ANALYSIS AND SIMULATION
OF
GROWTH AND YIELD
OF
CUT CHRYSANTHEMUM

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PROPOSITIONS

1. Interesting things are coming by accident.
   (The Tulips, Anna Pavord, 1999)

2. With boundaries of something we can explain everything of it, but without boundaries we cannot explain anything.

3. Plants are able to make a decision very much the way computers do.
   (Aphalo et al. 1999. Journal of Experimental Botany, 50: 1629-1634.)

4. Scientific models are not useful for practice, and practical models are not good for science; yet they need each other.
   (Kearney M. 1992. Acta Horticulturae, 313, 165-171)

5. Light use efficiency is a hyperbolic function of daily light integral.
   (this thesis)

6. Practical innovations should come from industry, rather than from science.

7. If you want to be happy for a lifetime, grow chrysanthemums.
   (A Chinese philosopher)

These propositions are a part of the thesis, "Analysis and Simulation of Growth and Yield of Cut Chrysanthemum" by Jeong Hyun Lee, Wageningen, The Netherlands,
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ANALYSIS AND SIMULATION OF GROWTH AND YIELD OF CUT CHRYSANTHEMUM

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ABSTRACT

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Seasonal variation in daily light integral naturally leads to seasonal variation in production and plant quality in year-round cut chrysanthemum (*Chrysanthemum*, Indicum group). Growers try to deliver constant product quantity and quality throughout the year by adapting plant density, day length, duration of long-day periods and supplementary lighting. Optimising crop management is very complex and requires a great deal of knowledge that is best represented by a generic model. There is, however, no such model available and there is also a lack of information on the dynamics of crop performance, i.e. dry mass production and leaf area index.

In this thesis, growth and yield of cut chrysanthemum were analysed and quantified, as related to radiation, planting date and plant density. A generic model, CHRYSIMv1.0, was derived from an existing photosynthesis-driven model, calibrated and validated for year-round cut chrysanthemum.

Final plant fresh and dry mass and number of flowers per plant decreased with plant density and this decrease was larger in summer than in winter. The observed variation in plant fresh mass can be described by a linear relationship with cumulative incident photosynthetically active radiation (PAR) per plant. Dynamics of aboveground total dry mass per m^2 (TDM) and leaf area index (LAI) were well described by the expolinear growth equation. Moreover a modified expolinear growth equation, formulated as a function of accumulated daily incident PAR was used to derive the light use efficiency (LUE, g MJ^{-1}) for closed canopies. LUE showed a hyperbolic relation to daily incident PAR and LUE was used to determine the maximum crop growth rate (g m^{-2} d^{-1}) at closed canopy. However, it was hard to generalise growth and yield of cut chrysanthemum under a wide range of crop growing conditions and in this approach measured LAI is still required as an input. These limitations lead to the development of a model for predicting LAI and use of it with a generic model for predicting growth and yield of year-round cut chrysanthemum.

Dynamics of LAI can be simulated by the combination of increase in leaf dry mass (LDM) and specific leaf area of new leaves (SLA_n). Dynamics of LDM could be adequately described using a Gompertz function to describe dry mass partitioning to the leaves. SLA_n was linearly related to the inverse of the daily incident PAR, to temperature and to plant density. Dynamics of LAI were satisfactorily simulated for independent experiments and for commercially-grown crops.

CHRYSIMv1.0 was validated, using measured LAI and dry matter partitioning to the organs as an input, to check first possible errors in crop photosynthesis, maintenance respiration and dry mass conversion efficiency. Global radiation outside, inside greenhouse temperature and CO_2 concentration were also input to the model. Simulated TDM was equal to measured TDM in summer (natural light) only, whereas a large under-estimation occurred at constant shade, and in winter. At low light LUE was largely underestimated by CHRYSIMv1.0. Calibrating the parameters of the photosynthesis light response curve of the leaves, i.e. initial light use efficiency, ε, and maximum leaf photosynthetic rate, P_{gmax}, based on one experiment resulted in largely improved simulations of TDM in all experiments, but unrealistic parameter values. Finally some limitations for application of CHRYSIMv1.0 are discussed in this thesis.

Key words: chrysanthemum, crop growth, development, explanatory model, expolinear growth, dry mass, dry matter partitioning, fresh mass, leaf area index, light interception, light use efficiency, plant density, season, simulation, validation, year-round.

To my wife, Hyun Jeong Tag

CONTENTS

I. GENERAL INTRODUCTION

Greenhouse horticulture is the most intensive and sophisticated form of crop production among agricultural production systems (Challa and Van Straten, 1993; Bakker and Challa, 1995). At present, greenhouse crop production systems are closer than ever to generating plant products independent of season, and are therefore referred to as 'plant factories' (Hashimoto, 1993) or 'the greenhouse industry' (Bakker and Challa, 1995). Modern greenhouses have sophisticated computerized control systems for (dynamic) control of greenhouse environmental conditions such as temperature, water vapour pressure, CO_2-concentration, radiation, day length and root environment, presenting numerous options to creatively control the most essential production factors, based on outside weather conditions, inputs (set points) and type and growth stage of the crop (Bakker *et al.*, 1995; Heuvelink, 1996). Vast knowledge, however, is required to optimise these production systems in terms of balancing production costs and economic returns (Challa and Van Straten, 1993; Lentz, 1998). Furthermore, due to the large variation of plant species and cultivars grown, each with different properties and requirements, cultivation system control has become more complex (Challa *et al.*, 1994; Heuvelink, 1996). Several authors (Krug 1989; Challa, 1990; Lentz, 1998) have discussed this complexity for greenhouse systems in general, and they concluded that crop growth models could help to define optimal production strategies.

YEAR-ROUND CUT CHRYSANTHEMUM

Cut chrysanthemum (*Chrysanthemum*, Indicum group), a short-day plant, naturally blooms in the autumn of the Northern Hemisphere. In the past, cut chrysanthemum was mostly grown under natural day length conditions (outside, or in unheated glasshouses). Chrysanthemum supplies to the flower market were therefore seasonally limited (Spaargaren, 2002). However, since 1961 the use of blackout screens and artificial lighting in heated greenhouses has led to effective day length control, such that cut flowers can be produced at any time of year. As a result, cut flower production in the Netherlands has rapidly increased (Spaargaren, 2002). In 2000, glasshouses for cut chrysanthemum covered 774 ha in the Netherlands, which is 21% of the entire area of cut flower cultivation in Dutch glasshouses (Spaargaren, 2002). The present value of cut chrysanthemum production in the Netherlands amounts to approximately € 319 million

(Spaargaren, 2002). Coming second after rose, chrysanthemum dominates the flower market.

Sophisticated year-round production programs for cut chrysanthemum, built upon growers' empirical knowledge, scientific research and the development of new cultivars, involve more than four crops per greenhouse area per year. Therefore cut chrysanthemum is one of the most intensive crops in greenhouse horticultural production systems (Machin, 1996). Chrysanthemum growers have to be able to carry out their production program with great accuracy every week of the year, and operate with a high decision making frequency (Machin, 1996). While seasonal variation in daily light integral naturally leads to seasonal variation in production and plant quality, chrysanthemum growers are commercially challenged to deliver constant product quantity and quality throughout the year. To maximize productivity and minimize variation in plant quality, growers therefore vary plant density, day length and duration of long-day periods (Langton *et al.* 1999). In the cut flower market, plant mass is one of the most important quality aspects, and this has been shown to be largely affected by the amount of light per plant (Langton *et al.* 1999). Particularly plant density is an important and effective crop management factor in determining final quality and productivity (Van der Hoeven *et al.*, 1975). In the Netherlands, chrysanthemum growers decide in advance on plant density, when they order rooted cuttings for their next crop. Whereas greenhouse temperature can be effectively controlled throughout the year in modern greenhouses, daily light integral varies largely. However, supplementary assimilation light, which is increasingly applied in year-round cut chrysanthemum, may reduce seasonal variation in daily light integral and hence increase crop quality and production. Yet the optimal use of supplementary lighting, considering plant density, final plant mass, financial investments and returns, is not well quantified. In complex production systems such as these, growers could benefit from crop growth models to optimise farm management.

RELATIONSHIP BETWEEN LIGHT AND PLANT DENSITY IN CUT CHRYSANTHEMUM

Plant density is an important determinant of plant quality and yield (number of harvested stems). Manipulation of the number of plants per area has resulted in widely variable plant growth and quality of cut chrysanthemum (Van der Hoeven *et al.*, 1975; Langton *et al*, 1999). At sufficient water and nutrient supply and effective pest and disease management, variation in plant growth and quality is mainly determined by competition for light among individual plants (Langton *et al.*, 1999). Therefore optimizing the amount of light per plant during the crop growth period is an important strategy to control plant growth and final quality.

The daily amount of light intercepted by a crop strongly influences its growth rate (Monteith, 1977). Plant density affects light interception before the canopy closes, and hence plant density affects crop growth to some extent. The amount of intercepted light integral before canopy closure depends on leaf area per plant, number of plants, day length, duration of long-day periods and daily light integral. However, when the canopy is closed the fraction of intercepted light will reach its maximum (Monsi and Saeki, 1953). Therefore plant density may not be a key factor influencing crop growth rate. Nevertheless, plant density does have strong effects on plant morphological aspects such as plant size, stem length, number of lateral branches and number of flowers (Van der Hoeven *et al.*, 1975; Carvalho and Heuvelink, 2001). Clearly, in year-round cut chrysanthemum yield and plant quality are strongly interconnected.

Supplementary assimilation light results in increased production, improved crop quality and decreased production time for chrysanthemum (Eng *et al.*, 1985; Anderson, 1990; Vernooij and Ploeger, 1999). However, important practical questions about application of assimilation light remain, particularly concerning (1) optimal use of supplementary lighting considering both plant growth and economic aspects, and (2) suitable plant densities throughout the year at different levels of supplementary light intensity. An almost infinite number of experiments would be required to answer these questions, because of the large number of possible combinations of leading factors such as planting week, assimilation light intensity and plant density. Crop simulation models are valuable additional tools in this situation, as valid models allow for swift and accurate crop growth prediction for a large range of input combinations. These predictions will assist in answering the aforementioned questions. In addition, economic information such as electricity price and market prices for different qualities of cut chrysanthemum is needed to determine the economical optimum for plant density and supplementary lighting intensity.

CROP GROWTH MODELS

Crop growth models are powerful tools to describe and understand complex systems, compare different scenarios, and recapitulate acquired knowledge (Marcelis *et al.*, 1998). Therefore, models can be used as tools for research and education, in decision support systems and greenhouse climatic control systems, for prediction and production planning, and in policy analysis (Challa, 1985, 1988, 1990; Gary *et al.*, 1998; Lentz, 1998; Marcelis *et al.*, 1998). In general, a distinction can be made between descriptive and explanatory models. Descriptive models usually consist of one or more mathematical equations, which are derived from measured data sets (Penning de Vries *et al.*, 1989). In contrast, explanatory models consist of quantitative descriptions of mechanisms and processes, and are based on scientific theory and hypotheses (Penning de Vries *et al.*, 1989). The predictive potential of descriptive models is larger than of explanatory models as the former include all unknown effects, although its model parameters often lack biological meaning (Marcelis *et al.*, 1998; Ishag and Dennett, 1998). However, descriptive models and its model parameters are dependent on species or location (Marcelis *et al.*, 1998), which is a major limitation to applying these models to variable conditions. Nevertheless, descriptive models are useful to summarize measurements as model parameters are relatively easy to estimate (Larsen, 1990; Kage *et al.*, 2001ab). In addition they are useful in on-line greenhouse climatic control systems because few state variables are included and computing time is short (Larsen, 1990; Marcelis *et al.*, 1998).

Explanatory models for crop growth are mostly photosynthesis-driven models based on the amount of intercepted light by plant leaves, and hence predict assimilation (Marcelis *et al.*, 1998). Subsequently, loss of assimilates to respiration and conversion of assimilates into structural dry mass are calculated, and partitioning of assimilates (or dry mass) into individual organs is estimated. Finally, fresh mass can be estimated from calculated dry mass (Marcelis *et al.* 1998). These models are used to predict dry mass production as an indicator for crop physical yield, as a function of greenhouse environmental conditions (Kano and Van Bavel, 1988; Lieth and Pasian, 1991; Dayan *et al.* 1993; Gary *et al.*, 1995; Heuvelink, 1996). Explanatory photosynthesis-driven models have successfully been applied and validated for greenhouse tomato and cucumber crops (De Koning, 1994; Marcelis, 1994; Heuvelink, 1996; Marcelis and Gijzen, 1998). Compared to descriptive models, explanatory models have much more potential for application in complex year-round crop production systems, in terms of dynamic climatic control, production planning, crop management and economic evaluation. According to Lentz (1998), optimal set points for short term and long term cultivation periods cannot possibly be determined without explanatory crop models. However, although the use of explanatory models has received attention in the greenhouse research for many years, application of these models for predicting yield response to greenhouse environmental conditions is still limited to a few fruit-vegetable species and some ornamental crops (De Koning, 1994; Heuvelink, 1996; Marcelis *et al.*, 1998; Marcelis and Gijzen, 1998). Before practical application, models need to be validated in detail not only at the yield level, but also at the level of underlying processes (Heuvelink, 1996). The main obstacles for validation and application of explanatory models in greenhouse production systems are lack of information, for most greenhouse crops, on dry mass dynamics in relation to (comprehensive) climatic data, and poor quantification and generalization of dry mass partitioning into organ and leaf development (Heuvelink, 1995a; Marcelis *et al.*, 1998).

CHALLENGES TO MODELLING YEAR-ROUND CUT CHYSANTHEMUM

As mentioned earlier, crop performance dynamics are not well studied for many (ornamental) greenhouse crops, including cut chrysanthemum. Available data are often limited to final yield, final plant quality, and crop growth conditions in the vegetative phase. Growth curves are usually missing, and climatic data are often lacking or limited to overall figures during the crop growth period. Apart from this soaring lack of data, modelling greenhouse crop performance is challenged further by the problem of predicting leaf area development, which is a weak part of photosynthesis-driven models even as this information is essential to the process of crop light interception described by these models.

The problem of predicting leaf area has been well reviewed by Marcelis *et al.* (1998). Principally, two approaches to prediction of leaf area development are available: (1) leaf area may be described as a function of plant developmental stage or (2) leaf area may be predicted from simulated leaf dry mass (Marcelis *et al.*, 1998). Commonly, photosynthesis-driven models predict leaf area development based on simulated leaf dry mass and specific leaf area (SLA). However, according to Marcelis *et al.* (1998), this approach shifts the modelling problem from predicting leaf area to estimating SLA and dry mass partitioning into leaves. SLA is sensitive to environmental factors and sink-source ratios, whereas dry mass partitioning into leaves is highly species-dependent (Marcelis *et al.*, 1998). Acock *et al.* (1979) formulated a simple and promising model for the SLA of chrysanthemum considering light and temperature, but this model has not yet been validated. As for dry mass partitioning into leaves, this was shown to be constant during the vegetative phase of dry mass increase (Acock *et al.*, 1979), but strongly declined during the generative phase of chrysanthemum (Hughes and Cockshull, 1971; Karlsson and Heins, 1992). None of these authors, however, have attempted to generalize dry mass partitioning into leaves, nor tried to predict leaf area development for cut chrysanthemum. Generalizing dry mass partitioning into leaves has only been done for arable crops, using Gompertz equation as a function of developmental stage (De Visser, 1994), and as a function of the day after emergence (Tei *et al.*, 1996).

AIM AND OUTLINE OF THIS THESIS

The aim of this study is to generalize the dynamics of crop growth performance for year-round cut chrysanthemum in terms of dry mass production and leaf area development, and to apply an existing explanatory model to cut chrysanthemum to determine its response to radiation and cropping strategies, specifically plant density management. This aim is approached by (1) describing and analysing the dynamics of growth and yield of greenhouse-grown cut chrysanthemum as influenced by planting date (season), plant density, and their interaction; (2) generalizing the effect of radiation and plant density on dry mass dynamics of year-round cut chrysanthemum with biologically meaningful parameters; (3) predicting leaf area development based on dry matter partitioning into leaves and specific leaf area of new leaves; (4) adaptation, validation, calibration and evaluation of an explanatory model for the prediction of dry matter production of year-round cut chrysanthemum.

For this study, the photosynthesis-driven model TOMSIM (Bertin and Heuvelink, 1993; Heuvelink, 1995b) was selected as explanatory model, as TOMSIM is built and validated based on a series of comprehensive experiments. TOMSIM is based on SUCROS87 (Spitters *et al.*, 1989), and on a crop photosynthesis model of Gijzen (1992). The photosynthesis module of TOMSIM is not specific to tomato (Heuvelink, 1996) and hence may be applied to other greenhouse crop species such as chrysanthemum. For this study, the module for calculating light intensity has been adjusted to the growing conditions of cut chrysanthemum in terms of supplementary assimilation light intensity and day length control. The resulting model, CHRYSIMv1.0 (Chrysanthemum simulator version 1) has the same structure as TOMSIM (Heuvelink, 1995b), consisting of a standard and adjusted model. The model computes daily crop growth rate (g m^{-2}), based on daily crop gross assimilation rate (P_{gd}) and maintenance respiration (R_m). In the standard model, P_{gd} depends on crop leaf area and radiation, while R_m is a function of temperature and plant organ biomass. In the adjusted model (Heuvelink, 1995b) a reduction factor for R_m is included, which is a negative exponential function of simulated relative growth rate (RGR).

The study is described and presented in four chapters. In Chapter II, long-term growth analyses are presented based on greenhouse experiments, conducted to obtain comprehensive data on dynamics of chrysanthemum dry mass production and leaf area index with detailed climatic data. Those data are needed to extend knowledge on dynamics of crop growth performance and for model development, calibration and validation. In Chapter II-1, the effect of planting date and plant density on dynamics of dry mass production and leaf area index are described and analysed. In addition, effects of planting date and plant density on the relationship between yield and intercepted light are quantified. Theoretically, crop growth rate is approximately linearly related to daily light integral. Hence, a relative increase of light should result in proportional yield increases, but firm experimental proof for year-round greenhouse crops is lacking (Challa *et al.* 1994, Challa and Bakker, 1999). In Chapter II-2, this question is addressed in greenhouse experiments with different combinations of planting date, supplementary assimilation lighting, shading levels and plant densities. In addition, an attempt is made to generalize crop growth in relation to factors with biologically meaningful model parameters.

Predicting leaf area index is a crucial component of photosynthesis-driven models based on light interception. Combining dry matter partitioning into leaves and specific leaf area appears to be a promising approach to predicting leaf area index. In Chapter III, this approach is applied to generalize leaf area index for cut chrysanthemum, based on seasonal experiments.

Structure and application of the photosynthesis-driven model CHRYSIMv1.0 is presented in Chapter IV. Using the measured data of Chapter II-2, model inputs are environmental factors (radiation, temperature, CO_2), dry mass partitioning and leaf area index. This chapter includes an evaluation of the standard model, as well as an adjusted model with maintenance respiration reduced depending on simulated RGR, and a calibrated model implemented with a generalized crop growth rate (as in Chapter II-2) based on daily global radiation averaged over several years.

In the general discussion (Chapter V) limitations of the model for application in ornamental crops are considered, specifically in terms of predicting physical yield by photosynthesis-driven models. In addition, possible improvements to the model are discussed, including the addition of quality aspects of cut chrysanthemum to the photosynthesis module.

II. ANALYSIS OF GROWTH AND YIELD

II.1. EFFECTS OF PLANTING DATE AND PLANT DENSITY ON CROP GROWTH OF CUT CHRYSANTHEMUM

Lee JH, Heuvelink E, Challa H 2002. Effects of planting date and plant density on crop growth of cut chrysanthemum. Journal of Horticultural Science and Biotechnology. 77, 238-247

ABSTRACT

The effects of planting date (season) and plant density (32, 48 or 64 plants m^{-2}) on growth of cut chrysanthemum (*Chrysanthemum*, Indicum group) were investigated in six greenhouse experiments, applying the expolinear growth equation. Final plant fresh and dry mass and number of flowers per plant decreased with plant density and this decrease was larger in summer than in winter. Stem length hardly responded to plant density and total dry mass production per m^2 linearly increased with plant density. Plant dry matter content was not influenced by plant density. Plant dry matter content, plant fresh and dry mass, number of flowers per plant, stem length and biomass production per m^2 were all higher in summer than in winter. Final plant fresh mass (y; g) showed a linear relationship with cumulative incident photosynthetically active radiation (PAR) per plant (x; MJ $plant^{-1}$) ($y = 16.7x + 28.0$, $R^2 = 0.97$). This relationship implies proportionality between incident light per plant and plant density (at the same final plant fresh mass), showing that plant density effects were primarily mediated through competition for light. Dry mass production in time could be described accurately by the expolinear growth equation with three regression parameters: maximum relative growth rate (r_m; assumed to be independent of plant density), maximum absolute growth rate (c_m) and lost time (t_b). r_m was 2.4 times higher and c_m was 4.1 times higher in summer than in winter and no effect of plant density on c_m was observed, whereas t_b decreased linearly with increased plant density. Using these parameters and measured maximum leaf area index (LAI) for calculating dynamic growth patterns of LAI, resulted in large over- or under-estimations, except for summer-grown crops. When an extended expolinear growth function was fitted simultaneously on dry mass production and LAI in time, accurate time curves for LAI were obtained, whereas dry mass production was only accurately described for the summer crops. Only under rather constant radiation levels during a cultivation (summer), could accurate descriptions for both dry mass

production and LAI increase in time be obtained. Light use efficiency (LUE), the slope of the linear relationship between crop growth and cumulative intercepted PAR, varied between 3.4 g MJ^{-1} in summer and 5.3 g MJ^{-1} in winter and LUE slightly increased with plant density.

INTRODUCTION

Daily light integral varies strongly throughout the year in northern Europe and as a consequence crop production and product quality varies. For many crops, including cut chrysanthemum, a constant ratio (light use efficiency, LUE, g MJ^{-1}) between intercepted radiation and biomass production has been observed (Monteith, 1994; Heuvelink *et al.*, 2002). Hence, chrysanthemum plant dry mass tends to be much higher in summer than in winter (Hughes and Cockshull, 1971; Van der Hoeven *et al.*, 1975; Langton *et al.*, 1999). Furthermore, crop management, e.g. plant density can have an influence on crop productivity and plant quality (Langton *et al.*, 1999). Increased plant density increases the productivity per unit area whereas the individual plant mass decreases, e.g. for tomato (Heuvelink, 1995c) and for cut chrysanthemum (Van der Hoeven *et al.*, 1975; Langton *et al.*, 1999; Heuvelink *et al.*, 2002).

Growers have to produce the right amount and right quality at the right moment under pressure of the market throughout the year (Langton *et al.*, 1999). Growers of cut chrysanthemum, a short-day (SD) plant, therefore vary plant density and duration of the long-day (LD) period with the season and they reduce the variation in daily light integral throughout the year by using supplementary assimilation light. By using a longer duration of the long-day period and applying lower plant densities and supplementary assimilation light in winter, Dutch cut chrysanthemum growers are able to reduce seasonal variation in plant mass to a factor two only (Lee *et al.*, 2002), whereas natural daily light integral varies by a factor eight between summer and winter.

Optimising the production system for cut chrysanthemum with its many variables is very complex. Besides the factors discussed above also temperature and CO_2 play an important role. This complexity has been discussed for greenhouse production systems in general by several authors (Krug 1989; Challa, 1990; Lentz, 1998), who concluded that crop growth models could help defining optimal strategies. Models, in particular photosynthesis-driven models, are powerful tools to recapitulate our knowledge to describe and understand complex systems and to compare different scenarios (Marcelis *et al.*, 1998). For the development, calibration and validation of such models quantitative information, especially dynamics of crop growth and crop growth characteristics e.g. leaf area index (LAI), are needed under a range of conditions (Heuvelink, 1995a). For many ornamental greenhouse crops, including cut chrysanthemum, however, dynamics of crop performance in time have hardly been studied. Concerning dynamics of crop growth, the expolinear growth equation provides biologically meaningful parameters as shown by several authors (Goudriaan and Monteith, 1990; Goudriaan, 1994; Dennett and Ishag, 1998; Ishag and Dennett, 1998). This growth equation, however, has not been thoroughly investigated for year around cultivated crops.

The aim of the present work is to describe and analyse the dynamics of growth and yield of greenhouse-grown cut chrysanthemum as influenced by planting date (season) and plant density and their interaction. Six greenhouse experiments, with planting dates throughout the year, each with three plant densities were conducted. The expolinear growth equation and the LUE concept were used to generalise the growth measurements. In future papers, the detailed periodic crop measurements combined with climatic data presented here, will be used for the development, calibration and validation of an explanatory crop growth model for cut chrysanthemum.

MATERIALS AND METHODS

EXPERIMENTAL SET-UP

Six experiments with different planting dates were conducted during three years (Table 1) using two cultivars of cut chrysanthemum (*Chrysanthemum* (*Indicum* group)) i.e. 'Reagan Improved' (Expt. 1, 2, 4 and 6) and 'Vyking' (Expt. 3 and 5; CBA, Aalsmeer, The Netherlands). The experiments were conducted in two (Expt. 1 and 6), three (Expt. 2 and 4) or four (Expt. 3 and 5) compartments (12 m × 12.8 m) that were part of the multispan Venlo-type glasshouse at Wageningen University, The Netherlands (Lat. 52 °N). Rooted cuttings of chrysanthemum were obtained from a commercial propagator (Fides Goldstock Breeding, Maasland, The Netherlands), and planted at 32, 48 or 64 plants m^{-2} in each compartment (plots randomized). Plants were grown by single stem on four or eight-parallel soil beds (1.125 m wide and 10.25 m length per bed, a border soil bed was always present on both sides of the experimental soil beds). All beds had a movable wire netting (maze size: 0.125 m × 0.125 m) system, consisting of a frame which included the heating pipes, to support the crop. LD was given at 16 h for 14 days after planting in Expt. 2 and 3 and at 19 h for 21 days in Expt. 1 and 6 by incandescent lamps (5-6 μmol m^{-2} s^{-1} PAR measured with a 1 m line quantum sensor, LI-191 SA, LI-COR, USA) and was at natural day length (about 15 h) for about 21 days after planting in Expt. 4 and 5. SD was given at 10 h in Expt. 2, 3 and 5 and at 11 h in Expt. 1, 4 and 6 by using a blackout screen until the end of the experiment. Incandescent lamps were continuously turned on during day hours of the LD and SD period for Expt. 1, 2, 3 and 6.

Soil was stem-sterilized before starting each of the Expt. 1, 2 and 5 and nutrient condition in the soil before starting each experiment was adjusted according to soil analysis (BLGG, Naaldwijk, The Netherlands). During cultivation, when soil moisture level (pF; tensiometer, DM-8, Nieuwkoop, Aalsmeer, The Netherlands) reached a value of about 2, irrigation was performed by micro sprinklers (overhead or on-the-ground system) with a nutrient solution (EC=1.2 dS m^{-1}, pH=5.6) for 4-5 min followed by water application for 1-1.5 min in order to prevent damage to the leaves. Pest and disease control were according to an integrated pest management (IPM) scheme, using biological and chemical agents. No growth regulators were applied.

The terminal bud was removed when this bud separated from the lateral buds and final harvest was conducted for all plant densities at the same date, i.e. when three or four flowers were fully open (ray florets horizontal) for plants grown at 48 plants m^{-2}.

TABLE 1. Basic information on the six glasshouse experiments. Dates are expressed as day of the year (day 1 = 1 January).

	Experiment					
	1	2	3	4	5	6
Year	2000	1999	1998	1999	1998	1999
Cultivar[a]	R	R	V	R	V	R
Planting day	12	29	55	126	177	273
Number of long days	21	17	15	22	21	21
Number of short days	61	56	54	53	60	60
Last day of the experiment	94	102	124	201	258	354
Duration of cultivation (d)	82	73	69	75	81	81
Outside global radiation[b] (MJ m^{-2} d^{-1})	2-7	4-9	4-12	17-19	14-7	6-2
Incident ΣPAR[c] (MJ m^{-2})	91	110	129	305	231	73
Average glasshouse temperature (°C)	17.2	18.7	18.3	21.4	20.4	19.2
CO_2 concentration[d] (μmol mol^{-1})	415	447	370	407	395	432

[a] R=Reagan Improved, V=Vyking

[b] Average over first two weeks of cultivation and last two weeks of cultivation

[c] Cumulative incident daily photosynthetically active radiation over the whole cultivation

[d] Between 10:00 and 16:00 h inside the glasshouse and averaged over the whole growing period

GREENHOUSE CLIMATE

Greenhouse temperature set point for heating was 18°C for day and 19°C for night except for Expt. 1, where day/night temperature set points were 16/17°C. Set-point temperature for ventilation was always 1°C higher than for heating. Greenhouse temperature was measured with PT100 elements. CO_2 concentration in each compartment was measured by a CO_2 analyzer (URAS G, Hartmann & Braun, Frankfurt, Germany) and maintained between 350 - 400 μmol mol^{-1} by enriching with pure CO_2. Global radiation was measured with a solarimeter (Kipp and Sons, Delft, The Netherlands) outside the greenhouse. Greenhouse temperature, CO_2 concentration inside the greenhouse and outside global radiation intensity were recorded every 5 min by a commercial VitaCo system (Hoogendoorn, Vlaardingen, The Netherlands).

Daily photosynthetically active radiation (PAR, MJ m^{-2} d^{-1}) inside the greenhouse was calculated based on measured daily integral of outside global radiation and greenhouse transmissivity. From daily global radiation integral, half-hourly values for diffuse and direct PAR were calculated according to Gijzen (1992) and instantaneous greenhouse transmissivity was determined using Bot's (1983) model, parameterised as in Heuvelink *et al.* (1995). This model predicts transmissivity for direct radiation based on solar position, greenhouse roof angle, dimensions of the roof construction parts, transmissivity of the glass panes and the orientation of the greenhouse. For the greenhouse described by Heuvelink *et al.* (1995) measured and simulated transmissivity for diffuse radiation was 0.62, whereas for the present greenhouses transmissivity was 0.49 (average of 42 positions measured on a cloudy day). Therefore, instantaneous greenhouse transmissivity was calculated as for the greenhouse of Heuvelink *et al.* (1995) and then divided by 0.62 and multiplied by 0.49. Daily PAR takes into account the loss of radiation by SD treatment and additional PAR from the incandescent lamps. Daily intercepted PAR was calculated as daily incident PAR multiplied by the fraction of PAR intercepted by the crop (= $1-e^{(-k \cdot LAI)}$; k = 0.72, see below). Accumulated incident PAR (ΣPAR, MJ m^{-2}) was obtained as the integral of daily PAR inside the greenhouse from planting day until final harvest day.

MEASUREMENTS

Destructive measurements were carried out every 7 to 10 days or every 3 to 4 days until start of SD in Expt. 1 and 6. Samples were taken from 5 (Expt. 4), 6 (Expt. 1, 2 and 6) or 8 (Expt. 3 and 5) plants per experimental plot, excluding border plants in two rows on each side of a bed. Stem length, number of flowers (including buds), total leaf area

(LI-COR Model 3100) and plant fresh and dry (105 °C for 14 h in a ventilated oven) mass were determined. No root measurements were conducted.

EXPOLINEAR GROWTH EQUATIONS

Two regressions (fittings) were conducted to describe dry mass production and LAI in time, based on the periodic measurements. First, a regression was performed on measured dry mass production in time only, using the simple expolinear equation (Goudriaan and Monteith, 1990):

$$W = (c_m / r_m) \cdot \ln[1 + e^{(r_m \cdot [t - t_b])}] \qquad (1)$$

where W (g m^{-2}) is dry mass at time t (d), and r_m (g g^{-1} d^{-1}) is the maximum relative growth rate in the exponential phase and c_m (g m^{-2} d^{-1}) is the maximum absolute growth rate in the linear phase. t_b, (d) is the lost time to indicate the apparent time lost during canopy development before all radiation is intercepted; it determines the position of the curve on the time-axis (Goudriaan and Monteith, 1990). The weakest assumption in this simple expolinear equation is that leaf area ratio (LAR, m^2 g^{-1}) remains constant during the growing season and hence LAI increases indefinitely (Ishag and Dennett, 1998). An extended expolinear growth equation for describing a realistic growth pattern of leaf area was suggested by Goudriaan (1994):

$$W = [c_m^* \cdot f_m / r_m] \cdot \ln[1 + e^{(r_m(t - t_b))}] \qquad (2)$$

$$LAI = \frac{1}{k} \ln[\frac{1 + e^{(r_m \cdot (t - t_b))}}{1 + e^{(r_m \cdot (t - t_b) - k \cdot LAI_m)}}] \qquad (3)$$

where c_m^* is the potential maximum absolute growth rate, f_m (= $1 - e^{(-k \cdot LAI_m)}$) is the maximum fraction of light intercepted at maximum leaf area index (LAI_m), and r_m and t_b are fitted parameters from the simple equation. LAI_m is the maximum leaf area index and k is light extinction coefficient. Potential growth rate, c_m* can be calculated by c_m/f_m, where c_m is the fitted value from the simple expolinear equation. Thus it can be ensured that the calculated total dry mass production in time is the same as for equation (1). LAI progression in time can be calculated from equation (3) using the fitted parameters from the simple equation (1) as shown by Ishag and Dennett (1998). These authors, however, showed over- or under-estimation of LAI using the parameters from the simple equation for legume crops. Alternatively to this first method, in a second regression procedure, a simultaneous fitting for both measured total dry mass and LAI using equation (2) and (3) was conducted.

In both fitting procedures r_m was assumed to be independent on plant and k was fixed for all experiments. In an experiment k was measured to be 0.87 (unpublished data), but this may not be representative for all planting dates in this study and therefore a theoretical value of 0.72 was assumed, based on a spherical leaf angle distribution (Goudriaan and Van Laar, 1994). Each fitting was performed by weighted least squares (Ishag and Dennett, 1998) using the non-linear fitting procedure of the SPSS software package (version 10, SPSS company, Chicago, USA). In the second fitting procedure periodically measured LAI was multiplied by a factor 100 in order to have a similar scale and weighting as the measured dry mass (g m^{-2}).

AN EMPIRICAL MODEL FOR PLANT FRESH MASS

A relationship between total plant fresh mass (*TFM)* of year-round cut chrysanthemum and radiation and plant density (p_d; plant m^{-2}) has been presented by Langton *et al.* (1999):

$$TFM = \frac{1}{a + \frac{1}{c + d \cdot RAD_g} p_d} \tag{4}$$

where $a = 0.00119$ plant g^{-1}, $c = 1881.4$ g m^{-2} and $d = 4.006$ (g MJ^{-1}) and RAD_g = accumulated outside global radiation integral (MJ m^{-2}) with adjusted photoperiod. These three regression parameters were estimated, based on a wide range of plant spacings (82.6-244.3 cm^2 per plant, which is equal to 121- 41 plants m^{-2}) and an accumulated global radiation integral ranging from 236.9 to 1262.1 MJ m^{-2} (Langton *et al.*, 1999).

COMPARISON OF MEANS AND PARAMETERS

Effects of planting date, plant density and their interaction were tested by analysis of variance based on a split-plot design using the Genstat software package (Genstat 5 Committee, 1993). The plant density effect was separated in a linear and a quadratic component. For significant ($P < 0.05$) effects, means were separated by Students *t*-test ($P = 0.05$), using the least significant difference (LSD) based on the minimum number of replications. Additionally polynomial trend for a qualitative treatment of plant density was also tested.

RESULTS

CLIMATIC DATA

Clear differences between experiments in global radiation levels were observed (Table 1). Expt. 1, 2 and 3 were planted in January or February and showed a rapid increase in daily global radiation during the experiment, whereas the opposite was observed for Expt. 6, which was planted at the end of September. Global radiation was high and rather constant for Expt. 4 and also for Expt. 5 except for the last weeks where radiation decreased by 50 %. As a consequence of the different global radiation levels, accumulated incident PAR was about 4 times higher in Expt. 4 compared to Expt. 6 and values for the other experiments were intermediate. Daily glasshouse temperature was 3-4 °C higher in summer than in winter (Table 1) and almost constant during a cultivation, except for Expt. 4 and 5. In Expt. 4, daily glasshouse temperature averaged over 14 days rose from 20 °C to 24 °C during the last month of the experiment and in Expt. 5 it rose from 19 °C to 22 °C during the first month of the SD treatment and thereafter remained at about 19 °C until the end of the experiment. These increased temperatures resulted from the high radiation levels in summer combined with closure of the blackout screen partly during daytime, as natural daylength was about 15 h, whereas photoperiod during SD treatment was 11 h for Expt. 4 and 10 h for Expt. 5. As a result of CO_2 enrichment, CO_2 concentration was above ambient in all experiments, although not to the same extent (Table 1).

FINAL PLANT CHARACTERISTICS

Strong seasonal and plant density effects on several plant and crop characteristics were observed (Fig. 1 and Table 2). Number of flowers per plant, plant fresh mass and plant dry mass decreased with plant density, this decrease being larger in summer than in winter (Fig. 1). Final plant fresh mass at 48 plants m^{-2} (Fig. 1B), was 2.7 times higher in Expt. 4 than in Expt. 6 (for plant dry mass this factor was 3.2) and plant mass in the other experiments was intermediate. The differences in ratio (2.7 versus 3.2) can be explained by variation in the dry matter content throughout the season: plant dry matter content was about 2 point % higher (13.3 % instead of 11.2 %) in Expt. 4 than in Expt. 6 (Table 2). Stem length showed an optimum response to plant density with a maximum length at 64 plants m^{-2}, however, differences between densities were only small (< 6 %).

Stem length was highest in Expt. 4 and lowest in Expt. 3. Total biomass production per m^2 showed a linear increase with plant density and was highest for Expt. 4, and lowest for Expt. 6.

TABLE 2. Effect of season (Experiment) and plant density on dry matter content (DMC), stem length and total dry mass production (TDM) of glasshouse-grown cut chrysanthemum at final harvest.

Factor		DMC (%)	Stem length (cm)	TDM (g m^{-2})
	1	11.7	63.6	351
	2	12.6	73.7	408
Experiment	3	11.8	57.9	382
	4	13.3	96.6	831
	5	12.5	84.1	693
	6	11.2	84.9	263
	LSD[1]	0.6	3.3	65
	32	12.2	73.9	459
Plant density (plants m^{-2})	48	12.2	77.2	515
	64	12.3	78.2	566
F-probabilities				
Experiment		< 0.001	< 0.001	< 0.001
Plant density		0.466	< 0.001	< 0.001
Linear		0.225	< 0.001	< 0.001
Quadratic		0.884	0.056	0.841
Experiment × Plant density		0.309	0.349	0.795

[1] Least Significant Difference (P=0.05) for comparing experiment means.

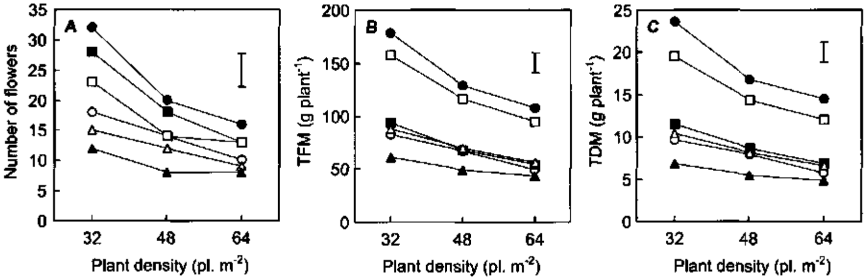

FIG. 1. Effect of the interaction between season (experiment) and plant density on (A) number of flowers per plant (B) total plant fresh mass (TFM) and (C) total plant dry mass (TDM) for glasshouse-grown cut chrysanthemum. Symbols indicate Expt. 1 (○), Expt. 2 (■), Expt. 3 (△), Expt. 4 (●), Expt. 5 (□) and Expt. 6 (▲). Vertical bars represent standard errors for interaction means

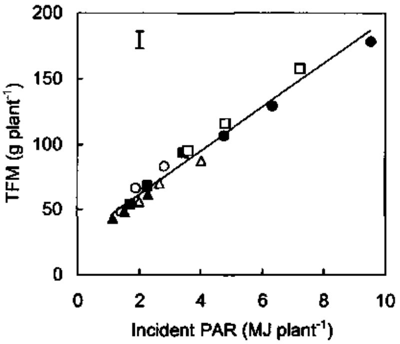

FIG. 2. Relationship between total plant fresh mass (TFM) and incident PAR integral per plant over the whole cultivation period of glasshouse-grown cut chrysanthemum. Regression line: $y=16.7x+28.9$ ($R^2=0.97$). Symbols indicate Expt. 1 (○), Expt. 2 (■), Expt. 3 (△), Expt. 4 (●), Expt. 5 (□) and Expt. 6 (▲). Vertical bar represents standard error of regression.

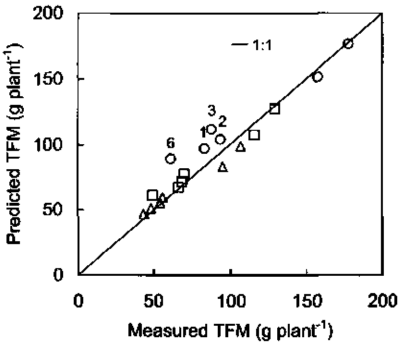

FIG. 3. Predicted total plant fresh mass (TFM) according to equation 4, plotted against measured TFM from six experiments with glasshouse-grown cut chrysanthemum at three plant densities (32 (○), 48 (□) or 64 (△) plants m^{-2}). Numbers indicate experiments.

Figure 2 shows that final plant fresh mass increased linearly with increased amount of light per plant. This relationship implied that 1 MJ additional light per plant over the whole growing period would increase plant fresh mass by 16.7g. Langton *et al.* (1999) reported a formula predicting plant fresh mass as a function of global radiation and plant density (equation 4), which could well describe plant fresh mass in the present study (Fig. 3). However, plant fresh masses at lower plant densities in the present experiments, were overestimated except for Expt. 4 and 5.

DRY MASS PRODUCTION AND LAI IN TIME

In all experiments, total dry mass production showed an exponential increase followed by a constant linear growth phase (Fig. 4). The expolinear growth equation with three parameters (equation 1) could accurately describe the dry mass increase in time (Fig. 4 solid lines and Table 3). Parameters r_m, c_m and t_b were significantly influenced by season whereas only t_b showed a linear decrease with increased plant density (Table 3). r_m was about twice as high for the crops planted May (Expt. 4) or June (Expt. 5) than for the crops planted in January (Expt. 1 and 2) or February (Expt. 3). c_m was about four times higher in Expt. 4 than in Expt. 6.

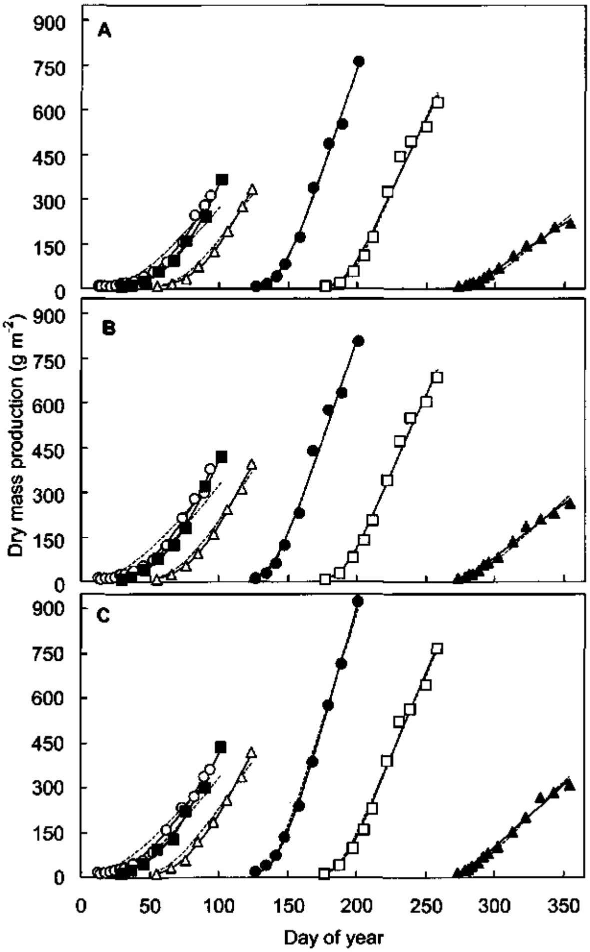

FIG. 4. Dynamics of dry mass production for glasshouse-grown cut chrysanthemum in six experiments (Expt. 1 (○), Expt. 2 (■), Expt. 3 (△), Expt. 4 (●), Expt. 5 (□) and Expt. 6 (▲)) at three-plant densities (A: 32, B: 48 or C: 64 plants m^{-2}). Lines represent fitted curves for the simple expolinear growth equation (equation 1, solid lines) and for the extended expolinear growth equation (equations 2 and 3), simultaneously fitting dry mass production and LAI (dashed lines).

TABLE 3. Parameters for the simple expolinear growth equation (equation 1) obtained by fitting periodic dry mass production measurements for glasshouse-grown cut chrysanthemum. Values between brackets are means over three plant densities.

Experiment	Density (pl. m^{-2})	r_m[1] (d^{-1})	c_m (g m^{-2} d^{-1})	t_b (d)
	32	-	10.6	53.9
1	48	-	9.6	45.1
	64	-	8.2	37.6
		0.062	(9.5)	(45.6)
	32	-	10.7	37.7
2	48	-	10.3	32.3
	64	-	9.5	28.1
		0.076	(10.2)	(32.7)
	32	-	8.4	29.5
3	48	-	8.8	25.1
	64	-	8.7	21.1
		0.087	(8.6)	(25.5)
	32	-	13.6	19.4
4	48	-	13.5	13.5
	64	-	16.0	17.1
		0.136	(14.3)	(16.5)
	32	-	9.8	14.4
5	48	-	10.4	12.9
	64	-	11.1	11.8
		0.169	(10.5)	(13.0)
	32	-	3.1	6.5
6	48	-	3.6	3.6
	64	-	4.2	2.7
		0.145	(3.6)	(4.2)
	32	-	9.6	26.0
Mean[2]	48	-	9.7	21.5
	64	-	10.0	19.5
LSD[3]		0.018	1.8	4.9
F-probabilities				
Experiment		< 0.001	< 0.001	< 0.001
Plant density		-	0.685	< 0.001
Linear		-	0.418	< 0.001
Quadratic		-	0.767	0.192
Experiment × Plant density		-	0.414	0.083

[1] r_m was assumed to be equal for all three plant densities

[2] Values averaged over the six experiments

[3] Least Significant Difference (P=0.05) for comparing experiment means.

LAI in time showed a sigmoid pattern in all experiments, its final value was highest for crops planted in May (Expt. 4) and June (Expt. 5) and it increased with plant density (Fig.5).

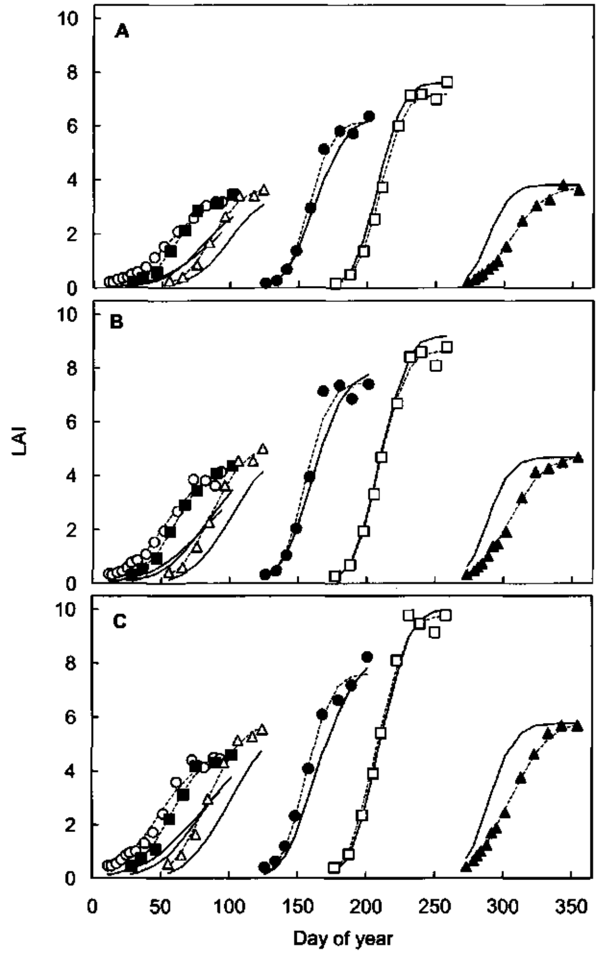

FIG. 5. Dynamics of LAI for glasshouse-grown cut chrysanthemum in six experiments (Expt. 1 (○), Expt. 2 (■), Expt. 3 (△), Expt. 4 (●), Expt. 5 (□) and Expt. 6 (▲)) at three-plant densities (A: 32, B: 48 or C: 64 plants m^{-2}). Lines represent curves calculated from the simple expolinear growth equation (equation 1) fitted for dry mass production (solid lines) and for the extended expolinear growth equation (equations 2 and 3), simultaneously fitting dry mass production and LAI (dashed lines).

TABLE 4. Parameters for the extended expolinear growth equation (equations 2 and 3) obtained by fitting simultaneously periodic dry mass production measurements and leaf area index of glasshouse-grown cut chrysanthemum. Values between brackets are means over three plant densities.

Experiment	Density (pl. m^{-2})	r_m[1] (d^{-1})	c_m* (g m^{-2} d^{-1})	t_b (d^{-1})	LAI_m
	32	-	5.8	28.1	3.4
1	48	-	5.6	20.4	4.3
	64	-	5.2	15.4	4.7
		0.078	(5.5)		(4.2)
	32	-	5.7	19.0	3.5
2	48	-	5.9	14.2	4.4
	64	-	5.6	10.6	4.7
		0.098	(5.8)		(4.2)
	32	-	6.7	19.0	3.8
3	48	-	6.8	14.0	5.1
	64	-	6.5	9.5	5.7
		0.106	(6.7)		(4.9)
	32	-	13.4	18.2	6.1
4	48	-	13.3	12.7	7.5
	64	-	14.7	13.8	7.6
		0.166	(13.8)		(7.1)
	32	-	10.3	16.7	7.2
5	48	-	10.6	13.4	8.6
	64	-	10.7	10.0	9.7
		0.168	(10.5)		(8.5)
	32	-	4.2	18.2	3.7
6	48	-	4.4	13.4	4.7
	64	-	4.9	10.1	5.8
		0.095	(4.5)		(4.8)
	32	-	8.1		4.8
Mean[2]	48	-	8.2		6.0
	64	-	8.4		6.7
LSD[3]		0.009	0.8	1.7	0.4
F-probabilities					
Experiment		< 0.001	< 0.001	< 0.001	< 0.001
Plant density		-	0.319	< 0.001	< 0.001
Linear		-	0.139	< 0.001	< 0.001
Quadratic		-	0.825	< 0.001	0.010
Experiment × Plant density		-	0.135	< 0.001	0.075

[1] r_m was assumed to be equal for all three plant densities

[2] Values averaged over the six experiments

[3] Least Significant Difference (P=0.05) for comparing experiment means; for t_b LSD for comparing experiment × plant density interaction means is presented.

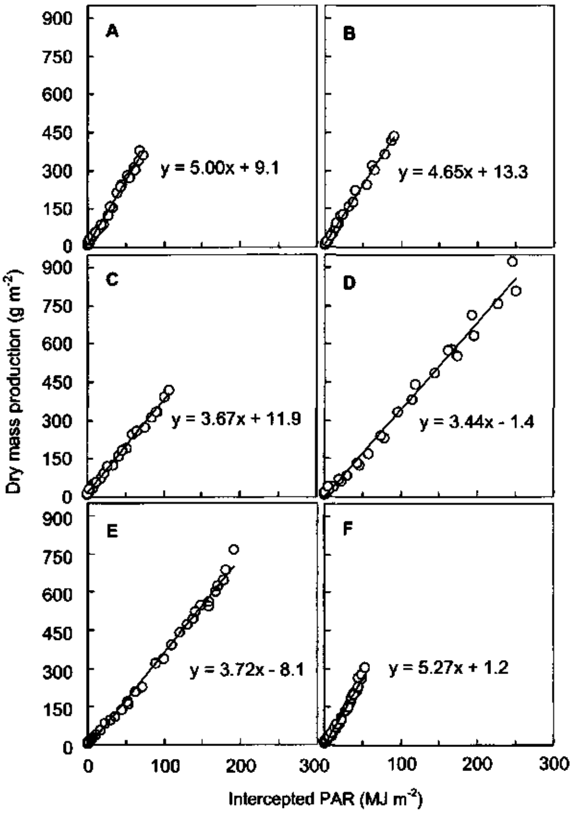

FIG. 6. Periodic measurements of dry mass production (○) at three plant densities plotted against cumulative intercepted PAR for glasshouse-grown cut chrysanthemum in six experiments (A, Expt. 1; B, Expt. 2; C, Expt. 3; D, Expt. 4; E, Expt. 5; F, Expt. 6). Lines represent linear regressions of which equations are shown in the graphs. R^2 for each linear regression was larger than 0.98.

Calculated LAI (Fig. 5 solid lines), based on the expolinear growth equation fitted for biomass production and measured maximum LAI, closely followed observed LAI for all plant densities in Expt. 4 and 5. In Expt. 1, 2 and 3 calculated LAI strongly underestimated observed LAI, whereas in Expt. 6 LAI was strongly overestimated. Hence, a simultaneous fitting of total dry mass production and LAI, using the extended expolinear growth equation (equations 2 and 3) was conducted. Estimation of LAI greatly improved in all experiments (Fig. 5 dashed lines and Table 4), but especially in Expt. 1 and 2 the description of dry mass production was less accurate (Fig. 4 dashed lines).

LIGHT USE EFFICIENCY

Periodic measurements of dry mass production showed a strong linear relationship with accumulated intercepted PAR in all experiments (Fig. 6). However, the slope of the regression line, which represents LUE, was not the same for all experiments. The lowest value was observed for the crop planted in May (Expt. 4) and the highest value was observed for the crop planted at the end of September (Expt. 6). LUE showed a small linear increase with plant density (LUE = 3.75 + 0.0073 × plant density; $P = 0.007$, $R^2 = 0.99$).

DISCUSSION

PLANT BIOMASS

Plant fresh mass is an important quality parameter for cut chrysanthemum. A fourfold variation in plant fresh mass, resulting from different planting dates and plant densities, was closely linearly related to available incident light per plant over the whole growing period (Fig. 2). Also Langton *et al.* (1999) reported a close relation between accumulated radiation per plant and plant fresh mass. However, their relationship contains three regression parameters (equation 4), whereas the present one has only two regression parameters. The relationship of Langton *et al.* (1999), with their parameter values (equation 4), gave in general a good prediction for plant fresh mass in the present experiments (Fig. 3), despite the use of a different cultivar and perhaps a different glasshouse transmissivity. However, at 32 plants m^{-2} in Expt. 1, 2, 3 and 6, equation 4 overestimated plant fresh mass. This may be, because 32 plants m^{-2} is outside the density range (40 - 121 plants m^{-2}) used by Langton *et al.* (1999) for determining the parameter values in equation 4.

In the present experiments, all densities were harvested on one date, whereas it is commonly found that a higher density delays flowering (Langton *et al.*, 1999). However, it is expected that the present procedure (harvest on one date) compared with harvest of each density plot 'when ready' will give almost identical results, as difference in harvest date between the lowest and the highest density would have been 3 to 5 days (Lee *et al.*, unpublished data).

The observed linear relationship (Fig. 2) between plant fresh mass (TFM) and incident PAR integral per plant over the whole growing period ($\Sigma PAR/P_d$) implies that, when light integral is 1 % higher, a 1 % higher plant density (P_d) can be used, without effecting plant fresh mass, as the relationship in Figure 2 can be reformulated as $P_d = \Sigma PAR \times 16.7 / (TFM-28.9)$. According to equation 4, plant density could increase by 0.90 % to 0.94 % (so also almost 1 %) as a result of a 1 % increase in total incident light integral in the range from 70 to 300 MJ m^{-2} incident PAR. This proportionality between incident PAR and plant density (at the same plant fresh mass) clearly shows that plant density effects in glasshouse-grown cut chrysanthemum are primarily mediated through competition for light. Hence, competition for water and nutrients is not or hardly playing a role, as one may expect for modern glasshouse cultivations.

STEM LENGTH AND NUMBER OF FLOWERS PER PLANT

A larger number of LDs will result in longer stems, as this results in a longer vegetative period and therefore the production of more leaves and internodes. Higher average day temperature increases stem elongation rate in chrysanthemum, resulting in taller plants (reviewed by Carvalho and Heuvelink, 2001) and hence the tallest plants were observed in Expt. 4 (longest duration of the LD period highest average temperature and). Expt. 3 showed the shortest stems, in agreement with the shortest duration of the LD period and a low average glasshouse temperature (Table 1). Differences in stem length between experiments are also partly the result of cultivar differences. For example, Expt. 2 (cv. Reagan Improved) and Expt. 3 (cv. Vyking) have almost the same duration of the LD period and the same average temperature and light integral, whereas stem length was 27 % higher in Expt. 2. This difference in stem length resulted from shorter internodes for 'Vyking', as the number of leaves on the stem was almost the same in Expt. 2 and 3 (not shown). Despite the statistically significant effect of plant density on stem length, a doubling in plant density from 32 to 64 plants m^{-2} resulted in only 6 % increase in stem length. Also Van der Hoeven *et al.* (1975) reported only a small increase in stem length (9 %) with a doubling in plant density.

The decrease in number of flowers per plant with increasing plant density (Fig. 1A) agrees with observations of Van der Hoeven *et al.* (1975). They also observed a larger plant density effect on the number of flowers per plant for a summer crop than for a winter crop. These results also agree with Carvalho *et al.* (2002) who reported a positive relationship between biomass per plant and the number of flowers. However, also temperature influences flower initiation and development (e.g. Adams *et al.*, 1998). A supra-optimal average 24 h temperature in Expt. 4 (24 °C during the last month of the experiment) may explain why the higher light sum (Table 1) and biomass production in this experiment compared to Expt. 2, did not result in more flowers per plant. This high temperature may have delayed or even inhibited formation and development of second order flowers on the lower part of the axillary stems.

EXPOLINEAR GROWTH FUNCTIONS

Dynamics of dry mass production in time were accurately described by the simple expolinear growth equation (Fig. 4). The higher r_m and c_m in summer compared to winter (Table 3), is likely to be the result of higher light level and higher temperature in summer (Table 1). t_b corresponds to the reciprocal of r_m with fixed initial fraction of light intercepted (Goudriaan, 1994) and hence an increase in r_m by temperature (Monteith, 2000) or radiation (Hughes, 1973) will result in a decrease in t_b. This is not reflected in our results (Table 3), as for example in Expt. 6 t_b is extremely small due to the fact that daily radiation integral decreased drastically during the experiment, which resulted in a decrease in the growth rate of a closed canopy. However, the equation is based on the assumption of a constant growth rate when the canopy is closed and hence c_m (fitted on the data for the whole growth period) will be an underestimation for the growth rate in the middle of the cultivation. As a result of this, t_b will be underestimated. Exactly the opposite holds for early spring crops: radiation level increases and therefore growth of a closed canopy increases and c_m will be an overestimation of crop growth rate in the middle of the cultivation. As a result of this, t_b will be overestimated. Increased plant density decreased t_b (Table 3), since initial fraction of light intercepted is higher at higher plant density.

When the dynamics of LAI were calculated, based on fitted parameters for the expolinear dry matter increase in time and a measured maximum LAI, as presented by Ishag and Dennett (1998), only in summer accurate descriptions of LAI in time were obtained (Fig. 5). This results from over- or underestimation of t_b as explained above. In spring crops, t_b is over-estimated and hence a delay in predicted LAI occurs, whereas in autumn t_b is under-estimated, resulting in much faster predicted than observed LAI development. Simultaneous fitting of measured dry mass production and LAI development using equations 2 and 3 resulted in good predictions of LAI development in time in all experiments (Fig. 5). However, dry matter production was described accurately only in summer and a particularly poor fit was obtained in Expt. 1 and 2 (early spring crops). The lower values of potential maximum growth rate (c_m*) than actual maximum growth rate (c_m) were not expected, because maximum fraction of intercepted radiation is always less than 1 at maximum LAI (Goudriaan, 1994) and hence c_m* should be higher than c_m (Table 3 and 4). For Expt. 1, 2 and 3, t_b was on average about 50 % lower in the simultaneous fitting (Table 4) than in the fitting on dry mass production alone (Table 3) and r_m was higher in the simultaneous fitting. We conclude that fitting expolinear growth functions for dry mass production alone, or fitting on dry mass production and LAI development simultaneously, gave accurate descriptions only under more or less stable radiation levels (summer). Goudriaan and Monteith (1990) mention that their analysis, leading to the expolinear growth equation, is only valid when there is little change in the receipt of radiation on a weekly basis. They consider this condition satisfied, which is true for field crops, grown in a rather limited part of the year. However, this condition is certainly not satisfied for year-round greenhouse crops.

RELATIONSHIP BETWEEN LIGHT INTERCEPTION AND DRY MASS PRODUCTION

The observed linear relationship between crop growth and cumulative intercepted radiation (Fig. 6) has also been reported by others for many crops (Monteith, 1994). Theoretically, the regression line should go through the origin. However, for five of the six regressions, the intercept differed slightly, however statistically significant, from zero. As intercepts were not much different from zero, fitting without intercept would hardly change the slopes (LUE) and therefore our conclusions would be the same. Measurements clearly showed variation in LUE among experiments and even a slight increase in LUE with plant density. Kage *et al.* (2001b) observed a reduction in LUE with daily PAR for field-grown cauliflower crops. A reduction of LUE at high light intensities is to be expected, based on light saturation of photosynthesis at leaf level, which also occurs, although to a much lesser extent, at crop level (Heuvelink *et al.*, 2002). Furthermore, increased light intensities result in a larger fraction of direct radiation, which is used less efficiently than diffuse radiation (Gijzen, 1992). The observed small increase in LUE with increased plant density may be explained by a reduced average light intensity per leaf at higher plant density.

In a previous paper, we reported a LUE between 2.7 and 4.1 g MJ^{-1} for cut chrysanthemum in a shading experiment in summer, assuming a glasshouse transmissivity of 63 % (Heuvelink *et al.*, 2002). However, measured glasshouse transmissivity was only 49 % for our glasshouses, resulting in a 30 % increase in calculated LUE values. Hence, using the measured instead of the estimated glasshouse transmissivity for the data of Heuvelink *et al.* (2002) results in a LUE range almost exactly equal to the one presented here (3.4 - 5.2 g MJ^{-1}).

CONCLUSIONS

The linear relationship between light integral per plant and plant fresh mass (Fig. 2), provides an accurate summary of the observations in our experiments, however, it can not be used as a generalisation. For example, plant fresh mass also depends on CO_2 concentration (Hughes and Cockshull, 1972) and temperature (Karlsson and Heins, 1992) and hence these climatic factors will influence the relationship between light integral per plant and plant fresh mass. The same is true for LUE (Fig. 6), which appeared to be rather constant within an experiment, but showed a clear seasonal influence being much higher in winter than in summer. Fitting expolinear growth functions for dry mass production alone, or fitting on dry mass production and LAI development simultaneously, gave accurate descriptions only under more or less stable radiation levels (summer). For an accurate description and generalisation of the present data, the approaches tested here, though very valuable, are all too limited. Therefore, the present data will be used for development, calibration and validation of an explanatory crop growth model. Such a model is expected to be able to simulate observed growth patterns accurately under the wide range of glasshouse climatic conditions used. For chrysanthemum, such a model does not exist yet (Marcelis *et al.*, 1998).

II-2. USING THE EXPOLINEAR GROWTH EQUATION FOR MODELLING CROP GROWTH IN YEAR-ROUND CUT CHRYSANTHEMUM

Lee JH, Goudriaan J., Challa H. Effects of planting date and plant density on crop growth of cut chrysanthemum. (Submitted)

ABSTRACT

The aim of this study was to predict crop growth of year-round cut chrysanthemum (*Chrysanthemum,* Indicum group) based on a model of maximum crop growth rate as a function of daily incident photosynthetically active radiation (PAR, MJ m^{-2} d^{-1}), using the expolinear growth equation. Four experiments for developing an empirical crop growth model and three experiments for validating the model were conducted in glasshouse compartments. In the four experiments for model development, chrysanthemum crops received different light regimes (natural light, shading to 66 % and 43 % of natural light, and supplementary assimilation light [HPS, 40-48 μmol m^{-2} s^{-1}]), at different plant densities (32, 64 and 80 plants m^{-2}), and seasons (planting in January, May-June and September). Greenhouse temperatures (19-21 °C) and CO_2 concentrations (349 - 432 μmol mol^{-1}) were similar between experiments.

The fitted expolinear growth equation as a function of time ($EXPO_T$) or as a function of incident PAR integral ($EXPO_{PAR}$) effectively described periodically measured total dry mass (R^2 > 0.98). However, growth parameter estimates for the fitted $EXPO_{PAR}$ were more suitable than $EXPO_T$ as they were not correlated to each other. Coefficients of $EXPO_{PAR}$ were the relative growth rate per incident PAR integral (RGR_{PAR}, [MJ $m^{-2}]^{-1}$) and light use efficiency (LUE, g MJ^{-1}) at closed canopy. In all four experiments no interaction effects between treatments on crop growth parameters were found. RGR_{PAR} and LUE were not different between HPS and natural light treatments, but were significantly increased when light levels were reduced by shading in the summer experiments. There was no consistent effect of plant density on growth parameters.

RGR_{PAR} and LUE showed hyperbolic relations with daily incident PAR averaged over 10 day periods after planting (RGR_{PAR}) or before final harvest (LUE). Based on those relations, maximum relative growth rate (g g^{-1} d^{-1}) and maximum crop growth rate (g m^{-2} d^{-1}) were successfully described by rectangular hyperbolic relations to daily incident PAR integral. TDM simulated over time was in good agreement with TDM

measured in three independent experiments, using daily incident PAR integral and leaf area index as inputs.

Based on these results it is concluded that the expolinear growth equation is a useful tool for quantifying cut chrysanthemum growth parameters and comparing growth parameters between different treatments, especially when light is the growth-limiting factor. Under controlled environmental conditions the regression model worked satisfactorily, hence the model may be applied as simple tool for understanding crop growth behaviour under seasonal variation in daily light integral, and for planning cropping systems of year-round cut chrysanthemum. However, further research on leaf area development in cut chrysanthemum is required to advance chrysanthemum crop growth prediction.

INTRODUCTION

Year-round cut chrysanthemum (a short-day plant) is grown in intensive industrialised cultivation systems, with scheduled planting and harvesting throughout the year. Hence, prediction of crop growth over time is important for maximizing cropping system efficiency. However, compared to greenhouse vegetable crops, growth prediction has yet to be established for cut chrysanthemum (Marcelis *et al.*, 1998). Seasonal variation in daily light integral is a major limiting factor for dry-mass production and product quality in chrysanthemum (Hughes and Cockshull, 1971, 1972; Van der Hoeven *et al.*, 1975; Langton *et al.*, 1999; Chapter II-1). Temperature strongly influences plant development (Karlsson and Heins, 1992; Adams *et al.*, 1998), and is, in modern greenhouses, a factor that can be controlled reasonably well throughout the year.

Physiological plant processes are too complex to be described by simple models, but simplifications are often useful for interpolating or extrapolating measured data. Theoretically, crop growth rate is approximately linearly related to daily light integral (Challa *et al.* 1994a, Challa and Bakker, 1999). Hence, a relative increase of light can result in proportional yield increases, but firm experimental proof for year-round greenhouse crops is lacking (Challa *et al.* 1994a, Challa and Bakker, 1999). When nutrients, water, pests and diseases are not limiting, maximum crop growth rate can be largely explained by the ability of the crop to intercept and utilise radiation at a closed canopy (De Wit *et al.*, 1978). Crop light use efficiency (LUE, g MJ^{-1}) has been defined as dry mass production per unit of intercepted photosynthetically active radiation (PAR, MJ m^{-2}) (Monteith, 1977; 1994). The LUE concept has often been used for analysing and modelling crop growth (Bonhomme, 2000), due to its simplicity and supporting experimental evidence (Kage *et al.*, 2001b). Bonhomme (2000) reported that variation in LUE is considered small if environmental conditions are not seriously growth limiting, such that crop growth rate is directly proportional to light interception. However Lee *et al.* (Chapter II-1) found that, despite adequate nutrients, water, and pest management, LUE varied widely between seasons, ranging from 3.4 to 5.3 g MJ^{-1} intercepted PAR for glasshouse-grown cut chrysanthemum. Moreover, the seasonal variation in LUE raised doubts about the linear relationship between intercepted light integral and accumulated dry mass production in year-round cultivated crops, where growth periods include conditions of seasonally decreasing or increasing daily light integral. Therefore, LUE may use as an intermediate parameter for analysing and modelling crop growth in year-round cut chrysanthemum.

Dry mass production of chrysanthemum over time follows a pattern of exponential growth followed by linear growth until reaching a commercial stage (Chapter II-1). The overall growth pattern of chrysanthemum, therefore, has been effectively described by the expolinear growth equation (Goudriaan and Monteith, 1990; Goudriaan, 1994), though with large seasonal variation in growth parameters (Chapter II-1). The expolinear growth equation has been used in many crops to describe crop growth dynamics and interpret measured data, as the equation contains biologically meaningful parameters, i.e. maximum relative growth rate (r_m, g g^{-1} d^{-1}), maximum absolute growth rate (c_m, g m^{-2} d^{-1}) and lost time (t_b, d) (Goudriaan and Monteith, 1990; Goudriaan, 1994; Tei *et al.*, 1996; Both *et al.*, 1997; Dennett and Ishag, 1998; Ishag and Dennett, 1998; Monteith, 2000). r_m characterizes the exponential growth phase and c_m the linear growth phase at complete light interception by the canopy, while t_b represents time lost before the linear growth phase is attained (Goudriaan and Monteith, 1990; Goudriaan, 1994). Lee *et al.* (2002) reported that parameter estimation for the expolinear growth equation is problematic when daily light integral varies systematically during the crop growth period, and Goudriaan and Monteith (1990) have worried about using the expolinear model for such conditions. Since variation in crop growth is the final result of variations in environmental conditions throughout the crop growth period, Tei *et al.* (1996) proposed that fitting empirical models to measured dry-mass production could improve the accuracy of estimating dependent variables if the independent variable in the model is replaced by environmental time, that is, considering the interdependent variables daily light integral, temperature integral and CO_2 concentration (Aikman and Scaife, 1993; Tei *et al.*, 1996). Therefore, in the case of modelling crop growth under temporally varying environmental conditions, the problem of estimating parameters for the expolinear growth equation could be solved by considering environmental time instead of days after planting.

The main objective of this study was to develop a regression model with biologically meaningful parameters, to model the effect of radiation and plant densities on crop growth rate for year-round cut chrysanthemum. Seven experiments were conducted in semi-commercial glasshouse compartments. For developing the model of crop growth rate as a function of daily incident photosynthetically active radiation integral (PAR, MJ m^{-2} d^{-1}), four experiments were conducted under similar greenhouse temperatures and CO_2 concentrations during the crop growth period. These experiments were conducted in three different seasons and treatments included supplementary assimilation light, natural light, shading and three plant densities. As greenhouse temperature and CO_2 concentration were similar between experiments, daily light integral was the major limiting factor for crop growth in these four experiments. Fitting of the expolinear growth equation, therefore, was implemented with the incident PAR integral ($EXPO_{PAR}$) as only independent variable. In this approach, the growth parameters r_m, c_m and t_b of the expolinear growth equation can be replaced by the relative growth rate per incident PAR integral (RGR_{PAR}, g g^{-1} [MJ $m^{-2}]^{-1}$), the maximum light use efficiency (*LUE*, g MJ^{-1}) in the linear growth phase during full light interception by the crop, and lost incident PAR (L_b, MJ m^{-2}), respectively. To improve accuracy of estimated growth parameters, the growth equation was reformulated to reduce correlation between parameters. Based on those estimated parameters, an empirical model was developed for daily crop growth rate as a function of daily incident PAR integral. Finally, three independent experiments were conducted to generate input data (measured initial dry mass, daily incident PAR and leaf area index) for model validation.

MODEL DESCRIPTION

MODEL DESCRIPTION

The expolinear growth model as a function of time (t) has three parameters, i.e. maximum relative growth rate (r_m, g g^{-1} d^{-1}) in the exponential phase, maximum growth rate (c_m, g m^{-2} d^{-1}) in the linear phase and lost time (t_b, d) to indicate the apparent time lost during canopy development before all radiation is intercepted; it determines the position of the curve on the time-axis (Goudriaan and Monteith, 1990; Goudriaan, 1994).

$$TDM = (c_m / r_m) \cdot \ln[1 + e^{(r_m \cdot (t - t_b))}] \qquad [1]$$

A detailed formulation of expolinear growth (Eqn. [1]) has been presented by Goudriaan and Monteith (1990) and Goudriaan (1994), and this model has been applied with cut chrysanthemum Lee *et al.* (2002). Therefore, only the specific approach to estimate the regression coefficients is detailed here. Equation [1] can be rewritten by replacing the independent variable (time) with the accumulated daily incident PAR integral inside the greenhouse ($\int PAR$, MJ m^{-2}), and by substituting the growth parameters r_m, c_m and t_b with their respective analogies.

$$TDM = (LUE / RGR_{PAR}) \cdot \ln[1 + e^{(RGR_{PAR} \cdot (\int PAR - L_{PAR}))}] \qquad [2]$$

where RGR_{PAR} ([MJ $m^{-2}]^{-1}$) is the relative growth rate per incident PAR integral in the exponential growth phase, LUE (g MJ^{-1}) is light use efficiency in the linear growth phase, and L_{PAR} is the lost daily incident PAR integral (MJ m^{-2}). $\int PAR$ (MJ m^{-2}) is the accumulated daily incident PAR integral. In general, the parameters in equations [1] and [2] are strongly correlated (Goudriaan and Monteith, 1990; Goudriaan 1994). Particularly, the parameters t_b and L_{PAR} strongly correlate with r_m and RGR_{PAR}, respectively (Goudriaan and Monteith, 1990). Hence, L_{PAR} in equation [2] can be decomposed as

$$L_{PAR} = -\ln[\frac{f_0}{1 - f_0}] \Big/ RGR_{PAR} \qquad [3]$$

where f_0 is the initial fraction of light interception by the initial leaf area index (LAI_0), $f_0 = 1 - e^{k \cdot LAI_0}$. Therefore equation [2] can be rewritten as

$$TDM = (LUE / RGR_{PAR}) \cdot \ln[1 + \frac{f_0}{1 - f_0} \cdot e^{(RGR_{PAR} \cdot \int PAR)}] \qquad [4]$$

At the start, accumulated incident PAR is set to zero assuming no growth at planting date. Hence, initial total dry mass (TDM_0) can be derived from equation [3] by

$$TDM_0 = (LUE / RGR_{PAR}) \cdot \ln[1 + \frac{f_0}{1 - f_0}] \qquad [5]$$

The fraction of light (f_0) can be eliminated from equation [4] because

$$\frac{f_0}{1 - f_0} = e^{TDM_0 \cdot RGR_{PAR} / LUE} - 1 \qquad [6]$$

Hence, equation [4] can be rewritten as

$$TDM = (LUE/RGR_{PAR}) \cdot \ln[1 + (e^{(TDM_0 \cdot RGR_{PAR}/LUE)} - 1) \cdot e^{(RGR_{PAR} \cdot \int PAR)}] \qquad [7]$$

Assuming a constant leaf area ratio (LAR, m^2 g^{-1}) throughout the crop growth period,

$$RGR_{PAR}/LUE = k \cdot p_l \cdot SLA_n = k \cdot LAR \qquad [8]$$

where k is the light extinction coefficient, p_l is the fraction of dry matter partitioned into new leaves and SLA_n is the specific leaf area of new leaves (m^2 g^{-1}). Hence, equation [7] can be rewritten as

$$TDM = (\frac{1}{k \cdot LAR}) \cdot \ln[1 + (e^{(TDM_0 \cdot k \cdot LAR)} - 1) \cdot e^{(\int C_{\max} \cdot k \cdot LAR)}] \qquad [9]$$

where $\int C_{\max}$ is the accumulated maximum crop growth rate (C_{max}, g m^{-2}), C_{max} is the maximum crop growth rate (g m^{-2} d^{-1}) at fully closed canopy, and k is assumed constant at 0.72 (Goudriaan and Van Laar, 1994). C_{max} was estimated by multiplying the daily incident PAR (MJ m^{-2} d^{-1}) with LUE (see results). Actual crop growth rate (GR, g m^{-2} d^{-1}), therefore, can be calculated as

$$GR = C_{\max} \cdot (1 - e^{k \cdot LAI}) \qquad [10]$$

Assuming a constant leaf area ratio (LAR) over time, the LAI growth rate can be calculated by multiplying GR with a constant LAR and hence it purely depends on GR.

MATERIALS AND METHODS

Seven experiments (Table 1) with different planting dates were conducted during two years using cut chrysanthemum (*Chrysanthemum,* Indicum group), cultivar Reagan Improved. Experiments were conducted in compartments (12.0 m × 12.8 m) that were part of a multispan Venlo-type glasshouse at Wageningen University, The Netherlands (lat. 52 °N). Experiments 1-4 were used for model development and experiments 5-7 were used for model validation (Table 1).

Block-rooted cuttings of cut chrysanthemum were obtained from a commercial propagator. Plants were grown as single stems on eight parallel soil beds (1.125 m × 10.250 m each bed), separated by borders. All beds had a movable system consisting of a frame, which included heating pipes, and wire netting (mesh size: 0.125 m × 0.125 m) to support the crop. Each experimental crop was exposed to a varying number of long days (LD) and short days (SD) (Table 1). LD was given at 16 h (Expt. 6) or 19 h (Expts. 1, 2 and 7) for 7-22 days using control lighting by incandescent lamps (CON, 4-6 μmol m^{-2} s^{-1}) or high-pressure sodium lamps (HPS, 42-57 μmol m^{-2} s^{-1}, SON-T 400W, Philips, The Netherlands), whereas in experiments 3 and 4 LD was given by only natural light (about 15 h). SD's of 10 h (Expt. 6) and 11 h (Expts. 1-5, and 7) were implemented from day 17-21 onwards until ending the experiments, using blackout screens. Lamps were continuously turned on during day hours of LD and SD periods (Expts. 1, 2, 5 and 6) or were controlled based on outside global radiation (Exp. 7). In the latter case, lamps were turned on at less than 150 W m^{-2} and turned off at more than 250 W m^{-2} global radiation intensity. For experiments 1, 2 5, and 6, compartments were installed with both HPS and incandescent lamps (3.5 m above soil surface), whereas experiment 7 had only HPS lamps. In experiments 3 and 4 (only natural light), two different white screens with different transmissivity were used for shading the crops.

TABLE 1. Basic characteristics of the seven greenhouse experiments used for model development (D) and validation (V). Dates are expressed as day of year (day 1 = 1 January). N is the number of harvests during the experimental crop growth period.

Expt.	Year	Planting date	Number of long days (LDs)	Number of short days (SDs)	Final harvest date	Plant density (Pl. m^{-2})	N
1	2000	12	21	58	91	32,48,64	14
2	1999	126	22	53	201	"	9
3	1999	273	21	60	354	"	13
4	2000	160	21	55-60	236-241	32,64,80	14
5	2000	12	21	58-61	91-94	32,48,64	14
6	1999	29	17	56	102	"	8
7	2000	250-264	7-21	63	334	64	12

Expt.	Global radiation[a] (MJ m^{-2} d^{-1})	Temperature[b] (°C)	$[CO_2]$[c] (μmol mol^{-1})	Expt. goal
1	2-7	21.0	415	D
2	17-19	21.4	407	D
3	6-2	19.2	432	D
4	22-15	22.1	349	D
5	2-7	17.2	415	V
6	4-9	18.7	447	V
7	8-2	19.8	407	V

[a] Averaged over first two weeks and last two weeks of cultivation.

[b] 24h average greenhouse temperature, averaged over the whole growing period.

[c] Measured inside the greenhouse between 10:00 and 16:00 h, averaged over the whole growing period.

TABLE 2. Average daily incident photosynthetically active radiation integral (incident PAR integral) in the experiments used for developing the model.

Experiment	Day interval	Average incident PAR[1] (MJ m^{-2} d^{-1})			Light intensity of lamps[2] (μmol m^2 s^{-1})	
		CON	HPS	SD	CON	HPS
1	0-19	0.49	1.10	0.23	3.5±0.4	48.1±3.2
	20-39	0.93	1.31	0.40		
	40-59	1.30	1.67	0.46		
	60-end	1.47	1.84	0.80		
	Average	1.09	1.48	-		
2	0-19	1.49	1.99	0.47	4.8±0.8	39.6±0.5
	20-39	0.98	1.28	0.39		
	40-59	0.69	0.98	0.26		
	60-end	0.44	0.73	0.21		
	Average	0.89	1.24	-		
3	0-19	3.96	-	1.34	-	
	20-39	3.92	-	1.20	-	
	40-59	3.99	-	1.52	-	
	60-end	4.22	-	1.04	-	
	Average	4.01	-	-	-	
4	0-19	4.81	-	1.58	-	
	20-39	2.96	-	1.11	-	
	40-59	3.52	-	0.84	-	
	60-end	3.32	-	0.96	-	
	Average	3.64	-	-	-	

[1] HPS: assimilation lighting by high-pressure sodium lamps; CON: control lighting by incandescent lamps; SD: standard deviation.

[2] Light intensity from the lamps was measured inside the greenhouse during night conditions.

Shading screens were placed 1.5 m above the soil surface on fixed rectangular frames, covering two soil beds each. An irrigation pipe was placed on the each soil bed (Expt. 3), or both on soil beds and under the shading screens (Expt. 4), in each compartment.

For each light treatment, intensity of supplementary lighting was measured by a 1 m line quantum sensor (LI-191 SA, LI-COR, USA) in 18 equally spaced places at crop level during late evening. Side effects from HPS assimilation lamps were minimised by installing the same light treatments in adjacent compartments. Side effects within compartments were minimised by attaching aluminium foil on half of the luminaries near the control treatments (day length provided by incandescent lighting). Adjusting their position and distance to ensure homogeneous light distribution of assimilation light on the crops, light intensities were measured (Table 2). Above and below the shading screens light intensity was measured in 27 places (equally spaced) using a 1 m line quantum sensor (LI-191 SA, LI-COR, USA) in Expt. 3. In Expt. 4 two quantum sensors (LI-190SA, LI-COR, USA) were placed permanently under each type of screen and read every 5 min in one of the compartments. The shading ratio in Expts. 3 and 4 was calculated by linear regression of light intensity above and under the screen. The same screens were used in both experiments. Light transmission of the two shading screens were 65 % ± 3.4 % and 45 % ± 3.0 % for Expt. 3 and 66 % ± 1.6 % and 42 % ± 1.6 % for Expt 4. Since the difference between the transmissions found in two experiments was marginal the values 66 % ± 1.9 % and 43 % ± 1.9 % averaged over the two experiments were used. Daily incident PAR (MJ m^{-2} d^{-1}) inside the greenhouse compartment was calculated according to Bot (1983), Gijzen (1992), Heuvelink *et al.* (1995). More detailed information about the calculation of incident PAR in these greenhouse compartments has been described elsewhere (Lee *et al.*, 2002). Additional light from the lamps and light reduction by SD treatments were included in the daily incident PAR integral. Daily incident PAR integral under shading screens is a proportion of daily light integral of non-shading treatment in Expts. 3 and 4.

Day/night temperature set point was 21/20 °C for Expt. 1, 17/16 °C for Expt. 5 and 18/19°C for other experiments. The ventilation temperature was 1 °C higher than the indicated day/night temperature set point. CO_2 concentration in each compartment was measured by a CO_2 analyser (URASG, Hartman & Braun, Germany) and remained at least 350 μmol mol^{-1} by pure CO_2 enrichment in all experiments except for Expt. 2, where CO_2 concentration was maintained at 400 μmol mol^{-1} in two compartments. Global radiation (assessed with Kipp and Zonen solarimeter, Delft, The Netherlands), greenhouse temperature (PT 500 element) and CO_2 concentration was recorded every 5 min by a commercial VitaCo climatic control system (Hoogendoorn, Vlaardingen, The Netherlands).

EXPERIMENTAL TREATMENTS AND EXPERIMENTAL DESIGN

Experiments 1, 2, 5 and 6 were conducted in two (Expts. 1, 2 and 5) or three (Expt. 6) compartments with two levels of control lighting (incandescent lamps for daylength, CON) and supplementary assimilation lighting (HPS) in each half of a compartment. Within each lighting plot three plant densities (32, 48 and 64 plants m^{-2}) were randomly distributed on two soil beds in each half of a compartment according to a split plot design. Expts. 3 and 4 were conducted in three compartments with three light levels

(100 %, 66 % or 43 %) in each compartment and within each light level three plant densities (32, 48 and 64 plants m^{-2} for Expt. 3 and 32, 48 and 80 plants m^{-2} for Expt. 4) were randomly distributed on two soil beds according to a split-plot design. Expt. 7 was conducted in two compartments under HPS (56.6 ± 0.8 μmol m^{-2} s^{-1}) with three different durations of LD (experimental unit) obtained by three planting dates at one-week interval as a complete randomised design and plants were planted at 64 plants m^{-2}. In Expts. 1, 2, 5 and 6 a border soil bed was present on both sides of the two experimental beds in each half of the compartments. In Expts. 3, 4 and 7 a border soil bed was present at each side of the compartment.

PLANT MEASUREMENTS

Destructive measurements were carried out every 3 to 12 days until final harvest. Samples were taken from 5 to 6 plants per experimental plot, excluding border plants in two rows on each side of a bed. Total leaf area per plant was measured (using a LI-COR Model 3100), as well as fresh and dry mass (dried at 105 °C for 14 h in a ventilated oven) of leaves (including petioles), stems and flowers (including buds). No measurements on roots were made. All measurements were recorded for individual plants, for each experimental plot and replication.

MODEL VALIDATION

Three independent experiments were used for crop growth model validation using measured initial total dry mass (TDM_0, g m^{-2}), leaf area index (LAI) and daily incident PAR (MJ m^{-2} d^{-1}) inside greenhouse. As mentioned in the model description, leaf area ratio (LAR) is defined by specific leaf area (SLA_n) and fraction of dry matter partitioned into leaves (P_l), but P_l strongly varies throughout plant development (Hughes and Cockshull, 1972; Karlsson and Heins, 1994) whereas SLA_n varies with temperature and incident PAR integral (Acock *et al.*, 1979). Therefore, it may not be feasible to ignore variation in LAR to calculate LAI dynamics for flowering cut chrysanthemum. To address this problem, total dry-mass production in time was calculated as accumulated GR (Eqn. [10]) with initial TDM and measured LAI as input. Excel software was used for model validation. In addition, Prism® (GraphPad Software Inc, San Diego, USA) was used to fit measured LAI by a cubic spline curve (Motulsky, 1999), in order to obtain the daily fraction of light intercepted by the crop for equation [10].

STATISTICAL ANALYSES OF MEASUREMENTS AND MODEL PARAMETERS

Regression coefficients for equations 1, 2, 4 and 7 were estimated by minimising the residual sum of squares (least squares method), using the non-linear fitting procedure of the SPSS software package (version 10, SPSS company, Chicago, USA). Using SPSS, Pearson correlation coefficients were estimated to select the best equation for estimating crop growth parameters, that is, the equation with no significant correlations between estimated parameters. Of the selected equation, estimated parameters RGR_{PAR} and LUE were subjected to treatment effect tests. Effects of light regime, plant density and their interaction were tested by analysis of variance (ANOVA) based on the experimental design for experiments 1-4 using the Genstat software package (Genstat 5 Committee, 1993). Light regime and plant density effects were separated in a linear and a quadratic component. For significant ($P < 0.05$) effects, means were separated by student t-tests ($P = 0.05$) using least significant differences (LSD).

RESULTS

GREENHOUSE CLIMATE

Average daily greenhouse temperature (average over 24 h) and CO_2 concentration (average between 10:00-16:00) and daily global radiation outside are presented in Table 1 and average daily incident PAR integral in four experiments in Table 2. Daily incident PAR varied largely between experiments due to season and supplementary assimilation lighting, whereas average greenhouse temperature and CO_2 concentration were rather constant during the growing period except for experiment 3, in which greenhouse temperature increased later in the growing period (Chapter II-1, Table 1 and 2).

FITTING OF EXPOLINEAR GROWTH EQUATIONS

Fitting of the expolinear equation as a function of time (Eqn. [1]) and as a function of incident PAR integral (Eqn. [2]) effectively described the observed TDM in all experiments. Although fitting of equation [1] to periodic measured TDM accounted for over 98 % of the variance, its estimated parameters were strongly correlated with each other (Table 3). Furthermore, these estimates were particularly biased when daily light integral drastically changed during the crop growth period in experiments 1 and 2. These problems can be solved by fitting the model as a function of incident PAR integral (Eqns [2], [4] and [7]). Although fitting of either equations [2] or [4] adequately described TDM dynamics as a function of incident PAR integral, strong correlations remained between RGR_{PAR} and L_{PAR} (Eqn. [2]) and RGR_{PAR} and f_0 (Eqn. [4]) (Table 3). Therefore, measured TDM was fitted as function of daily incident PAR by equation [7], to analyse and generalise estimated crop growth parameters without significant correlation between parameters (Table 3).

TABLE 3. Correlation matrix for estimated parameters of equations 1, 2, 4, and 7.

Equation	Parameters	RGR_{PAR}	LUE	r_m	c_m
1	c_m	–	–	-0.222^*	1.000
	t_b	–	–	-0.770^{**}	0.313^{**}
2	LUE	0.043	1.000	–	–
	L_{PAR}	-0.811^{**}	-0.235^*	–	–
4	LUE	0.043	1.000	–	–
	F_0	0.711^{**}	−0.023	–	–
7	LUE	0.065	1.000	–	–
	TDM_0	−0.139	0.176	–	–

** Correlation is significant at the 0.01 level (2-tailed)

* Correlation is significant at the 0.05 level (2-tailed).

ESTIMATED GROWTH PARAMETERS

Using the fitted $EXPO_{PAR}$ (Eqn. [7]), TDM dynamics as function of incident PAR integral showed a pattern of exponential growth followed by linear growth, which was in good agreement with measured TDM in all experiments (Figs. 1-2). Estimated initial TDM was identical to measured initial TDM in all experiments. Since there were no significant correlations between parameters of equation [7] (Table 3), treatment effects on estimated parameters could be unambiguously determined (Table 4 and 5). In all four experiments, no interaction effects between treatments were observed. In experiments 1 and 2 there was no significant effect of assimilation lighting and plant density on crop growth parameters (Table 4). However, the overall average of RGR_{PAR} appeared to be higher in experiment 1 than in experiment 2, whereas LUE was higher in experiment 2 than experiment 1 (Table 4), indicating a seasonal effect on crop growth parameters. In experiments 3 and 4, RGR_{PAR} and LUE were significantly different between light levels, and increased linearly with decreasing light level (Table 5). No plant density effects on growth parameters were detected in experiment 3, whereas RGR_{PAR} and LUE at 32 plants m^{-2} were significantly different from the highest plant densities in experiment 4 (Table 5). In the latter experiment, crop growth parameters appeared to show a linear trend to plant density (Table 5).

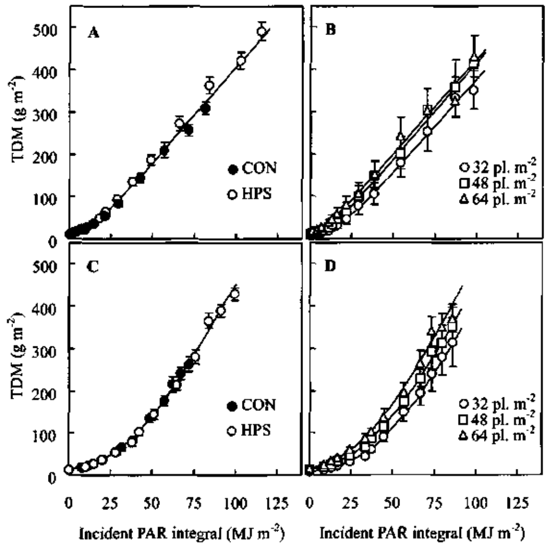

FIG. 1. Dynamics of total dry mass production (TDM) of cut chrysanthemum as a function of daily incident PAR integral. Graphs are separated by effects of light (A, C) and plant density (B, D) on dry-mass production for crops planted in January (A, B) and September (C, D). Vertical bars indicate standard errors of mean measured TDM.

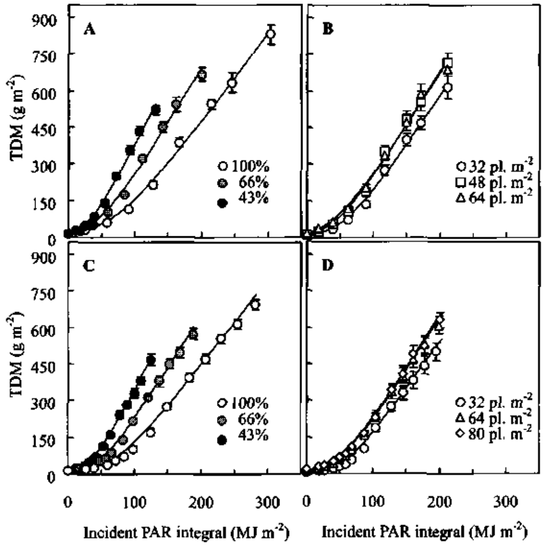

FIG. 2. Dynamics of total dry mass production (TDM) of cut chrysanthemum as a function of daily incident PAR integral under different shading treatments in two summer experiments (A, B: Expt. 3, C, D: Expt. 4). Graphs are separated by effects of light levels (A, C) and plant density (B, D) on dry-mass production for crops planted in May (A, B) and June (C, D). Vertical bars indicate standard errors of mean measured TDM.

TABLE 4. Effects of supplementary lighting and plant density on relative growth rate per incident PAR integral (RGR_{PAR}) in the exponential growth phase, and on light use efficiency (LUE) in the linear growth phase at closed canopy, estimated by the expolinear growth equation as a function of accumulated incident PAR integral for crops planted in January 2000 (Expt. 1) and September 1999 (Expt. 2).

Treatment		Expt 1		Expt 2	
		LUE (g MJ^{-1})	RGR_{PAR} $(MJ\ m^{-2})^{-1}$	*LUE* (g MJ^{-1})	RGR_{PAR} $(MJ\ m^{-2})^{-1}$
Light[1]	CON	4.33	0.1176	6.66	0.0620
	HPS	4.72	0.1169	6.72	0.0629
Density	32	4.44	0.1104	6.50	0.0626
	48	4.62	0.1165	6.67	0.0622
	64	4.51	0.1249	6.91	0.0626
	LSD[2]	0.55	0.0532	0.72	0.0079
F-probabilities					
Light		0.149	0.497	0.926	0.857
Density		0.703	0.691	0.368	0.877
	Linear	0.734	0.421	0.184	0.830
	Quadratic	0.470	0.936	0.872	0.664
Light×Density		0.098	0.623	0.063	0.056

[1] HPS: assimilation lighting by high-pressure sodium lamps, CON: control lighting by incandescent lamps.

[2] Least significant difference (P = 0.05) for comparing means.

GENERALISATION OF RGR_{PAR} AND LUE PARAMETERS

As mentioned before, RGR_{PAR} defines the exponential growth phase and LUE the linear growth phase at closed canopy. Estimated RGR_{PAR} and LUE were plotted against daily incident PAR in the period after planting (RGR_{PAR}) or before final harvest (LUE), using daily incident PAR averaged over 10 day periods instead of over the whole growing period (Fig. 3) because of large seasonal variation in daily incident PAR integral throughout the crop growth period (Table 2). Using this approach, RGR_{PAR} and LUE showed hyperbolic relations to averaged daily incident PAR integral (Fig. 3), which accounted for 52 % and 66 % of variance in RGR_{PAR} and LUE, respectively. Furthermore the ratio between the regression of RGR_{PAR} and LUE in Figure 3 is identical to the product of $k \cdot LAR_0$ as mentioned before (Goudriaan and Monteith, 1990).

TABLE 5. Effects of supplementary lighting and plant density on relative growth rate per incident PAR integral (RGR_{PAR}) in the exponential growth phase, and on light use efficiency (LUE) in the linear growth phase at closed canopy, estimated by the expolinear growth equation as a function of accumulated incident PAR integral for crops planted in May 1999 (Expt. 3) and June 2000 (Expt. 4).

Treatment		Expt 3		Expt 4	
		LUE (g MJ^{-1})	RGR_{PAR} $(MJ\ m^{-2})^{-1}$	*LUE* (g MJ^{-1})	RGR_{PAR} $(MJ\ m^{-2})^{-1}$
Light[1]	100%	3.63	0.0344	3.47	0.0401
	66%	4.34	0.0497	4.23	0.0520
	43%	5.23	0.0694	5.44	0.0639
	LSD	0.50	0.0064	0.54	0.0093
Density	32	4.22	0.0517	3.85	0.0652
	48	4.68	0.0511	-	-
	64	4.30	0.0507	4.55	0.0479
	80	-	-	4.74	0.0429
	LSD[2]	0.55	0.0072	0.52	0.0075
F-probabilities					
Light		<0.001	<0.001	<0.001	0.002
	Linear	<0.001	<0.001	<0.001	<0.001
	Quadratic	0.212	0.053	0.076	0.509
Density		0.196	0.959	0.008	<0.001
	Linear	0.751	0.781	0.002	<0.001
	Quadratic	0.081	0.961	0.639	0.442
Light×Density		0.055	0.130	0.155	0.742

[1] Light level created by two white shading screens. Percentage indicates proportion of light transmitted by shading screens (100% light level for non-shading treatments).

[2] Least significant difference (P=0.05) for comparing means.

Therefore, the initial LAR of 0.0327 $m^2\ g^{-1}$ can be derived from the ratio between the two non-linear regressions when daily incident PAR equals zero. As daily light integral largely varies with season in Northern Europe, seasonal variation in LAR_0 for year-round cut chrysanthemum might be described by a rectangular hyperbola as function of daily incident PAR integral ($MJ\ m^{-2}\ d^{-1}$):

$$LAR_0 = a + b \big/ (1 + d \cdot PAR) \qquad [11]$$

where $a = 0.0109\ m^2\ g^{-1}$, $b = 0.0218\ m^2\ g^{-1}$ and $d = 0.9186\ [MJ\ m^{-2}\ d^{-1}]^{-1}$. Hence seasonal variation in initial LAR can be described as a function of incident PAR throughout the year.

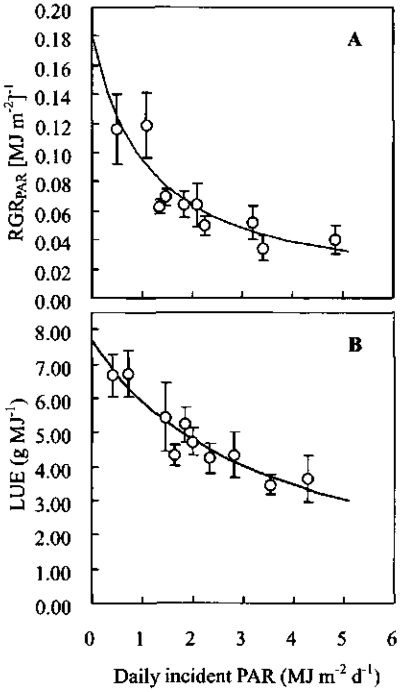

FIG. 3. Correlations between average daily incident PAR and relative growth rate per incident PAR integral (RGR$_{PAR}$, A) and light use efficiency (LUE, B). Vertical bars indicate standard deviation of parameter estimates. Daily incident PAR in the period after planting (RGR$_{PAR}$) or before final harvest (LUE) is averaged over 10 day periods. Regressions are, A: $1/RGR_{PAR} = 5.5172(\pm 1.344) + 5.0679(\pm 0.505) \times PAR$, $R^2 = 0.52$, $n = 78$ and B: $1/LUE = 0.1299(\pm 0.008) + 0.0397(\pm 0.003) \times PAR$, $R^2 = 0.66$, $n = 78$.

The maximum relative growth rate (RGR$_{max}$, d^{-1}) at early growth phase and maximum crop growth rate (C$_{max}$, g m^{-2} d^{-1}) at fully intercepted incident PAR can be extrapolated from the regressions of RGR$_{PAR}$ and LUE (Fig. 3) by multiplying with daily incident PAR integral (PAR, MJ m^{-2} d^{-1}). In figure 3, regressions of RGR$_{PAR}$ and LUE are therefore identical to the ratios RGR_{max}/PAR and C_{max}/PAR, respectively. Maximum relative growth rate (RGR$_{max}$) as a function of daily incident PAR integral (PAR, MJ m^{-2} d^{-1}) can be formulated as

$$RGR_{\max} = RGR_{PAR0} \cdot RGR_i \cdot PAR / (RGR_i + RGR_{PAR0} \cdot PAR) \qquad [12]$$

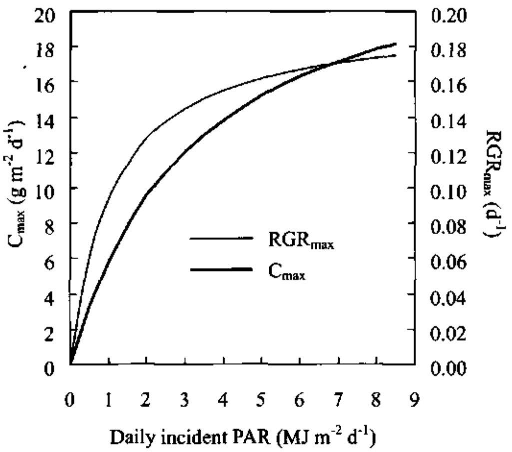

FIG. 4. Maximum relative growth rate (RGR_{max}, d^{-1}) and maximum crop growth rate (C_{max}, g m^{-2} d^{-1}) derived from the hyperbolic relation to incident PAR described in Fig. 3.

where RGR_{PAR0} is initial relative growth rate per incident PAR integral, equal to 0.1813 g g^{-1} [MJ m^{-2}]$^{-1}$, and RGR_i is the intrinsic maximum relative growth rate (d^{-1}), equal to 0.1973 g g^{-1} d^{-1} (Fig. 4).

Using the same approach as with RGR_{max}, maximum crop growth rate (C_{max}) as a function of daily incident PAR integral (PAR, MJ m^{-2} d^{-1}) can be formulated as

$$C_{max} = LUE_0 \cdot C_i \cdot PAR/(C_i + LUE_0 \cdot PAR) \qquad [13]$$

where LUE_0 is initial LUE, equal to 7.70 g MJ^{-1}, and C_i is the intrinsic maximum crop growth rate, equal to 25.18 g m^{-2} d^{-1}, which can be limited by factors other than radiation, i.e. CO_2 concentration at high daily light integral and temperature (Fig. 4).

Based on the theoretical relationship between RGR_{PAR} and LUE, equation [9] may be derived from equation [7]. Assuming a constant LAR, growth rate of LAI is proportional to crop growth rate. Hence TDM calculated from equation [9] provides an accurate value, as accumulated crop growth rate of equation [10] is based on simulated LAI, at constant LAR over growth period (Eqn. [11]) (data not shown).

MODEL VALIDATION

In flowering chrysanthemum, fraction P_l decreased systematically with increased TDM (Hughes and Cockshull, 1972), whereas in vegetatively grown chrysanthemum SLA_n

varied with temperature and incident PAR under closed canopy (Acock *et al.*, 1979). Therefore, P_l and SLA_n were not suitable to use as constant values for model validation in this study. Alternatively, measured LAI was used as input for validating the generalised model for crop growth rate formulated by equation [10]. Three independent experiments (Expts. 5-7 in Table 1) were used to simulate TDM dynamics over time, using daily incident PAR and leaf area index as input data. Simulated crop growth patterns adequately described measured TDM in all independent experiments (Fig. 5). For experiment 5, simulated TDM overestimated measured TDM for the crop grown at 17 °C under natural light conditions, whereas they were almost identical for the crop grown at same temperature under assimilation lighting.

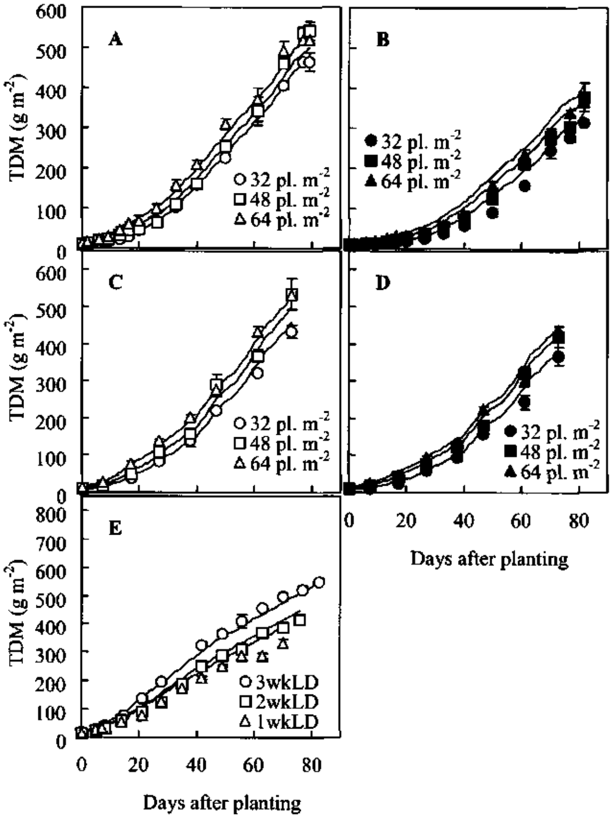

FIG. 5. Simulated dynamics of total dry mass production (TDM) over time using three independent experiments (A, B: Expt. 5; C, D: Expt. 6; E: Expt. 7). Graphs are separated by light treatment (open symbols: HPS lighting, closed symbols: control lighting) with three plant densities in experiment 5 and 6 and three long day (LD) periods in experiment 7. Vertical bars indicate standard errors of mean measured TDM.

DISCUSSION

The fitted expolinear growth equation as a function of incident PAR integral ($EXPO_{PAR}$) described periodically measured TDM significantly better than the equation as a function of time ($EXPO_{T}$), for all experiments particularly experiment 2 (data not shown). A similar approach of fitting empirical models has been used for describing TDM dynamics of lettuce, onion and red beet (Tei *et al.* 1996). Using equation [7], TDM dynamics as related to accumulated daily incident PAR integral were effectively described, and crop growth parameters were successfully estimated without significant correlations between parameters. Therefore treatment effects on estimated parameters could be unambiguously tested in this study.

Relative growth rate per incident PAR integral in the exponential growth phase (RGR_{PAR}) and light use efficiency in the linear growth phase of the crop (LUE) were effectively explained by hyperbolic relationships to averaged daily incident PAR (Fig. 3). It is worthwhile to compare LUE as estimated by $EXPO_{PAR}$ with LUE estimated by the slope of the linear relationship between accumulated light integral and accumulated dry mass production (LUE_{IN}). For the summer experiment, LUE estimated by $EXPO_{PAR}$ (3.6 g MJ^{-1}) in the present study was almost consistent with LUE_{IN} (3.4 g MJ^{-1}) in Chapter II-1. However, in the control treatment of experiment 2 in the present study, LUE estimated by $EXPO_{PAR}$ (6.7 g MJ^{-1}) (Table 5) was higher than LUE_{IN} (5.3 g MJ^{-1}). Based on the overall relation between LUE and daily incident PAR in this study and evidence of variation in LUE in a range of incident PAR of 2-5 MJ m^{-2} d^{-1} for cauliflower (Kage *et al.* 2001b), linear regression may underestimate LUE_{IN} at closed canopy, when the daily light integral drastically decreases such as in experiment 2 (Table 2). When daily incident PAR drastically increases such as in experiment 1, LUE_{IN} may be overestimated Therefore LUE can have non-linear relationships with intercepted PAR integral and accumulated dry mass production when daily light integral systematically varies during the crop growth period (Table 2).

Because of the hyperbolic relations of RGR_{PAR} and LUE to daily incident PAR integral, maximum relative growth rate (RGR_{max}) and maximum crop growth rate (C_{max}) have a rectangular hyperbolic relation to daily incident PAR. A similar response of RGR to daily incident PAR was found for young tomato plants, cucumber and sweet pepper (Nilwik, 1981; Bruggink and Heuvelink, 1987; Bruggink, 1992; Challa *et al.*, 1994a). From those studies, it was concluded that variation in RGR was mainly due to variation in LAR. Moreover, based on results of the present study and work by other authors (Challa and Schapendonk, 1984; Karlsson *et al.*, 1987; Cockshull *et al.*, 1992; Olesen and Grevsen, 1997; Kage et al, 2001b), it can be concluded that crop growth rate is dependent on daily incident PAR and not proportional to light. The saturation response to incident PAR of maximum crop growth rate at closed canopy is to be expected, as light saturation of photosynthesis at leaf level is reflected at crop level. Furthermore, at increased light level in summer the fraction of direct light is higher, but used less efficiently compared to winter season's diffuse radiation (Gijzen, 1992). Moreover, at low daily PAR integral in low light regions, the role of maintenance respiration (R_m) relative to crop gross assimilation rate ($P_{gc,d}$) should be considered (Heuvelink *et al.*, 2002). R_m is not affected by assimilation light (Heuvelink *et al.*, 2002). If R_m uses a large part (≥ 50 %) of $P_{gc,d}$, a proportional increase in $P_{gc,d}$ will result in a more than proportional increase in growth, which is proportional to $P_{gc,d}$ minus R_m (Heuvelink *et al.*, 2002). Cockshull *et al.*, (1992) found for tomato crops that loss of dry mass was less than relative loss of light by shading. In the present study, a similar response to reduced light level by shading screens was found in the summer experiments (Fig. 2). This response could be due to improved LUE when shading reduces daily light integral.

Based on the rectangular hyperbolic relation to daily incident PAR, crop growth rate can be used to simulate dry mass production of year-round cut chrysanthemum crops. Although many authors have found effects of temperature and CO_2 concentration on crop growth, the model developed in the present study is a function of light only. In addition, this model assumes that the light compensation point is zero. According to Penning de Vries and Van Laar (1982), it may be assumed that maintenance respiration equals 1.5 % of dry mass per day. When LAR and LUE considered as the value of LAR_0 and LUE_0 in the present study, light compensation point calculated as 0.08 MJ m^{-2} d^{-1} (Bruggink and Heuvelink, 1987). Because this value is negligible compared to daily incident PAR integral in the present study, the model assumption of a light compensation point of zero appears acceptable. Model validation using independent experiments was satisfactory, as the model effectively simulated dry-mass production using measured LAI, initial dry mass and daily incident PAR integral as input data. The only overestimation of dry-mass production occurred when the model was applied to the crop grown at lower temperature and lower daily incident PAR (Expt. 5). This discrepancy may be due to erratic generalisation of LUE through extrapolation of the hyperbolic relation in the lower light range, particularly as LUE varied largely in this range (Expt. 2). In addition, it may be due to possible variation in the light extinction coefficient between seasons or during the crop growth period.

Equation [9] may be used as a simple method for calculating dry-mass production under the assumption that LAR is constant throughout crop growth. Under the same assumption, the growth rate of LAI may be simulated by the variation in crop growth rate. In fact, results of simulating TDM assuming a constant LAR were not different from simulating TDM with input of LAI (data not shown). LAR is strongly correlated to light as well as crop growth stage, due to the variation in SLA_n and dry matter partitioning into leaves. Dry mass partitioning into leaves has been found to greatly vary with plant dry mass in flowering chrysanthemum (Hughes and Cockshull, 1972), whereas it was shown to remain almost constant under large variation in temperature and daily light integral in vegetatively grown chrysanthemum (Acock *et al.*, 1979). Furthermore, SLA_n is strongly correlated with light and temperature (Acock *et al.*, 1979). Prediction of LAI is a crucial subject in crop growth modelling, as the accurate estimation of crop growth rate depends on it. Further research on leaf area development in cut chrysanthemum is required to enable development of an LAI model for this crop.

Given these considerations, the expolinear growth equation proved to be a useful tool for analysing measured TDM of cut chrysanthemum. In the present work cut chrysanthemum was harvested before senescence and was measured in terms of total plant dry mass. Hence, growth components of relative growth rate and crop growth rate could easily be assessed by fitting the equation to periodically measured TDM under constant light conditions during crop growth. However, if systematic variation in environmental factors occurs, growth parameters may be estimated using environmental time as independent variable.

CONCLUSIONS

In this study LUE was successfully modelled by fitting an expolinear growth equation as a function of incident PAR integral to periodic measured TDM. Model coefficients were related to relative growth rate per incident PAR integral in the exponential growth phase, and to LUE during the linear growth phase at closed canopy. Based on generalisation of LUE, maximum crop growth rate as a function of daily incident PAR could be modelled for cut chrysanthemum. This is a significant result, considering that previous studies on crop growth rate are mostly limited to theoretical analysis. Furthermore, this study provides a first thorough study of maximum crop growth of cut chrysanthemum based on experimental evidence. Therefore the collected data and presented modelling approach may serve as a reference in the field of crop growth models for cut chrysanthemum.

III. LEAF AREA DEVELOPMENT

SIMULATION OF LEAF AREA DEVELOPMENT BASED ON DRY MATTER PARTITIONING AND SPECIFIC LEAF AREA FOR CUT CHRYSANTHEMUM

Lee JH, Heuvelink E. Simulation of leaf area development based on dry matter partitioning and specific leaf area for cut chrysanthemum. Annals of Botany. (in press)

ABSTRACT

This work aims at predicting time courses of leaf area index (LAI) based on dry matter partitioning into the leaves and on specific leaf area of newly-formed leaf biomass (SLA_n) for year-round cut chrysanthemum. In five greenhouse experiments, each consisting of several plant densities and planted throughout the year, periodic destructive measurements were conducted to develop empirical models for partitioning and SLA_n. Dry matter partitioning into the leaves, calculated as incremental leaf dry mass divided by incremental shoot dry mass between two destructive harvests, could be described accurately ($R^2 = 0.93$) by a Gompertz function of relative time R_t. R_t is 0 at planting date, 1 at the start of short-day and 2 at final harvest. SLA_n, calculated as the slope of a linear regression between periodic measurements of leaf dry mass (LDM) and LAI, showed a significant linear increase with the inverse of the daily incident photosynthetic active radiation (incident PAR, MJ m^{-2} d^{-1}), averaged over the whole growing period, the average greenhouse temperature and plant density ($R^2 = 0.74$).

The models were validated for two independent experiments and with data from three commercial growers, each with four planting dates. Measured shoot dry mass increase, initial LAI and LDM, plant density, daily temperature and incident PAR were input in the model. Dynamics of LDM and LAI were predicted accurately by the model, although in the last part of the cultivation LAI was often overestimated. The slope of the linear regression of simulated against measured LDM varied between 0.95 and 1.09. For LAI this slope varied between 1.01 and 1.12. The models presented in this study are important for the development of a photosynthesis-driven crop growth model for cut chrysanthemum.

INTRODUCTION

Explanatory models have an open modular character, which enables integration of knowledge at the level of underlying processes and transfer to other crops as only a part of the modules may need adaptation rather than the complete model (Heuvelink, 1996). For greenhouse fruit vegetables, explanatory photosynthesis-driven models have been developed and thoroughly validated for the dynamics of dry mass production and dry mass partitioning by several workers (De Koning, 1994; Marcelis, 1994; Heuvelink, 1996). Contrary to vegetable crops, the number of photosynthesis-driven models for ornamental crops is very limited (Marcelis *et al.*, 1998).

The accuracy of photosynthesis-driven models greatly depends on an accurate prediction of leaf area, as intercepted light largely determines crop growth (Heuvelink, 1999). However, prediction of leaf area index (LAI) is still a weak part of these models. Two approaches of simulating plant leaf area development are predominantly used: (1) leaf area is described as a function of plant developmental stage, or (2) leaf area is predicted from simulated leaf dry mass (Marcelis *et al.*, 1998). The former approach is often inaccurate for greenhouse crops, because of a large fluctuation in radiation (almost year around cultivation), whereas leaf area development is often strongly influenced by radiation (Marcelis *et al.*, 1998). Simulation of leaf area based on simulated leaf dry mass and specific leaf area (SLA) is a more flexible approach and it has been applied for several crops, e.g. lettuce (Van Henten, 1994), tomato (Heuvelink 1999) and rose (Lieth and Pasian, 1991). A module for partitioning to the leaves and a module predicting SLA are needed for prediction of LAI dynamics in this way. In such an approach, SLA is assumed to be constant, or simulated as a function of plant age, physiological age, season, developmental stage and plant density or environmental conditions (Marcelis *et al.*, 1998). Gary *et al.* (1995) calculated leaf area mainly as a function of temperature and physiological age. These authors distinguished between storage and structural leaf dry mass and allowed structural SLA to vary between a minimum (full satisfaction of growth demand) and a maximum (minimum leaf thickness) value. This may be a promising way for the mechanistic simulation of SLA and thus leaf area expansion; however, in this approach a lot of parameters have to be estimated and Gary *et al.* (1995) did not validate this part of their model.

In contrast to a tomato crop, which showed a constant partitioning to the leaves as a fraction of the total growth of the vegetative parts (Heuvelink, 1999), for chrysanthemum this fraction was constant during the vegetative phase only (Acock *et al.*, 1979). Partitioning to the leaves strongly declined as fraction of total plant growth and total vegetative growth during the generative phase of chrysanthemum (Hughes and

Cockshull, 1971; Karlsson and Heins, 1992). SLA of new leaf biomass (SLA_n, increase of LAI divided by increase of leaf mass) for chrysanthemum has been described as a function of average daily radiation integral and temperature by Acock *et al.* (1979). However, for chrysanthemum, to the best of our knowledge, no attempt has been made to predict LAI during growth, although it looks promising to do this based on dry matter partitioning into the leaves and SLA_n based on Acock *et al.* (1979). Such a module for prediction of LAI would strongly contribute to the applicability of photosynthesis-driven crop growth models for cut chrysanthemum (Heuvelink *et al.*, 2001). Unfortunately, there is not only a lack of quantitative data on dry matter partitioning into the leaves and SLA_n throughout the growing period of cut chrysanthemum, but also the empirical module for SLA_n (Acock *et al.*, 1979) is based on measurements in the vegetative phase and at high LAI only.

In this study we aim at the prediction of LAI development for cut chrysanthemum based on dry matter partitioning into the leaves and SLA_n. An accurate prediction of dry matter partitioning into the leaves and SLA_n is needed, as both have a strong positive feedback on LAI and total biomass production (e.g. Heuvelink, 1999). Five greenhouse experiments were conducted with different planting dates combined with several plant densities. These experiments were used for determining the general pattern of dry mass partitioning towards the leaves, calibrating an existing empirical module for SLA_n (Acock *et al.*, 1979) and for the development of a new module predicting SLA_n. Moreover, the model for LAI prediction is validated with two independent experiments and with several data collected from commercial growers.

MATERIALS AND METHODS

GENERAL EXPERIMENTAL SET UP

Seven experiments were conducted in greenhouse compartments (12 m × 12.8 m) of a multispan Venlo-type glasshouse at Wageningen University, The Netherlands (lat. 52 °N) in different seasons in 1999 and 2000 (Table 1). Block-rooted cuttings of cut chrysanthemum (*Chrysanthemum*, Indicum group), cultivar Reagan Improved (CBA, Aalsmeer, The Netherlands) were obtained from a commercial propagator. Crops were planted on four or eight parallel soil beds (1.125 m × 10.25 m per bed, a border soil bed was always present on both sides of the experimental soil beds) at three plant densities

TABLE 1. Basic information on seven greenhouse experiments with cut chrysanthemum 'Reagan Improved' for development (D), calibration (C) and validation (V) of the models. Dates are expressed as day of year (day 1 = 1 January). N is number of destructive measurements per treatment.

Expt	Year	Planting day	Number of long-days	Number of short-days	End day	Plant density (pl. m^{-2})	N
1	2000	12	21	58	91	32,48,64	14
2	1999	29	17	56	102	32,48,64	8
3	1999	273	21	60	354	32,48,64	13
4	1999	126	22	53	201	32,48,64	9
5	2000	160	21	55	236	32,64	14
6	1999	22	22	56	102	32,48,64	8
7	2000	250-264	7-21	63	334	64	12

Expt	Global radiation[a] (MJ m^{-2} d^{-1})	Temperature[b] (°C)	$[CO_2]$[c] (μmol mol^{-1})	Expt for
1	2-7	21.0	415	D,C
2	4-9	18.7	447	D,C
3	6-2	19.2	432	D,C
4	17-19	21.4	407	D,C
5	22-15	22.1	349	D,C
6	4-9	18.7	447	V
7	8-2	19.8	407	V

[a] Average over first two weeks of cultivation and last two weeks of cultivation.
[b] 24 h average greenhouse temperature, averaged over the whole growing period.
[c] Between 10:00 and 16:00 hours inside greenhouse and averaged over the whole growing period.

(32, 48 or 64 plants m^{-2}) in two or three compartments. Five experiments were used for developing and calibrating the models for dry matter partitioning into leaves and SLA_n and two experiments were used for model validation (Table 1).

The general crop management has been described previously (Lee *et al.*, 2002). Experiments were conducted in two (Expts 1, 3 and 7) or three (Expts 2, 4, 5 and 6) compartments with three plant densities except for Expt 7 (Table 1). Expts 2, 3 and 4 in this study are the same as Expts 2, 6 and 4 described by Lee *et al.* (2002). Expt 1 was conducted parallel to Expt 1 of Lee *et al.* (2002); however, in two other greenhouse compartments heated to a higher greenhouse temperature of 21 °C. In Expt 5 the crop was planted at 32, 64 and 80 plants m^{-2}, but measurements at 80 plants m^{-2} were not used so as to keep plant densities the same for all experiments. In Expt 6 each compartment half received supplementary lighting, provided by either incandescent lamps (4.8 ± 0.8 μmol m^{-2} s^{-1}) or high-pressure sodium lamps (HPS, 39.6 ± 0.5 μmol m^{-2} s^{-1}, SON-T 400W, Philips, The Netherlands). In Expt 7 three planting dates, with one-week intervals, were applied to obtain 3, 2 or 1 week of long-day (LD) period. The crop was planted at 64 plants m^{-2} and received supplementary assimilation light (HPS, 57.6 ± 0.8 $\mu mol\ m^{-2}\ s^{-1}$).

LD was given at 16 h for 17-22 d after planting (Expts 2 and 6) and at 19 h for 7-21 d (Expts 1, 3 and 7) by incandescent lamps or HPS lamps and natural day length (about 15 h) was applied in Expt 4 and 5 for 21-22 d after planting (Table 1). Short day (SD) was given at 10 h (Expts 2 and 6) or at 11 h (Expts 1, 3, 4, 5 and 7) using a black out screen until the end of an experiment. Lamps were continuously turned on during day hours of the LD and SD period except for Expt 7, where the lamps were turned on at less than 150 W m^{-2} and turned off at more than 250 W m^{-2} global radiation outside the greenhouse.

GREENHOUSE CLIMATE

Greenhouse temperature set point for heating was 18 °C for day and 19 °C for night except for the Expt 1, where day/night temperature set points were 20 °C/21 °C. Set-point temperature for ventilation was always 1 °C higher than for heating. Measuring and recording of greenhouse climate data has been described previously (Lee *et al.*, 2002). CO_2 concentration in each compartment was maintained between 350 and 400 $\mu mol\ mol^{-1}$ by enriching with pure CO_2. Average daily greenhouse temperature (averaged over 24 h) and CO_2 concentration (averaged between 10:00-16:00) and daily global radiation outside are presented in Table 1.

Daily photosynthetic active radiation inside the greenhouse compartment (incident PAR, MJ $m^{-2}\ d^{-1}$) was calculated according to Lee *et al.* (2002), applying a greenhouse transmisivity for diffuse radiation of 0.49, measured on a cloudy day. Supplementary light (assumed to be 100 % diffuse) and light reduction by blackout screens in the SD period were taken into account in the calculation of daily incident PAR.

PLANT MEASUREMENTS

Destructive measurements were carried out every 3 to 12 days until final harvest in all experiments. Samples were taken from 5 or 6 plants per experimental plot, excluding border plants in two rows on each side of a bed. Total leaf area (LI-COR Model 3100) and fresh and dry (105 °C for 14 h in a ventilated oven) mass of leaves (including petioles), stems and flowers were measured. No measurements on roots were conducted.

DRY MATTER PARTITIONING INTO THE LEAVES

The fraction of shoot dry mass partitioned to the leaves was calculated as the increment of leaf dry mass divided by the increment of shoot dry mass between two adjacent destructive measurements and negative values were assumed to be zero (Kropff and Van Laar, 1993). The relationship between this fraction and relative time (R_t) (Karlsson and Heins, 1992) was described with a Gompertz curve:

$$F = C \cdot \exp(-e^{[-B \cdot (R_t - M)]}) \qquad (1)$$

where F is the fraction of dry mass partitioned to the leaves, C represents the maximum fraction, B represents the steepness and direction of the curve and M represents R_t for the inflection point of the curve. For $B > 0$, the value of F will increase from zero to C with increasing R_t, whereas for $B < 0$ F decreases from C to zero. R_t was scaled from 0 to 2: R_t is 0 at planting date, R_t is 1 at the start of SD and 2 at final harvest and R_t in between 0-1 and 1-2 is obtained by linear interpolation of days after planting or start of SD. Parameters in Eqn. 1 were determined by the non-linear fitting procedure in SPSS software package (version 10, SPSS company, Chicago, USA), applied to all partitioning data from Expts 1 to 5.

SPECIFIC LEAF AREA OF NEW LEAVES

Specific leaf area of new leaves (SLA_n, $m^2\ g^{-1}$) is difficult to derive for each interval between two destructive measurements and hence the slope of the linear relationship between leaf dry mass ($g\ m^{-2}$) and LAI ($m^2\ m^{-2}$) was used for estimating SLA_n (Kropff and Van Laar, 1993). This implies the assumption of a constant SLA_n during each cultivation of chrysanthemum. An existing empirical model of SLA_A (Eqn. 2) of new leaves (Acock *et al.*, 1979) was validated with estimated SLA_n:

$$SLA_A = a + b \cdot T + c / I \qquad (2)$$

where I represents average daily incident photosynthetic active radiation (400-700 nm; $MJ\ m^{-2}\ d^{-1}$) and T average greenhouse temperature (°C), both averaged over the whole growing period. Regression coefficients a, b and c, have been estimated by Acock *et al.* (1979) as 5.23 $m^2\ kg^{-1}$, 0.617 $m^2\ kg^{-1}\ °C^{-1}$ and 43.74 $m^2\ kg^{-1}\ MJ\ m^{-2}\ d^{-1}$, respectively. As conditions in the present experiments, including the cultivar, were quite different from those of Acock *et al.* (1979) we also calibrated the regression parameters in Eqn. 2 using the non-linear fitting procedure in SPSS. Furthermore, SLA_n was predicted according to Eqn. 2, but extended with a linear term for plant density and with parameters calibrated on the SLA_n values from Expts. 1 to 5.

TABLE 2. Basic information on the commercially-grown crops used for model validation. Dates are expressed as day of year (day 1 = 1 January). For each crop 4 destructive measurements were conducted in 2001.

Season	Grower[a]	Cultivar[b]	Planting day	Number of long-days	Number of short-days	End day	Plant density (Pl. m^{-2})
Winter	1	S	31	15	55	101	57
	2	W	364	28	57	82	40
	3	W	9	28	50	87	44
Spring	1	S	106	10	55	171	62
	2	W	90	16	50	156	60
	3	W	92	10	48	150	58
Summer	1	S	171	13	55	239	60
	2	W	171	13	58	242	55
	3	W	153	11	54	218	58
Autumn	1	S	239	15	62	316	53
	2	W	250	24	50	324	48
	3	W	244	20	55	319	45

Season	Grower[a]	Global radiation[c] (MJ m^{-2} d^{-1})	Temperature[d] (°C)	[CO$_2$][e] (µmol mol^{-1})
Winter	1	8-11	20.3	1241
	2	3-6	18.6	957
	3	2-5	18.9	1065
Spring	1	15-22	21.7	526
	2	11-20	20.4	405
	3	8-17	21.1	544
Summer	1	23-16	23.0	438
	2	23-16	22.5	420
	3	21-20	23.3	432
Autumn	1	10-3	20.6	546
	2	10-3	20.1	412
	3	11-3	20.4	380

[a] Grower 1 applied supplementary lighting (high pressure sodium lamps; 52.4 µmol m^{-2} s^{-1}) for 293 h during LD period and 221 h during SD period for winter crop, for 79 h only during LD period in spring crop and for 150 h only during SD period in Autumn. Other growers used incandescent lamps with cyclic lighting during LD period for winter crops.

[b] S = Reagan Elite Sunny, W = Reagan Elite White.

[c] Average over first two weeks of cultivation and last two weeks of cultivation.

[d] 24h average greenhouse temperature, averaged over the whole growing period.

[e] Between 10:00 and 16:00 hours inside greenhouse and averaged over the whole growing period.

VALIDATION OF THE MODELS

Periodic measurements of total dry mass (TDM, g m^{-2}) from independent experiments (Expts 6 and 7 in Table 1) and from crops of commercial growers (Table 2) were fitted with a cubic spline function by Prism® (GraphPad Software Inc, San Diego, USA) in order to obtain daily crop growth rates (g m^{-2} d^{-1}). Leaf growth rate (LGR, g m^{-2} d^{-1}), was calculated by multiplying the partitioning to the leaves calculated with Eqn. 1 with this daily crop growth rate. Leaf dry mass (LDM; g m^{-2}) resulted from initial LDM and the cumulative LGR. The daily increase in LAI (m^2 m^{-2} d^{-1}) was calculated by multiplying predicted LGR (g m^{-2} d^{-1}) with predicted SLA_n (m^{-2} g^{-1}). LAI resulted from initial LAI and the cumulative daily increase in LAI. Initial values were input to the model and originated from destructive measurements at planting date.

COMMERCIAL CROPS FOR VALIDATION

Plant measurements were conducted in four seasons in 2001, at three growers and measurements were conducted four times during a cultivation, i.e. at planting, at start of SD, halfway the SD period and at commercial harvest stage (anthesis). Commercial crops were planted at densities between 40 and 62 plants m^{-2} and were grown at temperatures between 18 and 23 °C and CO_2 concentrations varied between 380 and 1200 μmol mol^{-1} depending on the season (Table 2). The commercial greenhouses were Venlo-type glasshouses, however, with a much higher greenhouse transmissivity of 68-70 % (measured on a cloudy day) and much bigger cultivation area (more than 1 ha) compared to the compartments in which the experiments were conducted. Cultivars Reagan Elite White and Reagan Elite Sunny, used by the commercial growers, are very similar to "Reagan Improved" used in the experiments, however, the duration from start of SD to final harvest is about 4 days shorter than for "Reagan Improved" (CBA, Aalsmeer, The Netherlands).

RESULTS

MODEL DEVELOPMENT

One Gompertz curve (Eqn. 1) could well describe ($R^2 = 0.93$) the relationship between dry mass partitioned to the leaves and relative time for all five experiments (Fig. 1A). In the early growth stages, dry mass partitioned towards the leaves was 65 % of the total amount of the dry-mass produced and this fraction was (almost) zero at anthesis. No statistically significant interaction effect between experiment and plant density and no effect of plant density alone (Fig. 1B) on any of the three parameters of the Gompertz

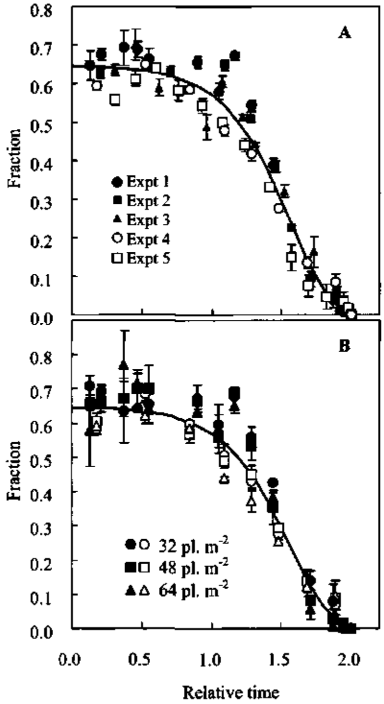

FIG. 1. Fraction of the dry mass partitioned to the leaves as a function of relative time (0, planting date; 1, start of SD; 2, commercial harvest date) for glasshouse-grown cut chrysanthemum planted in January (Expts 1 and 2), May or June (Expts 4 and 5), or September (Expt 3) (A; symbols represent values averaged over plant densities) and the effect of plant density on this fraction in Expts 1 (closed symbols) and 4 (open symbols) (B). Bars indicate standard error of means when larger than symbols. A Gompertz curve (Eqn 1) was fitted to the data (parameter values: $C = 0.649 \pm 0.008$, $B = -3.65 \pm 0.17$ and $M = 1.565 \pm 0.010$; $R^2 = 0.93$).

curve was observed. However, all three parameters were significantly affected by experiment (season). This effect can be seen in Figure 1A, as in general measured fractions in Expt 4 and 5 (open symbols) are below the curve, whereas fractions for Expts 1, 2 and 3 (closed symbols) are above the Gompertz curve.

A very close linear relationship ($R^2 > 0.98$) between measured LDM (g m^{-2}) and LAI during crop growth was observed in each of the five experiments. The slope of these lines was taken as an estimate for SLA_n. Applying Eqn. 2 with the parameter values determined by Acock *et al.* (1979) and the daily incident PAR and greenhouse

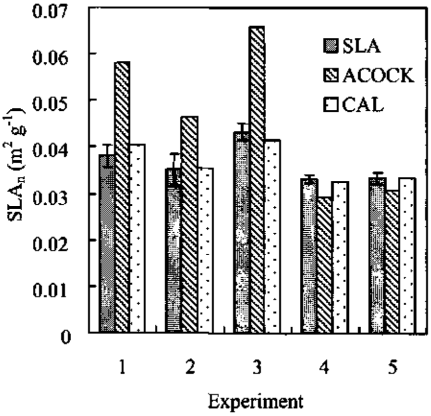

FIG. 2. Specific leaf area of new leaves (SLA_n) calculated as: the slope of a linear relationship between LDM (g m^{-2}) and LAI (m^2 m^{-2}) for five experiments (SLA); the values calculated with Eqn 2 using parameter values of Acock *et al.* (1979) (ACOCK; a = 5.23 m^2 kg^{-1}, b = 0.617 m^2 kg^{-1} $°C^{-1}$ and c = 43.74 m^2 kg^{-1} MJ m^{-2} d^{-1}); and values calculated with Eqn 2 with calibrated parameters (CAL; $a = 8.85 \pm 5.73$ m^2 kg^{-1}, $b = 0.961 \pm 0.615$ m^2 kg^{-1} $°C^{-1}$ and $c = 12.60 \pm 1.86$ m^2 kg^{-1} MJ m^{-2} d^{-1}). Averaged daily incident PAR and temperature over the whole growing period were input in Eqn 2. Vertical bars indicate standard error.

temperature averaged over the whole growing period for each experiment, resulted in a strong overestimation of SLA_n for Expts 1, 2 and 3 (Fig. 2). For Expts 4 and 5, predicted SLA_n was almost equal to the measured values. With Eqn. 2, after calibrating the regression parameters for the present experiments, a better prediction (Fig. 2) was obtained. The slope of the regression line (no intercept) relating predicted to measured SLA_n was 0.995 ($R^2 = 0.51$), indicating on average a perfect agreement, but with much scatter. By adding a term for plant density (P_d) to Eqn. 2, predictions were hardly changed, but scatter was much reduced (Eqn. 3; slope of regression line = 0.996; R^2 = 0.67). Therefore, SLA_n (m^2 kg^{-1}) was calculated by

$$SLA_n = a + b \cdot T + c / I + d \cdot P_d \qquad (3)$$

with $a = 3.99 \pm 8.59$, $b = 0.989 \pm 0.383$, $c=12.76 \pm 1.5$ and $d = 0.0873 \pm 0.0262$, and the variance accounted for being 74 %.

VALIDATION OF LEAF DRY-MASS PRODUCTION AND LAI

Observed leaf dry mass (LDM, g m^{-2}) production patterns in time in Expts 6 and 7 could be predicted well (Fig. 3), based on the partitioning function from figure 1. Moreover, simulated dynamics of LAI in time also agreed well with measured patterns, although some overestimation at high density occurred in Expt. 6 (Fig. 4). The slope of the linear relationship (no intercept) between measured and simulated LDM was 0.98 for Expt. 6 and 1.06 for Expt. 7, whereas for LAI these values were 1.12 for Expt. 6 and 1.01 for Expt. 7 (Table 3). Furthermore, by applying the simple relationship describing dry mass partitioning into the leaves as a function of relative time (Fig. 1) and the function describing SLA_n as function of daily incident PAR, temperature and plant density (Eqn. 3), observed and predicted LDM and LAI in 12 commercial crops (3 growers times 4 planting dates) showed very good agreement (Fig. 5 and Table 4).

TABLE 3. The coefficients of the linear relationship (without intercept) between measured and predicted leaf dry mass (LDM) and measured and predicted leaf area index (LAI) for two independent validation experiments.

	Experiment	Slope	S.E.	R^2
LDM	6	0.975	0.010	0.984
	7	1.063	0.007	0.994
LAI	6	1.119	0.012	0.983
	7	1.007	0.010	0.987

TABLE 4. The coefficients of the linear relationship (without intercepts) between measured and predicted values of leaf dry mass (LDM) and leaf area index (LAI) for the commercially-grown crops for model validation in 4 seasons.

	Season	Slope	S.E.	R^2
LDM	Winter	0.949	0.012	0.995
	Spring	1.019	0.023	0.986
	Summer	1.062	0.018	0.992
	Autumn	1.085	0.036	0.967
	Overall	1.037	0.013	0.981
LAI	Winter	1.010	0.016	0.992
	Spring	1.041	0.016	0.993
	Summer	1.097	0.024	0.987
	Autumn	1.112	0.038	0.965
	Overall	1.068	0.013	0.981

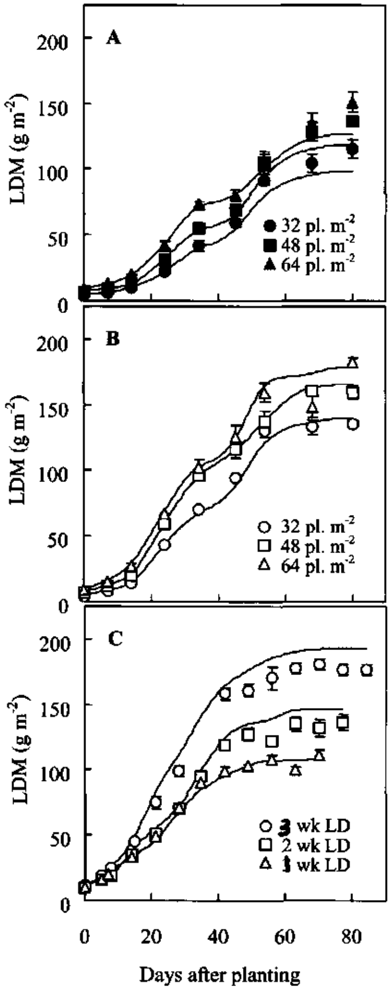

FIG. 3. Simulated dynamics of leaf dry mass accumulation (LDM) over time for two independent experiments (Expt 6, A and B; Expt 7, C). Crops were planted in winter (A and B) or autumn (C) at three plant densities (32, 48 or 64 plants m^{-2}) (A and B) or 3, 2 or 1 week LD (C) grown without (A) or with supplementary assimilation lamps (B, C). Bars indicate standard error of means when larger than symbols.

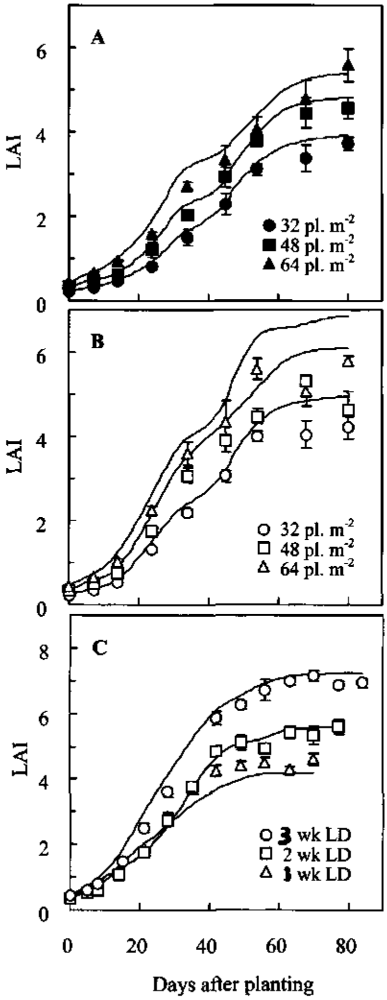

FIG.4 Simulated dynamics of leaf area index (LAI) in time for two independent experiments (Expt 6, A and B; Expt 7, C). See caption of Fig. 3 for further details.

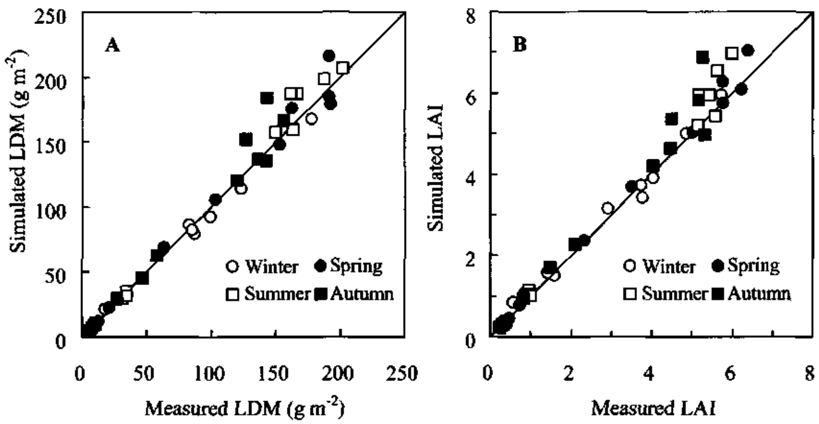

FIG. 5. The relationship between measured leaf dry mass (LDM) and simulated LDM (A) and between measured leaf area index (LAI) and simulated LAI (B), using independent data for model validation from 3 commercial growers during four seasons. Lines represent 1:1 relationship. Coefficients of the linear relationship for each season are presented in Table 4.

The slopes of the linear relationship between predicted and observed LDM varied between 0.95 and 1.09, whereas for LAI this slope varied between 1.01 and 1.11 (Table 4). Some overestimation of LDM and LAI was observed in summer and autumn, at the end of the cultivation (Fig. 5).

DISCUSSION

DRY-MASS PARTITIONING INTO THE LEAVES

The fraction of the dry mass partitioned to leaves has been reported to be constant during the early, vegetative phase (Hughes and Cockshull, 1971; Acock *et al.*, 1979), whereas this fraction decreases rapidly with flower developed in chrysanthemum (Hughes and Cockshull, 1971). Our results also show such a pattern, which could be described accurately as a function of relative time by a Gompertz curve (Fig. 1). A similar approach describing dry mass partitioning into the leaves was used by De Visser (1994) as a function of the developmental stage of onion and by Tei *et al.* (1996) as a function of the day after emergence for onion and red beet.

Only a few studies report on dry mass partitioning into leaves in chrysanthemum. Acock *et al.* (1979) observed almost no influence of temperature (10-30 °C) or daily incident PAR (1.9-9.2 MJ m^{-2} d^{-1}) on dry mass partitioning into the leaves for a vegetative crop. However, Hughes and Cockshull (1971) and Karlsson and Heins (1992) reported that the fraction of dry mass partitioned into leaves increased with decreased light intensity, whereas the effect of CO_2 concentration (Hughes and Cocksull, 1971) and day and night temperature (Karlsson and Heins, 1992) on this fraction seemed to be small.

In the present study, we found no significant effect of plant density on the partitioning to the leaves (Fig. 1B). This agrees with observations of Reuben and Mnzava (1982) in *Amaranthus cruentus*. However, an effect of experiment (season) on all three parameters of the Gompertz curve was observed (Fig. 1A). This seasonal effect was not taken into account as it was preferred to keep the model simple. Furthermore, our greenhouse experiments do not allow a sound separation of the seasonal effect in a light and a temperature component, which would be needed for a generalisation. Using a generalized pattern may lead to over- or underestimation of LDM and hence LAI. Overestimation of LAI was observed at the end of Expts 4 and 5 (data not shown). Since at the end of the cropping period LAI is high, resulting in interception of almost all light (closed canopy), overestimation of LAI hardly influences light interception and hence simulated crop growth rate. Therefore we accepted the general pattern for partitioning to the leaves, without adding specific effects of e.g. light, temperature or plant density which would have resulted in a more accurate prediction of LAI in the last weeks of cultivation. This general pattern of partitioning into the leaves was validated with independent experiments and data from several commercial growers. Even though there were large differences in crop management and environmental conditions between our experiments and the commercially-grown crops, predicted leaf growth based on measured shoot dry mass agreed very well with measured leaf growth (Fig. 5). Possible specific cultivar effects have not been investigated here. However, the ratio between LDM and shoot dry mass has been reported to vary between 0.59 and 0.77 for 15 cultivars at a shoot dry mass of 1 g (De Jong and Jansen, 1992). Hence, the parameters of the partitioning curve (Fig. 1) are likely to be cultivar specific.

It may be that partitioning into the leaves can be described even more accurately by determination of a real developmental stage x-axis for figure 1. So far, only a rather rough linear interpolation of relative time between planting date, start of SD and final harvest date was applied. The model for dry-mass partitioning into the leaves is incomplete, as it needs final harvest date (anthesis) as input. Time from start of SD until anthesis primarily is a cultivar characteristic. A study on predicting the time to flowering from the start of SD has been reported by Larson and Persson (1999). They discussed the lack of information from the breeders as one of the main problems, since at least 25 new chrysanthemum cultivars become available every year. For known cultivars, one can also apply reference schedules, i.e. planting date, number of long days, expected final harvest date (e.g. Roelofs *et al.*, 2001; Spaargaren, 2002) to obtain the time axis for partitioning.

SPECIFIC LEAF AREA

Specific leaf area of newly formed leaf dry mass (SLA_n) has been predicted as a linear function of temperature and the inverse of daily light integral (Eqn. 2) by Acock *et al.* (1979). However, Eqn. 2 with the parameter values of Acock *et al.* (1979), showed a large overestimation of SLA_n for the present crops (Expts 1, 2 and 3; Fig. 2). This discrepancy could be explained, since Acock *et al.* (1979) derived their equation for vegetative chrysanthemums only, under limited crop size (LAI > 2.2) and for relatively high incident PAR (1.9-9.2 MJ m^{-2} d^{-1}). The latter may explain why predictions for the summer experiments (Expt 4 and 5) were quite accurate as PAR levels were within the range of Acock *et al.* (1979). Since Acock *et al.* (1979) did use a different cultivar than the one used in the present experiments, this may also explain differences in SLA_n.

Eqn. 2 with calibrated parameters showed good agreement with measured SLA_n, and adding a positive linear relationship with plant density (Eqn. 3) improved prediction of SLA_n even more. The variation in SLA depends on the light intensity or season, which agrees with the literature (Hughes and Cockshull, 1972; Nederhoff, *et al.*, 1992; Heuvelink and Marcelis, 1996; Heuvelink, 1999). In addition, in chrysanthemum a small effect of temperature was found (Hughes and Cockshull, 1972). A positive effect of plant density on SLA was also found for other crops, e.g. potato (Vos, 1995), tomato (Heuvelink and Marcelis, 1996) and *Impatiens capensis* (Maliakal *et al.*, 1999), which might be explained by the lower average light level on the leaves at higher plant densities. Furthermore, SLA decreases with increasing CO_2 concentration (325-1500 μmol mol^{-1}; Hughes and Cockshull 1972), but CO_2 concentration is not represented in Eqn. 3. However, using Eqn. 1 and Eqn. 3 for simulating LAI, with total crop growth rate, initial LDM and intitial LAI, temperature, incident PAR and plant density as input, gave accurate predictions for crops grown in commercial greenhouses. Apparently CO_2 effects in SLA_n are not very large, as commercial crops received much higher CO_2 concentrations (especially in winter), compared to our experiments used for model development. The parameter values in Eqn. 3 are likely to be cultivar specific. De Jong and Jansen (1992) observed for 15 cut chrysanthemum cultivars a variation in the ratio between leaf area and LDM between 0.0344 and 0.0468 m^2 g^{-1} at a shoot dry mass of 1 g for plants grown in the same environmental conditions.

Many authors have attempted to predict LAI using a constant SLA, SLA as a function of developmental stage and day of year or sink/source relationship e.g for tomato or rose (Marcelis *et al.*, 1998). Often LAI is largely overestimated before canopy closure (Heuvelink 1999; Lieth and Pasian, 1991). In this study, prediction of LAI before canopy closure (LAI ≈ 3) agreed very well with measurements (Fig. 4 and 5B), using a simple approach based on dry mass partitioning into the leaves as a function of relative time and SLA_n as a function of daily incident PAR, temperature and plant density. This approach is valuable for photosynthesis-driven crop growth models, as their accuracy strongly depends on prediction of light interception.

CONCLUSIONS

Predicted LAI based on dry-mass partitioning into the leaves and SLA of new leaf biomass agreed well with measurements in validation experiments and for data from commercial growers. This approach, though demonstrated here for cut chrysanthemum, seems applicable for many other crops as well. Since no models for prediction of LAI dynamics in cut chrysanthemum were available, this work could be a valuable contribution towards a mechanistic photosynthesis-driven crop growth model for this crop. Heuvelink *et al.* (2001) introduced such a model, and the present results provide a possibility to adjust and improve this existing model.

IV. VALIDATION OF AN EXPLANATORY MODEL

DRY MASS PRODUCTION IN CUT CHRYSANTHEMUM: MODEL VALIDATION

Lee JH, Bakker M, Heuvelink E, Challa H. Dry mass production in cut chrysanthemum: model validation. *(Submitted)*

ABSTRACT

The objective of the present study was to validate a photosynthesis-driven model (CHRYSIMv1.0) for dry mass production in year-round cut chrysanthemum. Based on cultivation methods for this crop, options for management improvement include the duration of long and short day period and its daylength control and adjustment of supplementary lighting and plant density. Therefore, greenhouse experiments were conducted with different combinations of natural light, supplementary assimilation light, shading and plant densities, during different seasons. The model was applied to compute daily crop growth rate (g m^{-2}), based on daily crop gross assimilation rate (P_{gd}) and maintenance respiration (R_m). In the standard model, P_{gd} depends on crop leaf area and radiation, while R_m is a function of temperature and plant organ biomass. In the adjusted model (Heuvelink, 1995b) a reduction factor for R_m is included, which is a negative exponential function of simulated relative growth rate (RGR). Initial organ dry mass, leaf area index (LAI), dry matter partitioning into different plant organs, daily global radiation, and hourly greenhouse temperature and CO_2-concentration were model inputs.

Dynamics of aboveground total dry mass (TDM, g m^{-2}) were similar between measured and predicted values during the summer period (natural light), whereas the model largely underestimated TDM in winter and for (constantly) shaded conditions. Underestimation was more apparent at higher levels of shading, and occurred in both standard and adjusted models. Even when daily gross assimilation was converted to dry mass at an R_m equal to zero, model simulations still underestimated measured dry mass for the winter period and heavily shaded conditions. The discrepancies between measurement and simulation were summarised by light use efficiency (LUE, g MJ^{-1}). Simulated LUE at\closed canopy largely underestimated the measured LUE at lower light conditions, whereas for crops grown under natural light conditions in the summer

simulated and measured LUE were almost similar. Although LUE simulated by the adjusted model showed a strong improvement compared to LUE simulated by the standard model, it did not solve the large underestimation at lower light conditions. Therefore, the adjusted model was calibrated by changing the conversion efficiency from assimilates to dry mass, specific maintenance respiration coefficients and parameters in the leaf photosynthesis response curve, i.e. initial light use efficiency (ε) and maximum gross photosynthetic rate (P_{gmax}) on the basis of an experiment, which was conducted with shading screens and three plant densities in summer.

Changing conversion efficiency (inverse of assimilate requirement for production of dry mass) and specific maintenance coefficients was not satisfactory for heavily shaded condition, whereas the discrepancies between measured and simulated TDM were largely reduced in all experiments by applying a high value of ε combined with a low P_{gmax}. Although this calibration resulted in a satisfactory prediction of TDM, the calibrated value of ε was extremely high compared to literature values, and the calibrated value of P_{gmax} was relatively low. This suggests that optimisation of model parameters should not be restricted to ε and P_{gmax} but should also include other parameters such as the conversion efficiency and specific maintenance respiration coefficients. Moreover, such calibrated parameters should be supported by direct measurements for year-round cut chrysanthemum.

INTRODUCTION

Crop growth models are important tools to understand the complexity of crop growth under variable environmental conditions. In the greenhouse horticultural sector models have a wide range of potential applications, e.g. for research, planning, greenhouse climatic control, decision support and education (Challa, 1985, 1988, 1990; Jones *et al.*, 1991; Seginer, 1993; Heuvelink, 1995ab; Gary *et al.*, 1998). The application of crop growth models in horticulture has been thoroughly reviewed and discussed by Lentz (1998), Gary *et al.* (1998) and Marcelis *et al.* (1998).

In a previous study by Lee *et al.* (Chapter II-2), chrysanthemum crop growth rate throughout the year was effectively described by rectangular hyperbolic relations to daily incident photosynthetically active radiation (PAR, MJ m^{-2} d^{-1}). Although this regression model accurately predicted crop growth rate for the limited range of environmental conditions evaluated in the corresponding experiments (temperature,

CO_2-concentration), the model is not applicable to a wider range of crop growth conditions or to other crops. In contrast to descriptive (regression) models, explanatory models have a much larger potential to generalize crop growth for a wide range of greenhouse crops and growth conditions, due to their open modular structure (Heuvelink, 1996). Most explanatory crop models are photosynthesis-driven (Marcelis *et al.*, 1998). For vegetables and fruits many explanatory models have been developed and put into practice, but for the large group of ornamental crops only few models are available (De Koning, 1994; Marcelis, 1994; Heuvelink, 1995abc, 1999; Marcelis *et al.*, 1998; Marcelis and Gijzen, 1998).

TOMSIM (Bertin and Heuvelink, 1993; Heuvelink, 1995b), an explanatory photosynthesis-driven model based on SUCROS87 (Spitters *et al.*, 1989) and the greenhouse crop model of Gijzen (1992), has successfully been applied for greenhouse tomato crops. Since the photosynthesis module of TOMSIM is not specific to tomato (Heuvelink, 1996), it may be applied to other greenhouse crop species. TOMSIM computes daily crop growth rate (g m^{-2} d^{-1}) based on daily crop gross assimilation rate (P_{gd}, g CH_2O m^{-2} d^{-1}) and maintenance respiration (R_m, g CH_2O m^{-2} d^{-1}), converting assimilate to dry mass using a conversion efficiency factor. P_{gd} depends on crop leaf area and radiation, while R_m depends on temperature and plant organ biomass (in the standard model). The model has been developed, validated, and calibrated based on series of experiments during several years (Bertin and Heuvelink, 1993; Heuvelink, 1995b; 1999). According to Heuvelink (1995b), the standard model tends to underestimate crop growth rate when crop biomass is high and light conditions are low. Therefore, Heuvelink (1995b) proposed an adjusted model in which R_m is reduced at low relative growth rate.

The objective of the present work was to validate, calibrate and evaluate an explanatory model for the prediction of dry matter production in year-round cut chrysanthemum. Year-around cut chrysanthemum was chosen as a model crop for validating an existing photosynthesis-driven model (TOMSIM), because the production of cut chrysanthemum is one of the most intensive cultivation systems among floricultural greenhouse crops and the crop is successfully grown in winter season (Machin, 1996). Furthermore, optimising such dynamic and intensive cultivation systems is extremely difficult. A generic model can be a useful tool to understand and control these systems, as well as assist the grower in making complex decisions.

In the present work, model validation was based on greenhouse experiments investigating the growth of cut chrysanthemum at different planting dates (seasons), light intensities (fixed shading, assimilation lighting), plant densities and at somewhat different CO_2 concentration between experiments. In this study, model validation was limited to predicting dry mass production. Measured initial plant organ dry mass and leaf area, plant density and dry mass partitioning into leaves, stems, flowers and roots were used as model input. Measured hourly greenhouse temperature and CO_2-concentration, and daily global radiation were additional input data. Although it is possible to compute LAI dynamics by combining simulated dry matter partitioning into leaves with specific leaf area of new leaves (Chapter III), the module for predicting LAI was not included in this study in order to concentrate on possible errors in crop photosynthesis, R_m and dry mass conversion.

Using the standard version of the model TOMSIM (Heuvelink, 1995b), a discrepancy between measured and simulated dry mass production of year-round cut chrysanthemum may be expected at lower light conditions, because in winter dry mass production is much higher than for tomato while the duration of the cultivation periods was similar (Chapter II; Heuvelink, 1995ab). Since the adjusted version of TOMSIM, in which the effect of relative growth rate on maintenance respiration is included, has been simulate effectively the dynamics of crop growth for tomato dry mass production throughout the year, the adjusted version may provide better predictions for chrysanthemum dry mass production under low light conditions than the standard model. This hypothesis was tested in the present study. Where the adjusted model did not adequately predict chrysanthemum dry mass production, model parameters such as the conversion efficiency from assimilate to dry mass, maintenance respiration rate, and parameters of the leaf photosynthetic response curve, were calibrated to the experimental chrysanthemum data. Furthermore, model behavior was analyzed at low and high dry mass at closed canopy under different light intensity and two slightly different CO_2 concentrations. Calculated LUE at closed canopy from both standard and adjusted model was compared to a regression model to incident PAR based on measurement (Chapter II-2).

GENERAL MODEL DESCRIPTION

For the present study, a photosynthesis-driven crop growth model for cut chrysanthemum, CHRYSIMv1.0 was derived from the tomato model TOMSIM (Bertin and Heuvelink, 1993; Heuvelink, 1995b). Dry mass production in CHRYSIMv1.0 is modeled similarly as in TOMSIM. Daily crop growth rate may be computed using the standard model or the adjusted version (Heuvelink, 1995b). In the standard model, daily crop growth rate (*dW/dt*, g m^{-2} d^{-1}) is calculated as:

$$dW/dt = C_f \cdot (P_{gd} - R_m) \qquad [1]$$

where P_{gd} is daily crop gross assimilation rate (g CH_2O m^{-2} d^{-1}), R_m is daily maintenance respiration rate (g CH_2O m^{-2} d^{-1}) and C_f is an efficiency factor for the conversion of assimilate to dry mass. P_{gd} depends on canopy light absorption, and is mainly determined by crop leaf area and incoming radiation. P_{gd} is derived from integration of the instantaneous value of crop gross photosynthesis, which is computed by integrating leaf photosynthesis rates at various leaf layers over the entire canopy using Gaussian integration (Goudriaan, 1986; Gijzen, 1992; Goudriaan and Van Laar 1994). R_m depends on temperature and plant organ biomass with specific maintenance respiration coefficients for each plant organ. According to Heuvelink (1995b), the standard model tends to underestimate crop growth rate for tomato when the relative growth rate (RGR) is low (i.e. at low radiation and/or high biomass). Therefore, Heuvelink (1995b) proposed an adjusted form of TOMSIM in which maintenance respiration is reduced during periods of lower relative growth rate:

$$dW/dt = C_f \cdot (P_{gd} - R_m \cdot (1 - e^{-\beta \cdot RGR})) \qquad [2]$$

where β is a regression parameter (d) and RGR is relative growth rate (d^{-1}). Heuvelink (1995b) estimated a value of 33 for β, based on results of a winter experiment. The value of RGR is obtained by averaging simulated RGR over the five days directly preceding the present date, or, when less than five days preceded this date, by averaging over the actual number of preceding days (Heuvelink, 1995b).

Leaf gross photosynthesis is determined by a negative exponential light-response curve to absorbed PAR (Spitters, 1986; Gijzen, 1992; Goudriaan and Van Laar, 1994):

$$P_g = P_{g\max} \cdot \left(1 - e^{\left(-\varepsilon \cdot I_{abs} / P_{g\max}\right)}\right) \qquad [3]$$

where P_g is instantaneous leaf gross photosynthetic rate (mg CO_2 m^{-2} s^{-1}), P_{gmax} is maximum leaf gross photosynthetic rate at light saturation (mg CO_2 m^{-2} s^{-1}), ε is the leaf initial light use efficiency (mg CO_2 J^{-1}) and I_{abs} is the absorbed light by leaves (J m^{-2} s^{-1}). P_{gmax} and ε are affected by leaf temperature and CO_2 concentration (Appendix).

Incoming radiation is calculated from daily outside global radiation according to Spitters (1986), Bot (1983), Gijzen (1992) and Heuvelink *et al.* (1995). In this approach, transmissivity of direct radiation is predicted based on solar position, greenhouse roof angle, dimensions of the roof construction, transmissivity of the glass panes and orientation of the greenhouse. For the greenhouse described by Heuvelink *et al.* (1995) measured and simulated transmissivity for diffuse radiation was 0.62, whereas in the present study measured greenhouse transmissivity was 0.49 (averaged over 42 positions measured on a cloudy day). Therefore, instantaneous greenhouse transmissivity was calculated as in Heuvelink *et al.* (1995), divided by 0.62 and multiplied by 0.49. This simplified approach was followed because otherwise the transmission model (Bot, 1983) would have to be partially redesigned for the specific situation of a Venlo greenhouse with all kind of extra provisions such as screens etc.

Shading screens inside the greenhouse were open or closed depending on outside radiation intensity, while darkening screens were open or closed depending on time of day. The timing of these 'open' and 'closed' periods was taken into account in the model. Modules for controlling day length and supplementary assimilation light (switched on or off depending on time of day and outside radiation intensity) were added to the model. Supplementary assimilation light was assumed to be 100 % diffuse.

Contrary to TOMSIM, a time step of 30 minutes was used for calculating crop growth, in order to adequately deal with discontinuities caused by assimilation lighting and darkening screens.

MATERIALS AND METHODS

EXPERIMENTAL SET UP

Five greenhouse experiments with different combinations of natural light, supplementary assimilation light, shading and plant densities were conducted during two years using cut chrysanthemum (*Chrysanthemum*, Indicum group), cultivar Reagan Improved. Whereas detailed information on these experiments is provided in Chapter II-2, only a general outline of the experimental treatments is presented here. Experiments 1, 2, 3, 4 and 5 in the present paper are equivalent to experiments 1, 2, 7, 3, and 4, respectively, in Chapter II-2.

In experiments 1 and 2, chrysanthemum was grown at control lighting (CON, incandescent lighting for day length) and supplementary assimilation lighting (HPS, high pressure sodium lamps). Within each light treatment, crops were planted at three plant densities (32, 48 and 64 plants m^{-2}). In experiment 3, crops were exposed to a different number of long days (LDs). Three LD treatments were established by choosing three planting dates separated by one-week intervals. In all LD treatments, planting density was 64 plants m^{-2}. Experiments 4 and 5 were conducted at three light levels (100%, 66% or 43%). Within each light level, crops were planted at three plant densities (32, 48 and 64 plants m^{-2} in experiment 4, and 32, 64 and 80 plants m^{-2} in experiment 5).

In experiments 1-3, LDs of 19 h were implemented for 7-22 days after planting, using control lighting by incandescent lamps (CON, 4-6 μmol m^{-2} s^{-1}) or high-pressure sodium lamps (HPS, 42-57 μmol m^{-2} s^{-1}, SON-T 400W, Philips, The Netherlands). In experiments 4 and 5, LDs were established by natural light only (about 15 h light per day). Following the LD period, short days (SDs) of 11 h were implemented until the end of the experiments, using blackout screens. Final harvest occurred when flowering reached commercial stage (Chapters II-1, II-2), which could differ between treatments. In experiments 1 and 2, lamps were continuously turned on during day hours of LD and SD periods, whereas in experiment 3 lamps were controlled based on outside global radiation. In the latter case, lamps were turned on at less than 150 W m^{-2} outside global radiation and turned off at more than 250 W m^{-2} radiation intensity.

The day/night temperature set point was 21/20°C for experiment 1 and 18/19°C for all other experiments. Ventilation temperature was 1°C higher than the day/night temperature set point. CO_2-concentration, measured with a CO_2-analyser (URASG, Hartman & Braun, Germany), was maintained by pure CO_2-enrichment at 350 μmol mol^{-1} (experiments 1, 3, 4 and 5) or 400 μmol mol^{-1} (experiment 2). Global radiation (assessed with a Kipp and Zonen solarimeter, Delft, The Netherlands), greenhouse temperature (measured using a PT-500 element) and CO_2-concentration were recorded every 5 minutes by a commercial VitaCo climatic control system (Hoogendoorn, Vlaardingen, The Netherlands).

MODEL INPUT

Daily outside global radiation (MJ m^{-2} d^{-1}) is used as input in the model to generate the daily irradiance patterns based on the sine of the elevation of the sun above the horizon (Bertin and Heuvelink, 1993). Averaged hourly temperature (°C) and CO_2 concentration (μmol mol^{-1}) derived from the measured values in every 5 minutes was used as input. Initial plant organ dry mass per ground area (g m^{-2}), periodically measured leaf area index (LAI) and dry matter partitioning into leaves, stems, flowers and roots were input data for the model.

Fractions of total dry mass partitioned into leaves, stems, and flowers were calculated as the increment of individual plant organ dry mass divided by the increment of total dry mass between two successive destructive measurements (Kropff and Van Laar, 1993). On rare occasions negative increments were found, and then partitioning fraction was assumed to be zero. Calculated fractions were entered into the model, using those values as step functions for distributing assimilates to each plant organ. Based on experiments with plants grown in expanded clay grit, it was assumed that a constant fraction (0.1) of total crop growth was partitioned to the roots. Using averaged plant leaf area (m^2 $plant^{-1}$) from 5-6 plants, leaf area index values were obtained as the product of plant leaf area and number of plants m^{-2}. Daily LAI was obtained by linear interpolation between two successively measured values.

COMPARISON OF MODEL OUTPUT

In addition to comparing measured and simulated total dry mass production, measured and simulated crop light use efficiency (LUE, g MJ^{-1} of intercepted photosynthetically active radiation) were evaluated. The LUE concept has often been used for analysing crop growth (Bonhomme, 2000), due to its simplicity and supporting experimental evidence (Kage *et al.*, 2001ab). The linear relationship between intercepted daily light integral and total dry mass production is biased when daily light integral significantly changes during the crop growth period. Therefore, LUE was estimated by fitting an expolinear growth equation (Goudriaan and Monteith, 1990; Goudriaan and Van Laar, 1994) to simulated or measured TDM against accumulated daily incident PAR inside greenhouse from planting to final harvest (Chapter II-2).

CALIBRATION OF THE MODEL PARAMETERS

In addition to the reduction of maintenance respiration at low RGR (equation [2]), conversion efficiency, specific maintenance respiration coefficients and parameters of the leaf photosynthetic response curve were considered for model calibration (equations [2] and [3], Appendix).

$$P_g = COR_P \cdot P_{g\max} \cdot \left(1 - e^{\left(-COR_\varepsilon \varepsilon \cdot I_{abs} / COR_P \cdot P_{g\max} \right)} \right) \qquad [4]$$

where COR_P is a correction factor for P_{gmax} and COR_ε is a correction factor for ε.

ANALYSIS OF THE MODEL BEHAVIOUR

In order to analyse the general behaviour for the standard, adjusted and calibrated model the simulated LUE was compared with a reference LUE for a closed canopy derived from the experiments 1, 2, 4 and 5 (Chapter II-2). Comparing actual LUE values with simulated ones gives a narrow a view of model behaviour. A generalised LUE at closed canopy as a function of daily incident PAR were effectively described the dynamics of crop growth from planting to final harvest in year-round cut chrysanthemum as inputting measured LAI and daily incident PAR inside greenhouse (Chapter II-2). Therefore, the generalised LUE was used as a reference LUE to compare with simulated LUE from the simulated crop growth rate in this study. The reference LUE (LUE_R, g MJ^{-1}) showed a hyperbolic relation to daily incident PAR (I, MJ m^{-2} d^{-1}).

$$LUE_R = \frac{1}{0.1299 + 0.0397 \cdot I}, \quad R_2 = 0.66 \qquad [5]$$

Total crop growth rate (g m^{-2} d^{-1}) was simulated by the standard, adjusted, and calibrated models using fixed values for crop parameters, i.e. total dry mass, LAI, dry mass partitioning into plant organs and for day length (11 h as short day condition). The models set to simulate a daily total crop growth rate with fixed total dry mass and LAI at each day of a year. Fixed crop parameters entered into the model were TDM = 300 g m^{-2} or 600 g m^{-2} (root dry mass set to 10 % of TDM), LAI = 5, and fractions of partitioned dry mass = 0.5:0.5:0.0 or 0.0:0.5:0.5 for leaves: stem: flowers, with 10 % of total crop growth rate allocated to roots. The values of TDM and LAI were chosen as an approximation of measured TDM at closed canopy in this study and fractions of partitioned dry mass for leaves: stem: flowers were an approximation at the stage of flower initiation (0.5:0.5:0.0) or at the stage to final harvest (0.0:0.5:0.5) in this study. Daily global radiation data of selected months from the 1971-1980 weather records of De Bilt, The Netherlands (Breuer and Van de Braak, 1989) were used as model input. Furthermore, a temperature of 21.7 °C (averaged over five experiments) and a CO_2 concentration of 349 μmol mol^{-1} (average of experiment 5) or 415 μmol mol^{-1} (averaged over experiments 1-4) were set as constants in the model. The simulation period started at day 1 (1 January) and finished at day 365 (31 December).

Simulated LUE (g MJ^{-1}) was calculated as the ratio between simulated aboveground crop growth rate (g m^{-2} d^{-1}) divided by the product of a calculated daily incident PAR (MJ m^{-2} d^{-1}) from the model and the fraction of light intercepted (0.97) at LAI = 5. The reference LUE (LUE_R) was calculated according the equation [5] as inputting the daily incident PAR inside greenhouse from the model output.

RESULTS

MODEL VALIDATION WITH STANDARD AND ADJUSTED MODEL

There were large discrepancies between measured and simulated above ground total dry mass (TDM, g m^{-2}) in three different seasonal experiments using the standard model (Eqn.. 1) (Fig. 1 dashed lines). The standard model, in general, underestimated final TDM with 12 % (100 % light level in Expt. 5) upto 39 % (HPS in Expt. 2 and 43 % light level in Expt. 5). As mentioned before, reducing maintenance respiration (R_m) in dependence of the relative growth rate, using the adjusted model (Eqn. 2) resulted in increased total daily crop growth rate and hence it is not surprising that the results obtained with the adjusted model were better than with the standard model. Simulated TDM, however, did not reach the observed TDM except for the non-shaded crop in the summer experiment (Fig. 1, solid lines). In particular, TDM was relatively more underestimated with increasing shading in summer (Fig. 1B and Table 1). Furthermore, in Expts. 3 and 4 simulated TDM showed the same tendency as in Expts. 2 and 5 in different years (Table 1). When the regression parameter β in Eqn. (2) is set to 0, the simulated daily gross amount of gross photosynthesis (P_{gd}, g CHO_2 m^{-2} d^{-1}) is directly converted to crop growth ($R_m = 0$).

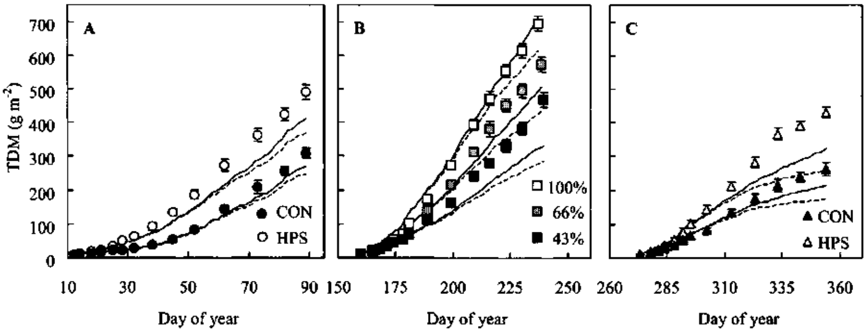

FIG. 1. Comparison between measured (symbols) and simulated (lines) total dry mass (TDM) for the crop growing from winter till spring (A, Expt. 1), in summer (B, Expt. 5) and from autumn till winter (C, Expt. 2) under natural light with incandescent light (CON), supplementary assimilation light (HPS) (A, C) and shading (B, 100 %: non shading, 66 %: 34 % shaded and 43 %: 57 % shaded by white shading screens above the crop). Vertical bars indicate standard error of means of measurements. ------ standard model, —— adjusted model.

TABLE 1. The coefficients of the linear relationship (without intercept) between measured and simulated total dry mass using the adjusted model in five experiments. SE is standard error of coefficients.

Experiments	Treatments[1]	Slope	SE	R^2
1	CON	0.886	0.008	0.994
	HPC	0.819	0.010	0.987
	Overall[2]	0.836	0.008	0.988
2	CON	0.857	0.015	0.968
	HPC	0.765	0.012	0.975
	Overall	0.790	0.010	0.967
3	3wk LD	0.802	0.011	0.993
	2wk LD	0.864	0.017	0.984
	1wk LD	0.922	0.016	0.989
	Overall	0.839	0.011	0.981
4	100%	1.023	0.014	0.989
	66%	0.878	0.016	0.979
	43%	0.746	0.011	0.985
5	100%	1.029	0.009	0.994
	66%	0.886	0.009	0.991
	43%	0.759	0.009	0.988

[1] Linear regression for all plant densities in each light condition.

[2] Overall coefficients of linear regression between all measured and simulated values

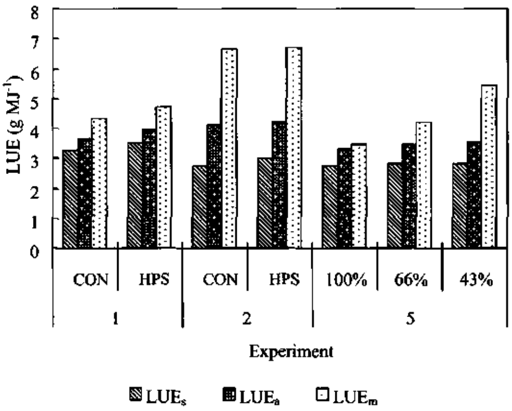

FIG 2. Light use efficiency (LUE, g MJ^{-1}) of the standard model (LUE$_s$), the adjusted model (LEU$_a$) and observed (LUE$_m$) at different light conditions in three experiments. See caption of Fig. 1 for further details.

Even with this theoretical assumption, however, TDM was underestimated in Expts. 2 and 3 and for the crop grown under heavy shading in Expts. 4 and 5, whereas TDM was overestimated for the crops grown without shading in Expts. 4 and 5 and in Expt. 1 (not shown). This proves that maintenance respiration alone cannot be responsible for the discrepancies observed and that other parameters also may need calibration.

Although the comparison of measured and simulated TDM over time (Fig. 1) is useful to evaluate the performance of the model, a comparison of measured and simulated LUE provides more detailed information for the analysis of the cause of the observed discrepancies. When comparing with both standard and adjusted models there were large discrepancies in LUE, particularly in Expt. 2 and under shading screens in Expt. 5 (Fig. 2), but not with the adjusted model for the crop grown without shading in Expt. 5 (Fig. 2). Furthermore, simulated LUE for Expt 5 was equal for both light levels, whereas the measured LUE increased with decreased light level (Fig. 2).

CALIBRATION OF THE MODEL

Experiment 5 was used to calibrate the adjusted model, because in this experiment there was a large variation in plant densities and light levels and furthermore there were frequent destructive measurements. The slope of the linear relationship without intercept between measured and simulated TDM defines the goodness of fit. In the ideal case it should attain the value 1. The slope was almost 1.0 at 100 % light, 0.89 at 66 % light, 0.76 at 43 % light without calibration of the adjusted model in Expt. 5 (Table 1).

To improve model performance the conversion efficiency from assimilate to dry mass (inverse of assimilate requirement; Appendix) and specific maintenance respiration coefficient were varied (Fig. 3). Changing assimilate requirement to obtain a good fit, no correction was needed with 100 % light, but a correction factor of 0.8 was needed for the 66 % light treatment and 0.6 for the 43 % light treatment (Fig. 3A). However, since the value of assimilate requirement is 1.37-1.49 g CH_2O g^{-1} of dry mass for different organs (Appendix), a correction factor of 0.6 would lead to the unlikely outcome that less assimilate would be needed than the amount produced, which is unlikely to occur. The correction factor for the specific maintenance respiration coefficients was 0.2 for the 66 % light treatment, whereas no satisfactory value was obtained for the 43 % light treatment (Fig. 3B). Because calibration of the model along these lines was not successful calibration was focused on the parameters of the photosynthesis light response curve of individual leaves (Eqn. 4).

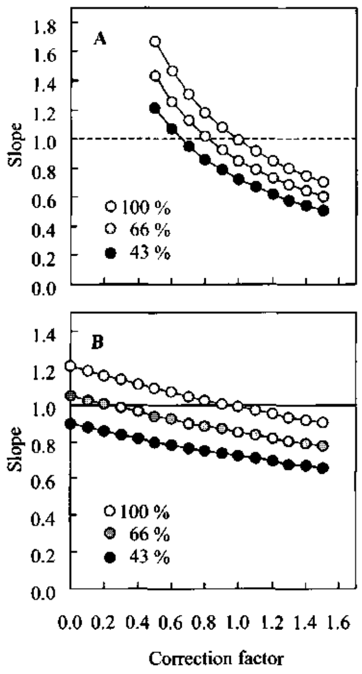

FIG 3. Effect of changing (through a multiplication factor varying from 0 – 1.5) assimilate requirement (A) and the specific maintenance respiration coefficient (B) on the slope of the linear relationship (no intercept) between measured and simulated (adjusted model) total dry mass at three different light levels for Expt. 5.

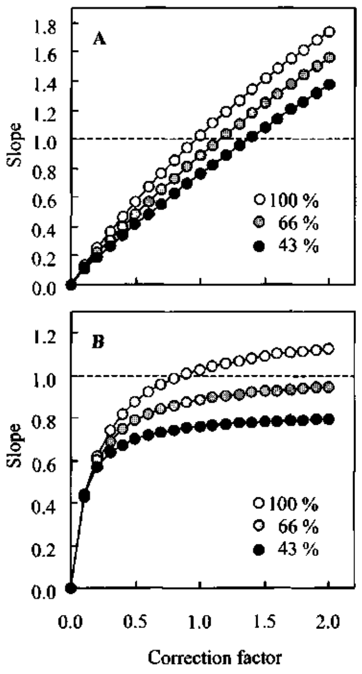

FIG 4. Effect of changing (through a multiplication factor varying from 0 – 2.0) ε (A) and P_{gmax} (B) on the slope of the linear relationship (no intercept) between measured and simulated (adjusted model) total dry mass at three different light levels for Expt. 5.

When changing only ε (through COR_ε), different correction factors were found at different light levels (Fig. 4A). COR_ε was 1.2 at 66 % light and 1.4 at 43 % light, but no correction was needed for the 100 % light treatment (Fig. 4A). When P_{gmax} was changed, the effect on the slope of linear relationship between measured and simulated dry mass production diminished with increasing COR_P (Fig. 4B).

For good fit of the model ε had to be increased and P_{gmax} had to be decreased. By iteration, a combination of COR_ε = 2.0 and COR_P = 0.29 for P_{gmax} proved to satisfactorily describe the results of Expt. 5 (Fig. 5), corresponding to the simulated ε = 25 µg CO_2 J^{-1} and P_{gmax} = 359 µg CO_2 m^{-2} s^{-1} and those are lower than the values in the other experiments (Table 2). The variations in ε and P_{gmax} through experiments were mainly caused by different CO_2 concentrations; the effect of temperature on ε and P_{gmax} in the range of 19-22 °C is small (Appendix).

The calibrated model was applied to the other experiments (Expts. 1-4). Compared to the adjusted model the calibrated model was far better able to describe the dynamics of dry mass production at different plant densities and light conditions (Figs. 1, 6 and 7).

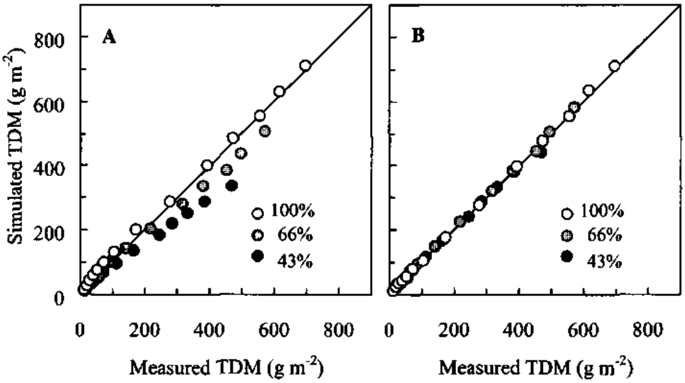

FIG 5. Measured versus simulated total dry mass (TDM) at three different light levels in Expt 5. (A) adjusted model (B) calibrated model.

TABLE 2. Calibrated initial light use efficiency (ε) (correction factor = 2) and maximum leaf photosynthesis (P_{gmax}) (correction factor = 0.29) in leaf photosynthesis light response curve (Eqn. 3 in text) based on average greenhouse temperature (24 h) and CO_2 concentration (between 10:00-16:00).

	Experiment				
	1	2	3	4	5
Temperature (°C)	21.0	19.2	19.8	21.4	22.1
CO_2 (μmol mol^{-1})	415.0	432.0	407.0	407.0	349.0
ε (μg CO_2 J^{-1})	26.4	27.2	26.6	26.2	24.9
P_{gmax} (μg CO_2 m^{-2} s^{-1})	429.8	452.1	424.2	423.0	358.6

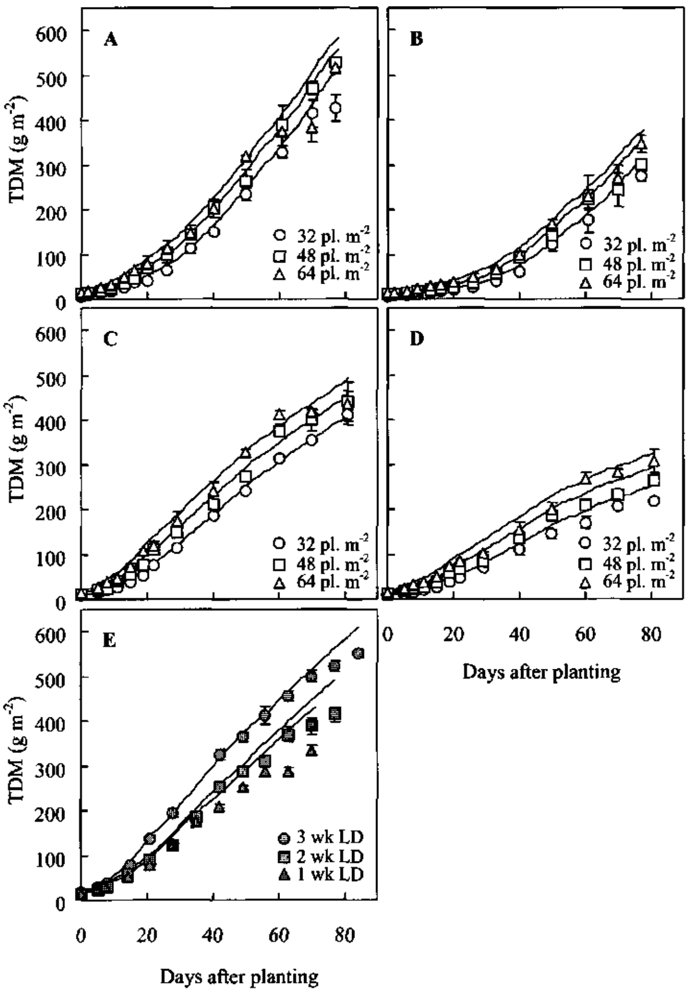

FIG 6. Dynamics of total dry mass (TDM) of measurements (symbols) and simulations according to the calibrated model (lines) for experiments 1 (A, B), 2 (C, D) and 3 (E), provided with a combination of natural light with supplementary assimilation light (HPS: A, C) and incandescent light (CON: B, D), at three plant densities and three different long-day periods for the crop grown at 64 plants m^{-2} (E).

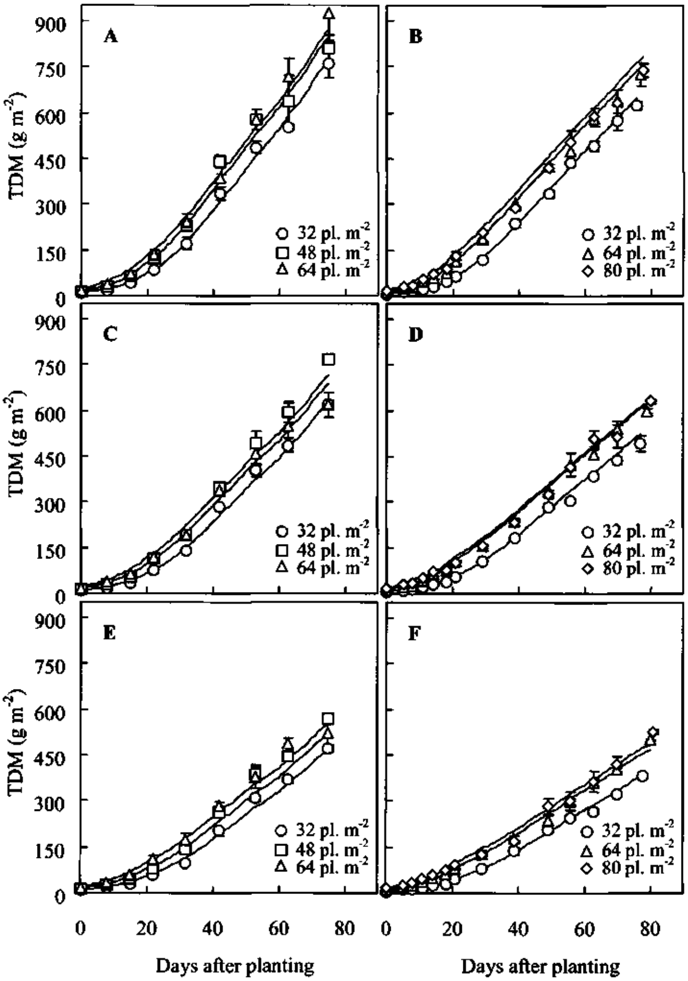

FIG 7. Dynamics of total dry mass (TDM) of measurements (symbols) and simulations according to the calibrated model (lines) for experiment 4 (A, C, E) and 5 (B, D, F) with the combination of 100 % (A, B), 66 % (C, D), and 43 % (E, F) light levels and three plant densities.

TABLE 3. The coefficients of the linear relationship (without intercept) between measured and simulated total dry mass using the calibrated adjusted model in five experiments. SE is standard error of coefficients.

Experiments	Treatments[1]	Slope	SE	R^2
1	CON	1.105	0.010	0.995
	HPC	1.084	0.013	0.988
	Overall[2]	1.090	0.009	0.990
2	CON	1.105	0.010	0.992
	HPC	1.022	0.010	0.991
	Overall	1.045	0.008	0.989
3	3wk LD	1.046	0.012	0.995
	2wk LD	1.120	0.016	0.993
	1wk LD	1.206	0.023	0.989
	Overall	1.093	0.013	0.986
4	100%	0.961	0.012	0.991
	66%	0.979	0.017	0.982
	43%	0.945	0.013	0.989
	Overall	0.964	0.008	0.988
5	100%	1.027	0.005	0.998
	66%	1.013	0.006	0.997
	43%	0.979	0.008	0.994
	Overall	1.013	0.004	0.996

[1] Linear regression for all plant densities in each light condition.

[2] Overall coefficients of linear regression between all measured and simulated values

The slope of the linear relation between measured and simulated TDM was between 0.96 and 1.09. However, the calibrated model overestimated measured TDM of the crop that received 1 week LD (Expt. 3), by as much as 21 % (Table 3).

ANALYSIS OF MODEL BEHAVIOUR

The performance of three different versions of the model, i.e. standard, adjusted and calibrated was compared with LUE_R values obtained from Eqn. (5). The comparison was made at fixed TDM 300 g m^{-2} (open symbols in Fig. 8) and 600 g m^{-2} (closed symbols in Fig. 8) assuming a closed canopy and CO_2 concentration of 349 μmol mol^{-1} (Fig. 8A) and 415 μmol mol^{-1} (Fig. 8B). LUE (g MJ^{-1}) was calculated as the ratio between simulated above ground crop growth rate (g m^{-2} d^{-1}) divided by the intercepted incident PAR at LAI = 5. Simulated crop growth rate was hardly changed by changing the fractions of dry mass partitioned between aboveground plant organs (not shown).

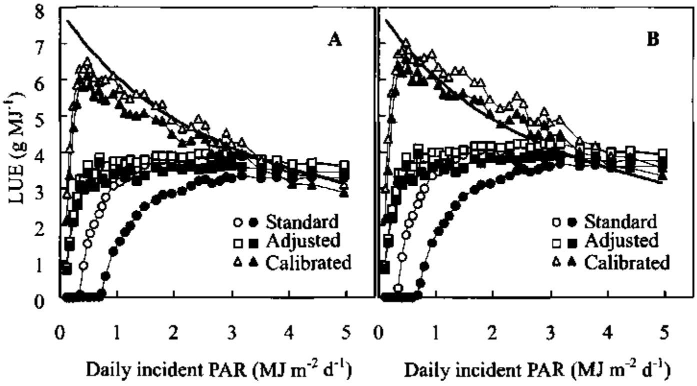

FIG 8. Light use efficiency (LUE g MJ^{-1}) according to the standard, the adjusted and the calibrated model with fixed total dry mass of 300 g m^{-2} (open symbols) and 600 g m^{-2} (closed symbols) at CO_2 concentration of 349 µmol mol^{-1} (A) and 415 µmol mol^{-1} (B). —— LUE_R (reference LUE).

Simulated LUE was similar for the three models at high light, independent of dry mass and CO_2 concentration (Fig. 8). The standard and the adjusted model, however, showed a large systematic underestimation of LUE at low light. The standard model was much more sensitive to dry mass than the adjusted and calibrated model (Fig. 8).

With the standard model growth was zero at daily light integral $\leq$ 0.26 MJ m^{-2} d^{-1} at 300 g m^{-2} of TDM (Fig. 8A), and $\leq$ 0.8 MJ m^{-2} d^{-1} at 600 g m^{-2} of TDM (Fig. 8). With the standard model there was often no growth at low light conditions prevailing at the end of the crop growth period in Expts. 2 and 3 and a too low crop growth rate with shading screens in summer experiments.

Taking the effect of RGR on R_m into account (Eqn. 2), LUE obtained with the adjusted model still deviated considerably from the reference LUE_R, in particular, at low light up to daily incident PAR of 2.0 MJ m^{-2} d^{-1} (Fig. 8). As consequence of that, simulated TDM was underestimated for the crop grown in winter and under shade screens in summer, whereas reasonable results were obtained with the non-shaded crop in summer (Fig. 1 and Table 1).

Changing ε resulted in a proportional change in LUE at all light regimes, whereas changing P_{gmax} resulted in asymmetric change in LUE at different light integrals. Combination of ε and P_{gmax}, therefore, will regulate the shape of the LUE response to incident PAR. After calibration of ε and P_{gmax} increasing LUE at low light regimes and diminishing LUE with increasing daily incident PAR was simulated, in accordance with LUE_R. Simulated LUE was increased by 10 % as CO_2 concentration increased by 19 % (Fig. 8). While the model was calibrated with only one experiment (Expt 5), the differences in TDM and CO_2 concentration between experiments could partly explain inconsistencies in the relationship between measured and simulated TDM.

DISCUSSION

The experimental data set represents conditions with largely differing light levels and associated differences in dry mass production (Fig. 1). Furthermore, temperature and CO_2 concentration were rather stable compared to daily global radiation through the crop growth period. These data are therefore very useful for model validation, when focus on radiation influences on crop growth.

In general the standard model underestimated dynamics of dry mass production, in particular at low light (Fig. 1). Similar problems under winter conditions, using the same leaf photosynthesis module, have been observed with rose (Kool and De Koning, 1995) and tomato (Heuvelink, 1995b). In contrast, the model overestimated dry mass production of rose in summer (Kool and De Koning, 1995), but underestimated dry mass production of tomato in summer (Heuvelink, 1995b). Overestimation of dry mass production in summer with rose has been explained by an overestimation of the leaf photosynthetic rate by the model (Kool and De Koning, 1995). Underestimation of dry mass production has been mainly attributed to an overestimation of maintenance respiration at high biomass under low light (Heuvelink, 1995b). In the standard model maintenance respiration is calculated by multiplying the dry mass of the plant parts with specific maintenance coefficients of individual organs that are only dependent on temperature. Hence maintenance respiration increases with plant mass. Many authors (Penning de Vries, 1975; McCree, 1982; Amthor, 1989; Gijzen, 1992), however, suggested that specific maintenance respiration coefficients also should depend on the metabolic activity of the crop. Therefore, Heuvelink (1995b) multiplied maintenance respiration with a relative growth rate dependent factor, mimicking the metabolic activity of the crop (Eqn. 2). In this way the dynamics of dry mass production of tomato could successfully be described for several seasonal experiments and grower's data sets (Heuvelink, 1995b). However, this adjusted model that worked well with tomato did not work well with chrysanthemum. It may be expected that the parameter β in Eqn. 2 would be dependent on crop species. However, if β would be much less than the current value (β = 33) the maintenance respiration would become almost zero at high biomass and low light. For example, simulated RGR at the end of Expt. 2 was 0.008 d^{-1} reducing maintenance respiration by 77 % in the adjusted model, compared to the standard model. Even when $\beta = 0$ and hence $R_m = 0$, the adjusted model underestimated TDM in Expt. 2 and 3 and the heavy shaded crops in Expts. 4 and 5, whereas the reverse was true in Expt. 1 and for the crop grown under 100 % and 66 % light in Expts. 4 and 5 (not shown). Underestimation of dry mass production in this study cannot only be explained by overestimation of maintenance respiration, but more likely underestimation of leaf photosynthetic rate at low light should play a role. Therefore calibration of β was not considered an option in this study.

Instead an analysis of the model behaviour was made by using LUE as a criterion. In Chapter II-2 a consistent description of LUE as a function of daily incident PAR inside greenhouse could be obtained for all experiments and treatments. This function was therefore used as a reference for comparison with different model configurations. It was observed that the discrepancy between reference and simulation was large at low daily light integral (Fig. 2). Therefore the leaf photosynthesis light response module was the first candidate for calibrating the adjusted model in this study. The parameters of the leaf photosynthesis light response curve are the initial light use efficiency (ε, mg CO_2 J^{-1}) and maximum leaf gross photosynthetic rate (P_{gmax}). Using one experiment (Expt 5) for calibration values for ε of 25 μg CO_2 J^{-1} and 359 μg CO_2 m^{-2} s^{-1} for P_{gmax} were obtained. The calibrated model described the dynamics of dry mass production for most experiments within 10 % discrepancy (Table 3 and Figs. 3, 5 and 6). The calibrated model could be considered suitable for prediction of dry mass production in cut chrysanthemum, especially if we were able to calibrate the model with more experiments.

However, ε and P_{gmax} represent crop physiological parameters that have not been measured directly in our experiments. The calibrated value of ε is much higher than the theoretical value of 17 μg CO_2 J^{-1} at high CO_2 concentration (Goudriaan and Van Laar, 1994) and a measured value of 9.9 μg CO_2 J^{-1} (Acock *et al.*, 1978a). Moreover, the calibrated values of P_{gmax} (Table 2) are much lower than the measured value of about 732 μg CO_2 m^{-2} s^{-1} at 400 μmol mol^{-1} and 20 °C (Acock *et al.*, 1978a).

There is a large discrepancy between calibrated, measured and theoretical values of ε, although ε is a stable parameter under different light and temperature conditions, whereas it varies with CO_2 concentration (Acock *et al.*, 1978ab; Warren Wilson *et al.*, 1992; Goudriaan and Van Laar, 1994; Kage *et al.*, 2001a).

These considerations, however, only will lead to lowering of the parameter ε and therefore do not contribute to the solution of the large underestimation of the dynamics of dry mass production under low light observed in this study. Alternatively, the standard or the adjusted model could be calibrated considering combinations of assimilate requirements, specific maintenance respiration coefficients and P_{gmax} without calibration of ε. When the assimilate requirement for all organs would be reduced by 10 %, overall crop growth in Expt 5 would increase by 9 %. The sensitivity of the model outcome to this parameter is comparable to that of ε with the adjusted model (Fig. 3A). When specific maintenance respiration was decreased by 10 % overall crop growth in Expt. 5 increased by 2 % at all light levels using the adjusted model (Fig. 3B). A combination of four parameters, ε and P_{gmax}, specific maintenance coefficients and assimilate requirements and perhaps other parameters could possibly provide a solution to improve the simulation results in this study. It was not feasible to optimise all parameters manually in this study. Moreover, none of these parameters has been measured experimentally in this study. Therefore, the parameter values of TOMSIM (Heuvelink, 1995b) were used, though they are not necessarily correct for chrysanthemum growing under low light.

Another possible source of error could be the estimation of light transmission by the greenhouse cover. Although the value of greenhouse transmissivity (Heuvelink *et al.*, 1995) was adjusted as a measured one in a cloudy day (0.49) in this study, this simplified approach may cause errors.

In our experiments only global radiation was measured and converted to photosynthetically active radiation (PAR) assuming a constant percentage of PAR (400-700nm) of 47 % for direct and diffuse radiation. In reality this percentage varies between 40 % for clear days to 60 % for very cloudy days and the monthly percentage PAR varied from 41 % in November and December to 49 % in July (Gijzen, 1992). Although the monthly percentage PAR in winter is lower than used in the model, the variation between clear and cloudy days was larger and this variation may have a direct effect on simulated instantaneous crop growth rate. Therefore it would be better to compare simulated light conditions inside the greenhouse and within the crop with measured values.

According to Karlsson and Heins (1992), dry mass partitioning to the root varies with developmental stage, light intensity and day and night temperature. A constant ratio (10 %) of dry mass partitioning to root, however, was assumed in this study. Although changing dry mass partitioning to the root would hardly change the shape of LUE (not shown), systematic variation in the dry mass partitioning to root in time or developmental stage (Karlsson and Heins, 1992) may cause errors in simulated above ground growth rate.

From the previous discussion it is clear that there are many possible solutions to solve the discrepancy between measured and simulated dry mass production. It is therefore important to measure the parameters involved directly under various conditions. However, it is not easy to approach them all, in terms of time, cost, space, and labour. Measurements on leaf and crop photosynthesis, nevertheless, seem to be a first step towards progress in this matter.

CONCLUSION

Because CHRYSIMv1.0 is based on generic, non crop-specific concepts good agreement between measured and predicted TDM could be obtained under suitable light conditions. Severe underestimation was observed at low light conditions. A good fit between predictions and observations could be obtained by increasing the light use efficiency in the leaf photosynthesis light response curve and simultaneously reducing the maximum leaf photosynthesis rate. It is quite unlikely that this adaptation of the model represents the real situation. On the basis of available evidence it is not possible to draw hard conclusions about the cause of these discrepancies, but there is some evidence that it concerns a general phenomenon that needs further investigation, especially in relation to greenhouse cultivation where low light conditions are common and relevant in year around cultivation.

Model validation is needed not only for dry mass production but also with regard to individual modules and related parameters. Without such a validation extrapolation to year-round cut chrysanthemum and other crops seems difficult, because it is impossible to ignore possible errors in the model. Especially validation and parameterisation under low light conditions is needed, together with detailed observations on climatic conditions, i.e. light, CO_2 concentration and temperatures within the crop, inside the greenhouse and over time.

APPENDIX

FUNCTIONS RELATED TO RESPIRATION

Maintenance respiration (R_m, g CH_2O m^{-2} d^{-1}) for the whole crop is a function of organ dry mass DM_i at actual temperature T_{act} (°C):

$$R_m = (M_l \cdot DM_l + M_s \cdot DM_s + M_r \cdot DM_r + M_f \cdot DM_f) \cdot Q_{10c}^{(0.1 \cdot (T_{ref} - T_{act}))} \qquad [6]$$

where M_i is the specific maintenance coefficient at reference temperature (T_{ref}, 25 °C) for leaves (*l*, 0.03 g CH_2O g^{-1} DM d^{-1}), stem (*s*, 0.015 g CH_2O g^{-1} DM d^{-1}), roots (*r*, 0.01 g CH_2O g^{-1} DM d^{-1}) and flowers (*f*, 0.01 g CH_2O g^{-1} DM d^{-1}). DM_i is the organ dry mass per unit of greenhouse area (g m^{-2}) for leaves (*l*), stem (*s*), roots (*r*) and flowers (*f*). Q_{10c} = 2 and represents the sensitivity of R_m to temperature (Spitters *et al.*, 1989).

Overall assimilate requirement (*ASR*, g CH_2O g^{-1} dry mass) is calculated for all plant parts separately and results in a conversion efficiency for assimilates to dry mass (C_f) according the Spitters *et al.*, (1989):

$$C_f = {}^{1}\!\Big/\!(ASR_l \cdot F_l + ASR_s \cdot F_s + ASR_r \cdot F_r + ASR_f \cdot F_f) \qquad [7]$$

where the assimilation requirement coefficients are 1.39 for leaves (ASR_l), 1.45 for stem (ASR_s), 1.37 for root (ASR_r) and 1.39 for flowers (ASR_f) and F_i is the fraction of dry mass distributed to organ for for leaves (*l*), stem (*s*), roots (*r*) and flowers (*f*).

FUNCTIONS RELATED TO LEAF GROSS PHOTOSYNTHESIS

The negative exponential response curve (Eqn. 3) is defined by two parameters P_{gmax} and ε modeled according to Goudriaan *et al.*, (1985).

The function P_{gmax} (mg CO_2 m^{-2} s^{-1}) is described by

$$P_{g\max} = \min(P_{nc}, P_{mm}) + R_d \qquad [8]$$

where P_{nc} is the maximum net photosynthetic rate (mg CO_2 m^{-2} s^{-1}), P_{mm} is the maximum endogenous photosynthetic capacity (mg CO_2 m^{-2} s^{-1}) and R_d is dark respiration (mg CO_2 m^{-2} s^{-1}). In the model P_{mm} increases linearly from 0 to 2 mg CO_2 m^{-2} s^{-1} with temperature from 5 to 15 °C, equals 2 mg CO_2 m^{-2} s^{-1} between 15 °C and 25 °C and decreases linearly from 2 to 0 mg CO_2 m^{-2} s^{-1} until 40 °C.

P_{nc} is calculated by

$$P_{nc} = \frac{1.83 \cdot (C_a - \Gamma)}{1.37 \cdot r_b + 1.6 \cdot r_s + r_m} \qquad [9]$$

where C_a is ambient CO_2 concentration (μmol mol^{-1}), r_m is the mesophyll resistance to CO_2 transport (s m^{-1}), r_b and r_s are the boundary layer resistance (s m^{-1}) and the stomatal resistance for water vapour diffusion (s m^{-1}) respectively. In the model mesophyll conductance ($1/r_m$) increases linearly from 0 to 0.004 m s^{-1} with temperature from 5 to 15 °C, remains constant between 15 °C and 25 °C and decreases linearly from 0.004 to 0 until 40 °C (Bertin and Heuvelink, 1993). temperature dependence of mesophyll conductance

Initial light use efficiency of leaf photosynthesis is described by

$$\varepsilon = \varepsilon_0 \cdot \frac{(C_a - \Gamma)}{(C_a + 2 \cdot \Gamma)} \qquad [10]$$

where C_a is the ambient CO_2 concentration and Γ is the CO_2 compensation concentration according to Brooks and Farquhar (1985)

$$\Gamma = 42.7 + 1.68 \cdot (T_l - 25) + 0.012 \cdot (T_l - 25)^2 \qquad [11]$$

where T_l is leaf temperature which is assumed to be equal to the ambient temperature.

Dark respiration is formulated by:

$$R_d = R_{d,20} \cdot Q_{10}^{[0.1 \cdot (T_l - 20)]} \qquad [12]$$

where $R_{d,20}$ is a constant dark respiration rate of the leaf (mg m^{-2} s^{-1}) at leaf temperature T_l (°C) and 20 °C respectively and Q_{10} the ratio between dark respiration at T_l+10°C and T. The value of Q_{10} used 2.

V . GENERAL DISCUSSION

The objectives of this study were to quantify and generalise crop growth dynamics of year-round cut chrysanthemum, and to apply an existing explanatory model to investigate the influence of daily light integral and crop management (specifically planting density) on the performance of this ornamental crop (Chapter I). These objectives were addressed by describing and analysing the dynamics of chrysanthemum growth and yield throughout the year (Chapter II-1), developing a regression model for chrysanthemum crop growth rate as influenced by daily light integral and plant density (Chapter II-2), and predicting leaf area development based on simulating dry mass partitioning into leaves and modelling specific leaf area of new leaves (Chapter III). These generalised relationships successfully predicted dynamics of chrysanthemum crop growth performances, i.e. dry mass production and leaf area index, as measured in independent experiments (Chapter II) and at commercial holdings (Chapter III). However, these models are likely to be insufficient for application to crops grown at climatic conditions different from those evaluated in the experiments on which the descriptive models are based. For example, the commercial chrysanthemum crops are usually exposed to higher CO_2-concentrations in winter than in summer by CO_2 enrichment (Lee *et al.*, 2002; Chapter III), which together with increased use of supplementary assimilation light enhanced plant growth and quality.

To circumvent the limitations of these descriptive models, an explanatory model was explored for predicting chrysanthemum crop growth under a wider range of climatic conditions. An existing model, TOMSIM (Heuvelink, 1995b) was adapted for chrysanthemum, resulting in the model CHRYSIMv1.0 (Chapter IV). This photosynthesis-driven model takes into account fundamental physiological processes and may adequately describe crop growth even for highly variable climatic conditions (light, temperature and CO_2-concentration). Hence, with CHRYSIMv1.0 the complex relationships between environmental factors and crop growth could be investigated more easily than based on descriptive models alone. Using comprehensive experimental data sets (Chapter II-2), CHRYSIMv1.0 was effectively validated for dry mass production of year-round cut chrysanthemum (Chapter IV). However, some discrepancies between measurements and simulations remained, particularly for winter and low light conditions. Similar model behaviour, of the same photosynthesis-driven model, has been reported for tomato (Heuvelink, 1995b) and rose (Kool and De Koning, 1996). In the case of tomato, reducing maintenance respiration, as a function of relative growth rate, was sufficient to remove discrepancies between simulated and measured crop growth (Heuvelink, 1995b). However, for chrysanthemum this was not effective (Chapter IV). Possible underlying problems with the experimental measurements and modelling of chrysanthemum are discussed in Chapter IV.

Nevertheless, the question remains why the adjusted model worked adequately for tomato but not for chrysanthemum, despite the fact that the TOMSIM model was built as general greenhouse (C_3) crop model. The main difference between tomato and cut chrysanthemum is that the former is an indeterminate crop while the latter is a determinate crop. Furthermore, tomato crops are tied up, trained and pruned, whereas cut chrysanthemum is grown without any manipulation of the crop structure. Therefore the light profile of the tomato canopy is optimised for an LAI of about 3 during the entire crop growth period, whereas the bottom layers of the chrysanthemum canopy, where LAI is often more than 3, receive only very low light intensity.

Calibration of the leaf photosynthetic response curve effectively removed discrepancies between measurements and simulations in this study (Chapter IV). However, uncertainties remain in estimating model parameters for assimilate requirements, specific maintenance respiration, light reduction within the canopy and leaf photosynthetic response (Chapter IV). Furthermore, validation and calibration of the explanatory model suggested some interesting areas for further exploration and model improvement. In particular, dynamics of crop growth performance at low light conditions and the effects of systematic variation in daily light integral due to seasonal changes should be focus of further study. In addition, the model has been validated only for average greenhouse climates (Heuvelink, 1995b; Chapter IV), while it was built to work for a wide range of climatic conditions. Validation of the model using data from crops grown at extreme (low and high) light intensities and temperatures could be an important exercise to further investigate and clarify discrepancies between measurements and simulations.

Despite these unsolved problems, the model may be applied to address some practical questions (Chapter I). Lee *et al.* (2002) applied the same photosynthesis-driven model, with only limited validation for dry mass production, to calculate economic optimum intensity for supplementary light, and to determine which plant densities generate the plant quality (fresh mass) required by flower markets during different seasons. Heuvelink *et al.* (2001) used this model to simulate the interaction effect between the duration of the long-day period and plant fresh mass. Hence, even with its shortcomings the explanatory model appears to be useful for calculating optimal production conditions quickly and effectively, at least when the input data to the model are reasonable values in practice.

Besides plant fresh mass, the number of flowers, stem length and plant shape of cut chrysanthemum are important aspects of plant quality. In fact, visual appearance of the flower bouquet has a much greater influence on final market price than plant fresh mass. Since chrysanthemum management practices not only influence physical yield but also plant quality development, the crop growth model would be more useful if output includes (quantified) visible plant qualities such as number of flowers, flower size, number of flower branches, stem length and plant shape. Although some progress has been made in predicting the number of flowers in cut chrysanthemum, showing a strong linear relationship between plant dry mass and number of flowers, further data are needed because of apparent seasonal effects on regression parameters (Heuvelink *et al.*, 2001; Carvalho *et al.*, 2002). In addition, there is some evidence that the number of flowers is related to the number of lateral stems and the light regime during the short-day period, specifically the duration of the night break, as has been found for spray chrysanthemum grown with cyclic lighting (Van Veen, 1969). In a recent review of the effects of greenhouse climate and plant density on chrysanthemum visual qualities, Carvalho and Heuvelink (2001) suggested that increased assimilate availability (brought about by higher light intensity, higher CO_2-concentrations and/or lower plant density) positively affects several visual quality aspects of chrysanthemum. In addition, light quality appears to influence visual characteristics.

Prediction of internode length and number of internodes and leaves has been investigated and discussed by several authors, and an empirical model has been developed (Jacobson and Willits, 1998; Langton and Cockshull, 1997). However, for cut chrysanthemum a model for stem length control is hardly used in practice, whereas for pot chrysanthemum internode length control by manipulating day and night temperature is more common. Recently, Schouten (2002) proposed a general model to predict temperature effects on internode length in cut chrysanthemum but an integrated approach to stem length was lacking. Although effects of daily temperature and day/night temperature cycles on stem length and internode length have been investigated for several cut flower species including chrysanthemum, developed models have been translated only limited greenhouse crop species for practical applications. Instead of predicting stem length based on internode length and number of leaves, that is independent of photosynthesis process, an approach would be to predict stem length based on photosynthesis and dry mass partitioning into stems, applying the concept of specific stem length (average stem length per g of stem dry mass, cm g^{-1}) (Kropf and Van Laar, 1993). The great advantage of this approach is that it could be built into a photosynthesis-driven model.

Finally, development and validation of the regression model (Chapter II) and CHRYSIMv1.0 (Chapter IV) was implemented for one chrysanthemum cultivar only. A further limitation is that the length of time between start of the short-day period and anthesis, which is primarily a cultivar characteristic, has not been predicted in this study (Larsen and Persson, 1999). Clearly, in addition to solving the modelling problems mentioned in Chapter IV, much more work needs to be done to modelling cut chrysanthemum. Ultimately, good teamwork between growers, breeders, advisors, automation companies and scientists is needed to bridge the gap between models developed by scientists and practical model application (Van den Bosch, 1998).

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CURRICULUM VITAE

Jeong Hyun Lee was born on 19 September 1970, in Jangheung-county, Jeollanam-do, The Republic of Korea. He entered College of Agriculture and Life Sciences, Chonnam National University in 1988 and completed his B.Sc. in Horticulture in 1994. During his B.Sc. study he joined the Chrysanthemum research student club. He continually studied in horticultural science at the same University and completed his compulsory courses for M.Sc. degree in August 1996. He worked at design of cultivation system for greenhouse crops and greenhouses structure using CAD software from 1994 to 1996.

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SUMMARY

Today, greenhouse cultivation is approaching more and more an industrial process, like a factory producing living products through all seasons. Like in a conventional factory, the production systems have a computerized environmental control system for controlling the crop growth process. Vast knowledge is required for optimising this complex production system. Moreover, a large variation of species and cultivars are grown with different properties and requirements in different cultivation systems making it is even more complicated to optimise the production system as a whole. Hence the use of models has been advocated for solving this type of problems in practice. Models are powerful tools for research, education, decision support, greenhouse climate control and prediction and planning of production and policy analysis. Although the predictive capability of descriptive models is high, explanatory models have much greater potentials for application in year-round crop production system, in terms of the dynamics of climatic control, production planning, crop management and economical aspects. These models had been applied for prediction of dry mass as indicator for physical yield of greenhouse crops as related to the environmental conditions in the greenhouse. Although explanatory models have been developed on a generic basis they have mainly been applied with greenhouse fruit vegetable crops.

The aim of this study was to apply an existing generic explanatory crop growth model for cut chrysanthemum in particular with respect to its response to radiation and crop management. This aim was approached by: (1) describing and analysing the dynamics of growth and yield (2) generalising the dynamics of dry mass production (3) predicting leaf area development based on dry matter partitioning into the leaves and specific leaf area of new leaves (4) adaptation of a well developed and validated explanatory model (TOMSIM) for use with chrysanthemum under conditions of controlled daylength and supplementary assimilation lighting (CHRYSIMv1.0.) and validation, calibration and evaluation of this model.

Dynamics of dry mass, leaf area index and final plants characteristics of six experiments were presented (Chapter II-1). Crops were grown at three plant densities and six planting dates during three consecutive years in semi-commercial size greenhouse compartments. Final number of flowers per plant, plant fresh mass and plant dry

mass decreased with plant density, this decrease being larger in summer than in winter. Final plant fresh mass at 48 plants m^{-2} was 2.7 times higher in summer than winter (for plant dry mass this factor was 3.2). Plant dry matter content between summer and winter varied between about 11-13 %. Stem length hardly responded to plant density and total dry mass production per m^2 linearly increased with plant density. Final plant fresh mass (y; g) showed a linear relationship with cumulative incident photosynthetically active radiation (PAR) per plant (x; MJ $plant^{-1}$) ($y = 16.7x + 28.0$, $R^2 = 0.97$). Dry mass production in time could accurately be described by the expolinear growth equation with three regression parameters: maximum relative growth rate (r_m; assumed to be independent of plant density), maximum absolute growth rate (c_m) and lost time (t_b). r_m was 2.4 times higher and c_m was 4.1 times higher in summer than in winter and no effect of plant density on c_m was observed, whereas t_b decreased linearly with increasing plant density. Using these parameters and measured maximum leaf area index (LAI) for calculating dynamic growth patterns of LAI, resulted in large over- or under-estimations, except for summer-grown crops. When an extended expolinear growth function was fitted simultaneously on dry mass production and LAI in time, accurate time curves for LAI were obtained, whereas dry mass production was only accurately described for the summer crops. Light use efficiency (LUE), the slope of the linear relationship between crop dry mass and cumulative intercepted PAR, varied between 3.4 g MJ^{-1} in summer and 5.3 g MJ^{-1} in winter and LUE showed a slightly linear increase with plant density (LUE = 3.75 + 0.0073 × plant density; $P = 0.007$, $R^2 = 0.99$).

The aim of Chapter II-2 was to predict crop growth of year-round cut chrysanthemum (*Chrysanthemum,* Indicum group) based on a regression model of maximum crop growth rate as a function of daily incident PAR (MJ m^{-2} d^{-1}), using generalised parameters of the expolinear growth equation. Four experiments for developing an empirical crop growth model and three experiments for validating the model were conducted in glasshouse compartments. In the four experiments for model development, chrysanthemum crops were grown at different plant densities (32, 64 and 80 plants m^{-2}), and seasons (planting in January, May-June and September) under shading screens (66 % and 43 % of natural light) or supplementary assimilation light (HPS, 40-48 μmol m^{-2} s^{-1}). Greenhouse temperatures (19-21°C) and CO_2 concentrations (349 - 432 μmol mol^{-1}) were similar between experiments. The fitted expolinear growth equation as a function of time ($EXPO_T$) or as a function of incident PAR integral ($EXPO_{PAR}$) effectively described periodically measured total dry mass ($R^2 > 0.98$). However, growth parameter estimates for the fitted $EXPO_{PAR}$ were more suitable as they were not correlated to each other. Coefficients of $EXPO_{PAR}$ characterised the relative growth rate per incident PAR integral (RGR_{PAR}, $[MJ\ m^{-2}]^{-1}$) and light use efficiency (LUE, g MJ^{-1}) at closed canopy. In all four experiments no interaction effects between treatments on crop growth parameters were found. RGR_{PAR} and LUE were not different between HPS and natural light treatments, but significantly increased when light levels were reduced by shading in the summer experiments. There was no consistent effect of plant density on growth parameters. RGR_{PAR} and LUE showed hyperbolic relations to average daily incident PAR averaged over 10 day periods after planting (RGR_{PAR}) or before final harvest (LUE). Based on those relations, maximum relative growth rate (g g^{-1} d^{-1}) and maximum crop growth rate (g m^{-2} d^{-1}) were successfully described by rectangular hyperbolic relations to daily incident PAR integral. Aboveground total dry mass (TDM, g m^{-2}) simulated over time was in good agreement with measured TDM in three independent experiments, using daily incident PAR integral and leaf area index as inputs. Based on these results it is concluded that the expolinear growth equation is a useful tool for quantifying cut chrysanthemum growth parameters and comparing growth parameters between different treatments, especially when light is the growth-limiting factor. Under moderate environmental conditions the regression model worked satisfactorily, hence the model may be applied as a simple tool for understanding crop response to seasonal variations in daily light integral, and for planning cropping systems of year-round cut chrysanthemum. However, information on leaf area development in cut chrysanthemum is required for crop growth prediction of chrysanthemum.

This problem was tackled in Chapter III, where leaf area index (LAI) was described on the basis of dry matter partitioning into the leaves and on specific leaf area of newly-formed leaf biomass (SLA_n) for year-round cut chrysanthemum. In five greenhouse experiments, at several plant densities and planting dates, periodic destructive measurements were conducted to develop empirical models for partitioning and SLA_n. The fraction of dry matter partitioned to the leaves, calculated as the increase in leaf dry mass divided by the increase in shoot dry mass between two destructive harvests, could be described accurately ($R^2 = 0.93$) by a Gompertz function of relative time R_t. R_t is 0 at planting date, 1 at the start of short-day and 2 at final harvest. SLA_n, calculated as the slope of a linear regression between periodic measurements of leaf dry mass (LDM) and LAI, showed a significant linear increase with the inverse of the daily incident PAR (MJ m^{-2} d^{-1}), averaged over the whole growing period, the average greenhouse temperature and plant density ($R^2 = 0.74$). The models were validated for two independent experiments and with data from three commercial growers, each with four planting dates. Measured TDM over time, initial LAI and LDM, plant density, daily temperature and incident PAR were input in the model. Dynamics of LDM and LAI were predicted accurately by the model, although in the last part of the cultivation LAI was often overestimated. The slope of the linear regression of simulated against measured LDM varied between 0.95 and 1.09. For LAI this slope varied between 1.01 and 1.12.

The objective of Chapter IV was to apply and validate an existing photosynthesis-driven model (TOMSIM) for dry mass production in year-round cut chrysanthemum. Two versions were compared, a standard version and an adjusted version, where maintenance respiration was made dependent on the relative growth rate of the crop (metabolic activity of the crop). Based on cultivation methods for this crop, options for management improvement include day length control, and adjustment of supplementary lighting and plant density. Therefore, greenhouse experiments were conducted with different combinations of natural light, supplementary assimilation light, shading and plant densities, during different seasons. The model was applied to compute daily crop growth rate (g m^{-2}), based on daily crop gross assimilation rate (P_{gd}) and maintenance respiration (R_m). In the standard model, P_{gd} depends on crop leaf area and radiation, while R_m is a function of temperature and plant organ biomass. In the adjusted model a reduction factor for R_m is included, which is a negative exponential function of simulated relative growth rate (RGR). Initial organ dry mass, leaf area index (LAI), dry matter partitioning into different plant organs, daily global radiation, and hourly greenhouse temperature and CO_2 concentration were model inputs. Dynamics of measured and predicted TDM (g m^{-2}) were similar during the summer period (natural light), whereas the model largely underestimated TDM in winter and under (constantly) shaded conditions. Underestimation was more apparent at higher levels of shading, and occurred in both standard and adjusted models. Even when R_m was completely set to zero, model simulations still underestimated measured dry mass for the winter period and heavily shaded conditions.

Comparing simulated and measured light use efficiency (LUE, g MJ^{-1}) provided better insight into model behaviour than comparing crop growth rates. Simulated LUE at closed canopy largely underestimated measured LUE at lower light conditions, but not for crops grown under natural light conditions in the summer period. The standard model often predicted no growth at low daily light integrals, whereas increased light resulted in higher TDM and maintenance respiration. For all experiments, discrepancies of TDM between measured and simulated by the adjusted model were largely reduced by calibration of the parameters of the leaf photosynthesis response curve, i.e. initial light use efficiency (ε) and maximum gross photosynthetic rate (P_{gmax}). Although this calibration resulted in satisfactory prediction of TDM, the calibrated value of ε was much higher than values from literature, and the calibrated value of P_{gmax} was relatively low. This suggests that optimisation of model parameters should not be restricted to ε

and P_{gmax} but should also include other parameters such as the assimilation requirement and specific maintenance respiration.

The objectives of this study, quantifying and generalising crop growth dynamics of year-round cut chrysanthemum, and validating and calibrating an explanatory model, CHRYSIMv1.0 to investigate the influence of daily light integral and crop management (specifically planting density) on the performance of this ornamental crop, were satisfied. Furthermore, validation and calibration of the explanatory model suggested some interesting areas for further exploration and model improvement (Chapter IV). Moreover the model does not directly cover certain aspects that are relevant to the growers, i.e. external quality of the final product. The crop growth model, therefore, would be more useful if output would include (quantified) visible plant quality such as number of flowers, flower size, number of flower branches, stem length and plant shape. Some progress on predicting stem length and number of flowers has been made, but there is still a gap between application into practice and the performance of a photosynthesis-driven model. Finally, development and validation of the regression model (Chapter II) and CHRYSIMv1.0 (Chapter IV) was valid for one chrysanthemum cultivar only. Clearly, in addition to solving the modelling problems mentioned in Chapter IV, much more work needs to be done to modelling cut chrysanthemum. Ultimately, good teamwork between growers, breeders, advisors, automation companies and scientists is needed to bridge the gap between models developed by (and for) scientists and practical model applications for year-round cut chrysanthemum.

SAMENVATTING

Het productieproces in de kasteelt lijkt tegenwoordig steeds meer op een industrieel proces. Het glastuinbouwbedrijf van nu lijkt op een fabriek die het hele jaar door levende producten maakt. Net als in een gewone fabriek is het productiesysteem voorzien van een computergestuurd klimaatbesturingssysteem om het groeiproces te sturen. Er is veel kennis nodig om dit complexe productiesysteem te optimaliseren. Bovendien wordt een grote verscheidenheid aan soorten en cultivars met verschillende eigenschappen geteeld, waarbij van uiteenlopende teeltsystemen gebruik wordt gemaakt. Dit maakt het nog gecompliceerder om het productiesysteem als geheel te optimaliseren. Vandaar dat het gebruik van modellen wordt bepleit om dit type problemen in de praktijk op te lossen. Modellen zijn een krachtig hulpmiddel voor onderzoek, onderwijs, ondersteuning van beslissingen, kasklimaat besturing, voor het voorspellen en plannen van productie en voor beleidsanalyses. Beschrijvende modellen zijn in het algemeen goed in staat om productie te voorspellen, maar verklarende modellen bieden veel grotere mogelijkheden voor gebruik in jaarrond productiesystemen, in termen van dynamiek van klimaatregeling, productieplanning, teeltsturing en economische aspecten. Verklarende modellen worden gebruikt om drogestofproductie te voorspellen, als maatstaf voor de fysieke opbrengst van gewassen in relatie tot het kasklimaat. Hoewel ze op generieke basis zijn ontwikkeld, worden verklarende modellen op dit moment hoofdzakelijk toegepast ten behoeve van de teelt van vruchtgroenten.

Het doel van deze studie was het modelleren van groei en productie van snijchrysant met behulp van een bestaand, generiek verklarend groeimodel, in relatie tot, met name, straling en teeltmaatregelen. Dit doel werd benaderd door: (1) beschrijven en analyseren van de dynamiek van groei en opbrengst, (2) generaliseren van de dynamiek van drogestofproductie, (3) voorspellen van de groei van bladoppervlak op basis van de drogestoftoedeling naar de bladeren en van de SLA van nieuw gevormde bladeren, (4) aanpassen, valideren, calibreren en evalueren van een verklarend model ten behoeve van chrysant (CHRYSIMv1.0). Een reeds ontwikkeld en goed gevalideerd verklarend model voor de tomaat (TOMSIM) werd hiertoe aangepast, rekening houdende met het gebruik van daglengtesturing en assimilatiebelichting bij chrysant.

De dynamiek van de drogestofproductie en van de bladoppervlakte-index (leaf area index;LAI) en plantkarakteristieken bij de eindoogst werd in 6 experimenten onderzocht

(Hoofdstuk II-1). Het gewas werd geteeld bij drie verschillende plantdichtheden in semi-commerciële schaal kascompartimenten met zes verschillende planttijdstippen gedurende drie jaren. Dynamische groeiparameters werden onderzocht door middel van de expolineaire groeifunctie. Het uiteindelijke aantal bloemen per plant, plantversgewicht en plantdrooggewicht daalden met toenemende plantdichtheid; deze daling was groter in de zomer dan in de winter. Bij 48 planten m^{-2} was het uiteindelijke plant versgewicht 2,7 maal hoger in de zomer dan in de winter (voor plant drooggewicht was deze factor 3,2). De drogestofgehaltes van de planten in de zomer en in de winter verschilden ongeveer fluctueerden tussen 11% en 13%. De stengellengte reageerde bijna niet op plantdichtheid en de totale drogestofproductie per m^2 nam lineair toe met de plantdichtheid. Het versgewicht van de plant bij de eindoogst (y; g) vertoonde een lineaire relatie met de totale hoeveelheid geaccumuleerde fotosynthetisch actieve straling (PAR) per plant (x; MJ $plant^{-1}$) ($y = 16{,}7x + 28{,}0$, $R^2 = 0{,}97$). De drogestofproductie kon nauwkeurig worden beschreven als functie van de tijd door de expolineaire groeicurve met drie regressieparameters: maximum relatieve groeisnelheid (r_m; er werd aangenomen dat deze onafhankelijk is van de plantdichtheid), maximum absolute groeisnelheid (c_m) en de vertraging (t_b). In de zomer was r_m 2,4 keer zo hoog en c_m 4,1 keer zo hoog als in de winter; er werd geen effect van plantdichtheid op c_m gevonden; t_b nam lineair af met toenemende plantdichtheid. Gebruik van deze parameters en de gemeten maximum LAI voor het berekenen van de dynamiek van de LAI, resulteerde in grote over- of onderschattingen, behalve voor het zomergewas. Als de uitgebreide expolineaire groeifunctie tegelijkertijd werd gefit op drogestofproductie en LAI, werd de groei van LAI wel nauwkeurige beschreven, maar drogestofproductie alleen bij het zomergewas. De efficiëntie waarmee licht gebruikt wordt (light use efficiency; LUE), de helling van de lineaire relatie tussen gewasgroei en de totale hoeveelheid onderschepte PAR, varieerde tussen de 3,4 g MJ^{-1} in de zomer en 5,3 g MJ^{-1} in de winter en LUE vertoonde een geringe lineaire toename met de plantdichtheid.

In Hoofdstuk II-2 werd de gewasgroei van jaarrondsnijchrysant veralgemeniseerd op basis van een empirisch model waarbij gewasgroei als functie van de dagelijkse inkomende fotosynthetisch actieve straling (PAR, MJ m^{-2} d^{-1}) beschreven werd. Hierbij werden parameters van de expolineaire groeicurve gebruikt. Om dit empirische gewasgroeimodel te ontwikkelen werden vier experimenten uitgevoerd in kascompartimenten; daarnaast werden nog 3 experimenten uitgevoerd om dit model te valideren. In de eerst genoemde vier experimenten werd snijchrysant geteeld bij verschillende lichtniveaus (ongeschermd en beschaduwing tot 66% en 43% lichtniveau door middel van schermdoek; daarnaast daglicht met of zonder 40-48 µmol m^{-2} s^{-1} assimilatiebelichting door middel van hogedruknatriumlampen), verschillende plantdichtheden (32, 64 en 80 planten per m^2) en verschillende seizoenen (planten in januari, mei-juni en september). Kastemperaturen (19-21°C) en CO_2 concentraties (349-432 µmol mol^{-1}) waren in deze experimenten nauwelijks verschillend. De expo-lineaire groeicurve, hetzij gefit als functie van de tijd ($EXPO_T$) of als functie van de op het gewas vallende PAR integraal ($EXPO_{PAR}$), gaf een goede beschrijving van het periodiek gemeten totaal drooggewicht ($R^2 > 0.98$). $EXPO_{PAR}$ leek beter bruikbaar dan $EXPO_T$, omdat de geschatte groeiparameters niet gecorreleerd waren. Coëfficiënten voor $EXPO_{PAR}$ waren de relatieve groeisnelheid per eenheid opvallende PAR (RGR_{PAR} [MJ $m^{-2}]^{-1}$) en de lichtbenuttingsefficiëntie (LUE, g MJ^{-1}) voor een gesloten gewas. In alle vier experimenten werd voor deze parameters geen interactie aangetoond tussen de verschillende factoren die onderzocht werden. RGR_{PAR} en LUE verschilden niet significant voor de teelt met en zonder assimilatiebelichting, maar namen significant toe bij laag licht onder schermdoek in de zomerteelten. Er was geen consistente invloed van plantdichtheid op de modelparameters. RGR_{PAR} en LUE vertoonden een hyperbolische relatie met de gemiddelde dagelijkse hoeveelheid PAR, gemiddeld over 10-daagse perioden vanaf planten (RGR_{PAR}) of juist voor de eindoogst (LUE). Gebaseerd op deze relaties werden potentiële relatieve groeisnelheid (g g^{-1} d^{-1}) en potentiële gewasgroeisnelheid (g m^{-2} d^{-1}) met succes beschreven als rechthoekige hyperbolische functie van de dagelijkse hoeveelheid PAR.

Het gesimuleerde verloop van totaaldrooggewicht in de tijd vertoonde een goede overeenkomst met de metingen in drie onafhankelijke experimenten, waarbij de dagelijkse invallende PAR integraal en de LAI modelinput waren. Op grond van deze resultaten kan worden geconcludeerd dat de expo-lineaire groeicurve bruikbaar is om de groeiparameters van snijchrysant te quantificeren en om behandelingen te vergelijken, in het bijzonder wanneer licht de limiterende factor is. Onder gecontroleerde klimaatscondities werkte dit empirische model naar behoren. Derhalve kan dit model toegepast worden als een simpel hulpmiddel om het gedrag van het gewas te begrijpen in relatie tot seizoensvariaties in dagelijkse stralingssom en voor het plannen van de jaarrondteelt van snijchrysant. Echter, informatie omtrent bladoppervlakteontwikkeling in snijchrysant is noodzakelijk om tot een voorspelling van gewasgroei te kunnen komen.

Het voorspellen van het verloop van de LAI, gebaseerd op drogestof toedeling naar de bladeren en het specifiek bladoppervlak van de nieuw gevormde bladbiomassa (SLA_n) was het onderwerp van hoofdstuk III. In vijf kas experimenten, met verschillende plantdichtheden en planttijdstippen, werden periodieke destructieve waarnemingen uitgevoerd om empirische modellen voor stofverdeling en SLA_n te ontwikkelen. De drogestoftoedeling naar de bladeren, d.w.z. de toename van het bladdrooggewicht ten opzichte van de totale drooggewichttoename tussen twee destructieve oogsten, kon goed beschreven worden (R^2 = 0.93) door een Gompertz functie van relatieve tijd. SLA_n, berekend als de helling van de lineaire relatie tussen blad drooggewicht (leaf dry mass; LDM) en LAI, vertoonde een significante lineaire toename met de inverse van de dagelijkse hoeveelheid fotosynthetisch actieve straling (PAR, MJ m^{-2} d^{-1}), gemiddeld over de gehele groeiperiode, de gemiddelde kastemperatuur en plant dichtheid (R^2 = 0.74). De geldigheid van het ontworpen model werd bevestigd met twee onafhankelijke experimenten en met data van drie commerciële telers, elk met vier planttijdstippen. Gebruik makend van de gemeten totale drogestoftoename, LAI en LDM aan het begin, plantdichtheid, dagelijkse temperatuur en PAR als invoer, kon de dynamiek van LDM en LAI nauwkeurig worden voorspeld. De helling van de lineaire regressie van de gesimuleerde versus de gemeten LDM varieerde tussen de 0,95 en 1,09. Voor de LAI varieerde deze helling tussen de 1,01 en 1,12.

Doelstelling van Hoofdstuk IV was het valideren van een bestaand, op fotosynthese gebaseerd, model voor drogestofproductie van tomaat (TOMSIM), ten behoeve van de jaarrond teelt van chrysant. Twee versies werden vergeleken: een standaard versie en een aangepaste versie, waarbij de onderhoudsademhaling afhankelijk werd gesteld van de relatieve groeisnelheid (metabolische activiteit) van het gewas. Mogelijkheden voor verbetering van de teelt zijn: optimaliseren van daglengte, bijbelichting en plantdichtheid. Daarom werden experimenten in de kas uitgevoerd met verschillende combinaties van natuurlijk licht, kunstlicht, beschaduwing en plantdichtheden en teeltseizoen. Het model werd gebruikt voor het berekenen van de dagelijkse groeisnelheid (g m^{-2}), gebaseerd op bruto assimilatie (P_{gd}) en onderhoudsademhaling van het gewas (R_m). In het standaard model hangt P_{gd} af van bladoppervlak en straling, terwijl R_m een functie is van temperatuur en biomassa van het gewas. In het aangepaste model is een reductie-factor voor R_m opgenomen. Deze reductie-factor is een negatief exponentiële functie van de gesimuleerde relatieve groeisnelheid (RGR).

Het drooggewicht van de organen en de LAI bij de aanvang van het experiment, de drogestoftoedeling naar de verschillende organen van de plant, de dagelijkse globale stralingssom en uurlijkse waarden van luchttemperatuur en CO_2-concentratie in de kas waren invoerparameters van het model. Het verloop van gemeten en voorspelde totale hoeveelheid bovengrondse drogestof (TDM, g m^{-2}) kwamen voor de zomerexperimenten (natuurlijk licht) goed overeen, daarentegen onderschatte het model TDM in de winterperiode en onder (constante) beschaduwing aanzienlijk. Deze onderschatting was sterker bij toenemende beschaduwing, en trad op bij het standaard zowel als het aangepaste model. Zelfs wanneer R_m volledig op 0 werd gesteld onderschatten modelsimulaties de drogestofproductie nog steeds, in vergelijking met metingen tijdens de winterperiode en bij intensieve beschaduwing. Het vergelijken van gesimuleerde en gemeten 'light use efficiency' (LUE, g MJ^{-1}) leverde een beter inzicht op in het gedrag van het model dan het vergelijken van gewasgroeisnelheden. Gesimuleerde LUE leidde, bij gesloten gewas en onder lagere lichtniveaus, tot een aanzienlijke onderschatting vergeleken met gemeten LUE. Dit gold echter niet voor gewas geteeld onder natuurlijk licht in de zomerperiode. Bij een geringe dagelijkse lichtintegraal voorspelde het standaard model vaak een groeisnelheid van nul. Toename van de dagelijkse hoeveelheid licht leidde tot een hogere TDM en onderhoudsademhaling. Verschillen tussen gemeten en gesimuleerde TDM in alle experimenten konden grotendeels worden weggenomen door kalibreren van parameters voor de fotosynthese-licht respons curve van het blad, zoals initiële lichtbenuttingsefficiëntie (ε) en maximale fotosynthesesnelheid (P_{gmax}). Alhoewel TDM na deze kalibratie bevredigend kon worden voorspeld, was de gekalibreerde waarde van ε veel hoger dan in de literatuur, en de gekalibreerde waarde van P_{gmax} relatief laag. Dit suggereert dat optimalisatie van modelparameters niet beperkt zou moeten blijven tot ε en P_{gmax}, maar dat hierin ook andere parameters zouden moeten worden betrokken, zoals assimilatenbehoefte en specifieke onderhoudsademhaling.

Aan de doelstellingen van deze studie, kwantificeren en generaliseren van de dynamiek van de gewasgroei van jaarrond snijchrysant en valideren en calibreren van een verklarend model, CHRYSIMv1.0 om de invloed van dagelijkse straling en teeltmaatregelen (in het bijzonder plantdichtheid) op het gedrag van dit siergewas te onderzoeken, is voldaan. Bovendien geeft validatie en calibratie van het verklarende model enige interessante gebieden voor verder onderzoek en verbetering van het model aan (Hoofdstuk IV). Verder bestrijkt het model niet alle gebieden die van belang zijn voor telers, o.a. uitwendige kwaliteit van het product. Het gewasgroeimodel zou daarom bruikbaarder zijn als de output ook (gekwantificeerde) uitwendige kwaliteit zoals aantal bloemen, bloemgrootte, aantal bloeiende takken, stengellengte en vorm van de plant zou omvatten. Er is enige vooruitgang geboekt bij het voorspellen van stengellengte en aantal bloemen, maar er is nog steeds een discrepantie tussen toepassing in de praktijk en de resultaten van een door fotosynthese gestuurd model. Tenslotte, ontwikkeling en validatie van het regressie model (Hoofdstuk II) en CHRYSIMv1.0 (Hoofdstuk IV) was alleen geldig voor één cultivar. Het is duidelijk, dat voor het oplossen van de problemen, genoemd in Hoofdstuk IV, er veel meer werk moet worden verricht om de snijchrysant goed te kunnen modeleren. Uiteindelijk is een goede samenwerking nodig tussen telers, veredelaars, voorlichters, automatiser ingsbedrij ven en wetenschappers om het gat tussen modellen ontwikkeld door (en voor) wetenschappers en een in de praktijk bruikbaar model voor de jaarrond teelt van chrysant te dichten.

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