Effects of Irradiation and Temperature on Shoot Growth and Development in Blue Holly (*Ilex* × *meserveae*)

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Abstract

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Evenly distributed production and sales of pot plants throughout the year would be the ideal situation for greenhouse companies with respect to labour input and planning. The market in Sweden, however, has two big selling seasons, the spring sales period with bedding plants, and the Christmas season. During summer, when the climate conditions outdoors are most favourable for cheap production of pot plants, most greenhouse companies chose to stop production since they meet a weak market in late summer and autumn. Blue holly (*Ilex* × *meserveae* 'Blue Princess' S.Y. Hu) was tested as a potential new greenhouse crop for summer production. This holly hybrid is an evergreen, hardy and woody plant that is normally used as a garden shrub or for Christmas decorations. The advantage of this hardy, woody plant is that the final product can be stored outdoors until the Christmas sales period.

The present study investigated the impact of greenhouse climate on growth of blue holly from rooted cuttings to small pot plants. In contrast to outdoor-grown shrubs, holly formed several periodic growth flushes when grown in climate conditions between 17 ºC and 26 ºC and irradiation levels of 0.6 to 5 mol m^{-2} d^{-1} (Skye sensors). The duration of one flush and the number of leaves produced were dependent on both irradiation and temperature levels. The individuals within the plant population, however, were poorly synchronized. In order to statistically prove the impact of climate on the growth oscillations, an analytical tool was developed. A *sine* function was modified to describe the growth oscillations and a value for the amplitude and the frequency of each individual plant could be estimated. The amplitude and frequency values were then analysed further for differences between the treatments.

Two growth environments were chosen for the growth analysis in blue holly: a heated greenhouse and climate chambers with artificial lighting (white cool fluorescent tubes). Oscillations in vegetative growth, shoot length, number of side shoots and dry weight were compared in respect of light quality and quantity as well as temperature. Due to the different oscillation patterns within the range of climate conditions tested, the oscillations were categorized to enable comparison. Shoot growth was almost continuous at high irradiation and high temperature conditions, while in cooler temperatures and low light conditions only one flush could be observed. In intermediate climate conditions pronounced oscillations of vegetative growth could be observed with up to three flushes within an experimental period of 93 days. The branching pattern in blue holly was linked to the vegetative growth oscillations. Side shoots only developed after the growth cessation period between two flushes. In treatments with pronounced oscillations, a higher number of side shoots could be observed.

Keywords: growth analysis, growth oscillations, irradiation, light, light quality, PPF, rhythmic growth, shade plant.

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Populärvetenskaplig sammanfattning

I Sverige är försäljningen av växthusproducerade prydnadsväxter säsongsberoende. Under våren och tidig sommar är efterfrågan på prydnadsväxter hög, under sommar och tidig höst säljs däremot färre krukväxter. I ett modernt växthusföretag med investeringstung styrutrustning är en jämn produktion året runt viktig för en god lönsamhet i företaget. I praktiken håller dock många växthusföretag stängt under sommaren, vilket gör det svårt att behålla kvalificerad personal. Situationen är olycklig, eftersom sommarens klimatförhållanden ger de bästa förutsättningarna för en billig produktion av prydnadsväxter i växthus. Ingen extra belysning behövs och kostnader för uppvärmning av växthusen är låga.

Doktorandprojektet initierades för att hitta och testa nya krukväxtkulturer som är lämpliga att producera i växthus under sommaren, men säljs först under julmånaden december. Dessutom skulle växterna vara härdiga och kunna lagras utomhus när de var färdigproducerade efter sommaren. En referensgrupp bildades där representanter från trädgårdsbranchen (Nils Andersen, Splendor Plant AB, Jonstorp; Roy Owesson, Mäster Grön, Helsingborg och Annika Öhman-Nilsson, GRO) och Sveriges lantbruksuniversitet tog beslutet att blå järnek (*Ilex* × *meserveae* ’Blue Princess’) skulle undersökas och testas som en potentiell ny växthuskultur. Järnek är en växt som redan används som prydnadsbuske utomhus och som snittgrönt för dekorationer till jul. Blå järnek är en korsning mellan den europeiska järneken (*Ilex aquifolium*) och den mycket härdiga *Ilex rugosa* som härstammar från norra Japan. Sorten ’Blue Princess’ producerar stora blågröna glänsande blad och röda bär, men har inte lika skarpa bladkanter som den europeiska järneken. Den ansågs därför vara lämplig som en krukväxt för inomhusdekoration.

I studien undersöktes järnekens tillväxt och utveckling under olika klimat-förhållanden (17, 21, 23, 26 ºC medeldygnstemperatur och olika instrålningar, för detaljer se arikel IV, sida 3). Järneken som är en vedartad växt vållar dock en rad svårigheter när det gäller styrning av produktionen. Skotten har ingen jämn tillväxt, utan växer i periodiska tillväxtcykler, ”flushes” (artikel I) som kan delas in i olika stadier (se bild sida 20). Klimatet påverkade tillväxtsvängningarna, men detta kunde inte bevisas statistiskt eftersom plantorna inte var synkroniserade d.v.s. plantorna började växa vid olika tidpunkter trots att de utsattes för samma behandling samtidigt. Vi utvecklade därför ett analysverktyg, som matematiskt kunde beskriva de olika tillväxtkurvorna från de olika klimatförhållandena (artikel II och III). Sidoskottsutvecklingen var knuten till svängningarna eftersom dessa bara utvecklades efter en period där inga nya blad producerades (Stage A i Fig. 4; sida 20). Högt antal sidoskott och jämna tillväxtsvängningar observerades när instrålningen var 2 mol per kvadratmeter och dag och en dygnsmedeltemperatur omkring 23 ºC. Detta klimat är lätt att uppnå under sommaren i nordeuropeiska växthus. Blå järnek har därför en stor potential som framtida sommarkultur i växthus. Experimenten visade dessutom att brist på rött ljus minskade sträckningstillväxten hos skotten och kort dag förlängde viloperioden mellan tillväxtcyklerna. Dessa två faktorer har betydelse för styrningen av produktionen, men behöver undersökas närmare. Även tidpunkten och metoden för sticklingsförökning kan ha inverkan på den efterföljande produktion och behöver testas innan odlings-rekommendationer ges.

Contents

Appendix

Papers I–IV

This thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Kosiba, A., Nothnagl, M., Alsanius, B.W. & Larsen, R.U. 2005. Influence of photosynthetic photon flux density (PPFD) and air temperature on vegetative growth and side shoot formation in greenhouse grown holly (*Ilex × meserveae* 'Blue Princess' S.Y. Hu). *European journal of horticultural sciences.* In press.

II. Larsen, R.U. & Kosiba, A. 2002. Modelling periodic plant growth using *sine* and *cosine* functions. *Acta horticulturae* 593, 145–150.

III. Kosiba, A., Nothnagl, M., Alsanius, B.W. & Larsen, R.U. 2005. Analysis of rhythmic growth in holly (*Ilex meserveae* 'Blue Princess'). *Scientia horticulturae* 104 (3), 325–337.

IV. Kosiba, A., Nothnagl, M., Alsanius, B.W., Gertsson, U.E. & Larsen, R.U. Comparison of greenhouse and climate chamber grown blue holly (*Ilex × meserveae* 'Blue Princess'). *Submitted manuscript.*

Papers I, II and III are reproduced by permission of the journals concerned.

Objective

The objective of this doctoral thesis was to investigate the impact of climatic factors on growth and developmental patterns of blue holly *(Ilex × meserveae*). Daily light integral (DLI), light quality and mean air temperature were studied as factors influencing vegetative growth and side shoot formation.

Introduction

Background

In Sweden, 48 million ornamental plants are produced yearly in a greenhouse area of 185 ha. After vegetable production, they account for the greatest fraction within protected cultivation. During the past 20 years, the number of greenhouse companies decreased gradually while the greenhouse area for protected cultivation remained at a stable level of 340 ha (SCB, 2003). This trend towards larger greenhouse companies started when the demand for greenhouse grown pot plants dropped during the 1980s. Most greenhouse companies had invested in computerized control of greenhouse climate, fertilization and irrigation during the sixties and seventies. Such high investments in equipment demand an even production and careful planning during the whole year to achieve profitability. The market in Sweden, however, is seasonally pronounced with a high demand for ornamental plants in spring and early summer and a minor peak of demand during the Christmas sales period. Due to this imbalance in demand and supply, many greenhouse companies experience either problems in keeping skilled staff or producing unprofitable crops during summer. This is a very unfortunate situation since outdoor climate conditions (temperature and light) during summer are most favourable for cheap production of ornamentals. In the late nineties, problems caused by variations in profitability during the year and empty greenhouses during the summer were considered to be the greatest challenge to the Swedish greenhouse industry. The Swedish Farmers' Foundation for Agricultural Research provided financial support for finding a solution and this PhD project was initiated. A reference group was formed with members from the greenhouse and nursery industry as well as wholesale traders.

Plant material

The reference group decided to test blue holly *(Ilex × meserveae* 'Blue Princess' S.Y. Hu) as a potential new greenhouse crop since blue holly:

- is already known as a plant for Christmas decorations
- produces many and decorative red berries and shiny dark green leaves
- is very hardy and can be stored outside in the Southern Scandinavian winter climate
- is suitable for indoor Christmas decorations since the leaf edges are not as sharp as in other common holly

For the Northern European market we considered a small pot plant, no larger than 20 cm from pot edge to shoot tip, as the ideal crop for Christmas. The plant had to be bushy with as many natural red berries as possible. Timing of production was regarded as most important. The economic ‘summer gap’, from the start of June until September, was to be used for production of a crop that is ready for shipping but can be stored outdoors until the sales period in December.

Ilex × *meserveae* is an evergreen ornamental shrub that belongs to the genus *Ilex* and the plant family *Aquifoliaceae*. *Ilex* is the largest genus within the family of *Aquifoliaceae,* containing thirty deciduous and more than 780 evergreen species which are domiciled worldwide (Galle, 1997). *Ilex* × *meserveae* is a hybrid between *Ilex aquifolium* L. and *Ilex rugosa* F. Schmidt. *Ilex aquifolium* is a broad-leaved species native to Europe, Western Asia and North Africa. This holly species has a high ornamental value due to its red fruits and glossy and dark green leaves (Fig. 1), but does not grow well on the east coast of the United States of America because of its sensitivity to extreme frost. *Ilex rugosa* is native to Northern Japan and its most important features are low shrubby growth habit and winter hardiness. During the 1940s the demand for broad-leafed hollies with good winter hardiness rose and Kathleen Meserve started hybridization of hollies in the late 1940s (Pair, 1984; Andrews, 1988). At the beginning of the 1950s she succeeded with crossings of *I. aquifolium* and *I. rugosa* and, as hoped, they inherited the glossy leaves of the male *I. aquifolium* parent and the increased winter hardiness of the female *I. rugosa* parent. She called the new hybrids blue hollies and the first surviving plants from cuttings were called ‘Blue Boy’ and ‘Blue Girl’.

Crop physiological aspects

In protected cultivation, climate – i.e. temperature, irradiation and photoperiod – has been used as a tool for production control in commercial production since the 1960s (Searle & Machin, 1968). In early commercial productions, the individual grower’s own experience and skills were crucial for good crop quality and right timing. Nowadays, growers have a great number of technical tools and the knowledge of many decades of investigations on the impact of climate (Brødum & Heins, 1993; Larsen & Hidén, 1995; de Smedt *et al.*, 1996), water supply (Mortensen, 2000), supplementary lighting (Weir, 1975; Mortensen & Gislerød, 1994; Van Labeke & Dambre, 1998) plant nutrition (Silberbush & Lieth, 2004), air humidity (Mortensen, 2001) and hormone spray (Forshey, 1982; Borden & Campell, 1984) on various crops’ growth and development. Timing and crop quality are, however, still most important for profitable production (Fisher *et al.*, 1996).

Plants are complicated and highly integrated systems with growth patterns that are genetically determined and modified by the environment. The formation of a leafy shoot is the result of a perfectly coordinated functioning of many sub-processes, which are affected *per se* by different factors (Crabbé & Barnola, 1996). Only one limiting factor of either internal or external character can constrain growth.

Temperature modifies the rate of growth and development due to its impact on photosynthesis (Farquhar & Caemmerer, 1982), respiration (Hansen *et al.*, 1994), nutrient uptake (Ingestad, 1979), enzyme kinetics (Farquhar, 1979) and relative humidity (Mortensen, 2000). At low temperatures the energy available is often too limited to maintain the biochemical processes for maintenance of growth. At too high temperatures, enzymes become inactivated or denatured, leading to plant stress or death (Larcher *et al.*, 1973). Although it is known that the temperature of the leaves can deviate substantially from the air temperature due to either high energy fluxes (Nobel, 1983) or transpiratory cooling (Hatfield & Burke, 1991), the moderation and monitoring of air temperature is a common approach when controlling plant responses (Berry & Raison, 1981). In greenhouse chambers the air movements vary depending on the temperature setpoint and the outdoor temperature and irradiation.

Figure 1. Developmental stages of blue holly *(Ilex* × *meserveae* ‘Blue Princess’ S.Y. Hu) during one season. 1) Vegetative growth. 2) Flower bud development and anthesis 3) Fruit ripening and mature fruits. Pictures: Andrea Kosiba.

During summer, in cooler treatments, the vents have to be opened more often than in warmer treatments in order to keep the set-point temperature. Both air temperature and air movement influence the air humidity which in turn has an impact on photosynthesis. In climate chambers, the air enters the chamber with the right temperature and humidity (Table 1) and the air movement is equal for all treatments. Temperature and humidity also affect the property of the growing medium. Together with irradiation, they affect both the medium itself and the activity of the plant. Changes in pH and electrical conductivity of the growing medium can lead to changes in water supply (Oki & Lieth, 2004) and availability of nutrients for the plant (Larcher, 1994). Water and nutrient supply, however, have to be sufficient in all treatments when different temperature levels are tested, but growth rates are probably not the same in all treatments. It was reported for *Ilex crenata* that the fertilizer source (controlled release fertilizer or soluble fertilizer) did not affect growth (Ruter, 1992). Since Gilliam & Wright (1978) reported that elevated nitrogen doses prior to the flush elicited flushing earlier than in the controls, we decided to use slow-release fertilizer, where the mineralization of nutrients can be assumed to be more consistent than with several individual doses of soluble fertilizer.

It was shown very early that plant growth rises with increased temperature until an optimum is reached (Sachs, 1864). Many processes are considered within the range where the growth process rate rises linearly with temperature. This includes empirical models such as prediction models for flowering in Easter Lilly (Fisher *et al.*, 1996; Fisher *et al.*, 1997; Fisher & Lieth 2000) or *Schlumbergera* (Larsen *et al.*, 1998). Chrysanthemum has such a low optimal temperature for growth and flowering that models based on the linear approach are not sufficient for accurate prediction (Larsen & Persson, 1998). Crop models are effective tools for prediction of yield or time of flowering in greenhouse production. Irrespective of the mathematical approach, the impact of greenhouse climate on the crop and the possibility to control the production time of the crop are of major importance. The basis for all models is the analysis of growth in a particular crop in different climate conditions. For most major greenhouse crops one or more models have been developed, for example in tomato (Heuvenlink, 1996), cucumber (Liebig, 1985; Marcelis, 1994), lettuce (Sweeney *et al.*, 1981), rose (Lieth & Pasian, 1991), chrysanthemum (Karlsson & Heins, 1985; Hidén & Larsen, 1994). In most fruit vegetable crops, leaf area and assimilate production and distribution are of major importance. In floricultural crops, the prediction of time to flower can be modelled by either temperature-driven models (Pasian & Lieth, 1994; Fisher & Heins, 1996; Larsen *et al.*, 1998) or responses to multiple environmental factors (Snipen *et al.*, 1998). The majority of existing models in horticulture are built with the focus on all plants within a crop without incorporating the variability in developmental stages within a population (Fisher & Lieth, 2000). Many floricultural crops are herbaceous plants and/or micropropagated and the variations in development within a population are low. In woody plants, however, variability within a population is higher due to their perennial character and the development of dormant structures. In this research field a stochastic approach of crop modelling is necessary to take the variability within the population into account.

As in herbaceous plants, temperature can affect woody plants directly by inducing injury or indirectly by affecting physiological processes. The status of the whole plant, such as age and developmental stage (Fig. 2), however, affects the level of climate factors' impact on growth of new shoots. Kozlowski & Pallardy (1997) summarized in their book *Growth Control in Woody Plants* internal and external growth factors affecting plant growth (Fig. 3). Their work visualized the complexity of woody plant growth.

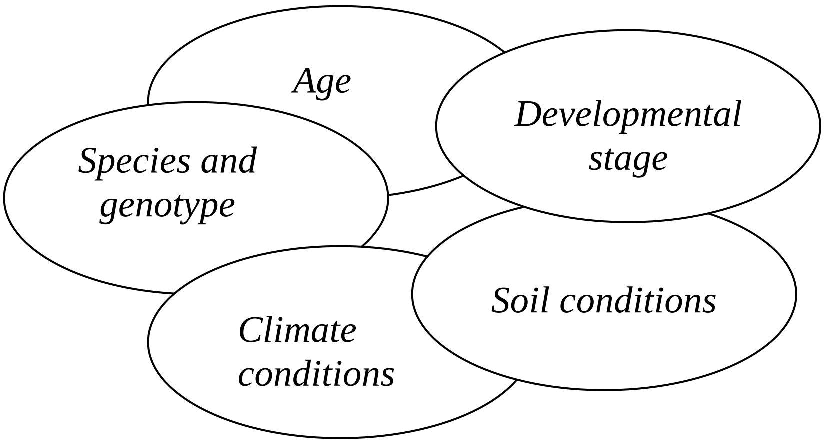

Figure 2. Factors affecting extension growth in woody plants (according to Kozlowski & Pallardy, 1997, modified).

In temperate zone woody plants, the perennial character of above ground organs requires structures to overcome unfavourable climate condition. The formation of buds, which are protected by bud scales, can be seen as the adaptation of plants to periods of unfavourable environmental conditions (Crabbé & Barnola, 1996). In red pine, the environmental conditions during bud formation influence the growth of the shoot in the subsequent year (Olofinboba & Kozlowski, 1973).

Temperature is closely connected with the phenomenon 'dormancy'. Perennial woody plants have to prepare for low temperatures by growth cessation and induction of frost hardiness. Research within the field of dormancy has been controversial from the beginning. Since dormancy is the absence of growth, and growth cessation can be caused by many factors (Fig. 3), the terminology was not consistent from the beginning. The abundance of terms developed when investigators named equivalent phenomena inconsistently. In 1987, Lang *et al.* tried to standardize dormancy classification although the overall understanding of dormancy is still limited. The same authors defined dormancy as 'a temporary suspension of visible growth of any plant structure containing a meristem'.

The most persistent theory about the physiological control of dormancy is the 'hormonal theory' (Dennis, 1994). It was believed that a delicate balance of promotive and inhibitory plant regulators kept the plants in a dormant stage. The research based on this theory, however, never succeeded in explaining how the onset and release of dormancy are controlled. More recent authors claim that the hormone theory repressed a more holistic view of dormancy. Crabbé & Barnola (1996) suggest that bud formation itself is the evidence of the establishment of dormancy. The same authors are very critical of the linear hormonal hypothesis and favour the findings of Romberger who already in 1963 considered that ‘bud formation is not strictly a matter of inhibited internodal and primordial growth’ and that bud scale formation ‘involves a specific kind of primordial development’. This matter of discussion is closely related to another field of research where the picture of control mechanisms is not clear either: rhythmic and periodic growth phenomena.

As early as the 1920s, rhythmic growth phenomena were described for *Quercus* and *Fagus* (Dostál, 1927) and the persistence of the oscillations was tested under consistent climatic conditions. In the 1940s, the flushing behaviour of the tea plant (*Camellia thea* Link.) was studied by Bond (1942; 1945) and the rhythmic flushing behaviour of cocoa (Greenwood & Posnette, 1949; Sale, 1968; Greathouse *et al.*, 1971) was investigated. Later on, horticultural crops like oak (Reich *et al.*, 1980; Alaoui-Sossé *et al.*, 1996; Mansour & Faÿ, 1998), *Ligustrum* (Kuehny & Halbrocks, 1993; Kuehny & Decoteau, 1994; Kuehny *et al.*, 1997) and holly (Mertens & Wright, 1978; Hershey & Paul, 1983) followed.

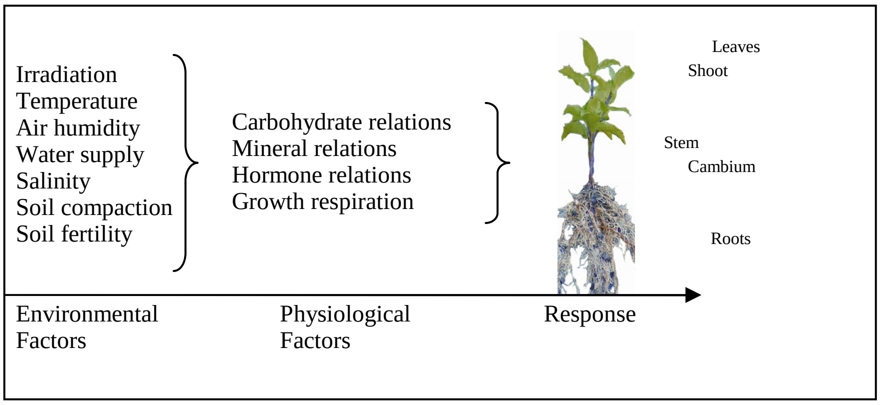

Figure 3. Illustration of environmental and physiological factors affecting growth in woody plants (according to Kozlowski & Pallardy, 1997, modified). Picture: Andrea Kosiba.

The mechanisms behind periodic growth are still not fully understood (Champagnat, 1989, Millet & Bonnet, 1990) and seem to be different for different species. Borchert (1973) suggested internal feedback in water balance, while El Morsy & Millet (1996) presented a study that indicated meristematic activity as the cause of rhythmic growth. As for dormancy, hypotheses on hormonal balance were discussed (Favre & Juncker, 1989; Whalley & Loach, 1978), but also assimilate distribution within the plant (Sleigh *et al.*, 1984; Kuehny *et al.*, 1997) has been investigated. For the tea plant (*Camellia thea*), an interaction between shoot and root growth was observed (Fordham, 1972), where in periods of maximum shoot growth, root growth seemed to be minimized, while for oak seedlings no coupling between root and shoot growth could be shown (Harmer, 1990).

In the Northern European countries, light is a limiting factor in greenhouses during a great part of the year. Many investigations were therefore focused on the effects and benefits of supplemental lighting (e.g. Nuernbergk, 1961; Weir, 1975). The quantity of light affects the production of assimilates and the developing parts of the plants are competing for the carbohydrates. The carbohydrate assimilation rises with rising light intensities until saturation is reached. At light intensities above the light compensation point, CO_2-concentration in the air becomes limiting to plant growth (Taiz & Zeiger, 1998). In vegetable production, such as tomato or cucumber, the production of fresh weight is most important. For harvest prediction in these crops, light and CO_2 concentration are therefore used as controlling factors (Heuvenlink, 1996). In ornamental plants, however, external quality of the crop is crucial for profitable production and factors affecting the morphology of the plant are important for harvest prediction (Dijkshoorn-Dekker, 2002).

Light quality is known to modify plant development (Smith, 1982; Mortensen & Strømme, 1987; Rajapakse *et al.*, 1999). Red and far red irradiation enhance extension growth (Rajapakse & Kelley, 1994) while blue irradiation inhibits extension growth (Marks & Simpson, 1999; Oyaert *et al.*, 1999; Runkle & Heins, 2001). Increased red:far-red ratios, however, reduce plant height in chrysanthemum (McMahon *et al.*, 1991; Rajapakse & Kelley, 1992). Irrespective of the kind of response, the place of perception is the phytochrome and other pigments in the leaf (Holmes & Smith, 1977; Cosgrove, 1994; Grindal *et al.*, 2000). Within those pigments a signalling pathway is started exhibited by phytohormones that enable the signals to reach all parts of the plant although perception took place in the leaves. One example of this is the shade avoidance reaction of plants (Taiz & Zeiger, 1998; Peer *et al.*, 1999). Due to a higher fraction of the far red irradiation transmitted by leaves, plants can ‘sense’ that they have competing plants nearby and start with greater extension growth (Ballaré, 1999). Cline & Deppong (1991) reported a connection between light quality and the strength of apical dominance for some trees species. Trees surrounded by vegetation are tall and slim and do apparently have a strong apical dominance, while high irradiation, to which solitary trees are exposed, seems to weaken apical dominance and leads to well branched trees. In the herbaceous long-day plant *Campanula*, however, far-red irradiation suppressed branching (Moe *et al.*, 1991). But not only light quality can alter the branching pattern. For *Dracena* (Donselman & Broschat, 1982) and apple trees (Lindhagen, 1996), a higher number of side shoots was reported for high irradiation treatments.

Daylength affects plant development. In most plants, vegetative growth is enhanced by long days and inhibited by short days (Garner & Allard, 1920; Kozlowski & Pallardy, 1997). The transition from vegetative to generative growth, however, can be triggered by either long or short days or can be completely independent of photoperiod (Thomas & Vince-Prue, 1997). The control of the daylength with blackout or darkening screens has been a common practice since the 1960s, enabling year-round production of short-day plants, such as chrysanthemum (Hidén & Larsen, 1994; Larsen & Persson, 1998) or kalanchoe (Bosse *et al.*, 1981).

Irradiation and temperature can be controlled at different levels depending on the growth environment or production site (Table 1). Besides the consistent temperature, the uniformity of the light source discriminates climate chamber from greenhouse conditions. Depending on the lamps used, the light quality in climate chambers can differ substantially from light conditions in a greenhouse (see Fig. 1 in paper IV). In greenhouses, different covering materials and shading screens can alter light quality as well as additional lighting with different lamp types can change the proportions of photons in the different wavelengths (Nuernbergk, 1961). Moreover, light from fluorescent tubes in the climate chamber is diffuse, while the direction of light in the greenhouse changes with the course of the sun. Irradiation can be measured with several different techniques and therefore the use of units is not consistent in the literature. The old units of lux and foot candle have been replaced in scientific publications with W m^{-2} and photosynthetic photon flux (PPF, mol s^{-1}) or photosynthetic photon flux density (PPFD, mol m^{-2} s^{-1}). The available brands of light sensors differ in sensitivity for certain wavelengths and the recordings from different sensors are not always comparable. In this study the brand of sensor is therefore always stated. Since irradiation fluctuates during the day and during the season, the sum of all irradiation during one day, calculated as a daily light integral (DLI), has become a common unit in research (Yeh & Hsu, 2004; Loehrlein & Craig, 2004). For this study, irradiation was measured with a spectroradiometer continuously with light sensors. Light sensors (Skye SKP 215) record the amount of photons in the photosynthetic active radiation region (PAR) with a flat photocell (Skye Instruments, Ltd, Llandringdod Wells, UK), while the spectroradiometer measures the light in W m^{-2} with a dome (Licor, Li-1800). For the comparison of the greenhouse and the climate chamber data, the continuous recordings of the light sensors were used as a measure for the fluctuation in DLI, but the absolute values for the DLI were calculated from the measurements with the spectroradiometer (paper IV).

In greenhouses, irradiation does not only provide photons for the crop, but also affects temperature inside the house. Irradiation is absorbed and converted into heat by the structures inside the house and the heat is trapped unless the greenhouse is ventilated (Laurie *et al.*, 1968). The difficulty in testing growth responses at different DLI and temperature levels lies in keeping all the other growth factors similar. Irradiation, temperature and air humidity influence each other, as soon as one of those factors is changed. Shading is a common practice in protected cultivation in order to avoid excessive heating of the greenhouse at high irradiation (Ball, 1985). During summer in Sweden, shading is often necessary. The shading cloth used can be of various materials, and besides the reduction of irradiation for photosynthesis, a change in light quality is possible. Moreover, air and canopy temperature are altered by different screen materials (Andersson, 1991). Depending on the crop, the impact of high temperatures or reduction of irradiation has to be balanced for growth and development of the crop and the timing of the sales date.

Plant propagation and plantlet development

It is known that vegetative cuttings can carry on characteristics of the stock plant to the plantlets (topophysis; Doorenbos, 1965; Van Labeke, 2000; Peer & Greenwood, 2001). We therefore decided to take cuttings for the experiments from stock plants with knowledge available about the physiological factors to which they have been exposed. For purchased rooted cuttings, such information is not obtainable.

Table 1. Control levels of climate in different growing sites.

	Temperature control	Light control	Air movement control	Application
Field	Limited	Limited	Limited	Agronomic production
Shade house	Frost protection	Protection against high irradiation	Wind reduction	Nursery production
Cold house	Fluctuations due to weather conditions, heating effect at high irradiations	Reduction of light due to reflection of cover material Fluctuating light levels	Protected environment Air movement through manually opened vents	Horticultural production, e.g. bedding plants
Heated greenhouse	Night minimum set-point Fluctuation during the day depending on irradiation	Reduction of light by reflection of cover material and shading screens Fluctuation in light levels	Protected environment Air movement when climate computer opens vents	Floricultural production Vegetable production
Climate chamber	Temperature is controlled ± 0.1 °C from set-point	Artificial light No fluctuations in light level	Constant air movement	Growth analysis studies

Moreover, for commercial propagation the entire shoot is used and both top and node cuttings can be found in a purchased batch. For several woody plant species, it has been reported that the position of the cutting affects the dry weight of the cutting and the sugar content of the rooted cutting (Van Labeke, 2000). For growth analysis, however, homogenous plant material is preferable. A mixture of different cutting types for our experiments was avoided and only top cuttings were used. General plant propagation recommendations for holly are available (Cook, 1993), but none especially for blue holly. Different propagation methods were therefore tested prior to plant propagation for the experiments.

Hypothesis

The initial main hypothesis of this thesis was that holly would perform continuous growth under greenhouse conditions and that the major factor affecting growth and development would be temperature. Since it is reported for apple trees (Lindhagen, 1996) and *Dracena* (Donselman & Broschat, 1985), we assumed that the number of side shoots would rise with rising DLI. Moreover, in literature for nurseries and gardeners, holly, *Ilex aquifolium*, which is one parent of the blue holly hybrid, is classified as a shade-tolerant plant (Sharman, 1992; Drake, 1993; Arkive, 2005). We assumed therefore that the shading practice in the greenhouses during high irradiation – to avoid undesirable heating – would not lead to major responses in blue holly.

As this hypothesis proved not to be applicable due to episodic growth, the focus of the thesis was directed towards the impact of climate on the oscillations in vegetative growth. We hypothesized that:

- Both light and temperature are decisive factors for provoking growth oscillations
- Growth oscillations are maintained in consistent climate conditions
- Side shoot formation is linked to growth oscillations
- Light quality does not affect canopy growth

Materials and methods

All experiments were performed in the experimental greenhouses and the phytotrone of the Swedish University of Agricultural Sciences in Alnarp (55°40´N, 13°05´E).

Cultivation practice

For this study four-year-old field-grown holly shrubs were used as stock plants. In June 2000, different cutting techniques, hormone concentrations and substrate mixtures were tested (Table 2). Two months prior to propagation the field-grown stock plants were planted in containers and placed in a heated greenhouse with 21 ºC set-point and outdoors in a shade house with watering facility. In all further experiments the best combination of the tested factors was used for propagation.

The cuttings were stuck in a mixture of peat-based growing medium (Hasselfors S) and perlite (Table 2) and kept in a mist chamber for eight to ten weeks. When propagated during seasons with natural short day, supplemental lighting with high-pressure sodium lamps (Philips, 400 W), to achieve a 16 h day, was provided. In the mist chamber set-points for root temperature and air temperature were 20 ºC and 22 ºC, respectively.

Table 2. List of propagation methods tested for blue holly (*Ilex* × *meserveae*).

	Level 1	Level 2	Level 3	Level 4
Cutting type	Top cutting	Heel cutting	–	–
IBA[x] concentration	No hormone	0.3%	0.6%	1%
Growth medium	30% perlite 70% medium	70% perlite 30% medium	–	–
Stock plant location	Greenhouse	Field	–	–

[x] Indole butyric acid

After the rooting phase the cuttings were transplanted in dark plastic pots with a diameter of 11 cm (greenhouse experiments) or acrylic tubes at a size of 30 cm and a diameter of 11 cm (climate chamber). Slow-release fertilizer (3 kg m^{-3}, 18N-6P-12K, 8 months) was always added as a top dress one day after transplanting. Nutrient release from the fertilizer was monitored in a plantless system for different temperature regimes resulting in non-significant differences at 15, 21 and 26 °C (data not shown).

Field-grown stock plants were transplanted in containers and kept in a heated greenhouse together with an assortment of ornamentals and their most common pests. The observed pests on holly were classified by Kersti Hesseldahl in 2001 (Svenska Predator).

Experimental set-up

Since it is almost impossible to achieve exactly the same climate conditions in two different greenhouse compartments, we decided to do the replication of the treatment in the same greenhouse compartment, but on separate benches. In the climate chambers the same positioning was chosen due to space restrictions. Further details are described in papers I and IV.

The ramified structure of woody plants causes competition for assimilates and nutrients within the plant (Kozlowski & Pallardy, 1997). To reduce the complexity of the experimental system, only one shoot per plant was allowed to develop. After transplanting the rooted cuttings regrowth was awaited for two weeks before the most prominent shoot was chosen. All other sprouting shoots were removed. The selected shoot was pinched to start the experiment.

The impact of photoperiod on holly was studied. Two groups of plants (n = 50) were exposed to the same DLI, but with long day (16 h) and short day treatment (8 h), respectively. The daylength treatments were achieved by two greenhouse compartments with blackout facilities. The same DLI for both treatments was attained by supplemental lighting with SON-T lamps (400 W, Philips) either during the day or as day extension. The rooted cuttings had reached the resting phase after the first flush, when exposed to the treatments.

Measurements and recordings

Air temperature was recorded with two thermocouples (type T) in each temperature chamber. The photosynthetic photon flux density (PPFD) was recorded at plant level using Skye SKP 215 quantum sensors (Skye Instruments Ltd, Llandringdod Wells, UK). The climate data were collected continuously at intervals of 5 s using a datalogger (Intab, Sweden).

The traditional measurement of shoot length for growth analysis did not work for holly due to the oscillating vegetative growth. Many leaves were unfolded during a very short time and leaves expand while still being attached to the shoot tip (Fig 4, stage C). The measurement of the length of the shoot up to the actual shoot tip would not have been possible without touching and thereby running the risk of disturbing shoot growth or harming the young leaves. Thus, the method of counting nodes was applied.

In the climate chamber experiment, the rooted cuttings were grown in transparent acrylic tubes to enable root observations. This method was adopted from studies with *Ilex crenata* (Mertens & Wright, 1978; Murdoch *et al.*, 1974). After transplantation, the existent roots were marked on the outside of the tube and the root tips of visible roots were marked outside the tube once a week during the entire experiment. At the end of the experiment the distance between the marks was measured.

Analysis of growth oscillations

To be able to compare treatments despite the poor synchronization of plants within treatments, an adapted *sine* curve (paper II) was fitted to each individual plant of the greenhouse (paper III) and climate chamber experiment (paper IV). The quality of root observations was evaluated by the number of continuous measurements of one single root. Only plants with more than six consecutive measurements were used for further analysis. From the observed root growth rates we calculated the accumulated root growth and the adapted *sine* curve could be fitted to the root growth curves. The root and shoot growth curves were simulated as growth rates and plotted against time. Then the data were evaluated visually, if the root-shoot growth was in phase or not.

The parameter values A and B, representing the amplitude and the frequency of the oscillation, were analysed further for differences between the treatments. Moreover, the different types of oscillation patterns were categorized (paper III) and plotted in percentage distribution for each treatment. The categories are presented in Fig. 3 in paper III and are defined as follows: 1F = one flush; 1FL = one flush with a resting period > 30 days; 2FT = a trend towards two flushes is visible, but the resting period is shorter than 10 days; 2F = two visible flushes with a resting period between 10 and 30 days; 2FL = two flushes with a resting period longer than 30; 3FT = a trend towards three flushes is visible, but the resting periods are shorter than 10 days; 3F = three visible flushes with a resting period between 10 and 30 days.

Results and discussion

Vegetative growth

Leaf unfolding

Blue holly shrubs grown outdoors perform one flush per season, in Southern Sweden starting at the end of May after flowering (Galle, 1997). Only during one unusually warm autumn (2000), a second flush per season could be observed. Several flushes, however, occurred in the more persistent climate of a heated greenhouse (Paper I). The course of one flush could be divided into different stages which are shown in Fig. 4.

The flush was initiated when the dormant terminal bud (stage A) started swelling (stage B). The first leaves unfolded and the stem followed by elongation (stage C). Leaf unfolding and stem elongation slowed down and the last leaves were unfolded (stage D). Stem elongation terminated, a terminal bud was formed and leaves expanded to full size (stage E). Finally the leaves became dark green and leathery, the lignification of the stem started and stage A was reached again.

As shown for many other woody and herbaceous plants (Garner & Allard, 1920; Snyder, 1972; Kozlowski & Pallardy, 1997), long day treatment enhanced vegetative growth in blue holly, while short day treatment led to growth cessation. This was most evident when we observed the number of plants switching from one stage of flush to the next. In long day conditions more than 70% of the plants had shifted from stage A (resting apical bud) to stage B (swelling of the apical bud) after 14 days (Fig. 5a), while in the short day treatment only 25% reached that stage (Fig. 5b). In long days all plants had started to grow after 9 days, while in short day all plants started to grow after one month. In the long day treatment the percentage of plants in the same stage varies between 90% and 100% (Fig. 5b). This may lead to the assumption that the synchronization in this treatment was good. However, this was not the case, since the shift from one stage to the next was not synchronized among individuals.

Growth oscillations

Temperature and DLI had an impact on the growth oscillations in holly. In some treatments (e.g. 4.7 mol m^{-2} d^{-1} and 25.8 °C) the plants grew nearly continuously while in others, only one evident flush occurred (0.6 mol m^{-2} d^{-1} and 18.3 °C). When analysing the growth curves based on the mean values for every treatment, only four of the 16 treatments resulted in visible periodic growth patterns (Paper I). Besides the impact of climate, this was due to poorly synchronized plants and different oscillation categories within one treatment (Paper III).

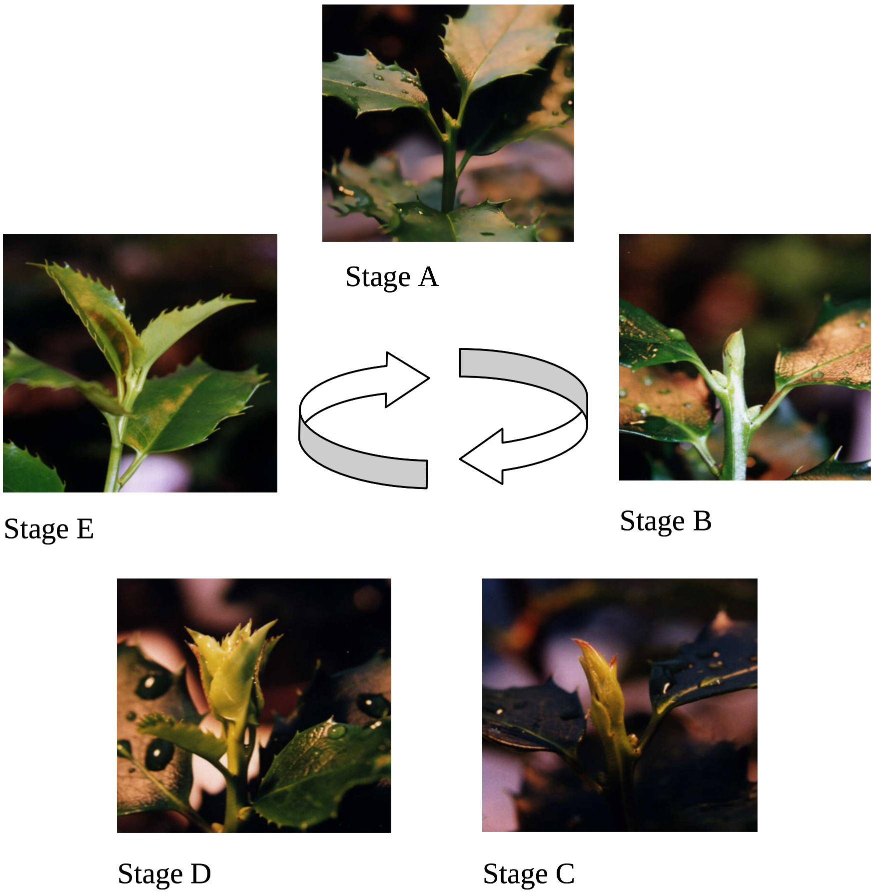

Figure 4. Developmental stages of the vegetative growth of Blue Holly (*Ilex* × *meserveae* 'Blue Princess'). Stage A) Dormant terminal bud. B) Terminal bud starts swelling. C) The first leaves start unfolding and the stem starts elongating. D) Leaf unfolding and stem elongation slow down. E) Stem elongation is terminated, the terminal bud is formed and the leaves expand to full size. Pictures: Andrea Kosiba.

After categorizing every single plant we found in almost every treatment individuals with oscillating growth behaviour, but the proportions varied substantially (Paper III). The fitting of the modified *sine* function (Paper II) to every individual plant resulted in values for the amplitude and for the frequency, respectively. For the amplitude significant differences within the DLI levels could be found at all temperatures (Paper III, Fig. 8). The frequency was only affected in the higher temperature levels. When the overall responses of amplitude and frequency were comparing (Paper IV, Fig. 6), the data for the climate chamber were more consistent than those for the greenhouse.

As possible mechanisms behind rhythmic growth in plants, changes in water status (Borchert, 1975) or hormonal status (Abo-Hamed *et al.*, 1981; Favre & Juncker, 1989), climate and nutrients (Sale, 1968; Phares, 1971; Farmer Jr., 1975) as well as carbon translocation (Hanson *et al.*, 1988; Dickson, 1989; Dickson *et al.*, 2000a; 2000b) were suggested. Since the oscillations can be altered by different climate conditions, but persist in consistent climate, we assume that it is most likely that a cyclic distribution pattern with the partitioning of limited assimilates either to the roots or the shoots could be the controlling factor for recurrent flushes (Botwright *et al.*, 1998). Further aspects are discussed in Papers I and III.

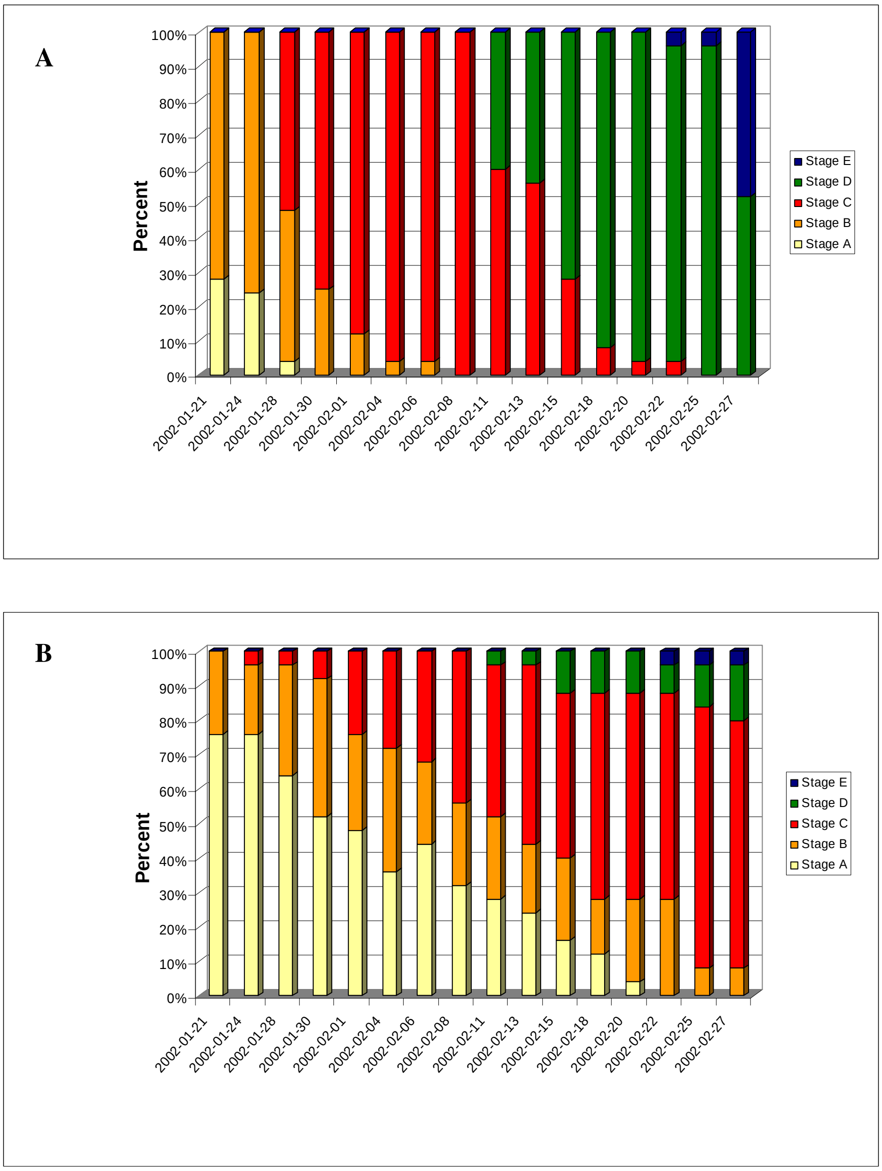

Figure 5. Effect of photoperiod on the developmental stages in vegetative growth of holly. A) long day treatment (16 h). B) short day treatment (8 h). n = 50.

Root-shoot growth

The root observation method adopted from Murdoch *et al.* (1974) and Mertens & Wright (1978) was not satisfactory for our purpose of studying root-shoot growth in blue holly. Many roots did not grow long enough along the acrylic tube wall to be observed for six consecutive weeks. We rated plants with at least six consecutive measurements as sufficient to see one period of a growth cycle. In no climate treatment consecutive root observations for all 10 plants could be made (Fig. 6). Only in the 26 °C treatments the number of plants with more than six consecutive measurements was higher in all irradiation treatments than in the measurements with less than six measurements. The remaining small number of plants with satisfying root observations did not show any conclusive picture as to whether root-shoot growth in blue holly could be considered as growing in phase or not (data not shown).

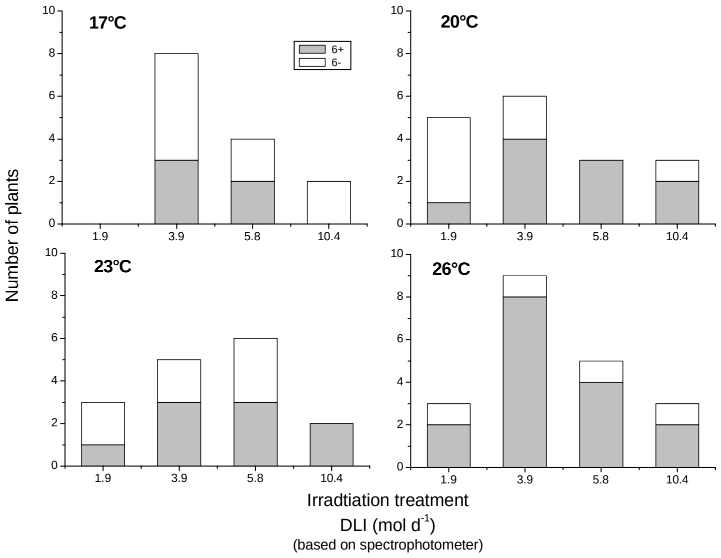

Figure 6. Number of plants with more (6+) or less (6–) consecutive root measurements (n = 10) in *Ilex* × *meserveae* ‘Blue Princess’ grown in transparent acrylic tubes in climate chambers at daily mean temperatures of 17, 20, 23 and 26 ºC and a DLI of 1.9, 3.9, 5.8 and 10.4 mol d^{-1} (Li-1800).

Ilex crenata (Mertens & Wright, 1978) showed episodic growth with the flush of root growth preceding shoot growth and for red pine seedlings, inversely leaf and root growth could be observed (Drew, 1982). Gilliam & Wright (1978) reported that the fertilization prior to shoot flush had an impact on the growth of the shoot, but that the shoot did not respond to applications made during the flush. Moreover, it was reported for *Ilex cornuta* (Ruter, 1992) that the method of fertilizer application (slow release or liquid fertilizer) had no influence on shoot growth.

Since our root observation data were patchy we could not draw any conclusion concerning the effect of fertilization. To eliminate the fertilization factor and especially the role of nitrogen (Gilliam & Wright, 1978) as a triggering factor for the growth oscillations, more studies with root observations and tissue N analysis in the leaves are needed. An alternative method for root analysis should therefore be reconsidered.

Side shoot formation

In the greenhouse, the number of side shoots was highest at 20.6 °C and differed significantly from all the other temperature treatments. At 2.1 and 3.7 mol m^{-2} d^{-1} (Skye) significantly more side shoots emerged from the main shoot compared to 0.6 and 4.7 m^{-2} d^{-1} treatment. In the climate chamber the optimum temperature for side shoot formation was 23 ºC. Side shoots only developed after the dormant phase of the shoot (data not shown) and they emerged from the base of the new flush, i.e. the oldest nodes of the flush. In treatments resulting in a high number of side shoots, side shoots even emerged from the youngest nodes of the previous flush. In paper I we were able to conclude that the best side shoot formation and pronounced periodic growth occurred in the same climate conditions. In paper III the categorization for the data of the greenhouse experiment showed that the most side shoots occurred in the categories 2F and 3F, which were the categories with the most evident growth oscillations. In the climate chamber the pattern of distribution within the different oscillation categories was not as clear under greenhouse conditions (Paper IV). The overall number of side shoots for the experiment in the greenhouse and in the climate chamber did not differ significantly. Since the side shoots only developed after the resting phase between two flushes, the number of leaves below the first side shoot was high in treatments with almost continuous growth (e.g. 25.8 °C) and low in treatments with a reduced leaf unfolding during one flush (e.g. 0.6 mol m^{-2} d^{-1}; paper I).

The initial hypothesis that the number of side shoot will rise with rising DLI as reported for apple (Lindhagen, 1996) and *Dracena* (Donselman & Broschat, 1985) could not be confirmed in our study. The highest number of side shoots occurred in climate conditions with relatively low DLI where we could observe pronounced oscillations in vegetative growth. We have two explanations for this result: (1) Increased side shoot formation is a strategy of holly to increase leaf area when exposed to lower light conditions, since common holly (*Ilex aquifolium*) is an understory species (Arkive, 2005). (2) The dominance of the apical bud is low during switch from the resting period to the swelling of the bud (stage A to stage B) and only during this phase the otherwise paradormant axial buds (Lang *et al.*, 1987) can compete for assimilates and develop.

For apple it was shown that 26 ºC led to more growth of side shoots (Tromp, 1993), which could not be confirmed with our experiments. Abbas *et al.* (1980) reported for apple that five days lasting cool temperatures (10 ºC) during early shoot development enhanced further side shoot development. The change of temperature during the different developmental phases of growth has not been subject of this study, but since we could show that climate has an impact on side shoot formation in holly, controlled changes in climate during development could be a tool to manipulate and shape holly plants without the use of chemicals.

Dry weight and leaf number

No interaction between daily light integral and temperature could be found for the growth oscillations or other variables measured at the end of the experiment. Irrespective of temperature level the DLI levels showed similar patterns for e.g. dry weight, leaf number or stem diameter and *vice versa*, both in the greenhouse and in the climate chamber (Paper I and IV). This pattern was also evident when parameter values of the amplitude (A) and frequency (B) were estimated (Paper III).

In the greenhouse the response curve for dry weight followed a curve with the optimum at 23 ºC. This result could not be confirmed with the climate chamber data, since we observed a linear rise of dry weight with rising temperature (Paper IV). Due to the steady climate the climate chamber results seem to be more reliable, showing that the optimum for dry weight production lies above the 26 ºC tested in our experiments. The deviations in dry weight between greenhouse and climate chamber could be explained by the light source. Cool fluorescent tubes emit little heat and moreover, in the climate chamber the air is moved all the time. In the greenhouse the plants were exposed to natural irradiation, which in the treatment with the highest DLI could have caused physiological stress for the plants by either high leaf temperatures or high root temperatures due to the use of black pots. The actual growth suppressing factor might therefore have been insufficient water supply due to high transpiration or evaporation from the substrate surface. A very thin shading cloth might have reduced, but probably not minimized this effect. The risk of poor water supply in treatments with high DLI, could be eliminated by the use of a tensiometer and additional watering as needed.

Evaluation of plant development

In the greenhouse, in the treatment where the *sine* function could best reflect shoot growth (95% of the plants) was at 23.9 °C and 2.1 mol m^{-2} d^{-1} (Skye). At 18.3 °C and 20.6 °C at 0.6 mol m^{-2} d^{-1}, all plants showed long resting periods (category 1FL and 2FL) and the *sine* function could not give a good fit to the shoot growth data (Paper III). In the climate chamber experiment, over 35% of the plants were classified as belonging to category 2FL. At higher amplitudes the *sine f*unction did not give a perfect fit to the data, resulting in lower R^2 values in these categories.

In Paper II, the model theory was presented. Climate chamber grown *Codiaeum* showed a persistent periodic growth pattern and the model fitted these data extremely well. Moreover, the data of the 15 plants observed by Welander (1988) must have been almost synchronized.

Since side shoot development is closely connected with the growth oscillation (Paper I and III), the *sine* function used in our study would be a suitable tool for a future prediction model. That the adapted *sine* function only resulted in satisfactory curve fitting when pronounced oscillations occurred is not a disadvantage as it is desirable to grow plants with many side shoots, hence at climate conditions were pronounced growth oscillations occur.

Commercial aspects

Plant propagation

Cuttings of blue holly plants which were propagated at the end of July (softwood phase) and with a treatment of 0.6% indole butyric acid (IBA) quick dip before sticking showed the highest rooting success (99%, Table 2). Moreover, the time of rooting was shortest during summer. This time of propagation, however, does not fit in with summer cultivation. When cuttings were taken during winter, the rooting success was still more than 90%, but depending on the weather, the rooted cuttings would have to be stored until transplantation for production in June. How this cold storage might influence further plant growth and development is not yet known. In commercial nursery production, cuttings are taken during summer. Depending on the date of cutting, the rooted cuttings preferably develop shoots until the onset of dormancy in autumn (Van Labeke, 2000). When cuttings are propagated during winter, they should not start to grow since they have to be cold-stored until the beginning of June. A misted rooting chamber with cold air and warm rooting substrate should therefore be tested as a possible propagation method for summer production in the greenhouse (Lindqvist, pers. commun.). For *Ilex crenata* cultivars it was shown that elevated nitrogen levels prior to the flush promoted the growth of the first flush (Scott, 1972; Gilliam & Wright, 1978). Yeager & Wright (1981) reported that nitrogen levels above 300 ppm increased the root:shoot ratio in *Ilex crenata* Thunb. ‘Helleri’ and reduced the time required for a shoot growth flush to occur. These results point out the possibility to control the vegetative growth flushes in blue holly with a fertilization strategy, but further investigations are needed.

Table 3. Date of propagation, duration of rooting and rooting success in *Ilex* × *meserveae* ‘Blue Princess’ S.Y. Hu.

Date	Duration of rooting	% successfully rooted
19 June 2000^{x}	9 weeks	81% ^{z}
12 Dec. 2000^{y}	10 weeks	91%
24 July 2001^{y}	8 weeks	99%
5 July 2002^{y}	9 weeks	97%

[x] Propagation methods presented in Table 2.

[y] Top cuttings from field-grown stock plants, 0.6% IBA.

[z] Mean of all tested treatments presented in Table 2.

Generative growth

Experiments within a master student’s project showed no significant differences for photoperiod as the eliciting factor for flower bud development. Furthermore, flower buds only occurred on mature shoots and when no other vegetative growth occurred on the same shoot (Engström, 2002). These results indicate that the amount of light and the developmental stage of the shoot do have a major impact on flower bud development. Especially the interaction between light and shoot development seem to be determining factors. If the plants are exposed to high light levels, they start a new flush cycle right after the last one is completed and no flower buds are developed. If the light levels are too low, it seems that the assimilate resources are not sufficient for flower bud development. This fact does not exclude the possibility that climate conditions during shoot development can be important to promote flower bud development as is known for apple (Tromp, 1993). When buds developed in greenhouse-grown plants, there were fewer flower buds per inflorescence compared to the stock plants outdoors (data not shown).

Within the male plant population flowering individuals could be found for the time span of two months, while the time period for female plants was only one month (data not shown). Under greenhouse conditions, the pollination of the dioecious holly plants has to be provided. In the greenhouse no natural pollinating insects are present and the air flow seems not sufficient. In orchards the use of honey bees is recommended to enhance pollination (Appelton *et al.*, 1996), but for the use in greenhouses, bumble bees might be more adequate, as they already are used commercially for the pollination of tomato (Biobest Biological Systems, 2005).

Pests in the greenhouse affecting holly

Stock plants in containers which were kept under heated greenhouse conditions with high pest pressure showed infestation with soft scales (*Saisettia coffeae*) and palm thrips (*Parthenothrips dracaenae*). The soft scales did not harm the plant itself, but were difficult to control and regenerated much faster in the greenhouse than in the field. It was, moreover, very laborious to remove the animals from the plant. Thrips were mostly found in the young leaves, but the damage was permanent and plants became unacceptable for marketing (Fig. 7). Leaf mealy bugs could be found on rare occasions.

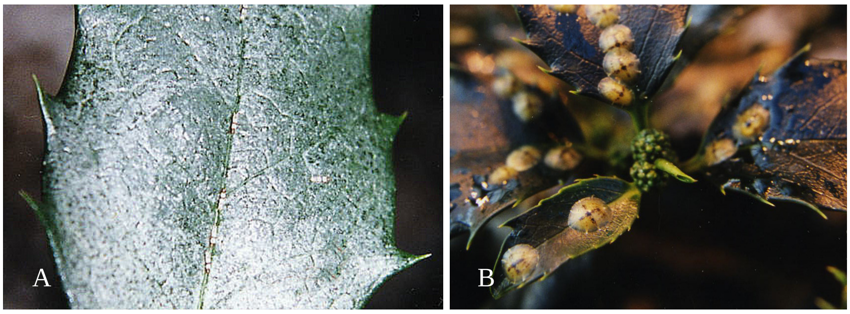

Figure 7. A) Palm thrips (*Parthenothrips dracaenae*) and B) soft scales (*Saisettia coffeae*) on blue holly *(Ilex* × *meserveae* ‘Blue Princess’ S.Y. Hu). Pictures: Andrea Kosiba.

Conclusions

The results confirmed our hypothesis that the vegetative growth oscillations in blue holly persist in constant climate. The tested daily mean air temperatures and daily light integrals (17, 20, 23 and 26 °C and 1.9, 3.9, 5.8 and 10.4 mol d^{-1}; Li-1800) altered the growth oscillations in a range from almost continuous growth to one distinct flush. Individuals with cyclic growth behaviour could be found in almost all treatments, but synchronization within treatments was poor. Competition between root and shoot growth for assimilates is likely to be the reason for the cyclic growth of the shoot, but could not be confirmed due to patchy data from the root observations. The growth oscillations are of major importance for the production of well branched holly pot plants, since individuals with pronounced growth oscillations also developed the highest number of side shoots. This assumption corresponds to the fact that *Ilex aquifolium* is a shade tolerant understory species (Stalter, 1979; Sharman, 1988; Arkive, 2005). A temporary loss of apical dominance during the switch from the dormant bud to the start of leaf unfolding (from stage A to stage B, see Fig. 4) might be a possible control mechanism to increase leaf area during sub-optimal light conditions. However, our study also showed that blue holly performed a shade avoidance growth when exposed to red and far-red light. Our hypothesis that light quality would not affect canopy growth could therefore not be confirmed.

Future research

Scientific aspects

In this study we exposed rooted cuttings to various climate conditions and investigated the impact of the climate on the growth response. Although uniform cuttings were used for the study, we had to cope with poorly synchronized plant material and by cultivation in growing medium, root growth could not be tracked satisfactorily. In future investigation we would therefore prefer to test micropropagated holly plants (Morte *et al*., 1991) and adapt a hydroponic or airoponic system to enable non-destructive root observations and N uptake measurements (Cabrera *et al*., 1995).

To prove our assumption that limited assimilates are partitioned in turns to the shoots and the roots of the plant, forcing it into a cyclic growth pattern, continuous photosynthesis measurements together with observation and analysis of shoot and root growth would be necessary and should be conducted for several growth cycles.

To get a deeper insight into the connection between the growth cycles and side shoot formation, continuous observations of the amount and type of phytohormones in the apical and the axillary buds would be needed.

Lang *et al.* (1987) defined the growth cessations between flushes as rhythmic dormancy, but the factors triggering dormancy (i.e. what type of dormancy: endo-, eco- or paradormancy) are not known. For ecodormant birch (i.e. dormancy induced due to external factors) an interruption of cell-to-cell communication in the apical meristem was reported by Van der Schoot (1996). Similar investigations during the dormant phase between the flushes might elucidate the type of dormancy occurring between flushes in holly.

Applied aspects

This thesis is a first step towards blue holly as a potential greenhouse crop for summer production. For a crop blueprint, the following questions have to be addressed:

- When is the best time during the year to take cuttings for summer production and how does the cooling treatment during transport and storage affect further growth responses in the greenhouse?
- Does competition between shoots alter growth oscillations that we observed during the experiments with only one shoot allowed to grow?
- What are the factors eliciting flower initiation and development?
- Could short day treatment be a tool to elicit pronounced resting periods which lead to good side shoot development?
- How can the plants be synchronized to obtain uniform production?
- Are bumble bees suitable as pollinating insects?

References

Abbas, M. F., Quinlan, J. D. & Buckley, W. R. 1980. Influence of early-season temperature on the growth and branching on newly-grafted apple trees. *Journal of horticultural science* 55, 437-438.

Abo-Hamed, S., Collin, H. A. & Hardwick, K. 1981. Biochemical and Physiological Aspects of Leaf Development in Cocoa (*Theobroma cacao*) VI: Homonal Interaction Between Mature Leaves and the Shoot Apex. *New phytologist* 89, 191-200.

Alaoui-Sossé, B., Ricaud, S., Barnola, P. & Dizengremel, P. 1996. Rhythmic growth and carbon allocation in *Quercus robur*. Sucrose metabolizing enzymes in leaves. *Physiologica plantarum* 96, 667-673.

Andersson, N. E. 1991. Relation between water vapour pressure difference and canopy temperature under different shading screen materials. *Tidskrift for planteavl* 95, 427-432.

Andrews, S. 1988. The Blue Hollies. *The gardener* 1, 43-45.

Appleton, B. L., Spivey, A. D. & French, S. C. 1996. Virginia cut holly production: Holly pollination and honey bees. *Virginia State University.* http://www.ext.vt.edu/pubs/holly/430-468/430-468.html (retrieved: 18 March 2005).

Arkive, Images of life on earth. Common holly (*Ilex aquifolium*). http://www.arkive.org/species/ARK/plants_and_algae/Ilex_aquifolium/more_info.html (retrieved: 23 March 2005).

Ball, V. 1985. Five other practical labor savers. *in: Ball Redbook - Greenhouse growing*. 14th edition. Reston Publishing Company, Inc. Virginia, USA. pp. 109-117.

Ballaré, C. L. 1999. Keeping up with the neighbours: phytochrome sensing and other signalling mechanisms. *Trends in plant science* 4, 97-102.

Berry, J. A. & Raison, J. K. 1981. Responses of macrophytes to temperature. *in: Encyclopedia of plant physiology. Physiological plant ecology I. Responses to the physical environment*. Springer Verlag. Berlin. pp. 277-338.

Biobest Biological Systems. 2005. Advantages of the use of bumblebees. http://207.5.71.37/biobest/en/bestuiving/voordelen.htm (retrieved 23 March 2005)

Bond, T. E. T. 1942. Studies in the Vegetative Growth and Anatomy of the Tea Plant (*Camellia thea* Link.) with Special Reference to the Phloem I. The Flush Shoot. *Annals of botany* 6, 607-633.

Bond, T. E. T. 1945. Studies in the vegetative growth and anatomy of the tea plant (*Camellia thea* Link.) with special reference to the phloem. II. Further analysis of flushing behaviour. *Annals of botany* 9, 183-216.

Borchert, R. 1973. Simulation of Rhythmic Tree Growth under Constant Conditions. *Physiologica plantarum* 29, 173-180.

Borchert, R. 1975. Endogenous Shoot Growth Rhythms and Indeterminate Shoot Growth in Oak. *Physiologica plantarum* 35, 152-157.

Borden, P. & Campbell, R. W. 1984. Response of *Ilex* × *meserveae* 'Blue Princess' to Hand Shearing and Three Growth Retardants. *Hortscience* 19, 285-287.

Bosse, G., Escher, F., Gugenhan, E., Kneipp, O. & Steib, T. 1981. *Kalanchoe blossfeldiana*. *in: Hauptkulturen im Zierpflanzenbau; Handbuch des Erwerbsgärtners*. Verlag Eugen Ulmer. Stuttgart. pp. 321-335.

Botwright, T. L., Menary, R. C. & Brown, P. H. 1998. Photosynthesis and assimilate partitioning during rhythmic growth of green tea (*Camellia sinensis* var *sinensis*). *Journal of horticultural science and biotechnology* 73, 806-811.

Brøndum, J. J. & Heins, R. D. 1993. Modeling Temperature and Photoperiod Effects on Growht and Development of Dahlia. *Journal of the American society for horticultural science* 118, 36-42.

Cabrera, P. I., Evans, R. Y. & Paul, J. L. 1995. Cyclic nitrogen uptake by greenhouse roses. *Scientia horticulturae* 63, 57-66.

Champagnat, P. 1989. Rest and activity in vegetative buds of trees. *Annales des sciences forestières* 46 suppl., 9s-26s.

Cline, M. C. & Deppong, D. O. 1999. The Role of Apical Dominance in Paradormancy of Temperate Woody Plants: A Reappraisal. *Journal of plant physiology* 155, 350-356.

Cook, A. D. 1993. Hollies: a gardener's guide. *Plants & gardens. Brooklyn botanic garden record.* 49.

Cosgove, D. J. 1994. Photomodulation of growth. *in: Photomorphogenesis in plants*. Kluwer Academic Publishers. The Netherlands. 631-658 pp.

Crabbé, J. & Barnola, P. 1996. A new conceptual approach to bud dormancy in woody plants. *in: Plant dormancy*. CAB International. pp. 83-113.

Dennis, F. G. 1994. Dormancy - What we know (and don´t know). *Hortscience* 29, 1249-1255.

Dickson, R. E. 1989. Carbon and nitrogen allocation in trees. *Annales des sciences forestières* 46 (Suppl.), 631-647.

Dickson, R. E., Tomlinson, P. T. & Isebrands J.G. 2000a. Allocation of current photosynthetate and changes in tissure dry weight within northern red oak seedlings: individual leaf and flush carbon contributing during episodic growth. *Canadian journal of forest research* 30, 1296-1307.

Dickson, R. E., Tomlinson, P. T. & Isebrands J.G. 2000b. Partitioning of current photosynthetate to different chemical fractions in leaves, stems, and roots of northern red oak seedlings during episodic growth. *Canadian journal of forest research* 30, 1308-1317.

Dijkshoorn-Dekker, M. 2002. Crop quality control system: a tool to control the visual quality of pot plants. *Dissertation, Wageningen University,* The Netherlands.

Donselman, H. & Broschat, T. K. 1982. Light-induced basal branching of *Dracaena marginata*. *Hortscience* 17, 909-910.

Doorenbos, J. 1965. Juvenile and adult phases in woody plants. In: Ruhland, W., ed., *Encyclopedia of plant physiology*, Vol XV. Differentiation and development. Part 1. Springer Verlag, New York, pp. 1222- 1235.

Dostál, R. 1927. Über die Sommerperiodizität bei *Quercus* und *Fagus*. *Berichte der deutschen botanischen Gesellschaft* 45, 436-447.

Drake, J. 1993. Honey, I crossed the rhododendrons. *Oregon´s Horticultural progress* 39, 30-34.

Drew, A. P. 1982. Shoot-root plasticity and episodic growth in Red Pine seedlings. *Annals of botany* 49, 347-357.

El-Morsy, A. A. & Millet, B. 1996. Rhythmic growth and optimization of micropropagation: The effect of excision time and position of axillary buds on in vitro culture of *Citrus aurantium* L. *Annals of botany* 78, 197-202.

Engström, E. 2002. The influence of different pre-treatments and day length treatments on growth and flower development on Blue Holly. *Master thesis, Swedish University of Agricultural Sciences, Sweden.* 8.

Farmer Jr., R. E. 1975. Growth and Assimilation Rate of Juvenile Northern Red Oak: Effects of Light and Temperature. *Forest science.* 21, 373-381.

Farquhar, G. D. & von Caemmerer, S. 1982. Modelling of photosynthetic response to environmental conditions. *in: Encyclopedia of plant physiology. Physiological plant ecology II. Water relations and carbon assimilation*. Springer Verlag. Berlin. pp. 549-588.

Farquhar, G. D. 1979. Models describing the kinetics of ribulose biphosphate carboxylase-oxygenase. *Archives of biochemistry and biophysics* 193, 456-468.

Favre, J. M. & Juncker, B. 1989. Variations in expression of episodic growth by *in vitro*-cultured shoots of oak (*Quercus robur* L.). *Annales des sciences forestières* 46 suppl., 206-210.

Fisher, P. R. & Heins, R. D. 1996. The greenhouse care system: A decision-support system for height control and scheduling of potted flowering plants. *Acta horticulturae* 417, 41-45.

Fisher, P. R., Heins, R. D., Ehler, N. & Lieth, J. H. 1997. A decision-support system for real-time management of Easter Lily (*Lilium longifolium* Thunb.) Scheduling and height-I. System description. *Agricultural systems* 54, 23-37.

Fisher, P. R. & Lieth, J. H. 2000. Variability in flower development of Easter lily (*Lilium longiflorium* Thunb.): model and decision-support system. *Computers and electronics in agriculture* 26, 53-64.

Fisher, P. R., Lieth, J. H. & Heins, R. D. 1996. Modelling flower bud elongation in easter lily (*Lilium longifolium* Thunb) in response to temperature. *Hortscience* 31, 349-352.

Fordham, R. 1972. Observations on the growth of roots and shoots of tea (*Camellia sinensis*, L.) in Southern Malawi. *Journal of horticultural science* 47, 221-229.

Forshey, C. G. 1982. Branching Responses of Young Apple Trees to Applications of 6-Benzylamino purine and Gibberellin A_{4+7}. *Journal of the American society for horticultural science* 107, 538-541.

Galle, F. C. 1997. *Hollies - The Genus Ilex*. Timber Press. Oregon, USA.

Garner, W. W. & Allard, H. A. 1920. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. *Journal of agricultural research* 18, 553-606.

Gilliam, C. H. & Wright, R.D. 1978. Timing of Fertilizer Application in Relation to Growth Flushes of 'Helleri' Holly (*Ilex crenata* Thunb.). *Hortscience* 13, 300-301.

Greathouse, D. C., Laetsch, W. M. & Phinney, B. O. 1971. The Shoot-growth Rhythm of a Tropical Tree, *Theobroma cacao*. *American journal of botany* 58, 281-286.

Greenwood, M. & Posnette, A. F. 1949. The Growth Flushes of Cacao. *The journal of horticultural sciences* 25, 164-174.

Grindal, G., Mortensen, L. M. & Moe, R. 2000. Manipulation of the Daylight Spectre for Growth Control. *Advances in floricultural research* 6, 75-82.

Hansen, L. D., Hopkin, M. S., Rank, D. R., Anekonda, T. S., Breidenbach, R. W. & Criddle, R. S. 1994. The relation between plant-growth and respiration - a thermodynamic model. *Planta* 194, 77-85.

Hanson, P. J., Isebrands, J. G., Dickson, R. E. & Dixon, R. K. 1988 . Ontogenetic pattern of CO_2 exchange of *Quercus rubra* L. leaves during three flushes of shoot growth. I. Median flush leaves. *Forest science* 34, 55-68.

Harmer, R. 1990. Relation of shoot growth phases in seedling oak to development of the tap root, lateral roots and fine root tips. *New phytologist* 115, 23-28.

Hatfield, J. L. & Burke, J. J. 1991. Energy exchange and leaf temperature behaviour of three plant species. *Environmental and experimental botany* 31, 295-302.

Hershey, D. R. & Paul J. L. 1983. Ion Absorption by a Woody Plant with Episodic Growth. *Hortscience* 18, 357-359.

Heuvenlink, E. 1996. Tomato growth and yield: quantitative analysis and synthesis. *Dissertation , Wageningen Agricultural University,* The Netherlands.

Hidén, C. & Larsen R.U. 1994. Predicting flower development in greenhouse grown chrysanthemum. *Scientia horticulturae* 58, 123-138.

Holmes, M. G. & Smith, H. 1977. The function of phytochrome in the natural environment - IV. Light quality and plant development. *Photochemistry and photobiology* 25, 551-557.

Ingestad, T. 1979. A definition of optimum nutrient requirements in birch seedlings. *Physiologica plantarum* 46, 31-35.

Karlsson, M. G. & Heins, R. D. 1985. Modelling of light and temperature effects on *Chrysanthemum morifolium*. *Acta horticulturae* 174, 235-240.

Kozlowski, T. T. & Pallardy, S. G. 1997. *Growth control in woody plants*. Academic Press. Sant Diego, California.

Kuehny, J. S. & Decoteau, D. R. 1994. Interrelationship of Nitrogen and Light on Episodic Growth of *Ligustrum japonicum*. *Journal of environmental horticulture* 12, 43-46.

Kuehny, J. S., Miller, W. B. & Decoteau, D. R. 1997. Changes in Carbohydrate and Nitrogen Relationsships during Episodic Growth of *Ligustrum japonicum* Thunb. *Journal of the American society for horticultural science* 122, 634-641.

Kuehny, J. S. & Halbrooks, M. C. 1993. Episodic whole plant growth patterns in *Ligustrum*. *Physiologia plantarum* 89, 33-39.

Lang, A., Early, J. D., Martin, G. C. & Darnell, R. L. 1987. Endo-, Para-, and Ecodormancy: Physiological Terminology and Classification for Dormancy Reasearch. *Hortscience* 22, 371-377.

Larcher, W. 1994. Die Umwelt der Pflanzen. *in: Ökophysiologie der Pflanzen*. Ulmer. Stuttgart. pp. 12-47.

Larcher, W., Heber, U. & Santarius, K. A. 1973. Limiting termperatures for life functions. *in: Temperature and life*. Springer Verlag. Berlin. pp. 195-263.

Larsen, R. U., Birgersson, A., Nothnagl, M. & Karlén, H. 1998. Modelling temperature and flower bud growth in November cactus (*Schlumbergera truncata* Haw.). *Scientia horticulturae* 76, 193-203.

Larsen, R. U. & Hidén, C. 1995. Predicting leaf unfolding in flower induced shoots of greenhouse grown chrysanthemum. *Scientia horticulturae* 63, 225-239.

Larsen, R. U. & Persson L. 1998. Modelling flower development in greenhouse grown chrysanthemum cultivars in realtion to temperature and response group. *Scientia horticulturae* 80, 73-89.

Laurie, A., Kiplinger, D. C. & Nelson, K. S. 1968. Greenhouses and related structures. *in: Commercial flower forcing: The fundamentals and their practical application to the culture of greenhouse crops*. 7th edition. McGraw-Hill , Inc. New York, USA. pp. 9-36.

Liebig, H. P. 1985. Model of cucumber growth and yield. II. Prediciton of yields. *Acta horticulturae* 156, 139-154.

Lieth, J. H. & Pasian, C. C. 1991. A simulation model for the growth and development of flowering rose shoots. *Scientia horticultureae* 46, 109-128.

Lindhagen, M. 1996. Model analysis of leaf unfolding rate in *Malus domestica* Borkh. *Scientia horticulturae* 67, 65-78.

Loehrlein, M. M. & Craig, R. 2004. The effect of daily light integral on floral initiation of *Pelargonium x domestica* L.H. Bailey. *Hortscience* 39, 529-532.

Mansour, A. & Faÿ, E. 1998. Rhythmic Growth Rings of Wood and Their Relationship with the Foliage in Oak Seedlings Grown in a Favourable Environment. *Annals of botany* 82, 89-96.

Marcelis, L. F. M. 1994. A simulation model for dry matter partitioning in cucumber. *Annals of botany* 74, 43-52.

Marks, T. R. & Simpson, S. E. 1999. Effect of irradiance on shoot development *in vitro*. *Plant growth regulation* 28, 133-142.

McMahon, M. J., Kelly, J. W., Decoteau, D. R., Young, R. E. & Pollock, R. K. 1991. Growth of *Dendranthema* x*grandiflorum* (Ramat.) Kitamura under Various Spectral Filters. *Journal of the American society for horticultural science* 116, 950-954.

Mertens, W. C. & Wright, R. D. 1978. Root and Shoot Growth Rate Relationships of Two Cultivars of Japanese Holly. *Journal of the American society for horticultural science* 103, 722-724.

Millet, B. & Bonnet, B. 1990. Growth Rhythms in Higher Plants. *Progress in clinical biological research* 341B, 835-851.

Moe, R., Heins, R. D. & Erwin, J. 1991. Stem elongation and flowering of the long-day plant *Campanula isophylla* Moretti in response to day and night temperature alternations and light quality. *Scientia horticulturae* 48, 141-151.

Morte, M. A., Olmos, E., Hellin, E. & Piqueras. 1991. Micropropagation of Holly (*Ilex aquifolium*). *Acta horticultureae* 289, 139-140.

Mortensen, L. M. 2000. Effects of air humitidy on growth, flowering, keeping quality and water relations of four short-day greenhouse species. *Scientia horticulturae* 86, 299-310.

Mortensen, L. M. 2001. Greenhouse climate and keeping quality of roses. *Acta horticulturae* 543, 199-202.

Mortensen, L. M. & Gislerød, H. R. 1994. Effect of summer lighting, plant density and pruning method on yield and quality of greenhouse roses. *Gartenbauwissenschaft* 59, 275-279.

Mortensen, L. M. & Strømme, E. 1987. Effects of Light Quality on some Greenhouse Crops. *Scientia horticulturae* 33, 27-36.

Murdoch, C. L., Criley, R. A. & Fukuda, S. K. 1974. An Inexpensive Method for the Study of Root Growth in Containers of Solid Media. *Hortscience* 9, 221.

Nobel, P. S. 1983. *Biophysical plant physiology and ecology*. Freeman and Company. San Francisco, USA.

Nuernbergk, E. L. 1961. Die Praxis der Kunstlichtbestrahlung. *in: Kunstlicht und Pflanzenkultur*. BLV Verlagsgesellschaft. München, pp. 73-145.

Oki, L. R. & Lieth, J. H. 2004. Effect of changes in substrate salinity on the elongation of *Rosa hybrida* L. 'Kardinal' stems. *Scientia horticulturae* 101, 103-119.

Olofinboba, M. O. & Kozlowski, T. T. 1973. Accumulation and utilization of carbohydrate reserves in shoot growth of *Pinus resinosa*. *Canadian journal of forest research* 3, 346-353.

Oyaert, E., Volckaert, E. & Debergh, P. C. 1999. Growth of chrysanthemum under coloured plastic films with different light qualities and quantities. *Scientia horticulturae* 79, 195-205.

Pair, J. C. 1984. Versatile Blue Hollies. *American nurseryman* 159, 51-52.

Pasian, C. C. & Lieth, J. H. 1994. Prediction of flowering rose shoot development based on air-temperature and thermal units. *Scientia horticulturae* 59, 131-145.

Peer, K. R. & Greenwood, M. S. 2001. Maturation, topophysis and other factors in relation to rooting in *Larix*. *Tree physiology* 21, 267-272.

Peer, W. A., Briggs, W. R. & Langenheim, J. H. 1999. Shade-avoidance responses in two common coastal redwood forest species, *Sequoia sempervirens* (*Taxodiaceae*) and *Satureja douglasii* (*Lamiaceae*), occurring in various light quality environments. *American journal of botany* 86, 640-645.

Phares, R. E. 1971. Growth of Red Oak (*Quercus rubra* L.) Seedlings in Relation to Light and Nutrients. *Ecology* 52, 669-672.

Rajapakse, N. C. & Kelly, F. W. 1992. Regulation of Chrysanthemum Growth by Spectral Filters. *Journal of the American society for horticultural science* 117, 481-485.

Rajapakse, N. C. & Kelly, J. W. 1994. Influence of spectral filters on growth and postharvest quality of potted miniature roses. *Scientia horticulturae* 56, 245-255.

Rajapase, N. C., Young, R. E., McMahon, M. J. & Oi, R. 1999. Plant Height Control by Photoselective Filters: Current Status and Future Prospects. *Horttechnology* 9, 618-624.

Reich, P. B., Teskey, R. O., Johnson, P. S. & Hinckley, T. M. 1980. Periodic Root and Shoot Growth in Oak. *Forest science* 26, 590-598.

Romberger, J. A. 1963. Meristems, Growth and development in woody plants. *U.S. Department of agriculture, forest service, technical bulletin* 1293.

Runkle, E. S. & Heins, R. D. 2001. Specific Functions of Red, Far Red, and Blue Light in Flowering and Stem Extension of Long-day Plants. *Journal of the American society for horticultural science* 126, 275-282.

Ruter, J. M. 1992. Leachate nutrient content and growth of two hollies as influenced by controlled release fertilizers. *Journal of environmental horticulture* 10, 162-166.

Sachs, T. 1864. Über die obere Temperaturgrenze der Vegetation. *Flora* 47, 22-32.

Sale, P. J. M. 1968. Flushing and leaf growth of cacao under controlled temperature conditions. *Journal of horticultural Science* 43, 475-489.

SCB, Statistics Sweden. 2003. The 2003 Horticultural consensus concerning 2002.

Scott, M. 1972. Fast growing container shrubs respond quickly to nitrogen feeds. *The grower* 3, 730-731.

Searle, S. A. & Machin, B. J. 1968. *Chrysanthemums the year round*. Blandford Press. London, UK.

Sharman, F. 1992. Plants for Shade. 2nd edition. *The royal horticultural society, Whisley handbook.* London. p. 16.

Silberbush, M. & Lieth, J. H. 2004. Nitrate and potassium uptake by greenhouse roses (*Rosa hybrida*) along successive flower-cut cycles: a model and its calibration. *Scientia horticulturae* 101, 127-141.

Sleigh, P. A., Collin, H. A. & Hardwick, K. 1984. Distribution of assimilate during the flush cycle of growth in *Theobroma cacao* L. *Plant growth regulation* 2, 381-391.

Smedt, V. de, Van Huylenbroeck, J. M. & Debergh, P. C. 1996. Influence of temperature and supplemental lighting on growth and flower initiation of *Clivia miniata* Regel. *Scientia horticulturae* 65, 65-72.

Smith, H. 1982. Light Quality, Photoperception, and Plant Strategy. *Annual review of plant physiology* 33, 481-518.

Snipen, L., Moe, R. & Soreng, J. 1998. Predicting time to flowering with a first passage time model. *Acta horticulturae* 456, 151-160.

Snyder, W. E. 1972. Growth and Flowering Responses of *Ilex crenata* 'Convexa' to photoperiodism. *Holly letter* 43, 1-7.

Stalter, R. 1979. Some Ecological Observations on an *Ilex* Forest, Sandy Hook, New Jersey. *Castanea* 44, 202-207.

Sweeney, D. G., Hand, D. W., Slack, G. & Thornley, J. H. M. 1981. Modelling the growth of winter lettuce. *in: Mathematics and plant physiology*. Academic Press. New York. pp. 219-229.

Taiz, L. & Zeiger, E. 1998. Photosynthesis: Physiological and ecological considerations. *in: Plant Physiology.* Sinauer Associates. Sunderland, USA. pp. 227-229.

Thomas, B. & Vince-Prue, D. 1997. *Photoperiodism in plants*. 2nd edition. Academic Press. San Diego, California.

Tromp, J. 1993. Lateral shoot formation and flower-bud formation in apple in the first year after budding as affected by air temperature and exposure to light. *Journal of horticultural science* 68, 255-260.

Van der Schoot, C. 1996. Dormancy and symplastic networking at the shoot apical meristem. *in: Plant Dormancy*. CAB International. Pp. 59-81.

Van Labeke, M.-C. 2000. Morphological studies and plant growth analysis of woody plants: a tool for optimization of phytotechnical decisions. *Dissertation, University of Gent*, Belgium.

Van Labeke, M.-C. & Dambre, P. 1998. Effect of supplementary lighting and CO_2 enrichment on yield and flower stem quality of *Alstroemeria* cultivars. *Scientia horticulturae* 74, 269-278.

Weir, J. 1975. Artificial lightning for commercial horticulture. *Lighting research and technology* 7, 209-225.

Welander, N. T. 1988. Acclimatization of *Codiaeum variegatum* L. 'Aucubaefolia' to changes in photon flux density. I. Leaf production. *Journal of horticultural science* 63, 271-277.

Whalley, D. N. & Loach, K. 1978. Modification of episodic growth in *Skimmia japonica* 'Rubella' by gibberellic acid treatment. *Scientia horticulturae* 9, 83-92.

Yeager, T. H. & Wright, R. D. 1981. Influence of nitrogen and phosphorus on shoot:root ratio of *Ilex crenata* Thunb. 'Helleri'. *Hortscience* 16, 564-565.

Yeh, D. M. & Hsu, P. Y. 2004. Differential growth and photosynthetic response of selected cultivars of English ivy to irradiance. *Journal of horticultural science and biotechnology* 79, 633-637.

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