McAvoy and Janes (1984) reported an interaction between root and air temperature on growth of *Chrysanthemum morifolium* 'May Shoesmith' grown on heated benches. Experiments of Mortensen (1982) failed to show a similar interaction for growth of *Chrysanthemum morifolium* 'Ramat', where root and air temperature were controlled independently. This difference may be due to the cultivars used, but also to the experimental conditions.

Reported positive effects of the root temperature on flowering may be related to a simultaneous temperature increase of the corm in *Cyclamen* (Fick and Widmer, 1989) or the shoot meristem in *Zantedeschia* (Corr and Widmer, 1990). The results with *Zantedeschia*, which is another *Aracea*, are in agreement with the results for *Spathiphyllum* in this study: growth (plant height) was influenced by the air temperature, while flowering was also influenced by the temperature of the root medium. Somewhat different results where obtained for *Dieffenbachia maculata* 'Perfection', (also an *Aracea*), where growth was increased at increasing soil temperatures up to 29°C, when grown at a low air temperature (13°C) (Conover and Poole, 1987). However, the growth response to increasing soil temperature was much smaller starting from a more usual temperature of 18.5°C (air and soil). Basal shoot formation appeared to be growth-related in their study, but the observed reduction at 29.5°C soil temperature and 18.5°C air temperature might also be due to hormonal changes as suggested in section 7.4. The observed decrease in number of axillary shoots in poinsettia up to 29°C root-zone temperature (Janes and McAvoy, 1982) conforms with observations in this study. The simultaneous increase in dry weight per shoot and in anthocyanin content was, however, in their study interpreted as an effect of the root temperature and not of the (slightly) increased air temperature, since air temperature had a negative effect on anthocyanin content. Lateral shoot growth was increased by root-zone heating with *Calceolaria* (White and Biernbaum, 1984), but data on shoot numbers were not presented; it is therefore not clear whether increased lateral shoot growth was due to enhanced initiation, or rate of plant growth as such.

It can be concluded, that reported interactions between root-zone and air temperature may not always have a physiological background. The ability of root-zone heating to substitute high aerial temperatures may be due to effects on microclimate. For potplants and bedding plants, therefore, more attention should be paid to the resulting microclimate, and the architecture of the crop when interpreting plant responses. For a crop with a low situated shoot meristem, coupling between root and shoot meristem temperatures is so strong, that an analysis of the sensitivity of different processes involved is very difficult.

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8. CONCLUSIONS FOR COMMERCIAL PRACTICE

8.1 Design of bench heating systems

There are large differences between bench heating systems in their transfer of heat to the crop. They may differ in relative contribution of heat transfer via convection, radiation and conduction, and in the way heat is distributed within the bench. Consequently, there are differences among bench heating systems in maximum root-zone temperature, vertical gradient of the air temperature, as well as the uniformity of root-zone and air temperature distribution (Vogelezang and Van Weel, 1989). Furthermore, maximum (root-zone) temperatures are dependent on confines for control (maximum temperature of heating water). Specifications for commercial bench heating systems should be related to crop requirements with respect to average and maximum acceptable root-zone and/or air temperature, which differ among species (Chapter 7). Bench heating systems with a high heat output, such as aluminium benches, can be used for crops with high root-zone and/or air temperature requirement or tolerance, such as foliage plants. When the maximum permissible root-zone temperature is lower (26°C, e.g. *Spathiphyllum*), other systems may be valuable as well, such as the polystyrene bottom with polythene heating tubes (section 3.1) or the plastic benchtop with heating tubes under a grid (Vogelezang and Van Weel, 1989). However, the heat distribution should be within acceptable limits to reduce heterogeneity among plants. A variation in root-zone temperature among pots of more than 3°C is not acceptable for crops sensitive to root-zone temperature, such as *Saintpaulia* (Chapter 3). Variation in air temperature should be within 2°C for e.g *Begonia* (optimum 18-19°C, Chapter 4) or *Spathiphyllum* (optimum 21-22°C, Chapter 6). This demand for a homogeneous heat distribution within the bench implies that materials used in the bench heating systems should be good transmitters of heat and that temperature difference between supply and return heating water is kept small. Furthermore, since differences in humidity of the potting soil among pots may lead to a variation in root-zone temperature, the root-zone should be kept close to saturation (Yang and Albright, 1985). This requires frequent watering of the plants, and bench heating should therefore preferably be combined with automized watering systems, such as drip irrigation with capillary matting or ebb and flood systems. The latter also reduces excessive evaporation from the bench bottom, thus reducing unnecessary heat losses.

A recent development in potplant cultivation is the introduction of transportable benches, which are in the majority of cases installed at large companies (> 10.000 m^2; Ploeger, 1992). The heating situation here is as poor as in traditional heating systems for potplants, since the primary heating source (steel pipes, ø 76 mm) is placed at some distance underneath the benches. Measurements at a commercial company showed the lowest air temperatures in the vicinity of the plants (unpublished results). Designs for the incorporation of bench heating in transportable benches have been made and await testing (Van Weel, pers. comm.).

8.2 Climate control in combination with bench heating systems

Potplants, grown on benches, are traditionally heated with two steel pipe heating systems placed overhead and at some distance under the benches. The control of these heating systems is usually based on one sensor for greenhouse air temperature (and humidity). The efficiency of these systems to control the climate in the vicinity of the plants depends on the reaction time of these heating systems (which is improved by a smaller diameter of the heating tubes), and the position of the heating pipes with respect to the canopy (affecting the heat transfer via convection) (Zandbelt, 1985). The position of the heating source is improved in bench heating systems compared to the traditional situation, but control could still be improved. A disadvantage of all commercial available bench heating systems is the fact that root-zone and air temperature cannot be controlled independently. Furthermore, bench heating systems have a slow response time (some hours), due the large total mass of the system.
Efforts have been undertaken to control the ratio of heat transfer to either bench bottom/root-zone or canopy layer with the help of forced air circulation; the vertical temperature distribution was, however, only slightly affected compared to the control without forced air circulation (Vogelezang et al., 1990).

The best option is therefore, to use bench heating systems for a base-load of the total heating demand. To utilize the system in the best way, the bench heating system should preferably be controlled by the actual root-zone temperature. The overhead heating system can supplement heating, whilst its control should be based on the air temperature just above the crop. In this way, control of root-zone and air temperature are to a certain extent separated. Restriction for maximum root-zone temperature might occur as a result of an undesirable high air temperature among the plants (e.g *Begonia*, section 4.1). Standardization of the position of the control sensor for root-zone temperature is necessary. In this study, the Pt-100 sensor for control of the root-zone temperature was placed 1 cm from the pot bottom. Highest root densities are normally found in this layer of the potting soil, and the root-zone temperature appeared most critical there (section 7.2); a position in the middle of pot would create supra-optimum temperatures in the lower layers.

The present-day strategies for climate control of potplants are primarily based on rather strict day and night temperature requirements. This is a disadvantage for optimal use of bench heating, due to the slow response time of this heating system. It may lead to a high contribution of the overhead heating system because it responds faster, compared to that of the bench heating system. A more flexible control of temperature on a 24-hour basis (De Koning, 1988), or allowing an average temperature over periods of several days instead of a fixed value, will increase efficient use of energy by 1) an increased use of waste heat by the bench heating system, and 2) a reduction of supplementary heating by the overhead heating system (which gives rise to greater thermal losses to the greenhouse cover, Zandbelt, 1985). Recently it was found, that tomato and kohlrabi accept deviating temperature if compensated within a certain period (De Koning, 1990; Liebig, 1988). However, possibilities for the integration of temperature regimes over longer periods have still to be evaluated for potplants. Furthermore, some restrictions might occur for plant processes which are sensitive to immediate temperature, such as stem elongation in response to day/night temperature regimes (Hendriks and Scharpf, 1985a; 1985b; Moe and Heins, 1990) or short temperature drops before or at sunrise (Cuijpers and Vogelezang, 1992; Moe, 1991).

8.3 Crop management

During the first years of application, growers were advised to a use a root-zone temperature equal to the air temperature (Meeuwissen, 1984). This study reveals, however, that tolerances to root-zone temperature are much higher than expected. The root-zone temperature was most critical for development processes, such as shoot formation and flowering (Chapter 7). Application of bench heating should therefore be carefully adopted for other flowering (pot)plants. No limitations of the root-zone temperature for growth became manifest up to 30°C (Chapter 7), and complications are therefore less likely to occur for foliage plants. The latter has been confirmed in recent experiments, where a number of foliage plants has been tested on heated aluminium benches (Verberkt, 1990; De Beer, 1992) and heated concrete floor (Van Leeuwen, 1992). Bench heating may also be valuable for crops in other branches of horticulture, such as young-plant cultivation of vegetable crops, production of cuttings and nursery stock plants. For the latter group, effects of the root-zone temperature on development processes, such as side shoot formation, might be an important aspect to consider. Keepability of the potplants evaluated in this study was not unfavourably affected by bench heating, but poinsettia shed their leaves more quickly after cultivation on heated benches (Ellis and Holder, 1986), and keepability is therefore a point to consider for other crops.

Effects of the air temperature on growth were most pronounced at a low Leaf Area Index (LAI). An increase in growth of *Ficus* and *Schefflera* achieved during the first three weeks of cultivation on heated benches (Table 5.2, Exp. 2), resulted in 2 weeks earlier spacing (data not shown), and this decrease in cultivation time persisted until the end of cropping time (Chapter 5). Relations between temperature, light level and LAI should be analysed in more detail to provide information for different stages of growth. This information is important for optimal cultivation and adequate spacing of potplants. Humidity among the plants did not detoriate with increasing root-zone temperatures in this study (Chapter 2). Incidence and development of fungal diseases for which relative humidity is an important aspect, such as *Botrytis* (Kerssies, 1992), is, therefore, not increased on heated aluminium benches. However, the influence of increased root-zone temperature on humidity might be less favourable when bench heating is combined with a humid bottom surface, such as a capillary mat. The root-zone temperature did influence the development of soil fungi, such as *Rhizoctonia solani* in *Nephrolepis exaltata* (Chase and Conover, 1987) and *Cylindrocladium spathiphylii* in *Spathiphyllum* (Chase and Conover, 1988; Kerssies and Vogelezang, 1990). This may have consequences for the use of bench heating systems. *Spathiphyllum* can be grown successfully on heated benches up to 26°C root-zone temperature (Chapter 6), but disease severity of *C. spathiphylii* is near optimal at this temperature and bench heating is therefore not advisable if there is a risk of *C. spathiphylii* infection (Chase and Conover, 1988; Kerssies and Vogelezang, 1990).

Electrical conductivity (EC) in the lower two-third layer of the potting soil was not much affected by different root-zone temperatures, but in the top layer accumulation of salt was increased at increasing root-zone temperatures (Table 5.5). However, high

EC levels in the top layer did not affect keepability, even if salts were rinsed back to the roots by watering on top of the potting soil during post-harvest life (Chapter 5). In all evaluated crops, there were no large differences observed in mineral composition of leaf tissue for the different temperature treatments (data not shown), indicating that supply of nutrients was sufficient for adequate uptake at all temperature treatments. However, a different situation occurred in small pots on heated benches (< 9 cm); a too high level of EC reduced growth of *Pteris cretica* 'Albolineata', and EC-level of the solution had to be adjusted for the different root-zone temperature treatments (Verberkt, 1990). To avoid accumulation of salt in the (upper layer) of the potting soil, evaporation from the potting soil should be reduced. However, a practical method is not yet available.

8.4 Economical evaluation

This study was part of a larger project investigating the possibilities of waste and reject heat application for the glasshouse industry (section 1.5). An economical study has been made by Van der Velden (1989), where 100% heating with natural gas was compared with heating with a low temperature base-load (from an external heating source) complemented with natural gas for peak-load. For potplants, the control situation consisted of two steel pipe heating systems placed overhead and at some distance under the benches. For the situation with low temperature heating, the pipe heating system under the benches was replaced by bench heating.

The polystyrene bottom with polythene heating tubes (as used in the experiments with *Saintpaulia*, Fig. 3.1) is the most profitable in all situations (e.g. with different condensers, heat consumption and gas prices). Compared to the aluminium bench with aluminium tubes, annual costs of the polystyrene bottom were lower, due to differences in investment costs for the bench heating systems (85 and 60 guilders.m^2 respectively). However, the proportion of waste heat in the total heat consumption on an annual base is lower for the polystyrene bottom compared to the aluminium bench (60 and 83% respectively at 40°C water temperature and 180 $W.m^{-2}$ heat capacity). Furthermore, some bench heating systems can also be used for ebb and flood watering, and might be installed solely for this purpose. When, in this case, extra costs of the bench heating system are not attributed to application of waste heat, the economic feasibility did not differ much among the bench heating systems. However, certain aspects of bench heating systems were not included in this economical evaluation, such as the uniformity of heat distribution and effects of root-zone heating on cultivation time. The latter has been taken into consideration in an economical evaluation of bench heating for the situation without (external) waste heat application. In this case, bench heating was most promising if the root-zone temperature shortened cultivation time, as for *Saintpaulia*. The increased production of *Saintpaulia* was enough to reduce the annual cost price for the polystyrene bottom; the aluminium bench might be of interest if ebb and flood watering is considered (Benninga and Van der Velden, 1990).

It can be concluded that there are differences in economical perspective among bench heating systems, but that no one system can be classed as the most outstanding. The polystyrene bottom is generally the most profitable, but cannot be used for ebb and flood watering. The aluminium bench has the highest heat output and can be used for ebb/flood watering, but is on the other hand very expensive in outlay. When investment costs for the bench heating systems are not attributed to waste heat application (from an external source), all evaluated systems were soon cost-effective (in terms of high comparable prices for 1 m^3 gas equivalent low temperature heating water) (Van der Velden, 1989). Waste heat is, therefore, of particular interest if bench heating systems are already installed on a nursery.

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SUMMARY

Most of the greenhouses are heated with high temperature water circulating through a pipe heating system. This water is usually derived from boilers heated with natural gas. As a result of increasing energy prices in the seventies, energy saving techniques were introduced, under which the use of flue gas condensers. This resulted in availability of low temperature heating water (about 40°C). Furthermore, application of low temperature heating water from external sources (waste and reject heat) became interesting.

Potplants, grown on benches, are traditionally heated with two separate steel pipe heating systems placed overhead and (at some distance) under the benches. The availability of low temperature heating water stimulated the development of bench heating systems for potplant cultivation. Compared to the traditional way of heating, there is a 'reversed' temperature gradient on heated benches inside the crop canopy, with a relatively high root-zone temperature compared to the air temperature. Knowledge about the response of potplants to increased root-zone temperature was lacking.

Aim of this study was to investigate responses of potplants to (increased) root temperature in order to optimize the use of bench heating systems. Six potplants were selected for research (*Saintpaulia*, *Begonia*, *Ficus benjamina*, *Schefflera*, *Spathiphyllum* and *Guzmania*), based on origin and architecture of the crops. Knowledge at crop level and at process level was integrated to provide a more general overview and understanding of the effects of root temperature, which may help to extrapolate results to a wider range of potplants.

Important aspects involved in the cultivation of potplants are rooting, growth, flowering and plant quality. Growth (dry weight) largely depends on crop photosynthesis and dry matter distribution within the plant. Root temperature may influence crop photosynthesis through its effect on LAI (Leaf Area Index) (at non-saturating light interception). Root temperature may affect photosynthesis also through water balance mediated effects on stomatal conductance. A significant portion of carbohydrates is respired, and root temperature may increase the loss in roots through increased maintenance respiration. For flowering potplants, effects on flower initiation and - development are important aspects.

The research, described in this thesis, is mainly carried out with an aluminium bench heating system under greenhouse conditions. The influence of this heating system on microclimate is described in Chapter 2. An aluminium bench provided a uniform horizontal temperature distribution. Some temperature gradient is inevitable, due to the temperature difference between supply and return water temperature, but heat transmitted well from heating tube to bench bottom in this bench construction. Variation among pots in root-zone temperature was larger than variation in bench bottom temperature, which might be due to differences in humidity of the potting soil. Up to 45 cm crop height, a rather constant vertical temperature gradient among the plants was measured on heated benches: an increase in bench bottom temperature of 2°C led to an increase in root-zone temperature of 1°C and an increase of air - and leaf temperature of 0.4°C (in the range 20-40°C bench bottom temperature and

17-20°C greenhouse air temperature). Humidity did not detoriate with increasing root-zone temperatures, which might be due to the ebb/flood watering system.

Increased root-zone temperatures (22-25°C) affected growth and flowering of *Saintpaulia* positively compared to the unheated control (17-19°C), and reduced cultivation time 10-15% without unfavourable effects on plant quality and keepability (Chapter 3). Similar results were obtained in Wisconsin tanks (in the range 13 to 26°C), which indicate that the results obtained on heated benches can be ascribed to root-zone and/or growing-point temperature. Effects on plant fresh weight were due to changes in percentage dry matter. Earlier flowering at increased root-zone temperature was due to faster plant and flower development only and not to earlier initiation. Marketable plants, grown on unheated and heated benches, did not show differences in fresh weight and dry matter distribution.

The influence of root-zone and air temperature on growth, flowering and keepability of *Begonia x hiemalis* is presented in Chapter 4. Root and air temperature were more critical for flowering than for growth rate of *Begonia*. In greenhouse experiments, an optimal temperature for flowering was 18-19°C in winter season, whereas root-zone temperatures in the range of 18 to 26°C were of less importance. An additional experiment with Wisconsin tanks in conditioned growth chambers confirmed these results at 18°C air temperature. Flowering was almost prevented at root-zone temperatures of 26°C and higher, in combination with a too high air temperature. Lowering the root-zone temperature in the generative stage of growth did not improve the flowering response, compared with a continuous high root-zone temperature of 29°C. The post-harvest experiment demonstrated similar tolerances for air and root-zone temperature.

Elevated root-zone (19 to 30°C) and/or air temperatures (19 to 23-24°C) had a positive effect on growth rate of *Ficus benjamina* and *Schefflera* in the beginning of the cultivation period (Chapter 5). For *Schefflera*, the air temperature was the most important factor, whereby differences in RGR (Relative Growth Rate) were mainly caused by differences in LAR (Leaf Area Ratio); differences in re-growth of roots after planting, due to root-zone temperature, were not reflected in the RGR in this crop. For *Ficus*, both NAR (Net Assimilation Rate) and LAR were affected by root and/or air temperature in this phase of cultivation. In later stages of growth, no effect of the root-zone temperature on growth could be detected. The lead in growth, built up during the first three weeks of cultivation, persisted until the end of cropping time without unfavourable effects on ornamental value (shoot formation in *Ficus*, internode length in *Schefflera*).

Bench heating increased the accumulation of salts in the top layer of the potting soil, but keepability was not affected, even if salts were rinsed back to the root-zones by watering on top of the potting soil during post-harvest life.

The effects of root-zone and air temperature on flowering and growth of *Spathiphyllum* and *Guzmania* are described in Chapter 6. The optimal air temperature for flowering of *Spathiphyllum* was 22°C, whereas root-zone temperatures in the range of 20 to 26°C were of less importance. Plant shape and size of *Spathiphyllum* was largely influenced by the air temperature (plant length, leaf size, plant weight). Increased root-zone temperatures decreased number of shoots, whereas shoot/root-ratio was increased. For *Guzmania*, effects on development time and quality of inflorescences were most pronounced. Both root-zone (19 to 26°C) and air temperatures (19 to 22°C) promoted flowering without negative effects on the quality of inflorescences. The reduction in size of inflorescences on highly heated benches was most likely due to supra-optimal root temperature (30°C).

In Chapter 7 similarities and differences in the results obtained for the six potplants under investigation were analysed. Roots had (visually) a finer structure and were more branched at increased root-zone temperatures in some crops. Water and nutrient uptake might have been enhanced at increased root temperature, due to an increased root surface area, but there is no evidence that these processes were limiting plant growth in the investigated temperature range. *Saintpaulia* is an exception, where a lower plant dry matter percentage was found at increased root temperatures, which might have been due to a reduced root resistance for water uptake at these temperatures. Effects of root-zone temperature on root distribution (*Begonia*, *Spathiphyllum*) were most likely due to adaptations to local supra-optimal temperatures.

Dry matter production was influenced more by the air than by the root-zone temperature in the investigated temperature range. Respiration losses in the roots, due to increased root temperature, might have been limited through improvement of the area/weight-ratio and/or shoot/root-ratio. Root-zone temperature affected dry matter percentage of *Saintpaulia* (see above), which resulted in increased plant fresh weight at increased root-zone temperature. This response may be attributed to the natural habitat of this crop in East Africa (warm and humid).

The number of lateral shoots was reduced in *Saintpaulia* and *Spathiphyllum* at increased root-zone temperatures. Effect of temperature on shoot initiation was most likely related to changes in the hormonal balance in these crops. Possible explanations are discussed.

Root-zone and air temperature requirements for optimal flowering response were crop specific. The optimal range was, however, larger for the root-zone than for the air temperature. For crops with a meristem situated close to the root-zone, effects of increased root-zone temperature might operate through the locally increased temperature of the shoot apex.

For the overall crop response, effects of the root-zone temperature were most pronounced on developmental processes, such as shoot formation and flowering. For flowering crops, a maximum root-zone temperature of 26°C might be used as a guide value. No limitations of the root-zone temperature for growth became manifest up to 30°C. An exception was *Saintpaulia*, where growth (fresh weight) was positively affected by increased root-zone temperature. In the literature reported interactions between root-zone and air temperature may not always have a physiological background. The ability of root-zone heating to substitute high aerial temperatures may be due to effects on microclimate (higher crop - than greenhouse air temperature).

In Chapter 8, consequences for the use of bench heating systems in commercial practice are discussed. Requirements for the design of bench heating systems are formulated. The best option for climate control is to use bench heating systems for a base-load of the total heating demand, preferably controlled by the actual root-zone temperature. Restriction for maximum root-zone temperature might occur as a result of an undesirable high air temperature among the plants. Suggestions for further optimization of strategies for climate control are presented.

Root-zone temperature was most critical for developmental processes (shoot formation, flowering), and application of bench heating should therefore be carefully adopted for other flowering (pot)plants. Complications are less likely to occur for foliage plants. Application of bench heating systems might be restricted as a result of undesirable effects of root temperature on keepability or development of soil fungi.

There are differences in economical perspective among the bench heating systems. The polystyrene bottom with polythene heating tubes is most profitable in situations with - or in the situation without external low temperature heating water, due to its low investment costs. The aluminium bench has the highest heat output and can be used for ebb and flood watering, but is on the other hand very expensive. External waste heat is of particular interest if bench heating systems are already present on a nursery.

SAMENVATTING

In de glastuinbouw worden de kassen over het algemeen verwarmd met buizenverwarming met een hoge aanvoer- en retour-watertemperatuur. De cv-ketel brengt dit water op de gewenste temperatuur, meestal door middel van verbranding van aardgas. Ten tijde van de energiecrisis, in de jaren zeventig, zijn voor de glastuinbouw een reeks van energiebesparende maatregelen ingevoerd, waaronder de toepassing van rookgascondensors. Hierdoor kwam verwarmingswater beschikbaar met een relatief lage watertemperatuur (circa 40°C). Tevens kwam de vraag naar voren in hoeverre rest- en afvalwarmte gebruikt kon worden voor kasverwarming.
Potplanten op tabletten worden traditioneel verwarmd met twee verwarmingsnetten, één boven in de kas en één (op enige afstand) onder de tabletten. De beschikbaarheid van verwarmingswater met een lage temperatuur leidde tot de ontwikkeling van tabletverwarmingssystemen voor de potplantenteelt. In vergelijking tot de traditionele wijze van verwarmen ontstaat op verwarmde tabletten een 'omgekeerde' temperatuurgradiënt in de omgeving van de plant, met een relatief hoge worteltemperatuur ten opzicht van de luchttemperatuur. Kennis over de gewasreacties van potplanten op een verhoogde worteltemperatuur was echter niet voorhanden.
Doel van dit onderzoek was het vaststellen en analyseren van reacties van potplanten op (verhoogde) worteltemperatuur met het oog op optimale benutting van tabletverwarming. Zes potplanten zijn geselecteerd voor dit onderzoek (*Saintpaulia*, *Begonia*, *Ficus benjamina*, *Schefflera*, *Spathiphyllum* en *Guzmania*), een keuze gebaseerd op herkomst en architectuur (opbouw) van de gewassen. Kennis omtrent gewasreacties en verklarende processen is geïntegreerd om een meer algemeen beeld te verkrijgen omtrent de effecten van worteltemperatuur, van waaruit geëxtrapoleerd zou kunnen worden naar andere potplanten.

Voor de teelt van potplanten zijn beworteling, groei, bloei en kwaliteit belangrijke aspecten. De groei (drooggewicht) hangt in hoge mate af van de gewasfotosynthese en de drogestof-verdeling binnen de plant. De invloed van worteltemperatuur op gewasfotosynthese hangt samen met de beïnvloeding van de LAI (Leaf Area Index) (zolang lichtonderschepping niet maximaal is) en de stomataire geleidbaarheid via effecten op de wateropname. Een aanzienlijk deel van de gevormde hoeveelheid assimilaten gaat verloren via onderhoudsademhaling, en een verhoogde worteltemperatuur kan het verlies in de wortels versterken. Voor de bloei van potplanten zijn effecten op bloeiinductie en bloeirealisatie van belang.

Het onderzoek in dit proefschrift is grotendeels uitgevoerd onder praktijkomstandigheden in kassen met verwarmde aluminium tabletten. De invloed van dit verwarmingssysteem op het microklimaat wordt beschreven in Hoofdstuk 2. Met aluminium tabletten is het mogelijk een uniforme horizontale warmteverdeling te creëren. Een zekere temperatuurgradiënt is onvermijdelijk als gevolg van het verschil in aanvoer- en retourtemperatuur, maar er is een goede warmteoverdracht van aluminium buis naar aluminium tabletbodem. De spreiding in pottemperatuur was groter dan de spreiding in tabletbodemtemperatuur, wat mogelijk het gevolg is van verschillen in vochtgehalte van de potgrond. Op verwarmde tabletten werd bij diverse gewassen een vrij constante verticale temperatuurgradiënt tussen het gewas waargenomen tot 45 cm gewashoogte: een toename van de tabletbodemtemperatuur van 2°C leidde tot een verhoging van de pottemperatuur van 1°C en een verhoging van de lokale lucht- en planttemperatuur van 0.4°C (in het bereik 20-40°C tablettemperatuur en 17-20°C kastemperatuur). De luchtvochtigheid werd niet verslechterd door een verhoogde worteltemperatuur, wat mede het gevolg kan zijn van de tabletconstructie met een kale teeltbodem en eb/vloed-watergeefsysteem.

Een verhoogde worteltemperatuur (22-25°C) beïnvloedde groei en bloei van *Saintpaulia* positief ten opzichte van de onverwarmde controle (17-19°C), wat resulteerde in een 10-15% kortere teeltduur, zonder dat kwaliteit en houdbaarheid nadelig beïnvloed werden (Hoofdstuk 3). In Wisconsin-tanks werd een identiek teeltresultaat behaald (in het bereik 13 tot 26°C worteltemperatuur), wat erop wijst dat de resultaten op verwarmde tabletten toegeschreven kunnen worden aan de wortel- en/of groeipunttemperatuur. Effecten op plant-versgewicht werden veroorzaakt door een veranderd drogestof-percentage. In een nadere analyse van de bloeirespons werden geen effecten op bloem-initiatie gevonden, wat erop duidt dat versnelde bloei bij een hogere worteltemperatuur een gevolg is van een snellere plant- en bloemontwikkeling. Veilrijpe planten, afkomstig van onverwarmde en verwarmde tabletten, verschilden niet in versgewicht en in verdeling van droge stof over blad-, stengel- en bloemdelen.

De invloed van wortel- en luchttemperatuur op groei, bloei en houdbaarheid van *Begonia x hiemalis* wordt beschreven in Hoofdstuk 4. Wortel- en luchttemperatuur waren van meer belang voor de bloei dan voor de groei van *Begonia*. In kasexperimenten werd voor bloei een optimale luchttemperatuur gevonden van 18-19°C in het winterseizoen, terwijl de worteltemperatuur van weinig belang was in het bereik 18 tot 26°C. In een additioneel experiment met Wisconsin-tanks in kunstlichtkamers werd dit resultaat bevestigd bij een luchttemperatuur van 18°C. Bloei bleef vrijwel achterwege bij een worteltemperatuur van 26°C en hoger, indien dit gecombineerd werd met een te hoge luchttemperatuur. Verlaging van de worteltemperatuur in de generatieve fase van de teelt, gaf geen verbetering in bloei vergeleken met een continue worteltemperatuur van 29°C. De houdbaarheid liet dezelfde toleranties zien ten aanzien van wortel- en luchttemperatuur.

Een verhoogde wortel- (19 tot 30°C) en/of luchttemperatuur (19 tot 23-24°C) had een positief effect op de groeisnelheid van *Ficus benjamina* en *Schefflera* in de beginfase van de teelt (Hoofdstuk 5). Bij *Schefflera* was de luchttemperatuur de meest bepalende klimaatfactor, en werden verschillen in RGR (Relative Growth Rate) grotendeels verklaard door verschillen in LAR (Leaf Area Ratio); verschillen in hergroei van wortels na oppotten, geïnduceerd door de worteltemperatuur, kwamen niet tot uiting in de RGR bij dit gewas. Bij *Ficus* werden in deze fase zowel NAR (Net Assimilation Rate) als LAR beïnvloed door wortel en/of luchttemperatuur. In latere fasen van de teelt konden geen effecten van de worteltemperatuur op groei meer vastgesteld worden. De teeltversnelling, opgebouwd in de eerste drie weken van de teelt, werd behouden tot het veilrijpe stadium zonder nadelige invloed op de kwaliteit van het gewas (scheutvorming bij *Ficus*, internodiënlengte bij *Schefflera*).

Tabletverwarming verhoogde de opeenhoping van zouten in de bovenste laag van de potgrond, maar dit had geen nadelige consequenties voor de houdbaarheid, zelfs als zouten werden teruggespoeld tijdens de na-oogstfase door bovenop water te geven.

De invloed van wortel- en luchttemperatuur op bloei en groei van *Spathiphyllum* en *Guzmania minor* wordt beschreven in Hoofdstuk 6. Bij *Spathiphyllum* werd een optimale luchttemperatuur van 22°C gevonden voor bloei; de worteltemperatuur kon in een groter bereik gevarieerd worden (20 tot 26°C) zonder nadelige effecten voor de bloeirespons. Plantvorm en -grootte werden in grote mate bepaald door de luchttemperatuur (plantlengte, bladgrootte, plantgewicht). Het aantal scheuten werd negatief beïnvloed door een verhoogde worteltemperatuur, terwijl de spruit/wortel-verhouding juist toenam. Bij *Guzmania* werden de voornaamste effecten gevonden op teeltsnelheid en bloemkwaliteit. Een verhoogde worteltemperatuur (19 tot 26°C), en een verhoogde luchttemperatuur (19 tot 22°C) versnelde de bloei zonder nadelige effecten voor de kwaliteit van de bloeiwijze. Bij extreme verwarming van de tabletten werd een reductie in omvang van de bloeiwijze gevonden, wat waarschijnlijk het gevolg was van te hoge worteltemperatuur (30°C).

In Hoofdstuk 7 worden de resultaten van de zes onderzochte gewassen in hun samenhang geanalyseerd. Bij een aantal gewassen is (visueel) een fijner en meer vertakt wortelstelsel waargenomen bij hogere worteltemperaturen. Water- en voedingsopname kunnen door een toegenomen worteloppervlak verbeterd zijn, maar genoemde wortelfuncties lijken de bovengrondse groei niet te beperken in het onderzochte temperatuurbereik. *Saintpaulia* vormt een uitzondering. Hier werd een lager drogestof-gehalte gevonden bij verhoogde worteltemperaturen, wat veroorzaakt kan zijn door een verminderde wortelweerstand voor wateropname bij die temperaturen. Effecten van worteltemperatuur op de wortelverdeling (*Begonia, Spathiphyllum*) waren waarschijnlijk het gevolg van aanpassingen aan lokale supra-optimale temperaturen.

Drogestof-produktie werd meer beïnvloed door de lucht- dan door de worteltemperatuur in het onderzochte temperatuurtraject. Respiratieverliezen in de wortels bij hogere worteltemperaturen zijn mogelijk beperkt door aanpassingen van het wortelstelsel in oppervlak/gewicht-verhouding en/of spruit/wortel-verhouding. Bij *Saintpaulia* heeft de worteltemperatuur het drogestof-gehalte beïnvloed (zie hierboven), wat resulteerde in een positief effect van worteltemperatuur op groei in versgewicht. Deze reactie lijkt samen te hangen met de herkomst van dit gewas in Oost-Afrika (warm en vochtig).

Een verhoogde worteltemperatuur heeft bij *Saintpaulia* en *Spathiphyllum* het aantal zijscheuten gereduceerd. Effecten van temperatuur op initiatie van scheuten zijn waarschijnlijk het gevolg geweest van een veranderde hormoonbalans in deze gewassen. Mogelijke verklaringen worden besproken.

Optimale wortel- en luchttemperatuur voor de bloei zijn gewasspecifiek. Het optimum voor de worteltemperatuur is echter breder dan dat voor de luchttemperatuur. Bij gewassen met een laaggelegen groeipunt lijkt de worteltemperatuur de bloei voornamelijk te beïnvloeden via een verhoging van de groeipunttemperatuur.

Voor de totale reactie van het gewas heeft de worteltemperatuur de grootste invloed op ontwikkelingsprocessen, zoals scheutvorming en bloei. Voor bloeiende planten kan een maximum van 26°C worteltemperatuur als richtlijn gehanteerd worden. Voor groeiprocessen zijn geen beperkingen gevonden tot 30°C worteltemperatuur. *Saintpau-*

lia vormde een uitzondering, waar groei (versgewicht) positief werd beïnvloed door een verhoogde worteltemperatuur. In de literatuur beschreven interacties tussen wortel- en luchttemperatuur hoeven niet altijd een fysiologische achtergrond te hebben. Het vermogen van wortelverwarming om hoge luchttemperaturen te vervangen kan het gevolg zijn van effecten op het microklimaat (hogere gewas- dan kasluchttemperatuur).

In Hoofdstuk 8 worden de consequenties voor toepassing van tabletverwarming in de praktijk besproken. Eisen ten aanzien van het ontwerp van tabletverwarmingssystemen worden geformuleerd. Verwarmde tabletten kunnen het beste gebruikt worden voor een basislast van de totale kasverwarming, waarbij er geregeld wordt op de actuele worteltemperatuur. Beperking ten aanzien van maximale worteltemperatuur kan voortkomen uit een ongewenste verhoging van de luchttemperatuur in het gewas. Suggesties voor verdere optimalisering van regelstrategieën worden gegeven.
De worteltemperatuur had de meeste invloed op ontwikkelingsprocessen (scheutvorming, bloei), en toepassing bij ander bloeiende planten dient daarom voorzichtig te geschieden. Complicaties zijn minder snel te verwachten bij bladplanten. Toepassing van tabletverwarming kan beperkt worden door ongewenste effecten van worteltemperatuur op houdbaarheid of ontwikkeling van bodemschimmels.
Er zijn verschillen in economische perspectieven tussen tabletverwarmingssystemen. Door de lage investeringskosten is de polystyreenbodem met polytheen verwarmingsslangen het snelst rendabel in zowel situaties met als zonder toepassing van externe laagwaardige warmte. Daarentegen kan met een aluminium verwarmd tablet een grotere bijdrage in de totale kasverwarming gegeven worden, en kan het gecombineerd worden met een eb/vloed-watergeefsysteem. Toepassing van externe laagwaardige warmte heeft een grote waarde indien tabletverwarming reeds aanwezig is op een tuinbouwbedrijf.

Curriculum vitae

José Vogelezang werd op 16 juli 1958 in Voorschoten geboren. In 1975 behaalde zij het HAVO-diploma aan het Lucas College te Voorschoten. De middelbare schoolopleiding werd voortgezet in Leiden, aan het Bonaventura College, en in 1977 werd het Atheneum-B diploma behaald. In 1977 begon zij haar studie aan de toenmalige Landbouwhogeschool in Wageningen. Na het kandidaatsexamen werd in 1980 gedurende een half jaar een praktijkstage in Davis (Californië) uitgevoerd op het gebied van de na-oogstfysiologie. In januari 1984 slaagde zij voor het doctoraal examen in de richting Tuinbouwplantenteelt met als bijvakken Entomologie, Voorlichtingskunde en Marktkunde en Marktonderzoek. Tijdens de ingenieursfase is als extra vak onderwijsbevoegdheid in de Biologie behaald.

In 1984 werd zij op tijdelijke basis aangesteld op het Proefstation voor de Bloemisterij (PBN) als onderzoeker 'rest- en afvalwarmte'. Dit onderzoek werd in projectverband uitgevoerd met onderzoekers van het Proefstation voor Tuinbouw onder Glas (PTG) en het Instituut voor Arbeid, Mechanisatie en Gebouwen (IMAG). In 1987 werd zij aangesteld als wetenschappelijk onderzoeker Kasklimaat binnen de afdeling Teelt van het PBN. Naast de afronding van het onderzoek 'rest- en afvalwarmte', waarvan de resultaten in dit proefschrift zijn beschreven, waren beheersing van uitwendige kwaliteit (morfogenese) en kwaliteitsproblemen bij potplanten belangrijke onderwerpen van onderzoek.