Light response in alpine species: Different patterns of physiological plasticity

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ABSTRACT

Light is one of the major stress factors that alpine plants face. Phenotypic plasticity of photoprotection mechanisms was analyzed in six alpine species growing in the Teide National Park (Canary Islands, Spain) at two different light exposures: full sunlight and 50% shading. Measurements of absorptance and chlorophyll fluorescence parameters obtained from induction kinetics and rapid light curves were performed. The studied species displayed high modulation capacity in most of the analyzed physiological traits, such as avoidance of light absorption, partitioning of the absorbed energy into consumption and/or dissipation, and its resultant resistance to high light, although in some cases opposite directions were observed. Three different response patterns were reported: 1) high adaptive plasticity response to light exposure, such as in *Spartocytisus supranubius* and *Scrophularia glabrata*, which could develop a high non-photochemical quenching or face higher levels of saturating irradiation at full sunlight exposure, 2) high modulation response in a non-adaptive direction, as found in *Adenocarpus viscosus,* which decreased its non-photochemical quenching at high irradiation, and in *Pterocephalus lasiospermus*, which increased photodamage of PSII and started decreasing ETR at low PPFD when developing at high light exposition, and 3) low physiological plasticity, as in *Echium wildpretii*, which could only modulate its leaf absorptance. Our data suggest that phenotypic plasticity should not always be considered as an adaptive response in nature.

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1. Introduction

Light is the most spatially and temporally heterogeneous factor affecting plants (Pearcy and Valladares, 1999). Plants can modulate their morphology and physiology in order to adjust to available light at different levels: crown morphology, phenology, gas exchange properties and area, anatomy and optical properties of the leaf (Valladares, 2003). The ability of a single genotype to produce multiple phenotypes in response to environment conditions is termed phenotypic plasticity (Bradshaw, 1965; Pigliucci, 2001; Valladares et al., 2007). Phenotypic plasticity is frequently considered as the variability among individuals of similar genotype, comparing species or population, since identical genotypes are often difficult to identify and compare (Valladares, 2003). It is often

quantified and depicted as reaction norms, which refer to the set of phenotypes that can be produced by an individual genotype that is exposed to different environmental conditions (Sultan, 1987). Reaction norms may be plastic or non-plastic. Thus, the phenotype may either change or remain fixed in response to environmental changes. Plastic reaction norms have been clearly recognized as a means of dealing with environmental heterogeneity (Schlichting and Pigliucci, 1998). However, this plasticity is not necessarily adaptive (Valladares, 2003). The adaptation of an organism to its environment is generally defined as the relative success in survival and reproductive output, known as fitness, which is a descriptor of an ongoing phenotype–environment interaction (Sultan, 1987). Thus, adaptive phenotypic plasticity has been understood as a factor in maintaining fitness under heterogeneous environmental conditions by increasing the number of tolerable habitats.

Several studies have focused on phenotypic plasticity in response to different light conditions using morphological and physiological traits (Nicotra et al., 1997; Sultan, 2000; Valladares et al., 2000a,b, 2002a, 2005a, 2005b; Balaguer et al., 2001; Yuan et al., 2016). Many physiological traits are involved in the adaptation to different environmental conditions. In the case of light

exposure, plants have developed several mechanisms in order to face with excessive light and to avoid photoinhibition.

Photoprotection mechanism associated with avoiding light absorption is the most common strategy to elude inactivation of photosystem II (PSII) and photosynthesis, rather than the dissipation of absorbed light energy (Takahashi and Badger, 2011). This strategy includes both crown structure (leaf angle and self-shading) and leaf optical characteristics. Leaf light absorptance (Abs) is the percentage of incident light that is neither reflected nor transmitted and that can be used by the photosynthetic apparatus. Abs can diverge since it depends on 1) the existence of reflectance structures and/or chemicals (hair, wax, etc.) (Holmes and Keiller, 2002), 2) the adjustment of chlorophyll content and other leaf pigments (Gausman, 1983), 3) the suitable movement and distribution of chloroplasts (Brugnoli and Björkman, 1992), and 4) mesophyll characteristics (Gausman, 1977).

One other mechanism described to deal with high radiation is the consumption or dissipation of absorbed light. Since the usage of light in photochemistry is limited, plants have developed non-photochemical processes that do not involve ATP formation nor reduction power. These processes can be evaluated by chlorophyll fluorescence relaxation kinetics measured in the dark period after the induction kinetics, which allow the calculation of regulated non-photochemical quenching yield (ϕ_{NPQ}). It involves all mechanisms that decrease fluorescence yield beyond photochemistry (ϕ_{PSII}) and the constitutive thermal energy dissipation ($\phi_{f,D}$) (Hendrickson et al., 2004). Thus, ϕ_{NPQ} is divided into energy-dependent quenching ($\phi_{NPQ,E}$), state-transition quenching ($\phi_{NPQ,T}$), zeaxanthin-dependent quenching ($\phi_{NPQ,Z}$) and photoinhibitory quenching ($\phi_{NPQ,I}$) components according to a) their relaxation kinetics in darkness after a period of illumination, b) their response to different inhibitors or c) its behavior in plant mutants (Allen et al., 1981; Krause et al., 1982; Krause, 1988; Horton and Hague, 1988; Nilkens et al., 2010). $\phi_{NPQ,E}$ is the major component of ϕ_{NPQ} and relaxes within seconds to 2–5 min. It requires the build-up of a proton gradient across the thylakoid membrane, which is involved in the activation of xanthophyll cycle and in some species possibly of the lutein epoxide cycle. Within 12–30 min, both $\phi_{NPQ,T}$ and $\phi_{NPQ,Z}$ are relaxed. The phenomenon of state transition by which the light harvesting complex of the photosystem II (LHCII) is phosphorylated and separates from PSII to associate with the photosystem I (PSI) does not significantly contribute to ϕ_{NPQ} in higher plants. In contrast, zeaxanthin epoxidation plays an important role in long-lasting ϕ_{NPQ}. The last component, $\phi_{NPQ,I}$, shows the slowest relaxation in the range of hours or even days and it is linked to photoinhibition of PSII. It is assumed that $\phi_{NPQ} = \phi_{NPQ,E} + \phi_{NPQ,T} + \phi_{NPQ,Z} + \phi_{NPQ,I}$. For more information, see Müller et al. (2001), Lichtenthaler et al. (2005), Lambrev et al. (2007), Roháček (2010) and Jahns and Holzwarth (2012).

Regarding to the consumption of the excess light, this can be enhanced by 1) increase in the capacity of the biochemistry of photosynthesis (Anderson et al., 1988; Heber et al., 1990), 2) photoreduction of O_2 (Schreiber and Neubauer, 1990; Savitch et al., 2000), and 3) other reduction reactions (Adams et al., 1989; Demmig-Adams and Adams, 1992). Overall, these processes determine the running of the electron transport chain and the level of excess light. Detailed information on the saturation characteristics of the electron transport chain can be provided by rapid light curves (RLC) (Ralph and Gademann, 2005), which have been reported to be closely related to the photosynthetic activity (Beer et al., 1998) and widely used in research (de Mattos et al., 1997; Lüttge et al., 1998; Franco et al., 1999; Valladares et al., 2005a). These saturation characteristics of photosynthesis have been interpreted as a measure of the irradiance level to which the leaf has become acclimated (Henley, 1993; MacIntyre et al., 2002).

Despite the abundant knowledge of morphological and physiological phenotypic plasticity in response to different light conditions in a wide range of ecosystems, mainly in mesic plants, less information is available for light acclimation in alpine plants (Clausen et al., 1940; Byars et al., 2007; Gonzalo-Turpin and Hazard, 2009; Gratani et al., 2012), which must deal with higher light irradiation. Our study focused on the physiological plasticity of six alpine species growing in the Teide National Park (Canary Island, Spain) under different light exposure by measurements of absorptance and the analysis of the induction kinetics and RLCs. Two main goals were aimed: 1) Are photoprotective mechanisms used by alpine plants modulated with environmental light? 2) Does plasticity response follow a similar pattern between the studied species?

2. Material and methods

2.1. Plant material, study area and experimental design

The high mountain ecosystem of the Teide National Park (Canary Island, Spain) spreads above 2000 m a. s. l. (Rivas-Martínez, 1995). Apart from the high thermic oscillation and the hard edaphic conditions with Leptosols as predominant soils (Rodríguez et al., 2014), an important stress factor of this ecosystem is the high irradiation, which can reach to 600–1100 W m^{-2} (2000–2200 μmol m^{-2} s^{-1}) due to both high altitude and low latitude.

The most representative species were selected, which include *Pterocephalus lasiospermus* Link *ex* Buch (Dipsacaceae), *Spartocytisus supranubius* (L. f.) Christ *ex* G. Kunkel (Fabaceae), *Scrophularia glabrata* Aiton (Scrophulariaceae), *Echium wildpretii* Pearson *ex* Hook. f. (Boraginaceae), *Adenocarpus viscosus* (Willd.) Webb & Berthel. (Fabaceae) and *Erysimum scoparium* (Brouss. *ex* Willd.) Wettst. (Brassicaceae), all evergreen Canary endemic species. Seeds were collected along the distribution of the species, randomly selected and germinated at the Teide National Park greenhouse at 2070 m a. s. l. Two-month-old seedlings were planted in pots, daily irrigated and located outside in two closed areas with different sunlight exposure: 1) a totally exposed area to natural sunlight (experimental group named EXP$_{100}$), and 2) a partially exposed area thanks to an artificial canopy that reduced light by 50% (EXP$_{50}$). This artificial canopy was made with a black plastic net with narrow holes which was assumed to produce a spectrally neutral shade under it. The entrance inside the canopy was oriented so that direct solar radiation never reached the plants. The effect of a possible diffuse light and a rim effect was corrected by a randomly disposition of the plants through the canopy. These different conditions were maintained during nearly two years and the assays were conducted in early April (favorable season). All species were represented by five plants (n = 5) in both experimental groups. Upper mature and healthy leaves were selected for the analysis, as it has been reported that the capacity for light acclimation is stronger in the adult life phase (Hoflacher and Bauer, 1982). In the case of *S. supranubius*, both the main photosynthetic tissues (stem) and short-lived leaves were analyzed.

2.2. Leaf absorptance determination

Absorptance was measured using Imaging-PAM fluorometer (blue light 450 nm, mini version, Walz GmbH, Effeltrich, Germany) in 2–4 mature and healthy leaves (or exposed stem) as technical replicates per plant. The average Abs was calculated from each of the 5 individuals per species and treatment. Imaging-PAM determines absorptance by measuring red (660 nm) and near infrared (780 nm) reflectance (Abs = 1−Abs$_{660}$/Abs$_{780}$), assuming a constant reflectance at near infrared for all species. Furthermore, it was also assumed that the Abs$_{660}$ are equal to Abs$_{450}$, which is the wave-