

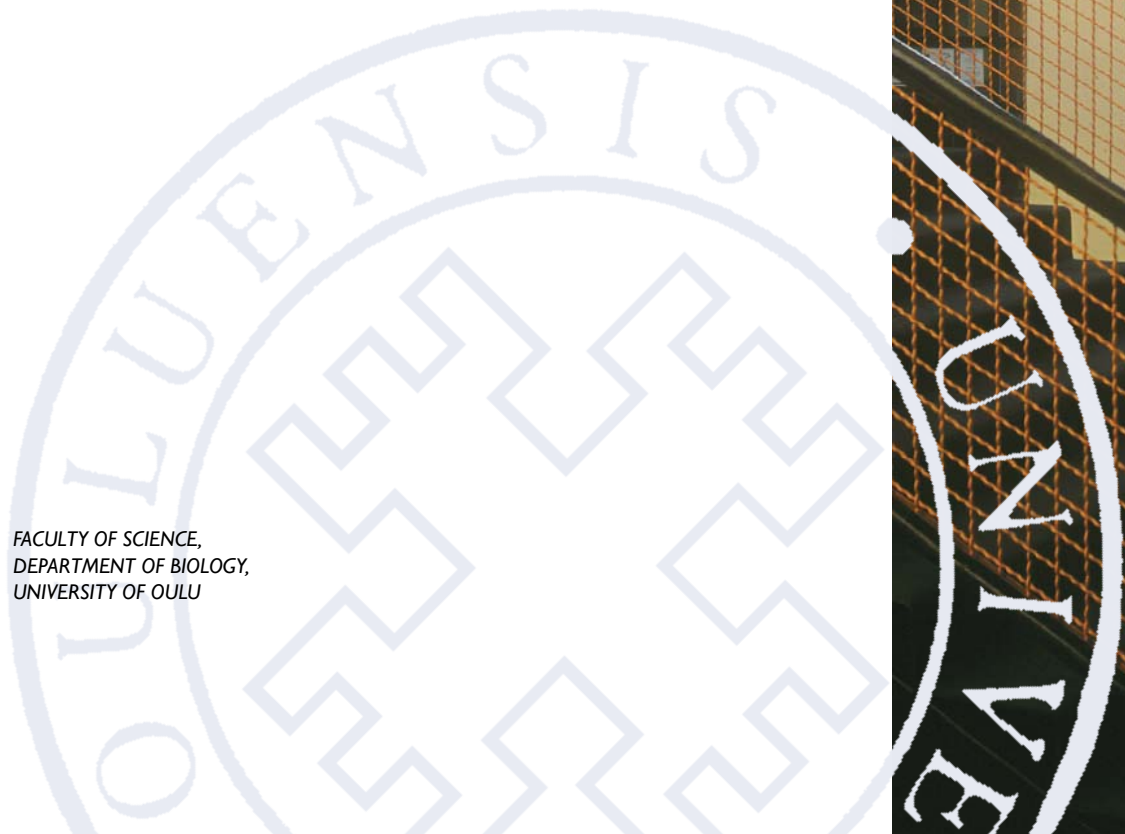
Marian Sarala

ELONGATION OF SCOTS
PINE SEEDLINGS UNDER
BLUE LIGHT DEPLETION

FACULTY OF SCIENCE,
DEPARTMENT OF BIOLOGY,
UNIVERSITY OF OULU

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MARIAN SARALA

**ELONGATION OF SCOTS PINE
SEEDLINGS UNDER BLUE LIGHT
DEPLETION**

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Supervised by
Docent Kari Taulavuori
Docent Erja Taulavuori

Reviewed by
Professor Eero Nikinmaa
Professor Jorunn E. Olsen

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Faculty of Science, Department of Biology, University of Oulu, P.O.Box 3000, FI-90014
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Abstract

The elongation response of Scots pine (*Pinus sylvestris* L.) seedlings to the removal of blue light (400–500 nm) was studied in field experiments in northern Finland. The seedlings were grown in orange or transparent plexiglass chambers or in ambient control plots. The orange plexiglass removed the blue wavelengths from sunlight, while the others served as controls. The experiment was conducted at sub-arctic (69°N) and mid-boreal (64°N) latitudes with three- and two-year-old seedlings originating from 67°N latitude. The response to blue light depletion was also investigated at the 69°N latitude in the following plant subjects: one-year-old Scots pine seedlings of northern (67°N) and southern (62°N) provenances, deciduous *Betula pubescens* ssp. *czerepanovii* and *Betula pubescens* f. *rubra* seedlings and herbaceous *Epilobium angustifolium* and *Glechoma hederacea* plants. Additionally, diurnal change in light quality at the 69°N latitude during the summer was measured.

The elongation of Scots pine seedlings was increased by the removal of blue wavelengths. The increase was more pronounced at the 69°N latitude, while at the 64°N latitude the response was smaller or absent. This is due to increased amount of scattered growth-inhibiting blue light during the nights at the high latitude.

The removal of blue light increased stem elongation in northern origin Scots pine seedlings much more compared to the southern origin seedlings, which suggests that the northern provenance is more sensitive to blue light. Irrespective of that, southern origins also suffer from reduced elongation in the north as they migrate according to climatic change scenarios. However, it is obvious that they grow longer than local origins in the north.

Morphological variables and photosynthetic pigments confirm that the increased elongation of Scots pine seedlings under blue light depletion is not a result of etiolation or it is only a marginal factor. Also, it was neither dependent on temperature nor photosynthesis and growth resources. Instead, the increased elongation is probably a photomorphogenic regulation response of metabolism. In addition, shade intolerant Scots pine, *Betula* seedlings and herbaceous *Epilobium angustifolium* responded stronger to blue light removal compared to the more shade-tolerant herbaceous *Glechoma hederacea*.

Keywords: Blue light, elongation, etiolation, gas exchange, life forms, morphology, pigments, *Pinus sylvestris*, resources, sub-arctic latitude

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Otso and Lumi for reminding me every day about what really is important in life.

Oulu, July 2010

Marian Sarala

List of original articles

The thesis is based on the following articles, which are referred to in the text by their Roman numerals:

- I Taulavuori K, Sarala M & Taulavuori E (2010) Growth responses of trees to arctic light environment. *Progress in Botany* 71: 157–169.
- II Taulavuori K, Sarala M, Karhu J, Taulavuori E, Kubin E, Laine K, Poikolainen J & Pesonen E (2005) Elongation of Scots Pine Seedlings under Blue Light Depletion. *Silva Fennica* 39(1): 131–136.
- III Sarala M, Taulavuori K, Taulavuori E, Karhu J & Laine K (2007) Elongation of Scots pine seedlings under blue light depletion is independent of etiolation. *Experimental and Environmental Botany* 60: 340–343.
- IV Sarala M, Taulavuori E, Karhu J, Savonen E-M, Laine K, Kubin E & Taulavuori K (2009) Improved elongation of Scots pine seedlings under blue light depletion is not dependent on resource acquisition. *Functional Plant Biology* 36: 1–10.
- V Sarala M, Taulavuori E, Karhu J, Laine K & Taulavuori K (2010) Growth responses and pigmentation of various species under blue light depletion. Manuscript.

Author's contribution: M. Sarala participated in carrying out the experiment in paper IV. She planned and carried out the experiments in papers II and III together with supervisors K. and E. Taulavuori and the experiment in paper V by herself. She was responsible for most of the height growth measurements (II–V) and all other morphological measurements (III and V). She was also responsible for the light measurements (I and II), gas exchange measurements (IV), statistical analyses and most of the laboratory work. She was the corresponding author for papers III–V, and participated in the writing of the papers I and II.

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1 Introduction

White light (day light) is electromagnetic radiation, which consists of ultraviolet-light (< 400 nm), visible light (400–800 nm) and infrared light (> 800 nm). Light affects plant growth in at least three ways: duration of light (day length) determines the length of growing period in some tree species (*e.g.* birches, willows) (Weiser 1970, Olsen *et al.* 1997, Junttila 2007), quantity of light speeds up photosynthesis to the saturation level of plant species (Teskey *et al.* 1994, Lambers *et al.* 1998, Taiz & Zeiger 2006) and quality of light (spectral distribution of light) affects photosynthesis through both blue- (400–500 nm) and red- (600–700 nm) light absorbing chlorophylls and blue light absorbing carotenoids. Light quality also controls plant morphogenesis, which is mediated at least by phytochrome, cryptochrome and phototropin pigments (Cashmore 1999, Parks *et al.* 2001, Franklin & Whitelam 2005, Briggs *et al.* 2006). Phytochromes mainly absorb red and far-red (700–800 nm) light, whereas cryptochromes and phototropins absorb blue light.

Light quality is determined by particles of the atmosphere in a way that after reaching the atmosphere the light coming from the sun hits atoms and molecules and scatters. Shorter wavelength blue light (400–500 nm) scatters stronger than longer wavelength red light (600–700 nm) (Minnaert 1987, Grimvall 1995, Karttunen *et al.* 1998). Light quality also depends on solar angle, which is determined by the diurnal rhythm and depends on latitude. Towards the north or during the sunrise and sunset the solar angle decreases and therefore sunlight must travel a longer distance through the atmosphere before reaching the earth's surface (Minnaert 1987, Karttunen *et al.* 1998). The diminished solar angle changes the quality of light as the shorter wavelengths of light increasingly scatter. Thus, towards high latitudes or in the twilight especially the amount of indirect, diffuse blue light increases in the atmosphere (Minnaert 1987). The sun shines from a low elevation particularly during the polar summer nights above the Arctic Circle (66.5°N).

Blue light induces many responses in plants such as phototropism, cotyledon/leaf expansion, leaf movement, chloroplast accumulation and movement, opening of stomata, anthocyanin accumulation, controlling of circadian rhythms (*e.g.* flowering time) and inhibition of hypocotyl/stem elongation (Christie 2007, Kang *et al.* 2008, Demarsy & Frankhauser 2009, Goh 2009, Li & Kubota 2009). The inhibiting effect of blue light on hypocotyl growth is very rapid, occurring after 30 seconds and is constant under continuous blue

light, at least in short-term experiments (Kigel & Cosgrove 1991, Parks *et al.* 1998, Parks *et al.* 2001, Weller *et al.* 2001, Ahmad *et al.* 2002). In Scots pine the hypocotyl elongation is also reduced when the plants are illuminated together with blue and red light (Fernbach and Mohr 1990). Separately given blue and red light has no effect on hypocotyl elongation. The red light converts the red-light-absorbing form of phytochrome (Pr) to the far-red light-absorbing form (Pfr). Thus, hypocotyl growth of Scots pine is controlled by the Pfr form of phytochrome, but blue light is required for the plants to become fully responsive to red light.

Plant morphology as well as pigmentation is affected also by darkness or low light quantity. In these conditions plants etiolate, which causes increased stem elongation, reduced branching and root development and accumulation of chlorophylls and carotenoids and changes in the leaf size and allocation of growth resources (McLaren and Smith 1978, Atkinson 1984, Warrington *et al.* 1988, de Kroon and Knops 1990, Salisbury & Ross 1992, Begna *et al.* 2002, Cookson and Granier 2006).

The quantity of light is reduced in the shade below a vegetation canopy. However, shade also changes the quality of light, because red and blue wavelengths are absorbed very effectively from sunlight by the canopy foliage (Smith 1982). Thus, under a canopy red to far-red light ratio (R/FR) and amount of blue light are reduced. Some plant species tolerate shading by other plants, some are shade-intolerant and some tolerate shade moderately. A reduction in R/FR ratio increases stem elongation of especially shade-intolerant plant species (McLaren and Smith 1978, Morgan & Smith 1979, Warrington *et al.* 1988, Smith and Whitelam 1997). Low R/FR ratio also increases petiole length and biomass of stem and reduces leaf area, branching, root weight and chlorophyll synthesis (Morgan *et al.* 1983, Warrington *et al.* 1988, Smith & Whitelam 1997). *Pinus sylvestris* is an evergreen, coniferous and shade-intolerant tree species, which increases elongation in a dense stand (de la Rosa *et al.* 1998).

Northern populations of Norway spruce (*Picea abies*) require far-red light to maintain epicotyl extension growth (Clapham *et al.* 1998). This requirement decreases towards lower latitudes of origin. Seedlings of the same species also respond similarly (Mølmann *et al.* 2006). Clapham *et al.* (2002) demonstrated that in northern, but not in southern populations of Scots pine, the secondary needle extension growth is maintained by far-red light. In addition, an exposure to red and far-red light de-etiolates the hypocotyls of northern natural populations of *Arabidopsis thaliana* more than the hypocotyls of southern populations (Stenøien

et al. 2002). Thus, plant populations of northern areas may respond more sensitively to the quality of light.

The aims of my thesis are to assess: (1) the effect of blue light removal on the elongation of Scots pine seedlings at sub-arctic and mid-boreal latitudes. (2) To compare the elongation of Scots pine seedlings originating from southern and northern provenances and the elongation of different life forms (i.e. evergreen vs. deciduous trees and herbaceous shade-intolerant vs. more shade-tolerant species) under light manipulation. (3) And to evaluate the mechanism behind the elongation response of the plants to the removal of blue light: Is the response related to temperature, etiolation or photosynthesis and acquisition of growth resources (carbohydrates, C/N ratio, N concentration and soluble proteins) or is it a photomorphogenic regulation response of metabolism?

2 Materials and methods

2.1 Study sites

The elongation of Scots pine seedlings was studied at 26° 0' E, 64° 48' N, 25 m above sea level (Muhos) in 2001 (IV). In 2002 the studies were conducted at two sites: at 64°N latitude and at 20° 47' E, 69° 3' N, 473 m above sea level (Kilpisjärvi) (II, III). In 2003 and 2008 the experiment was concentrated at the 69°N latitude (II, III, V).

2.2 Plant material

One-year-old Scots pine seedlings originating from 62°N and 67°N latitude (V) and two- and three-year-old Scots pine seedlings originating from 67°N latitude were studied (II, III, IV). The seeds of the one-year-old southern Scots pine seedlings were from grafted trees growing at 62°N latitude. The 35 selected trees from which the grafts have been taken grow in different parts of middle and eastern Finland at 62°N latitude. The effect of blue light removal on deciduous trees and herbaceous species of different levels of shade tolerance were studied with *Betula pubescens* spp. *czerepanovii* seedlings from 69°N latitude and *Betula pubescens* Ehrh. f. *rubra* Ulvinen seedlings from 64°N latitude and *Epilobium angustifolium* and *Glechoma hederacea* plants both from 65°N latitude (V). *Betula pubescens* spp. *czerepanovii* is a subspecies and *Betula pubescens* f. *rubra* is a mutant form of a deciduous tree species *Betula pubescens*, which is shade-intolerant especially in its early stage (Ellenberg 1988). *Epilobium angustifolium* is a herbaceous shade-intolerant species and *Glechoma hederacea* is a herbaceous more shade tolerating species (Ellenberg 1988, Sparks *et al.* 1996).

2.3 Removal of blue light

Chambers made of either orange or transparent plexiglass were used (II–V). The orange plexiglass removed the blue wavelengths (400–500 nm) from sunlight coming into the chambers. Wooden tables without chambers served as ambient control plots. A more detailed description of the experimental design is found in paper II. The quality of light in the experiment was checked with an Ocean Optics spectrometer (Model USB2000, Ocean Optics Inc., Dunedin, FL, USA) with a

cosine-corrected head to obtain spectral flux densities ($\mu\text{W cm}^{-2}$) from 400 to 800 nm. Temperatures and relative humidity in the chambers and control plots were recorded with data loggers (StowAway XTI, Rickly Hydrological Company, Columbus, OH, USA). The plants were well watered and positioned in the treatments without occurrence of mutual shading.

2.4 Light measurements

To obtain the relative changes in diurnal light quality, i.e. blue to red (B/R) and red to far-red (R/FR) light ratio, at the 69°N latitude measurements were conducted throughout the day and night with the Ocean Optics spectrometer at 10-min intervals and averaged for hourly values (I). The measurements were made on June 17–19 in 2008.

2.5 Morphological measurements

Main stem elongation was measured directly from Scots pine seedlings with a Vernier's calliper to obtain annual growth (II–V) and indirectly from photographs taken from the seedlings to determine daily and diurnal growth (IV). The length of branches and the diameter of new stem and old shoot and needle dimensions were measured with a Vernier's calliper (III, V). The elongation of roots was measured from one-year-old seedlings (V). The stem/stolon elongation and old and new stem/stolon diameter of *Betula* seedlings, *Epilobium angustifolium* and *Glechoma hederacea*, petiole elongation of *Betula* seedlings and *Glechoma hederacea* and branch elongation of *Epilobium angustifolium* was measured with Vernier's calliper (V). Leaf length, width and area of *Betula* seedlings, *Epilobium angustifolium* and *Glechoma hederacea* were determined from photographs with ImageJ (NIH). The total number of leaves was calculated from *Epilobium angustifolium* and the number of new leaves from *Glechoma hederacea*. Dry biomass of different plant parts of all the species, except for roots of herbaceous plants, was determined (III, V). Detailed descriptions of morphological measurements in papers III and V are found in Appendix 1.

2.6 Laboratory analyses

Photosynthesis, stomatal conductance to water vapour and water use efficiency was measured in a transparent box (0.3 x 0.5 x 0.6 m) from the previous year's

needles of two-year-old Scots pine seedlings with a Li-Cor 6400 Portable Photosynthesis System (Li-Cor Inc., Lincoln, NE, USA). From dried previous year's needles collected during the growing period of Scots pine, analyses were also carried out for carbohydrates (glucose, fructose and starch) according to Beutler *et al.* (1978), C/N ratio and total nitrogen using an EA 1110 CNSH-0 (EA/NA 1110, Fison Instruments, Milano, Italy) automatic element analyzer and soluble proteins according to Bradford (1976) (IV).

Concentrations of chlorophyll *a* and *b* and carotenoids were analyzed from needles and leaves according to Soukupova *et al.* (2000) (V). The amounts of the pigments were calculated according to Wellburn (1994).

2.7 Statistical analyses

Statistical methods used for data analysis included: 2-way ANOVA, 1-way ANOVA, analysis of covariance (ANCOVA) and independent samples *t*-test. All the analyses were performed using the SPSS software package.

3 Results

3.1 Light, temperature and humidity conditions

Blue wavelengths were removed by the orange plexiglass (II). During the night time the amount of blue light was high at both latitudes (I, IV). However, there was a bend after midnight at the 64°N latitude due to twilight during the period when the sun was set (IV). The removal of blue light decreased light quantity approximately 30%. The temperature inside the chambers was not affected by blue light removal (II, IV). During the fastest growth the relative humidity in the chamber treatments was similar at daytime both at 64°N and 69°N latitudes (Fig. 1).

3.2 Elongation of Scots pine seedlings under blue light depletion

Increased elongation of Scots pine seedlings under blue light removal was evident especially in each study at 69°N latitude (II, III, V), but also in one study at 64°N latitude (IV).

3.3 Effects of latitude and provenance on the elongation of Scots pine seedlings

The removal of blue wavelengths increased the elongation of three- and two-year-old Scots pine seedlings at the 69°N latitude. At the 64°N latitude blue light removal either had no effect on elongation (II, III) or increased it only slightly (IV). The elongation of one-year-old seedlings also increased under blue light depletion at the 69°N latitude. The increase was especially marked in the northern origin seedlings (V).

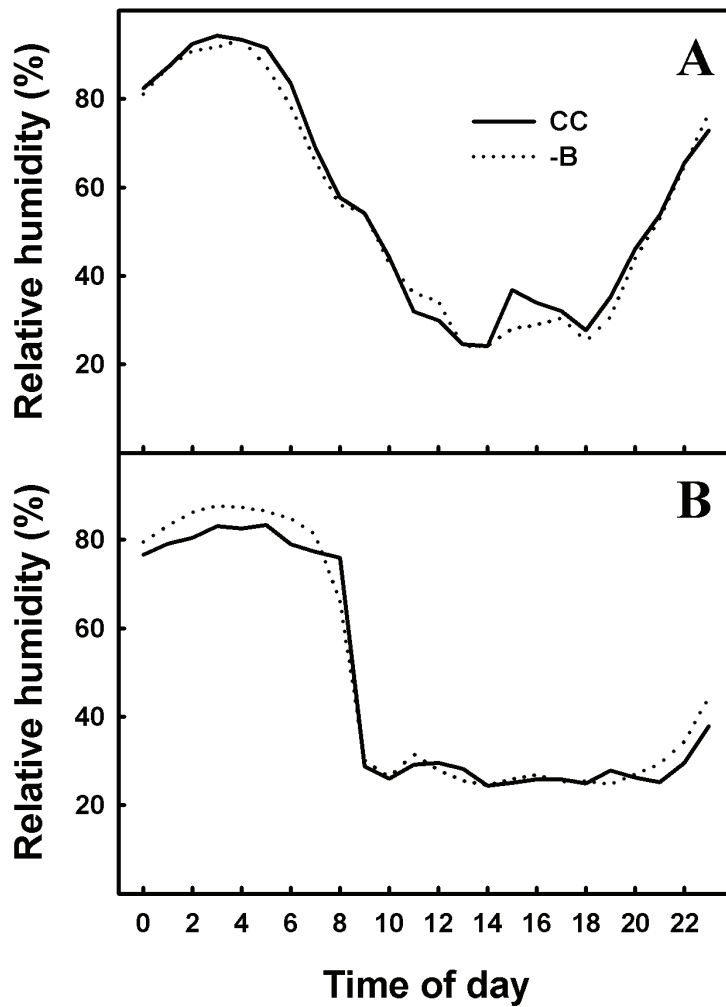


Fig. 1. An example of relative humidity inside transparent (CC) and orange (-B) chambers during the fastest growth of chamber seedlings on June 5th 2002 at 64°N (A) and on June 4th 2002 at 69°N (B) latitudes. During these days the maximum temperature inside the chambers at both sites was around +46°C.

3.4 Morphological changes other than elongation in Scots pine seedlings

Elongation of lateral branches, needle area and the biomass of the stem and needles of two- and three-year-old Scots pine seedlings increased under blue light depletion at the 69°N latitude (III). None of the variables were affected by the removal of blue wavelengths at the 64°N latitude. In one-year-old seedlings grown at the higher latitude, the branch and needle lengths of both origins were increased (V). In the seedlings of southern provenance the increase in branch elongation, however, was smaller compared to the northern seedlings. In the northern origin the removal of blue wavelengths also increased root length to some extent.

3.5 Changes in growth resources in Scots pine seedlings

Photosynthesis, stomatal conductance to water vapour or water use efficiency of the previous year's needles were unaffected by the removal of blue wavelengths. Also glucose, fructose and starch concentrations as well as C/N ratio, total N and soluble proteins, were not affected by the light manipulation (IV).

3.6 Changes in photosynthetic pigmentation in Scots pine seedlings

The accumulation of chlorophyll *a* and *b* and carotenoids in the previous year's needles of three-year-old seedlings and in the previous and current year's needles of one-year-old seedlings of both provenances were not affected by the removal of blue light (V).

3.7 Life form and light habitat

Also the elongation of deciduous tree seedlings (*Betula pubescens* ssp. *czerepanovii* and *Betula pubescens* f. *rubra*) increased under blue light depletion. In both *Betula* seedlings the removal of blue wavelengths also increased leaf area, leaf length and petiole length. The biomasses of leaves, stem and roots in both *Betula* seedlings were similar in both chamber treatments. The stem elongation, leaf area, leaf length and old stem diameter of *Epilobium angustifolium* increased by the removal of blue light while the total number of branches and the biomass

and number of leaves reduced. The elongation of the three longest branches, diameter of new stem and biomass of the stem were unaffected by the light manipulation in *Epilobium angustifolium*. In *Glechoma hederacea* the elongation of stolons, length of old petioles, stem diameter, biomass of the stem and leaves and number of new leaves were not affected by the removal of blue wavelengths. Area of the new leaves and new petiole length were, however, increased under blue light depletion.

The removal of blue light reduced the concentrations of chlorophyll *a* and *b* and carotenoids in *Betula pubescens* f. *rubra*. In *Epilobium angustifolium* and in *Glechoma hederacea* the concentrations of each pigment were unaffected by the treatments. Most of the morphological variables and also concentrations of the chlorophylls were significantly lower in ambient control plots in all plant species due to the cold weather (II, III, V).

In summary, in the shade-intolerant deciduous *Betula* tree seedlings and herbaceous *Epilobium angustifolium* the elongation of all the aerial plant parts increased under blue light depletion similarly as in the shade-avoiding evergreen Scots pine seedlings. In the herbaceous, more shade tolerant *Glechoma hederacea*, morphological variables responded less to the light manipulation.

4 Discussion

4.1 Elongation of Scots pine seedlings under blue light depletion

There are evidences that stem elongation of herbaceous plants is inhibited by illumination with blue light (Kigel & Cosgrove 1991, Parks *et al.* 1998, Parks *et al.* 2001, Weller *et al.* 2001, Ahmad *et al.* 2002). Also in Scots pine hypocotyl elongation is inhibited by an interaction of red and blue light in a short-term (9 d) experiment (Fernbach and Mohr 1990). Accordingly, the removal of blue wavelengths increased the elongation of Scots pine seedlings (II–V). To my knowledge this is the first research in which the effect of blue light removal has been studied in older seedlings of woody species throughout its entire annual elongation period. Temperature cannot explain the increase in elongation under blue light depletion, since the daily extreme temperatures between the chambers at both sites were equal as were the temperature sums accumulated in the chambers by the end of the experiments (II). In addition, the diurnal changes between the chambers were similar (IV).

Blue light induces stomatal opening very effectively, although red light is also able to promote it (Maleszewski *et al.* 2000). The red wavelengths may have compensated for the depletion of blue light in opening of stomata, especially after the amount of PAR exceeded the saturation level of photosynthesis for Scots pine ($> 800 \mu\text{mol m}^{-2} \text{s}^{-1}$; Wang *et al.* 1995). The temperatures inside the chambers rose close to 50°C from time to time and at the same time the relative humidity declined to 20–30% (Fig. 1, II). However, the relative humidity between the treatments remained close during the day. In addition, the seedlings were kept well watered throughout the experiments. Thus, despite the high temperature and equally low relative humidity in the chambers, the seedlings had been able to keep their stomata open. Thus, the water potential of the plants in both treatments has most obviously been good throughout the experiments. Therefore, it is unlikely that differences in water potential of the seedlings would be the reason for the increased elongation under blue light depletion.

4.2 Effects of latitude and provenance

The increase in elongation under blue light depletion was marked especially at the 69°N latitude of the experiment, while at the 64°N latitude the difference between

the treatments was either very small or non-existent (II, III, IV). To my knowledge this is the first research in which the effect of blue light removal on elongation is investigated in field conditions comparing two different latitudes. At the sub-arctic latitude (69°N) the amount of scattered blue light is high, especially during the night hours of polar summer (I). Thus, the more pronounced elongation of the seedlings at the higher latitude is likely to be the result of the greater amount of scattered blue light, which consequently inhibits the elongation of the seedlings in the transparent control chamber more effectively than at the lower latitude.

The removal of blue light increased the stem elongation of Scots pine seedlings of both northern and southern origins. However, the stem elongation and also the elongation of lateral branches and roots under blue light depletion were more remarkable in the northern origin suggesting that the seedlings from the northern provenance are more sensitive to blue light than the southern seedlings. Accordingly, northern plant populations also respond more sensitively to changes in red and far-red light (Clapham *et al.* 1998, Clapham *et al.* 2002, Stenøien *et al.* 2002, Mølmann *et al.* 2006).

As a consequence of global warming the vegetation is expected to move towards the north (ACIA 2005). In the northern light environment, which is rich in blue light during the low solar elevations, the elongation of especially shade-avoiding southern species and ecotypes will probably be reduced. Nevertheless, it is obvious that southern plants grow longer than local origins in the north.

4.3 Changes in other morphology and photosynthetic pigmentation

Stem elongation increases also due to etiolation in seedlings grown in darkness, but the development of leaves and roots is retarded (Salisbury & Ross 1992). Also in low light quantity the morphological variables, except for stem elongation, mainly decrease in *Pinus radiata* (Warrington *et al.* 1988). However, in one-, two- and three-year-old Scots pine seedlings grown under blue light depletion, needle growth and also branch elongation increased, while root growth was mainly unaffected (III, V). This indicates that no etiolation occurred.

Additionally, in a low light quantity chlorophyll *a* and *b* and carotenoid concentrations decrease (McLaren & Smith 1978). The removal of blue light, however, had no significant effect on the accumulation of chlorophyll *a* and *b* and carotenoids of Scots pine seedlings (V). Nevertheless, the new needles of one-

year-old Scots pine seedlings were light green under blue light depletion and also a slight decrease in chlorophyll *a* content was observed in the seedlings of northern origin. However, the concentrations of both chlorophylls were not affected by the removal of blue light in the southern origin. The removal of blue wavelengths diminished the total amount of light. Thus the possibility of etiolation cannot be totally excluded. On the other hand, the needle length of both Scots pine origins was increased by the removal of blue light. Therefore, the light green colour observed in the new needles under blue light depletion is probably due to spreading the chlorophylls to a wider area and not reducing the actual amount of chlorophylls. In addition, although the quantity of light slightly decreased it was above the Scots pine's saturation level of photosynthesis ($>800 \mu\text{mol m}^{-2} \text{s}^{-1}$; Wang *et al.* 1995) during the daytime. Thus, morphological measurements and analyses of photosynthetic pigment concentrations confirm that etiolation is not a significant factor in the increased elongation of Scots pine seedlings under blue light depletion, and strongly suggest that the increased elongation is a consequence of photomorphogenic regulation.

4.4 Changes in growth resources

The removal of blue light did not affect the assimilation of CO_2 , stomatal conductance or water use efficiency of Scots pine seedlings measured in a transparent (IV) or orange box (Sarala 2002). Thus, the removal of blue wavelengths did not cause either permanent change in the level of photosynthesis or directly in the assimilation. Also glucose, fructose and starch concentrations as well as C/N ratio, total N and soluble protein content were similar in both treatments throughout the experiment (IV). Therefore, the increased elongation of the seedlings grown under blue light depletion is independent of photosynthesis and resource acquisition. Instead, this is a second evidence for a photomorphogenic regulation response of metabolism, which leads to a better utilization of available stores by mediation of non-photosynthetic pigments phytochrome, cryptochromes and phototropin (Parks *et al.* 2001). Additionally, Scots pine seedlings were planted in nature both at 64°N and 69°N latitude at the end of two experiments. After seven years at 69°N latitude and one year at 64°N latitude, the seedlings grown under blue light depletion grew weaker compared to the seedlings grown in the control chambers (personal observation) indicating that the seedlings under blue light removal used more of their storages during the experiments leaving less resources for the following years.

4.5 Life forms and light habitat

The stem elongation of shade-intolerant species increases in low light quantity (Atkinson 1984, Warrington *et al.* 1988, de Kroon & Knops 1990, Begna *et al.* 2002). Also the removal of blue wavelengths increased the stem elongation of shade-intolerant deciduous *Betula* tree seedlings and shade-avoiding herbaceous *Epilobium angustifolium*. In a more shade-tolerant herbaceous *Glechoma hederacea* reduced light quantity and R/FR ratio did not affect the total length of primary stolons (Price & Hutchings 1996). Similarly in this study the removal of blue light had no effect on the stolon elongation of *Glechoma hederacea*.

Unlike in *Pinus radiata* seedlings growing in low light quantity (Warrington *et al.* 1988), no reduction was observed in the morphological variables of *Betula* tree seedlings under blue light depletion. However, low amount of light extends the leaf area of *Betula pubescens* (Atkinson 1984) as did the removal of blue wavelengths in *Betula pubescens* f. *rubra*. In shade-intolerant herbaceous species growing in low light quantity many morphological variables such as branching, number of leaves and leaf area decrease (McLaren & Smith 1978, Dong & de Kroon 1994, Begna *et al.* 2002, Cookson & Granier 2006). Similarly in *Epilobium angustifolium* blue light removal decreased branching and leaf number and consequently the total biomass of leaves. Nevertheless, the blue light depletion did not reduce the other measured variables. In more shade-tolerant plants petiole elongation increases, but most of the growth-related variables mainly decrease under low light and low R/FR ratio (Price & Hutchings 1996, Vermeulen *et al.* 2008). In *Glechoma hederacea* the elongation of new petioles and leaf area increased by the removal of blue wavelengths, while the other measured variables were unaffected. The leaf area growth of *Epilobium angustifolium* and *Betula* seedlings also increased under blue light depletion. This is in accordance with Eskins (1992), who reported that an increasing amount of blue light reduces the leaf area of *Arabidopsis thaliana*.

The concentrations of chlorophyll *a* and *b* and carotenoids reduce in low light quantity (McLaren & Smith 1978). However, no reduction was observed in most of the studied species under blue light depletion. The responses observed in morphology and pigmentation confirms that the increased elongation of plant species under blue light depletion is only marginally etiolation. However, in *Betula pubescens* f. *rubra* the contents of the pigments were decreased by the removal of blue wavelengths. Thus, this birch also responds strongly to the quantity of light, which is in agreement with the findings of Taylor & Davies

(1988) according to which the leaves of birch are very sensitive to changes in PAR.

5 Conclusions

The results undoubtedly indicate that the stem elongation of Scots pine seedlings increases by the removal of blue light. The shade-avoiding evergreen and deciduous woody species and herbaceous species responded similarly to the light manipulation, while a more shade-tolerant species was less influenced. The increase is mainly explained by a photomorphogenic regulation response of metabolism, since it was not dependent on temperature or photosynthesis and resource acquisition. The morphological measurements and analysis of photosynthetic pigment concentrations of various species support the interpretation of the results and confirm that the improved elongation could be only marginally related to etiolation.

The increase in elongation of Scots pine seedlings under blue light depletion was more pronounced at the sub-arctic latitude (69°N) of the experiment, while at the mid-boreal latitude (64°N) the increase was smaller or absent. At the higher latitude in the summertime the amount of scattered growth-inhibiting blue light passing to the transparent control chambers was high during the nights. Thus, the pronounced elongation at the high latitude and the smaller or non-existent difference at the lower latitude could be due to the growth-inhibiting effect of blue light, which increases gradually along increasing latitudes.

In the northern origin (67°N) Scots pine seedlings the removal of blue wavelengths increased the elongation of stem, branches and roots more than in those from the southern region (62°N). The result suggests that it responds more sensitively to blue light than the southern Scots pine seedlings. From the global change point of view, the elongation of southern species and ecotypes that migrate towards the north will probably reduce under conditions of a warming climate. Obviously they still grow taller than the local northern plants.

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Appendix

Table 1. Measured growth variables of Scots pine seedlings in paper III. Three-year-old seedlings grew both at (1) 64°N and 69°N latitudes and two-year-old seedlings at (2) 69°N latitude.

Measurement	64°N (1)	69°N (1)	69°N (2)
Stem elongation	x	x	x
Stem diameter		x	x
Stem biomass	x	x	x
Shoot diameter	x	x	x
Branch elongation	x	x	x
Branch no.	x	x	x
Needle area	x	x	x
Needle biomass	x	x	x
Fascicle density	x	x	x

Table 2. Measured growth variables of one-year-old *Pinus sylvestris* (Scots pine) seedlings from northern 67°N and southern 62°N provenances, *Betula pubescens* spp. *czerepanovii* and *Betula pubescens* f. *rubra* seedlings and *Epilobium angustifolium* and *Glechoma hederacea* plants in paper V. ^a Measurements are not taken from outdoor control seedlings.

Measurement	<i>Pinus sylvestris</i> northern/ southern	<i>Betula pubescens</i> spp. <i>czerepanovii</i>	<i>Betula pubescens</i> f. <i>rubra</i>	<i>Epilobium angustifolium</i>	<i>Glechoma hederacea</i>
Stem/old stolon elongation	x	x	x	x	x
Branch/new stolon elongation	x			x	x
Branch/stolon no.				x	x
Old shoot/stolon diameter	x		x	x	x
New stem/stolon diameter	x		x ^a	x ^a	x
Internode no.			x		
Needle length, width, thickness	x				
New leaf length, width and area		x	x	x	x
New petiole length		x	x		x
Old petiole length					x
Total leaf no.				x	
New leaf no.					x
New stem/stolon biomass	x				x
Old shoot/stolon biomass	x				x
Total stem biomass		x	x	x	
New needle/leaf biomass	x				x
Old needle/leaf biomass	x				x
Total leaf biomass		x	x	x	
New branch biomass	x				
Root biomass	x	x	x		
Root elongation	x				

Original articles

The thesis is based on following articles, which are referred to in the text by their Roman numerals:

- I Taulavuori K, Sarala M & Taulavuori E (2010) Growth responses of trees to arctic light environment. *Progress in Botany* 71: 157–169.
- II Taulavuori K, Sarala M, Karhu J, Taulavuori E, Kubin E, Laine K, Poikolainen J & Pesonen E (2005) Elongation of Scots Pine Seedlings under Blue Light Depletion. *Silva Fennica* 39(1): 131–136.
- III Sarala M, Taulavuori K, Taulavuori E, Karhu J & Laine K (2007) Elongation of Scots pine seedlings under blue light depletion is independent of etiolation. *Experimental and Environmental Botany* 60: 340–343.
- IV Sarala M, Taulavuori E, Karhu J, Savonen E-M, Laine K, Kubin E & Taulavuori K (2009) Improved elongation of Scots pine seedlings under blue light depletion is not dependent on resource acquisition. *Functional Plant Biology* 36: 1–10.
- V Sarala M, Taulavuori E, Karhu J, Laine K & Taulavuori K (2010) Growth responses and pigmentation of various species under blue light depletion. Manuscript.

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