



# Effect of vegetational shade and its components on stomatal responses to red, blue and green light in two deciduous tree species with different shade tolerance



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## ABSTRACT

Stomatal responses to red, blue and green light were measured in shade-midtolerant *Nothofagus alpina* and shade-avoidant *Betula pendula* seedlings grown in full sunlight (control, C-set), simulated vegetational shade (IUW-set), or with a single component of vegetational shade: decreased light intensity (I-set) or attenuated UV irradiance (U-set). In *N. alpina*, stomatal opening response to red light switch-on was stronger in IUW-set and U-set, than in C-set. The addition of medium blue light into the red (stomatal opening) induction light increased the stomatal response, and the stomata also responded sensitively to weak blue light in the IUW- and U-sets. The addition of green light into the red induction light did not change the stomatal response in any set. Yet in the U-set, the addition of green light into the red + (medium) blue or weak blue induction light decreased the stomatal response. Thus, vegetational shade had increased the photosynthesis-mediated stomatal light response, activated an additional stomatal response through blue light receptors, and let stomata insensitive to green light. The attenuated UV irradiance had the same effects as vegetational shade on the stomatal photosynthesis-mediated response and the additional blue light receptors-mediated response, but it also activated the green light reversal of blue light response. The stomata of leaves grown under decreased irradiance exhibited the same stomatal responses as the full-light-grown leaves. In *B. pendula*, stomatal responses to all the different types of light were remarkably weaker than those in *N. alpina*, and did not differ between themselves or between the different shade treatments. Thus, the modulation of stomatal light sensitivity participates in shade acclimation in shade-tolerating, but not in shade-avoiding deciduous tree(s).

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## 1. Introduction

The forest canopy is characterised by a deep vertical light gradient. The lower leaves of the canopy are strongly affected by vegetational shade (canopy shade) – the light intensity decrease and composition modifications that are caused by light absorption and reflection by upper shoots of the canopy (Smith, 1982). As the light availability of the growth environment is one of the basic determinants of plant morphophysiological characteristics (Franklin and Whitelam, 2005; Pinho et al., 2012), the effects of vegetational shade on the development of leaf traits have been measured in numerous studies. Amongst stomatal characteristics,

it has been found that in vegetational shade-grown leaves of woody plants, stomatal density is smaller (e.g., Givnish, 1988; Sack et al., 2003; Brodribb and Jordan, 2011) or similar (Nardini et al., 2012; Zhou et al., 2012), stomatal index is smaller (Kürschner, 1997; Poole et al., 1996; Sun et al., 2003), dimensions of stomata are bigger (Givnish, 1988; Rossatto and Kolb, 2010) or similar (Ashton and Berlyn, 1994; Sack et al., 2003; Brodribb and Jordan, 2011), and stomatal conductance is lower (Ashton and Berlyn, 1994; Brodribb and Jordan, 2011; Jensen et al., 2012). Yet there is lack of data about the effect of vegetational shade on stomatal sensitivity – the strength of response in stomatal conductance following a change in the environment. Georgieva et al. (2012) found that stomatal sensitivity to leaf water potential decrease was lower in *Haberlea rhodopensis* plants grown in deep shade under trees than in the plants grown in sun-exposed locations. It has also been found that, in the lower leaves of tree foliage (that are shaded by upper foliage branches), the stomatal sensitivity to rapid changes in light intensity is higher (Dang et al., 1997; Sellin and Kupper, 2004,

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2005) and the sensitivity to a decrease in air humidity is lower (Sellin, 2001; Sellin and Kupper, 2004, 2005) than in the sun-exposed leaves of the top foliage. However, these results do not give enough information about morphogenetic effect of vegetational shade, because edaphic and/or water conditions also differ between the various natural locations and between the top and base of tree foliage. As light is scanty and unstable under vegetational shade (Casal, 2012), more data are needed about the effect of vegetational shade on stomatal sensitivity to rapid increases in light intensity. CO<sub>2</sub> enters the leaves through stomata, and high stomatal light sensitivity is important for the efficient use of light energy in photosynthetic CO<sub>2</sub> fixing.

Stomatal conductance increases in response to a rapid increase in white light intensity. As white light consists of light of different colours, the stomatal response to white light is a sum of the responses to the different components of white light (Talbot et al., 2006; Shimazaki et al., 2007). Stomata are especially sensitive to blue light (Sharkey and Ogawa, 1987; Dumont et al., 2013), but the rate of stomatal opening in response to an increase in red light is also remarkable (Olsen et al., 2002; Bocalandro et al., 2012). Following green light switch-on, stomatal conductance increases only slightly (Frechilla et al., 2000,b; Talbot et al., 2002a,b; Wang et al., 2011) or even decreases (Talbot et al., 2002a; Kim et al., 2004). It is not known, whether the stomatal responses to all the different colours – the different components of the ‘rapid white light response’ or only some of them are modified by growing under vegetational shade.

Under vegetational shade, both the quantity and quality of light are different from those in full sunlight. The intensity of all light wavelengths (from ultraviolet to far-red) is smaller than in full sunlight, but the proportions of far-red and green wavelengths are increased because of enhanced transmission and reflection of these quanta by leaves (Folta and Maruhnich, 2007; Franklin, 2008; Casal, 2012, 2013). The morphogenetic effect of shade is the sum of the effects of all the different components of the shade (Casal and Sánchez, 1994; Franklin and Whitelam, 2005). It is found that some components of vegetational shade have an especially strong morphogenetic effect on some characteristics of plants. E.g., red and far-red light ratio has an especially strong effect on stem (Ballaré et al., 1991b; Pierik et al., 2004) and hypocotyl length (Ballaré et al., 1991a; Tao et al., 2008), and light intensity, on leaf angle (Pierik et al., 2004). Yet it is not known, which components of vegetational shade are most efficient for the morphogenesis of the ‘shade leaf mode’ values of stomatal light sensitivity.

Plants have two basic strategies to cope with shade – shade avoidance and shade tolerance. Shade-avoiding (shade-intolerant, light-demanding) species use their resources preferentially for growing out from the shade. Shade-tolerant species use their resources preferentially for efficient absorbing and use of the scanty light energy in shade conditions (Boardman, 1977; Gommers et al., 2013; Pierik and de Wit, 2014). It has been found that the stomata of shade-tolerant tree species are characterised by similar (Goodchild et al., 1972; Ashton and Berlyn, 1992; Aasamaa et al., 2001; Gamage et al., 2003) or higher (Ashton and Berlyn, 1994) stomatal frequency, similar (Goodchild et al., 1972; Ashton and Berlyn, 1994) or smaller (Aasamaa et al., 2001) stomatal length, and higher stomatal area as a proportion of leaf area (Ashton and Berlyn, 1994) as compared to stomata of shade-intolerant tree species. Stomatal conductance of shade-tolerant and shade-intolerant tree species is similar in plants grown in low to moderate light (Strauss-Debenedetti and Bazzaz, 1991; Ashton and Berlyn, 1992, 1994; Naidu and DeLucia, 1998; Cano et al., 2011), but in plants grown in high light, the conductance of shade-tolerant species is lower (Strauss-Debenedetti and Bazzaz, 1991; Ashton and Berlyn, 1992, 1994; Naidu and DeLucia, 1998; Aasamaa and Söber, 2001; Kuo et al., 2004). In our previous studies, we found

that stomatal sensitivities to rapid increase in white light intensity, and also the sensitivities to rapid changes in other basic conditions of the stomatal environment – in [CO<sub>2</sub>] and water potential of air and leaf, were almost all higher in shade-tolerant than in shade-intolerant tree species (Aasamaa and Söber, 2001, 2011). However, it is not known, whether the stomatal sensitivities to all the different colours, or only some of them are higher in shade-tolerant than in shade-intolerant species.

In this study, stomatal responses to red, blue and green light were measured in well-watered seedlings of a shade-midtolerant and a shade-avoidant deciduous tree species grown under full sunlight, under vegetational shade, or under separate components of vegetational shade – light with decreased intensity or without UV irradiance. The main hypotheses of the study were: (1) A single component of vegetational shade causes as strong acclimation in stomatal rapid light responses as the full vegetational shade. (2) Not all the stomatal colour responses, but the stomatal responses to only one or two colours differ significantly between the leaves (of same species) grown in different light conditions, or between shade-tolerant and shade-intolerant species.

## 2. Materials and methods

### 2.1. Plants

Two temperate deciduous tree species with different light demand: shade-midtolerant *Nothofagus alpina* (Popp. and Endl.) Oerst. (Read and Hill, 1985; Pollmann, 2005; Donoso et al., 2013) and shade-intolerant *Betula pendula* Roth (Laas, 1987; Ellenberg, 1998) were studied. Seeds of *N. alpina* were sown in spring 2010, and seeds of *B. pendula* in spring 2011, and the pots with the plants were well-watered throughout all the following period. They were kept in field conditions in summer (May–Sept) and in a glasshouse (t° minimum 6 °C) in winter. At the end of May 2012, the plants were transplanted to 3 l pots, to a soil mix composed of peat White 420 F6 (Kekkilä Oy, Vantaa, Finland), mixed soil from forest growing sites of *B. pendula* and *Tilia cordata* (Saint-Gobain Weber Oy Ab, Helsinki, Finland), and vermiculite (Vermipu Oy, Lapinjärvi, Finland) (5.3:2:1.8:0.9), and fertilized (2 g l<sup>-1</sup>) with Osmocote Exact (Oy Habitec AB, Vantaa, Finland) (15% N; 3.9 P; 10 K; 1.5 Mg; 0.45 Fe; 0.06 Mn; 0.056 Cu; 0.025 Mo; 0.02 B; 0.02 Zn). The pots were taken to the field and placed under four different types of light filters. The filters were: (1) control (C-set) – near-ambient full solar spectrum, ~90% light transmission, polyethylene, 04 PE-LD (Etola Group, Helsinki, Finland); (2) neutral shade (light intensity decreasing) (I-set) – full-spectrum (neutral density) shade, ~70% lower light transmission than C-set filter, in layers perforated mirror plastic E-Colour #270 Scrim (Roscolab Ltd., London, UK) and the polyethylene filter; (3) ultraviolet shade (UV attenuating) (U-set) – UV-A and UV-B blocking, ~90% PAR transmission, polyethylene terephthalate, E-Colour #226 U.V. (Roscolab Ltd., London, UK); (4) full vegetational shade (light intensity decreasing, UV attenuating, and light wavelengths proportions modifying) (IUW-set) – UV-A and UV-B blocking, ~70% lower (than C-set filter) and enhanced light transmission in green and far-red, polyethylene terephthalate, E-Colour #089 Moss Green (Roscolab Ltd., London, UK). The light transmission spectra of the filters are given in Fig. 1, and the differences in the light conditions of the sets are further described in Table 1. *B. pendula* trees were pruned (up to 10%) at the beginning and in the middle of August. The measurements of stomatal responses were made in August using only the leaves that had emerged under the filters. Before the measurements, the pots with the plants were taken to a dark laboratory where a candle was used as the only light source and a temperature close to 25 °C was maintained. The plants were

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