Unveiling the shade nature of cyanic leaves: a view from the 'blue absorbing side' of anthocyanins

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Abstract

Anthocyanins have long been suggested as having great potential in offering photoprotection to plants facing high light irradiance. Nonetheless, their effective ability in protecting the photosynthetic apparatus from supernumerary photons has been questioned in many instances, based upon the inexact belief that anthocyanins almost exclusively absorb green photons, which are instead poorly absorbed by chlorophylls. This suggestion also contrasts with the well-recognized 'shade syndrome' displayed by cyanic leaves: shade avoidance responses are activated indeed by excessive green light. Here we focus on the blue light absorbing features of anthocyanins, a neglected issue in anthocyanin research. We offer a comprehensive picture of the suite of molecular events activated in response to low blue-light availability, which we suggest to be responsible for the shade nature of cyanic leaves/individuals. As a corollary, this adds further support to the view of an effective photoprotective role of anthocyanins. We discuss about the morpho-anatomical adjustments imposed by the epidermal anthocyanin shield, mostly devoted at maximizing light harvesting, which make complex the analysis of the photosynthetic performance of cyanic vs acyanic leaves. Finally, we evidence major methodological issues for future research, which may help to draw conclusions on how and how much anthocyanins sustain photoprotection.

Introduction

Whether epidermal anthocyanins offer effective protection to plants facing excessive light is still a debated issue (for review articles, see Hughes, 2011; Manetas, 2006; Landi, Tattini, & Gould, 2015; Steyn, Wand, Holcroft, & Jacobs, 2002). There are several reasons responsible for this 'apparently irrelevant' discussion, since anthocyanins effectively absorb photons over a wide portion of the solar spectrum (Gould, Jay-Allemand, Logan, Baissac, & Bidel, 2018; Tattini et al., 2017). First, juvenile red leaves or leaves that became transiently red during the winter season (so-called 'winter reddening') have been compared to mature green leaves in many instances (Hughes, Neufeld, & Burkey, 2005; Kytridis, Karageorgou, Levizou, & Manetas, 2008; Ranjan, Singh, Singh, Pathre, & Shirke, 2014; Zeliou, Manetas, & Petropoulou, 2009; Zhang et al., 2018a). We note that many traits other than the biosynthesis of anthocyanins may largely vary because of leaf age or season, between cyanic and acyanic leaves (Rasulov, Bichele, Laisk, & Niinemets, 2014; Tattini et al., 2014). Second, light irradiance at which plants have been grown strikingly differs among studies. In

some instances, plants acclimated to relatively low irradiance (greenhouse/growth chamber studies) have been suddenly and transiently exposed to excessive light (Gould et al., 2018; Landi, Guidi, Pardossi, Tattini, & Gould, 2014; Logan, Stafstrom, Walsh, Reblin, & Gould, 2015). Other studies have instead compared cyanic and acyanic individual exposed for long periods to high light irradiance in the field (Liakopoulos et al., 2006; Tattini et al., 2017; Zhang, Zhong, Wang, Sui, & Xu, 2016). Third, there is the general, inexact belief that anthocyanins are effective in absorbing photons over the green region (over the 500-550 nm waveband), but quite ineffective in absorbing photons over other portions of the visible solar spectrum (Hughes, 2011; Kyparissis, Grammatikopoulos, & Manetas, 2007; Steyn et al., 2002). It has been argued, therefore, that anthocyanins may play only a marginal role in photoprotection (Liakopoulos et al., 2006; Neill & Gould, 1999; Nikoforou, Nikopoulos, & Manetas, 2011), given that chlorophylls mostly absorb over the blue (400-500 nm) and the red (600-700 nm), but poorly over the green portion of the solar spectrum. Nonetheless, light-induced depression in both maximal (F_v/F_m) and operational (Φ_{PSII}) photosystem II (PSII) quantum yield is lower in cyanic compared to acyanic leaves over a broad range of species (Gould et al., 2018; Hughes & Smith, 2007; Landi et al., 2014; Tattini et al., 2017). There is also evidence that photoinhibition (Long, Humphries, & Falkowski, 1994), estimated from morning-to-midday depression in photosynthesis is lower in 'constitutively' cyanic leaves (leaves that remain red throughout their entire life cycle) compared to the green counterparts (Tattini et al., 2014; 2017). This is consistent with the observation that, while having molar extinction coefficient () maxima in the 510-540 nm waveband, anthocyanins also substantially absorb blue photons (and red photons to a lesser degree, Fig. 1), depending on decoration and tissue molar concentration (Jordheim et al., 2016; Merzlyak, Chivkunova, Solovchenko, & Naqvi, 2008; Tattini et al., 2014; Gould et al., 2018).

It is a matter of fact, that the capacity of anthocyanins to absorb maximally over the green portion of the solar spectrum does not fit to the long-reported 'shade syndrome' displayed by cyanic leaves (Manetas, Petropoulou, Psara, & Drinia, 2003; Tattini et al., 2014, see end of section for details). High green light availability actually induces shade avoidance responses in leaves and individuals (Dhingra, Dies, Lehner, & Folta, 2006; Wang & Folta, 2013; Smith, McAuslan, & Murchie, 2017), as is the case of leaves growing in the understorey (true shade leaves), which perceive light strongly enriched in green and far-red (FR) wavelengths. Green light stimulates early stem elongation indeed, and opposes responses to blue- and red light-activated signaling pathways (e.g. blue/red light-induced stomata opening, Folta & Mahrunic, 2007). Transcripts encoding proteins of PSI, PSII and the stroma (psaA, psbD, and rbcL), which are long known to accumulate in response to high light, are largely downregulated upon a pulse of green light (Wang & Folta, 2013). We also argue that the shade nature of cyanic leaves is unlikely the result of the UV-screening ability of anthocyanins, which may be substantial for anthocyanins acylated with hydroxycinnamic acid derivatives (Jordheim et al., 2016; Tattini et al., 2014). Effective UV-absorbing compounds, such as the colorless flavonols, accumulate more in high light-exposed green leaves compared to the corresponding red counterparts (Tattini et al., 2014; 2017), consistent with the strong competition between flavonol and anthocyanin biosynthetic pathways (Yuan, Rebocho, Sagawa, Stanley, & Bradshaw, 2016). The lower UV-absorbing potential of red compared to green leaves should oppose indeed the shade avoidance response (Hayes, Velanis, Jenkins, & Franklin, 2014; Mazza & Ballarè, 2015). On the other hand, the ability of anthocyanins in absorbing over the red waveband, thus reducing the red (R) to far-red (FR) ratio (R/FR), as occurs when leaves grow under a dense canopy (Franklin, 2008), may be responsible for the shade syndrome displayed by cyanic leaves. The absorption spectra of anthocyanins, especially when conjugated with 'colorless' flavonoids (so-called co-pigmentation, Trouilas et al., 2016) may have an appreciable tail over the 600-630 nm waveband (Gould et al., 2018; Jordheim et al., 2016; Fig. 1). Since the epidermal concentration of colorless flavonoids is high (in the low mM range, Agati & Tattini, 2010) in both green and red leaves growing in sunlight (Tattini et al., 2014, 2017), co-pigmentation is strongly favored. However, the extent to which anthocyanin-induced decline in R/FR may contribute to the shade avoidance response in cyanic leaves needs deeper investigation: true shade leaves may experience R/FR ratios even an order of magnitude lower than that perceived by sun-exposed leaves (Fankhauser & Batschauer, 2016).

The functional significance of blue-light absorption by epidermal anthocyanins has been early-emphasized

(Chalker-Scott, 1999; Drumm-Herrell & Mohr, 1985), but largely ignored thereafter. Nonetheless, red stems of *Cornus stolonifera* transmitted just 25% of blue light compared to green stems (Cooney, Schafer, Logan, Cox, & Gould, 2015; Gould, Dudle, & Neufeld, 2010), and blue light absorption by the epidermal peel of activation-tagged *pap1-D*(*production of anthocyanin pigment 1- Dominant*) mutant of*Arabidopsis* was as much as 70% of the absorbance over the green-yellow waveband (Gould et al., 2018). The decline in blue photons reaching the photosynthetic apparatus limits the efficient use of incident radiant energy for photosynthesis and imposes to cyanic leaves a profound adjustment in the light harvesting system (Horton, 2012; Ruban, 2018). Consistently, cyanic leaves have much greater concentration of chlorophylls (Chl), a significantly lower Chl*a*to Chl*b* ratio (Chl*a* /Chl*b*) and, usually display lower photosynthetic rates than the green counterparts (Gould, Vogelmann, Han, & Clearwater, 2002; Menzies et al., 2015; Zhang et al., 2018a), unless when long exposed to high solar irradiance (Liakopoulos et al., 2006; Tattini et al., 2014; 2017). These observations well explain the shade syndrome displayed by cyanic leaves, even when growing in full sunlight (Manetas et al., 2003; Hughes et al., 2005; Tattini et al., 2017; Zeliou et al., 2009). In fact, red leaves are thinner, with less compact mesophyll tissues and lower proportion of palisade to spongy parenchyma with respect to green leaves (Boardmann, 1977; Franklin, 2008; Manetas et al., 2003; Kyparissis et al., 2007; Tattini et al., 2014). The shade nature of cyanic leaves is also manifested through a lower concentration of de-epoxided xanthophylls, and consequently, of a lower potential (or of a lower need, Tattini et al., 2017) to dissipate excess energy via nonphotochemical quenching (NPQ) compared to green leaves, irrespective of light availability (Landi et al., 2015; Tattini et al., 2014).

Here we discuss about the suite of molecular events, which operate at very different levels of scale (from cellular to organism, up to whole-plant levels), that follow blue light absorption by epidermal anthocyanins. We offer clear evidence that the blue light-absorbing properties of anthocyanins are responsible for the shade nature of cyanic leaves/individuals and, as a corollary, this strongly supports the view of an effective photoprotective role of anthocyanins, consistent with the notion that blue light contributes substantially to the action spectrum for photodamage (Takahashi et al., 2010).

Dissecting molecular events at the base of the shade nature of cyanic leaves

Low blue light availability evokes shade avoidance responses similar to those induced by low R/FR (Sellaro et al., 2010; Pedmale et al., 2016), and the cellular reprogramming because of blue light depletion may be even larger than in response to a decrease in R/FR (Ballarè & Pierik, 2017; Ballarè, Scopel, & Sanchez, 1990). Plants are very sensitive to changes in blue light irradiance, as up to 26% of gene expression varies in response to blue light, even on a very short, time-scale level (Jiao et al., 2003). This conforms to the notions that stems perceive reductions in blue light well before leaves are shaded, and that low blue light is an indicator of actual shading, whereas plants use the reduction in R/FR as an early warning signal of future competition (Ballaré et al., 1990; Keuskamp, Keller, Ballarè, & Pierik, 2012). As a consequence, the blue light absorbing properties of anthocyanins cannot be ignored when exploring response mechanisms of green vs red individuals to excessive light as well as to conclusively assess the photoprotective functions of anthocyanins.

While functional analysis of genes involved in secondary metabolite biosynthesis has been investigated in some instances(Jin et al., 2018; Kim et al., 2018; Torre et al., 2016), there is very limited information about molecular events that govern morpho-anatomical and physiological traits in red compared to green individuals (Tattini et al., 2017). Here we have extended the analysis of differentially expressed genes reported in Tattini et al. (2017) for purple and green basil, with special emphasis on a suite of blue light-responsive genes (Fig. 2), which regulate developmental processes at the base of the shade nature of cyanic leaves/individuals. Overall, low blue light-regulated genes aimed at maximizing light harvesting are over-expressed in purple leaves (Fig. 2). These include a gene coding for auxilin-like J-domain protein required for chloroplast accumulation response 1 (*JAC1*) under low blue light (Suetsugu, Kagawa, & Wada, 2005), thus re-locating chloroplasts perpendicular to the light flux (chloroplasts move to the periclinal cell wall). The expressions of genes coding for Chlorophyll*a*-*b* binding protein CP2410A (CAP10A), and the nitrogen fixing (niFU-like3) protein, all involved in light harvesting in PSI (Ganadeg, Klimmek, & Jansson, 2004; Yabe, Morimoto, Nishio,

Terashima, & Nakai 2004) are also higher in cyanic leaves. This is also the case of CURVATURE THYLAKOID 1A (CURT1A), which is effective in optimizing PSII photochemistry under low light conditions (Pribil et al., 2018). The need of 'maximizing' light harvesting in purple leaves is also well documented by the large expression of genes, such as *Far Red Impaired Response 1* (*FAR1*) and *Protochlorophyllide-a oxygenase (PTC52*), which promote Chl biosynthesis (Bartsch et al., 2008; Reinbothe et al., 2006; Tanaka, Tanaka, Tanaka, Yoshida, & Okada, 1998). As expected, a range of high light-responsive genes is downregulated in red basil. This includes the *Filamenting Temperature-Sensitive Z1* (*FtsZ1*) that promotes chloroplast division and the photo-relocation of chloroplasts toward the anticlinal wall of palisade cells (so-called chloroplast avoidance response, Dutta et al., 2017; Kong & Wada, 2011; Koniger, Delamaide, Marlow, & Harris, 2008). The transcript abundance of genes that encode for proteins that either reduce the synthesis (early light-induced protein2 ELIP2, Tzvetkova-Chevolleau et al., 2007) or sustain the catabolism of Chl (Chlorophyllase1, CLH1, Banaś, Labuz, Sztatelman, Gabrys, & Fiedor, 2011), and of Chl*b* (Non Yellow Coloring1, NYC1*,* Horie, Ito, Kusaba, Tanaka, & Tanaka, 2009), is also low in purple basil. Notably, red leaves have lower expression levels of both*EXECUTER1* (*EX1*) and *Plastid-Lipid-Associated 6* , (*PAP6*), which are genes involved in singlet oxygen-induced retrograde signal and in the transport of lipophilic antioxidants, respectively, under light stress (Langenkamper et al., 2011; Lee, Kim, Landgraf, & Apel, 2007). This increase in oxidative stress signaling (sensu Foyer, Ruban, & Noctor, 2017) displayed by green leaves adds further evidence to previous suggestions that anthocyanins are effective photoprotective pigments (Gould, 2004; Gould et al., 2010; Hughes et al., 2005, Hughes & Smith, 2007).

The expression of genes involved in the shade avoidance responses at leaf and whole plant levels is also higher in cyanic leaves. These include three members of the *Phytochrome Kinase Substrate* gene family (*PKS1, PKS3, PKS4*), which operate downstream of Phototropin1 (phot1) under low blue light irradiance, and act as negative regulators of phytochrome (PHY) signaling. Overexpression of*PKS* s promotes hypocotyl elongation and leaf flattening as well, early events in shade avoidance responses (de Carbonell et al., 2010; Lariguet et al., 2003). We also observe that the expressions of both*DWARF27* (*β-ϛαροτενε ισομεραση*), a gene involved in the first committed step of strigolactone biosynthesis and two genes, coding for members of the ABC (ATP BINDING Cassette) superfamily transport proteins (ABCG5 and ABCG11, also known as pleiotropic drug resistance (PDR) proteins) are low in purple basil. DWARF27 and ABCGs regulate canopy architecture, by promoting axillary branching indeed (Bienert et al., 2012; Kretzschmar et al., 2012; Yasuno et al., 2009), a common plant response to high light irradiance. Other relevant genes involved in shade avoidance responses such as *LONGIFOLIA 1/2* and a set of*EXPANSINs (1,4,8,10)* (Christie, 2007; Sasidharan, Chinnappa, Voesenek, & Pierik, 2008) are also overexpressed in red compared to green basil leaves. *LONGIFOLIA* and *EXPANSIN* both promote leaf and stem elongation, by enhancing polar cell elongation at the expense of cell proliferation (Lee et al., 2018), and disrupting noncovalent bonds between cellulose microfibrils and matrix polysaccharides, respectively (Choi, Lee, Cho, & Kende, 2003; Marowa, Ding, & Kong, 2016).

Consistent with their shade nature, red individuals invest less carbon to leaf construction, as also occurs when green leaves grow in low light. This is because R2R3MYB genes, such as the *MYB6* ,*MYB75* , *and MYB308* genes detected in our study, while promoting anthocyanin biosynthesis, repress the synthesis of early products of the general phenylpropanoid metabolism, including lignin (Bhargava, Mansfield, Hall, Douglas, & Ellis, 2010; Tamagnone et al., 1998). This is in line with the notion that blue light strongly promotes secondary cell wall thickening (Zhang et al. 2018b). It has been recently shown that a range of transcription factors that are responsive to low blue light irradiance, and involved in the regulation of leaf cell fate, are largely overexpressed in high light-grown red compared to corresponding green basil leaves (Tattini et al., 2017). This includes relevant members of the HD-ZIP family, such as *ATHB1, ATHB2* and*ATHB12* genes, which repress cell proliferation and the proper development of palisade cells, thereby sustaining shade avoidance responses (Ciolfi et al., 2013; Hur et al., 2015). Our findings are therefore consistent with and may conclusively explain why cyanic leaves are thinner, have much less compact mesophyll and lower leaf mass per area (LMA) with respect to acyanic leaves (Manetas et al., 2003; Kyparissis et al., 2007; Wang, Zhou, Jiang, & Liu, 2016), especially when growing in high light (Tattini et al., 2014).

The 'peculiar shade nature' of cyanic leaves: a perspective in anthocyanin research

Though cyanic leaves have a suite of morphoanatomical- and biochemical-related traits that closely resemble those usually displayed by green leaves growing in low light (true shade leaves), they also display features that are uncommon in shaded green leaves. First, while shade leaves typically saturate photosynthesis at much lower PPFD compared to sunny leaves, photosynthesis in cyanic leaves saturates at very similar or even higher PPFD than do the green counterparts (Fig. 3). This results simply on the ability of their epidermal anthocyanin filter in effectively absorbing photons otherwise available to chlorophylls, especially to Chl_b: the actual quantum yield for CO_2 assimilation is lower at moderate or greater at high light irradiance in red compared to green leaves (Tattini et al., 2014; 2017, Fig. 3). There is evidence indeed that red leaves have higher photosynthesis during the central hours of the day (Tattini et al., 2017), thus adding further support to the effective photoprotective functions of anthocyanins. Second, stomatal conductance in red leaves is higher or very similar compared to that of green leaves (Liakopoulos et al., 2006; Nikoforou et al., 2011; Tattini et al., 2017). This is unusual for true shade leaves, in which the excess of green compared to blue (and red) photons opposes the opening and the development of stomata (Chen, Xiao, Li, & Ni, 2012; Poorter et al., 2019). However, cyanic leaves sense both higher blue/green and red/green ratio compared to true shade leaves, and this may promote stomata opening (Smith et al., 2017). The matter deserves further investigation aimed at evaluating the relative contribution of blue, green and red signals (Merzlyak et al., 2008) perceived by cyanic leaves, to the downstream molecular events regulating the development and the aperture of stomata (Inoue & Kinoshita, 2017; Hiyama et al., 2017; Kang, Lian, Wang, Huang, & Yang, 2009).

The profound morpho-anatomical adjustments imposed by the epidermal anthocyanin shield makes complex the analysis of the 'photosynthetic performance' of cyanic vs acyanic leaves and, hence, of the photoprotective role of anthocyanins. For instance, Tattini et al. (2017) have shown that mesophyll conductance to CO_2(g_m) is substantially lower in purple than in green basil leaves growing in full sunlight (similar results have been observed in *Acer platanoides* , Fini unpublished data). This conforms to previous observations that g_m is usually lower in shaded than in sun-exposed green leaves (Campany, Tjoelker, von Cammer, & Duursma, 2016; Peguero-Pina et al., 2016). We hypothesize that the anatomical adjustments imposed by the shade-avoidance response, such as the accumulation of chloroplasts toward the periclinal cell walls (Wada, 2016) may force cyanic leaves to 'unusually high' stomatal conductance (compared to green leaves) to counter large limitations to CO_2 diffusion through the mesophyll (Tattini et al., 2017). As a result, the drawdown from actual (calculated from response curves of A_N to changes in chloroplast CO_2 concentration, A_N/C_ccurves) to apparent (calculated from response curves of A_N to changes in intercellular CO_2concentration, A_N/C_i curves) carboxylation efficiency ($V_{c,max}$) was indeed markedly higher in red compared to green basil leaves (Tattini et al., 2017). The lower carboxylation efficiency of red compared to the green counterparts reported in previous studies (Carpenter, Keidel, Pihl, & Hughes, 2014; Nikoforou, Nikopoulos, & Manetas, 2011; Ranjan et al., 2014) may merit extensive re-evaluation. In turn, this poses serious methodological issues regarding the effective photoprotective potential of cyanic vs acyanic leaves. We recall that photoprotection, a qualitative parameter in its nature, closely relates to photoinhibition and, hence, suitably quantified by high light-induced depression of photosynthesis, rather than photosynthesis *per se* . However, in most studies the degree of photoinhibition in cyanic vs acyanic leaves has been estimated through light-induced declines in F_v/F_m([?]F_v/F_m) and/or Φ_{PSII}([?]Φ_{PSII}). Nonetheless, when leaves largely differ for both g_s and g_m, neither [?]F_v/F_m nor [?]Φ_{PSII} are good proxies of photoinhibition: g_s, and particularly g_m are major constraints to photosynthesis, especially under high light irradiance. We conclude that quantifying the relative contribution of diffusional limitations to photosynthesis in cyanic vs acyanic leaves long-exposed to excessive light (when photoprotection really makes sense) will significantly improve our understanding on the actual photoprotective role(s) of anthocyanins.

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Figure legends

Figure 1. *In vivo* absorbance spectra of epidermal anthocyanins. Measurements were performed on intact leaves in red and green individuals of the same genotype (Photinia x Fraseri "Red Robin" and*Parthenocissus quinquefolia*) or of different cultivars (red-leafed *Ocimum basilicum* cv. "Purple Ruffle" and cv. "Red Rubin" compared to green-leafed *O. basilicum* cv. "Tigullio") using a spectrofluorimeter equipped with a double arm optical fibre bundle. Absorbance spectra were then calculated using the protocol of Agati,

Cerovic, Pinelli, & Tattini (2011), by measuring the Chl fluorescence excitation over the 350-700 nm spectral region, for emission at 730 nm. Theoretical background: the Chl Fluorescence Excitation Ratio (ChlFER) of green to red leaves corresponds to the ratio of epidermal transmittance (EpT) and, hence, $\text{ChlFER}_{\text{green/red}} = \text{EpT}_{\text{green/red}}$. According to the Beer–Lambert's law, A = -log T, thus log ChlFER is the difference in epidermal absorbance of red to green leaves: $\text{logChlFER}_{\text{green/red}} = \text{EpA}_{\text{red}} - \text{EpA}_{\text{green}}$. Since fluorescence spectroscopy is a highly sensitive technique and fluorescence emitted by chlorophylls is intense, logChlFER is more accurate than reflectance spectroscopy in measuring*in vivo* absorbance of leaf epidermis, especially in the UV-blue waveband. In fact, reflectance is very low over the 350-480 nm waveband, due to high absorbance of both epidermal located phenylpropanoids and photosynthetic pigments located in the adaxial mesophyll layers.

Figure 2. Heat map showing differentially expressed genes, based on $\log_2$ fold change of transcript abundance of purple ('Red Rubin') to green ('Tigullio') *Ocimum basilicum* leaves grown for four weeks in full sunlight, as detailed in Tattini et al. (2017). List of annotated genes and encoded proteins: (*JAC1*) auxilin-like J-domain protein required for chloroplast accumulation response1; (*FtsZ1*) Filamenting Temperature-Sensitive Z1; (*CAP10A*) Chlorophyll a-b binding protein CP2410A; (*NIFU3*) Nitrogen Fixation-like 3; (*CURT1A*), CURVATURE THYLAKOID 1A; (*FAR1*) Far Red Impaired Response 1; (*PTC52*) Protochlorophyllide-*a*oxygenase; (*ELIP2*) early light-induced protein 2; (*CLH1*) Chlorophyllase 1; (*NYC1*) Non Yellow Coloring 1; (*EX1*), EXECUTER1; (*PAP6*) Plastid-Lipid-Associated 6; (*PKS*) Phytochrome Kinase Substrate; (*LNG*) LONGIFOLIA; (*EXPA*) EXPANSIN; (*ATHB*) *DWARF27*) β-carotene isomerase.

Figure 3. Response curves of net photosynthesis (A_{N}) to changes in light irradiance (A_{N}:PPFD curves) in reddish vs green cultivars. (A) Response curves of green (green symbols) and black (red symbols) *Ophiopogon planiscapus* 'Nigrescens' grown in sunlight (redrawn from Hatier, Clearwater, & Gould, 2013). (B) Response curves of*Physocarpus amurensis* 'Maxim' (green symbols) and*Physocarpus opulifolius* 'Diablo' (red symbols) grown under natural sunlight (1000-1500 μmol quanta m-2 s-1 (redrawn from Zhang, Zhong, Wang, Sui, & Xu, 2016). (C) Response curves of *Acer platanoides* 'Summer Shade' (green symbols) and 'Crimson King' (red symbols) grown for three month in full sunlight (Fini, unpublished data). (D) Response curves of green (Tigullio, green symbols) and purple (Red Rubin, red symbols) *Ocimum basilicum* grown for four weeks in full sunlight (redrawn from Tattini et al. 2017).