UV-B induced morphological changes; an enigma

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ABSTRACT

UV-B induces complex changes in plant morphology, including decreases in petiole length, leaf area and/or increases in thickness together with shorter, but more branched stems. The resulting, compact, phenotype is widely reported in the literature. Yet, major questions remain with respect to the precise phenotype, the underlying mechanism, and the functional role. Complex dose-response curves, a mixture of transient and permanent morphological changes, and distinct effects on cell and organismal development, indicate that at least two distinct UV-B phenotypes exist. One phenotype is mediated through the UV-B photoreceptor UVR8, and has been linked to, amongst others, decreases in hypocotyl length and petiole elongation. The second UV-B induced phenotype is associated with generic, oxidative plant stress, as detailed by the concept of Stress Induced Morphological Responses (SIMR). Despite differences in underlying mechanism, both UV-B responses lead to a compact phenotype. The functional role of this phenotype remains unclear, and assertions that the phenotype contributes to UV-B protection remain unproven. A key target for future research is the development of markers that distinguish the two UV-B induced phenotypes, and therefore facilitate systematic studies of their functional role and environmental relevance.

Keywords

UV-B radiation, plant morphology, elongation, UV-B tolerance, stress, ROS

No two trees are the same to Raven.

No two branches are the same to Wren.

If what a tree of a bush does is lost on you,

You are surely lost. Stand still. The forest knows

(David Wagoner, "Lost" 1999)

1-INTRODUCTION

David Wagoner (1999) wrote in his poem "Lost" about the variation in architecture that is so characteristic of plants. The poem also refers to knowledge, information that is shared between organisms present in the forest environment, information that is important to all. Notwithstanding the poetic interpretation, these lines are in many ways an accurate statement on the high degree of variation in plant architecture, and the important ecological consequences of variation for the plant as well as the entire ecosystem. The intraspecific plasticity in plant architecture is controlled by endogenous growth processes and external environmental influences (Barthélémy and Caraglio, 2007). Morphological processes that determine plant architecture include primary growth (organogenesis and elongation), branching, morphological differentiation of axes, and positioning of reproductive structures (Barthélémy and Caraglio, 2007). Thus, plant architecture is dependent on the arrangement of what are, in essence, modular structures in a particular pattern.

Environmental parameters can impact on plant architecture by altering the arrangement of organs in a 3D structure, the identity of the organs formed, and/or the morphology of each organ. These responses to environmental cues are vital for optimising growth performance under different conditions. Especially, temperature, solar radiation, nutrient supply and rainfall are known to modulate organ identity, branching, tropisms, and phenology (Costes *et al*., 2013). The role of solar radiation is particularly complex as light constitutes both energy and information. Optimal intensities of Photosynthetically Active Radiation (PAR) can alter plant growth and overall plant architecture through the improved supply of photosynthates, while specific wavelengths control architecture via dedicated photoreceptors that perceive the informational content of light. Photoreceptors can perceive, and trigger responses to, minor changes in the direction, duration, dose and wavelength of light, and this underlies processes such as photoperiodicity, phototropisms and photomorphogenesis. The best documented examples of light mediated changes in plant architecture are those mediated by phytochrome (red/far-red responses including shade-avoidance), cryptochrome (blue light responses including hypocotyl elongation) and phototropin (blue light responses including effects on tropisms and leaf architecture) (Möglich *et al*., 2010; Galvão and Fankhauser, 2015). In recent years, the effects of ultraviolet-B (UV-B; 280 - 315 nm) radiation on plant architecture have also drawn the attention of the scientific community (Robson *et al*., 2015b) with research focussed on mechanistic, ecological and commercial aspects. In this chapter we will review the concept of

the UV-B phenotype, describing UV-B induced morphological changes, analysing underlying regulatory pathways, and exploring the functional importance.

2-THE UV-B PHENOTYPE

Reports on UV-mediated changes in plant architecture have been around for a considerable period. Brodführer reported that solar UV-radiation altered the architecture of the *Arabidopsis thaliana* inflorescence in 1955. Teramura (1983) concluded that "Ultraviolet-B radiation has been shown to affect anatomical and morphological plant characteristics" and this author lists UV-B effects such as "plant stunting, reductions in leaf area and total biomass, and alterations in the pattern of biomass partitioning into various plant organs". Since the publication of these early reports, many studies have shown that UV-B radiation can alter plant architecture (reviewed by Jansen 2002; Robson *et al*., 2015b). Generally, the term "UV-B phenotype" refers to a more compact plant. At the organismal level, the most common UV-B responses are decreases in leaf area and/or increases in thickness together with changes in leaf shape, shorter petioles and, in some cases, leaf curling (Yang *et al.,* 2008; Wargent *et al.,* 2009; Hectors *et al.,* 2010; Klem *et al.,* 2012, Robson and Aphalo, 2012). A few studies have also reported UV-effects on root development, and especially an increase in root-shoot ratio (Robson *et al*., 2015b). In parallel with UV-B induced decreases in leaf size, leaf venation also changes, with a notable decrease in the width of the mid-rib of soybean (*Glycine max*) leaves (Fatima *et al.,* 2016). Typically, stems will remain shorter, as detailed for various species (Barnes *et al.,* 1990; Hofmann and Campbell, 2011; Germ *et al.,* 2013). Although the length of the main stem may decrease in UV-B acclimated plants, overall stem length does not necessarily decrease due to enhanced axillary branching and/or tillering (cf. Jansen, 2002). For example, *Taxus chinensis* exposed to supplemental UV-B under growth room conditions displays an almost 6-fold increase in the number of secondary branches (Zu *et al*., 2010). Yet, caution is required when analysing published data on the UV-B phenotype. UV-B exposure conditions vary dramatically between research groups, and involve exposure to low or high UV-B doses, to filtered UV-B radiation or mixtures of UV-A, UV-B and UV-C radiation (all emitted by UV-B lamps), and to various UV-B:PAR ratios. Moreover, experiments are performed under indoor or outdoor conditions, and using different red:far-red ratios. Given such variation in experimental conditions, it is not surprising that there is considerable variation in observed UV-B phenotype, and that many studies fail to report the "prototype" UV-B phenotype of a "compact" plant.

Despite experimental variations, the existence of a UV-B phenotype has been firmly established. Studies with UV-B photoreceptor (UVR8) mutants have unambiguously shown the role of UV-B, and that of UVR8 in controlling plant architecture (Favory *et al*., 2009; Heyde and Ulm, 2012). Indeed, UVR8 was discovered in a screen for UV-B induced hypocotyl shortening (Favory *et al*., 2009). The failure of UVR8 mutants to undergo UV-induced shortening of the hypocotyl was the first evidence linking UVR8 to control of plant architecture. UVR8-deficient mutants do not just fail to display a shorter hypocotyl after UV-B exposure, but also petiole length, and therefore rosette diameter remain relatively large despite UV-B exposure (Hayes *et al*., 2014). Yet, UVR8-deficient mutants still display "dwarfing" when exposed to high UV-doses. Therefore, not all UV-B mediated effects on plant architecture are mediated by UVR8, and it must be concluded that there is more than one UV-B induced phenotype.

3-**EXISTENTIAL DOUBTS**

The UV-B phenotype in the natural environment

The UV-B phenotype is routinely observed in plants raised under supplemental UV-B in controlled conditions. Barnes *et al*., (1990) observed reductions in leaf length, leaf area, and shoot height, as well as increases in leaf and axillary shoot production across a collection of 12 dicot and monocot species kept in a glasshouse. Cooley *et al*., (2001) showed UV-B induced reductions in leaf area, petiole length, and leaf number in a range (but not all) of *Arabidopsis thaliana* accessions exposed for 21 days to supplemental UV-B under outdoor conditions. Yet, long-term outdoor studies have yielded more variable results. For example, Indian cress (*Tropaeolum majus*) grown outdoors under supplemental UV-B for three months, displayed no UV-induced alterations in specific leaf area, internode length, and petiole length (Germ *et al*., 2016). In contrast, work by the same group on common and tartary buckwheat (*Fagopyrum esculentum* and *F. tataricum*, respectively) grown outdoors under supplemental UV-B revealed strong UV-B induced decreases in leaf area, and plant height as well as increases in leaf thickness (Breznik *et al*., 2005). Few studies have explored the UV-B effect on morphology under natural-growth conditions. Sun *et al*., (2016) reported how leaf morphological traits of *Quercus guyavifolia* (Chinese Guava Leaf Oak) change along an altitudinal gradient on the Qinghai-Tibet plateau. With increasing UV-dose, leaf length, leaf length-width ratio, and petiole length all decreased. Although these data appear to suggest that a UV phenotype does occur in the natural environment, this is not necessarily the case, as other altitude dependant factors such as temperature and rainfall are similarly associated with leaf architecture. A more extensive experiment was done by Roro *et al*., (2016) who combined an altitudinal gradient with the use of UV-filters. This revealed that UV radiation decreases total leaf area, but increases stem branching and specific leaf area in pea plants (*Pisum sativum*) and this occurs especially at higher latitudes. Effects on branching and specific leaf area were particularly pronounced during the dry season, emphasising that other environmental factors moderate UV-B effects on morphology. Perhaps the most ecologically relevant data on UV-induced morphological change are those generated at Abisko Research station in Sweden where outdoor UV-supplementation studies lasted decades. In an early study, leaf thickness of *Vaccinium vitis-idaea* increased following two years of UV-supplementation, although co-existing *Vaccinium myrtillus* and *V. uliginosum* both developed thinner leaves in the same exposure experiment (Johanson *et al*., 1995). Tellingly, the year-on-year variation in leaf thickness of non-UV control plants was greater than the actual UV effect in each particular year. After seven years of UV-B treatment there were no discernible effects of UV-B on leaf thickness (Semerdjieva *et al*., 2003). These data underline that the UV-B phenotype is not reliably observed under natural conditions. It is likely that in many years the UV-B effects on plant architecture are masked by other environmental factors, such as light, temperature, and water availability, which are known to exert strong effects on plant architecture. Apart from environmental factors, there also appears to be a strong effect of plant genotype on the UV-B phenotype. Different Arabidopsis accessions display distinct morphological responses to the same UV-B treatment (Cooley *et al.,* 2001). Moreover, Klem *et al*., (2012) demonstrated the importance of leaf ontogeny for UV-B responses. Thus, rather than a simple on/off scenario, the induction of the UV-B phenotype is specific

phenomenon that can be observed under specific environmental conditions in specific species and/or ecotypes.

The UV-B phenotype as a transient phenomenon

Plant organs display determinate or indeterminate growth. Leaves typically have a final form and size, depending on environmental conditions. In contrast, stems often exhibit indeterminate growth. Awareness of growth patterns is essential when assessing the impact of an environmental factor on organ size. Unfortunately, single time-point studies constitute the bulk of knowledge about the UV-B phenotype, and these studies fail to clarify whether UV-B exposure leads to a permanently more dwarfed phenotype or slows down the expansion rate to yield a transiently smaller organism. Few studies have investigated this question, but it appears that both scenarios do occur. In silver birch (*Betula pendula*), leaf elongation is delayed by supplemental UV-B, but as elongation growth continues slightly longer in the UV-B exposed leaves, only a transient effect on leaf size is observed (Robson and Aphalo, 2012). In contrast, in downy birch (*Betula pubescens*) UV-B decreases the size of the fully developed leaf (Robson and Aphalo 2012). Effects on fully developed leaves were also described by Johanson *et al*., (1995) who reported UV-induced changes in leaf thickness in three *Vaccinium* species grown outdoors, under supplemental UV-B. Transient effects of UV-B on leaf morphology have been studied in some detail in *Arabidopsis thaliana*. Hectors *et al*., (2010) showed that supplemental UV-B initially mostly impeded longitudinal growth. However, in leaves exposed for longer periods to UV-B, the length:width ratio was restored as a result of a stronger impediment of elongation along the transverse axis of the leaf. Thus, not only are some UV-B effects transient, it also appears that plants are capable of compensatory responses that restore the geometric balance of the leaf. Lake *et al*., (2009) reported a transient effect of supplemental UV-B on leaf elongation in Arabidopsis. Following an initial (acute) phase of decreased growth, plants exposed to chronic UV-B exposure recovered growth. Interestingly, a permanent phenotypic effect was observed for the Arabidopsis *fah-1* mutant. This mutant is UV-sensitive as it lacks sinapic acid due to a mutation in the enzyme ferulate-5-hydroxylase. This observation implies that permanent, morphological UV-B effects are associated with stress, while transient UV-effects are associated with lower UV-B doses. Given the mixture of transient and permanent UV-B effects, a key message is that single time-point studies are inadequate for analysing UV-B induced morphological changes. Indeed, it cannot be excluded that the failure of some studies to detect a UV-B effect on plant morphology is due to the transient character of the UV-B phenotype, in combination with an unfortunate choice of time-point for analysis.

The dose response for induction of the UV-B phenotype

Nearly all reports on the UV-B phenotype are based on single-dose studies, and therefore fail to elucidate any dose-response relationship. The few studies that investigated the effects of different doses of UV-B on plant architecture show that the relationship is not necessarily linear. Brodführer (1955) revealed that increasing the UV-B dose from 2% to 33% of ambient solar UV-B resulted in an increase in the length of the main stem of the Arabidopsis inflorescence. Increasing the UV-B dose from 33% to 100% of solar UV-B did not cause a further increase in

stem length, but rather a substantial decrease in stem length. Similarly, low UV-doses increased inflorescence branching, while high doses inhibited the same process. Van de Staaij *et al.,* (1997) observed a similar (but inverse) bell-shaped UV-B dose-response. Low doses of UV-B decreased flower formation in *Silene vulgaris*, whilst higher UV-doses stimulated this process. An inverse, bell-shaped dose-response was also found by Qaderi *et al*., (2008) who reported that low doses of UV-B decreased the number of leaves in *Silene noctiflora*, although higher UV-doses increased leaf numbers. At present there are not enough dose-responses curves of UV-B mediated plant morphology to draw firm conclusions. However, the three examples of bell-shaped dose-response curves imply the possibility that distinct UV-B response pathways are triggered by low as opposed to high UV-B doses. Consistently, *uvr8-mutants* fail to display a shorter hypocotyl length when exposed to low doses of UV-B, but display a "dwarfing" response to high doses (Favory *et al.,* 2009).

The UV-B induced phenotype exists, and some of its architectural characteristics are mediated by the UV-B photoreceptor, UVR8. Nevertheless, reported dose-response curves, and mixtures of transient and permanent UV-B effects, strongly suggest that at least two different UV-B phenotypes do exist.

4-A mechanistic perspective on the UV-B phenotype

A cellular perspective

The size of plant organs is determined by interactions between genotype, physiology and environment, through effects on cell proliferation and expansion. During the proliferation phase, the size of densely cytoplasmic cells is relatively constant, while in the post-mitotic organ cells start to enlarge and this is often accompanied by increases in ploidy (Hepworth and Lenhard, 2014). Environmental factors can alter organ size through impacts on cell proliferation and/or cell expansion (Hepworth and Lenhard, 2014). However, this view is overly simplistic, as "compensatory" cell expansion can mask decreases in cell proliferation. Indeed, organ size is co-modulated by the identity of the organ itself, i.e. a top-down control function (Hepworth and Lenward, 2014). UV-B has been shown to decrease cell proliferation and/or cell expansion. UV-B can impede cell division through the accumulation of DNA-damage (primarily cyclobutane pyrimidine dimers and pyrimidine (6-4) pyrimidone dimers) which slow down the G1-to-S step in the cell cycle (Jiang *et al.,* 2011). Oxidative stress caused by UV-B exposure can also impede the cell cycle, through interactions with oxidative stress checkpoints (Tsukagoshi, 2012). The cell cycle block can facilitate DNA repair before further replication occurs (Jiang *et al.* 2011), but does not necessarily result in smaller numbers of cells in a particular organ, as plants can delay the transition from cell proliferation to expansion (Hepworth and Lenhard, 2014). Compensatory effects of UV-B radiation on cell expansion have been related to increases in ploidy. UV-B can enhance endoreduplication resulting in increased ploidy which, in turn, has been associated with cellular expansion (Radziejwoski *et al*., 2011).

UV-B exposure can inhibit cell proliferation (Wargent *et al.,* 2009), expansion (Hectors *et al.,* 2010), or have a complex effect on both processes. Both cell numbers and cell size decreased when a UV-sensitive *Arabidopsis thaliana fah-1* mutant was exposed to UV-B. This scenario

comprised a nearly 10-fold decrease in leaf area was likely associated with abiotic stress (Lake *et al*., 2009). In comparison, larger cells were reported on the abaxial (but not adaxial) leaf surface when wildtype Arabidopsis was exposed to the same UV-B dose (Lake *et al.,* 2009). Similarly, Wargent *et al.,* (2009) reported an increase in cell size in UV-B exposed Arabidopsis, although this was offset by a decrease in cell number. Hectors *et al*., (2010) found that UV-B had no measurable effect on the numbers of cells in Arabidopsis, but cell expansion was decreased by UV-B along a developmentally-controlled pattern. Thus, effects on cell size became apparent first for the distal zone, and only later for the middle and proximal zones of the leaf. These data emphasise the variation in UV-induced cellular responses, but also the importance of the developmental context of UV-B studies.

An anatomical perspective

There is a substantial knowledge gap between UV-B effects on epidermal cells, and on plant organs. In fact upscaling is complicated because tissues within a leaf respond differently to UV-B exposure. Leaf thickness increased substantially in blueberry (*Vaccinium corymbosum*) cultivar Legacy exposed for 40 days to supplemental UV-B, and this was due to increased thickness of the mesophyll (Reyes-Diaz *et al*., 2016). This observation is consistent with data by Robson and Aphalo (2012) who reported UV-B induced increases in palisade thickness in birch leaves, and by Nagel *et al*., (1998) who reported increases in hypodermal thickness of pine (*Pinus ponderosa*) needles. In lemon (*Citrus limon*) fruits UV induces cell wall thickening in the epidermis, as well as underlying parenchyma and collenchyma (Ruiz *et al*., 2016). Although Reyes-Diaz *et al*., (2016) reported increased mesophyll thickness in UV-B exposed blueberry cultivar Legacy, this was not the case for cultivar Bluegold. In the latter cultivar leaf thickening was associated with disorganisation of the mesophyll cells, and the formation of substantial intercellular cavities. Thus, under the same exposure conditions one blueberry cultivar appears to display a form of acclimation, whilst another cultivar displays stress, reinforcing the message that there is more than one UV-B mediated process that mediates alterations in plant architecture.

5-Underpinning regulatory mechanisms

UVR8 mediated control of plant architecture

Understanding of UVR8 mediated changes in plant architecture has increased in recent years. Interactions with hormonal pathways are a key feature of UVR8 activity. Hayes *et al*., (2014) demonstrated that UVR8 slows elongation growth through interactions with gibberellic acid (GA) and auxin metabolism. GA-homeostasis is affected through a UV-B mediated increase in GA2-oxidase transcript levels. Evidence for a drop in GA-concentrations is indirect, through an increase in (elongation inhibiting) DELLA proteins. Consistently, several other studies have reported induction of genes encoding GA-oxidases (cf. Vanhaelewyn *et al*., 2016). Peng and Zhou (2009) reported a decrease in actual GA levels in soybean (*Glycine max*). In contrast, Yang *et al*., (2004) showed that GA levels in tomato leaves doubled following UV-B exposure. Thus, measurements of GA-levels in UV-B exposed plants do not yet yield a coherent story.

There is good evidence for a role of auxin in UV-B mediated morphological changes. Auxin is a key regulator of elongation, axillary branching, leaf development, and root growth. Initially, auxins were associated with the UV-B phenotype based on architectural similarities between the UV-B phenotype and auxin mutants (Jansen, 2002). Hectors *et al*., (2012) demonstrated a UV-B mediated decrease in free auxin levels in young leaves of Arabidopsis, while Yang *et al*. (2004) reported an overall decrease in auxin levels in UV-B exposed tomato (*Solanum lycopersicum*). Hayes *et al*. (2014) showed UVR8 mediated effects on auxin homeostasis using *pDR5:GUS* reporter constructs. Consistently, UV-B acclimation involves the differential expression of a range of auxin-related genes (Favory *et al.,* 2009; Hectors *et al.,* 2010 & 2012; Hayes *et al.,* 2014; Vandenbussche *et al.,* 2014). Furthermore, the Arabidopsis auxin influx mutant *axr4-1*, and auxin biosynthesis mutant nit1-3 display relatively strong morphological responses to UV-B exposure (Hectors *et al.,* 2012). Thus, there is diverse evidence for a central role of auxin in mediating UV-B induced morphological acclimation.

Stress mediated control of plant architecture

It is unlikely that UVR8 mediated responses comprise the only mechanism of UV-B mediated changes in plant morphology. Favory *et al*. (2009) reported "dwarfing" of Arabidopsis UVR8-deficient plants grown in a solar sunlight simulator. UVR8-deficient plants are hypersensitive to UV-B stress due to a lack of protective responses (Heijde and Ulm, 2012), and it is likely that UV-B induced alterations in architecture of these mutants are associated with stress. The notion of Stress Induced Morphogenic Responses (SIMR) is based on the similarities in phenotype following exposure and acclimation to different stressors (Potters *et al.,* 2007). SIMR comprises a redirection of growth, rather than a cessation. The resulting phenotype can be more dwarfed, with increasing leaf thickness and/or branching (Potters *et al*., 2007). SIMRs are thought to be associated with generic stress-related processes such as enhanced production of Reactive Oxygen Species (ROS) and changed metabolism of auxin (Potters *et al.,* 2007). Although UV-B induced stress is considered to be rare in the natural environment, UV-B is potentially damaging to plants (Jansen and Bornman 2012). UV-B can trigger oxidative stress-responses (cf. Hideg *et al.,* 2013) including the activation of mitogen-activated protein kinase phosphatases (Besteiro and Ulm, 2013). UV-B mediated ROS production has also been linked with nitric oxide (NO) signalling (Lytvyn *et al*., 2016). UV-B induced NO has been linked with changes in microtubuli organisation (Krasylenko *et al.,* 2012), which in turn can affect morphology though regulation of cell division, cell elongation and initiation of lateral growth.

The generic SIMR is likely to play a key role under oxidative stress conditions caused by exposure to high doses of UV-B (for a discussion of high and low UV-B doses see Hideg *et al.,* 2013). In contrast, UVR8 mediated morphological responses can occur under very low UV-B fluences (Brown and Jenkins, 2008) (Fig. 1). Yet, the two potential response pathways are not mutually exclusive, and it is likely that there is considerable overlap of the two responses under the fluctuating UV-intensities that are characteristic of natural sunlight.

UV-B acclimation and its impact on morphology

UV-B induces a broad range of biochemical acclimation responses, some of which can interfere with the mechanism controlling plant growth, while others may affect growth through incurring a fitness cost (Fig. 1). UV-B induced changes in plant architecture and in the concentration of protective flavonoids are typically co-occurring phenomena. Flavonoids play a central role in UV-B protection due to their anti-oxidant and UV-screening properties (Agati and Tattini 2010). However, flavonoid aglycones are also regulators of polar auxin transport (Peer and Murphy 2007) and auxin stability (Mathesius 2001). Qi *et al*., (2003) reported a strong correlation between UV-B absorbing pigments, and thickness in developing pecan (*Carya illinoensis*) leaves. Similarly, Klem *et al*., (2012) showed that increases in leaf flavonol content correlated with decreases in specific leaf area in barley (*Hordeum vulgare*). Exposure of tobacco seedlings to exogenous flavonoids (quercetin and epicatechin) resulted in reduced leaf expansion, increased root length, but a decrease in lateral and adventitious roots (Mahajan *et al.,* 2011). These effects were associated with an increase in free auxin in the shoot, and this was hypothesised to be due to decreased basipetal auxin transport (Mahajan *et al.,* 2011). Previously, the association between flavonoids and auxin transport was demonstrated using Arabidopsis tt4 and ugt78d2 flavonoid mutants. These mutants display alterations in both auxin distribution and plant morphology (Peer *et al.,* 2007; Ringli *et al.,* 2008; Yin *et al*., 2013). Thus, data imply that flavonoids, through their effect on auxin transport, can "fine-tune" the plant phenotype mediated by either UVR8 and/or stress.

6-THE BIOLOGICAL FUNCTION OF THE UV-B INDUCED MORPHOLOGY

Many reports describing the UV-B phenotype refer to a potential role in protecting plants from UV-B stress. It has been hypothesised that thicker leaves contain "UV-free" zones (Day 1993; Jansen 2002). Yet, in most plant species very little (<10% of incident dose) UV-B reaches the mesophyll due to UV-screening by epidermal cells (Day 1993; Barnes *et al.,* 2008). Thus, the importance of leaf thickening for UV-B protection remains unproven, especially as UV-B transmission is patchy due to predominant UV-B penetration via stomatal pores and anticlinal cell walls (Day *et al.,* 1993). It has also been argued that a lack of elongation growth increases self-shading, and therefore decreases UV-B exposure. Yet, despite the obvious attraction of such a concept, shading does not necessarily equate to decreased UV-B exposure. The diffuse fraction of global UV-B irradiance is larger (0.57 to 0.91) than that of visible wavelengths (0.25 to 0.70) (Webb and Steven 1984) which results in relatively strong penetration of UV-B into canopies (Fig. 2). Within a forest canopy the UV:PAR ratio in sunflecks (i.e. exposure direct sunlight) isenhanced compared to sunlight in open environments , while in the shaded understorey the UV:PAR ratio can reach at least five times that of sunlight in the open (Yang *et al*., 1993; Brown *et al.,* 1994). Thus, a more dwarfed architecture does not necessarily reduce UV-B exposure, and may even increase the UV:PAR ratio which is considered to be an important determinant of UV-B stress.

Thus, there is no conclusive evidence that UV-induced alterations in morphology contribute to UV-B protection. The observation that some UV-B effects on morphology are transient (Lake *et al.,* 2009; Robson and Aphalo, 2012) implies, at best, a temporary role in UV-protection. Furthermore, the observation of bell shaped dose-response curves (Brodführer, 1955; Van de

Staaij *et al.*, 1997; Qaderi *et al*., 2008) triggers the question, how can opposing morphological responses be linked with a single, functional role. Given the lack of an obvious association between morphology and UV-B tolerance, the possibility that (aspects of) the UV-B phenotype have a function other than UV-protection should be considered.

An exciting hypothesis on the role of UV-B induced morphological changes was proposed by Hayes *et al*. (2014) who argued that UV-B, via the UVR8 photoreceptor, represses plant shade avoidance. Plants perceive shading through phytochrome which senses the decrease in red:far-red ratio. This triggers elongation growth involving, amongst others, PHYTOCHROME INTERACTING FACTORS (PIFs) and changes in auxin distribution. UV-B counters this response by triggering degradation of PIF4 and PIF5, while increasing DELLA stability (Hayes *et al*., 2014). The antagonistic interaction between UVR8 and phytochrome responses creates a system of "checks and balances" whereby elongation occurs under shaded conditions (low red to far-red ratio), while UV-B perception under exposed conditions impedes this process (Hayes *et al*., 2014). However, this is not necessarily the case as the UV:PAR ratio can be strongly enriched in the understory (Yang *et al*., 1993; Brown *et al.,* 1994)(Fig. 2) with the degree of enrichment depending on vegetation structure including species-specific leaf reflectance and absorbance (Robson *et al*., 2015b). To understand the antagonism between phytochrome and UVR8 pathways in plant shade responses, there is a need for experimental approaches that cover the natural range of variation in the red/far-red and UV-B fluences (Mazza and Ballaré, 2015).

The idea that UV-B induced morphology has a function different from increasing UV-B tolerance is intriguing. In the natural environment exposure to increasing doses of UV-B will normally be paralleled by exposure to increasing intensities of PAR, and therefore typically higher temperatures, and possibly drought ( ). Therefore, UV-B induced morphological changes might play a role in acclimation to high levels of PAR, heat and/or drought. A reduction in leaf area in combination with increased leaf thickness is a typical characteristic of a sun-leaf (Lichtenthaler *et al.,* 2007; Niinemets, 2010). Similarly, branching is associated with exposure to higher levels of PAR (Niinemets, 2010). Thus, it can be speculated that UV-B reinforces the co-occurring high PAR signal. A smaller but thicker leaf is typically associated with a decrease in transpirational water loss (Anyia and Herzog, 2004). Consistently, recent work by Robson *et al*. (2015a) demonstrated that UV-B exposure induced drought tolerance in silver birch (*Betula pendula*). In contrast, Bandurska *et al*. (2013) argued that there is no direct association between UV-acclimation and drought tolerance. Thus, while a role for the UV-B-phenotype in acclimation to various solar and/or weather conditions is not proven, it is an attractive prospect that deserves studying.

7-THE CONSEQUENCES OF UV-INDUCED MORPHOGENESIS FOR GROWTH

Morphological traits are good indicators of plant performance and adaptation (Poorter and Bongers, 2006), through effects on light capture, and photosynthetic performance. Alterations in leaf area and/or leaf thickness will alter light absorption, but also CO_2 availability, nitrogen use, heat load, transpirational water loss and self-shading (Nunes-Nesi *et al*., 2016). Thus, UV-B induced alterations in architecture will likely have consequences for growth, but few studies

have explored this. Some studies report UV-B induced changes in plant architecture, and concomitant decreased biomass accumulation (Breznik *et al*., 2005; Chen *et al*., 2016). Yet, it is likely that negative effects on biomass are due to parallel, damaging impacts of UV-B on the cellular machinery, rather than as a fitness cost of the new phenotype per sé. In some studies, UV-B induced morphological changes are not accompanied by a loss in shoot biomass (Barnes *et al*., 1990). This may be interpreted as meaning that UV-B induced morphological changes do not necessarily carry a yield penalty. However, this is far from proven, particularly as many studies are short, and therefore not suitable for visualising small incremental differences in biomass yield. Thus, the effect of UV-B induced morphological changes on plant biomass production remains largely unknown.

Alterations in architecture can have indirect effects on growth. For example, the spatial distribution of leaves will determine the microclimate which may, in turn, affect susceptibility for pest and pathogen attack (Costes *et al*., 2013, Ben-Yakir and Fereres, 2016). The best evidence for a potential yield penalty of the more dwarfed UV-B phenotype is generated by studies on plant-plant competition. UV-B-induced changes in morphology are large enough to affect competition for light capture in a canopy (Ryel *et al.,* 1990). Indeed, UV-B induced alterations in the competitive balance between wheat (*Triticum aestivum*) and wild oat (*Avena fatua*) were linked to alterations in the relative position of leaves (Barnes *et al.,* 1988). Yet, it is important to be aware that UV-B radiation can also affect plant-plant interactions through other routes, such as a stimulation of production and release of allelochemicals. For example, Li *et al*. (2009) found that allelopathic potential of *Zanthoxylum bungeanum* was stimulated under enhanced UV-B radiation.

8-A FUTURE PERSPECTIVE

UV-B induced changes in plant morphology comprise a decrease in elongation growth, resulting in a more compact plant displaying decreases in petiole length, leaf area and/or enhanced leaf thickness together with shorter, but more branched stems. Here, we argue that there are at least two distinct UV-B phenotypes. One phenotype is mediated by the UV-B photoreceptor UVR8. The second UV-B induced phenotype does not require functional UVR8 and is associated with plant stress. It is likely that both phenotypes do occur simultaneously in the natural environment. It is also likely that this mixture of two phenotypes is a cause of (1) contradictory information on UV-B induced morphological changes, (2) complex dose-response curves, (3) a mixture of transient and permanent morphological changes, and (4) distinct effects on cell and organismal development. To distinguish the two UV-B phenotypes, detailed dose-response curves and action spectra need to be developed. In turn, these can be used to identify molecular, physiological and/or biochemical markers representative for distinct phenotypes. Only, when this has been achieved, is there a realistic chance to explore the functional role of the UV-B phenotypes and to identify regulatory interactions with other environmental parameters which co-modulate plant morphology.

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460

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675 **Figure legends**

676

677 Figure 1. Low doses of UV-B can alter plant morphology via the UV-B photoreceptor, UVR8.
678 Alternatively, high UV-B doses can affect plant morphology through a generic Stress Induced
679 Morphogenic Response (SIMR), as has been observed for many distinct stressors. Interference of
680 flavonoids with auxin metabolism, and hence morphology, has been demonstrated, especially in
681 flavonoid mutants. A trade-off cost associated with UV-acclimation has been postulated, but not
682 conclusively demonstrated.

683

684

685 Figure 2. UV-B and PAR intensities are low under a canopy, compared to those of incident radiation.
686 Canopy transmittance of direct and diffuse radiation depends on vegetation characteristics, and the
687 heterogeneous structure of a canopy results in complex spatial patterns of irradiance. In shaded
688 areas, UV-B:PAR ratios may increase substantially due to the relatively large component of diffuse
689 radiation enriched in solar UV-B. High UV-B:PAR ratios have been associated with plant stress.

690

691 Figures

692

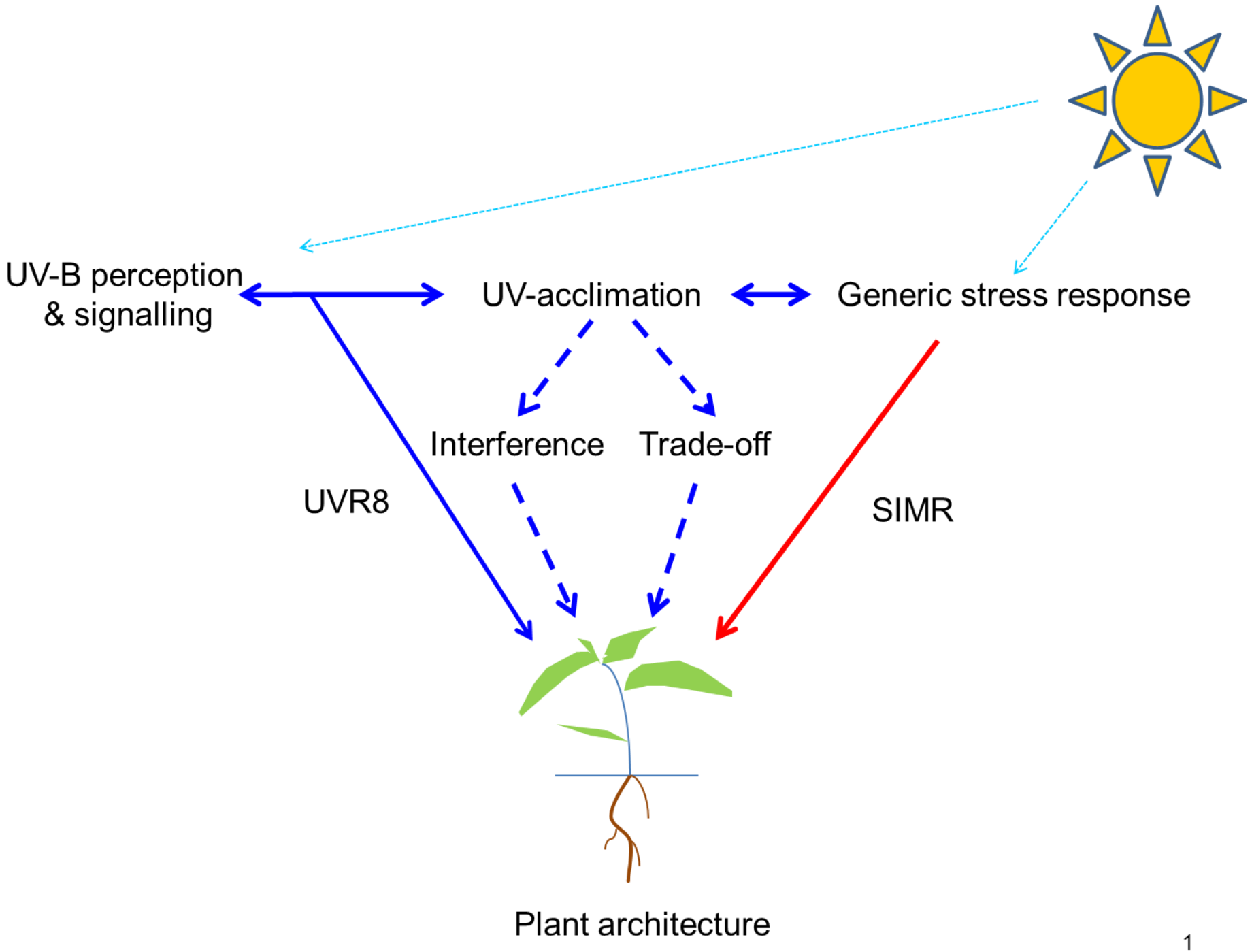
UV-B perception
& signalling
UV-acclimation
Generic stress response
Interference
Trade-off
UVR8
SIMR
Plant architecture

Figure 1. UV-B has been demonstrated to alter plant morphology via the UV-B photoreceptor, UVR8. Alternatively, UV-B can alter plant morphology through a generic Stress Induced Morphogenic Response, as has been observed for many distinct stressors. Interference of flavonoids with auxin metabolism, and hence morphology, has been demonstrated, especially in flavonoid mutants. Yet, this process has not been shown for UV-B induced flavonoids. Similarly, a trade-off cost associated with UV-acclimation has been postulated, but not conclusively demonstrated.

712

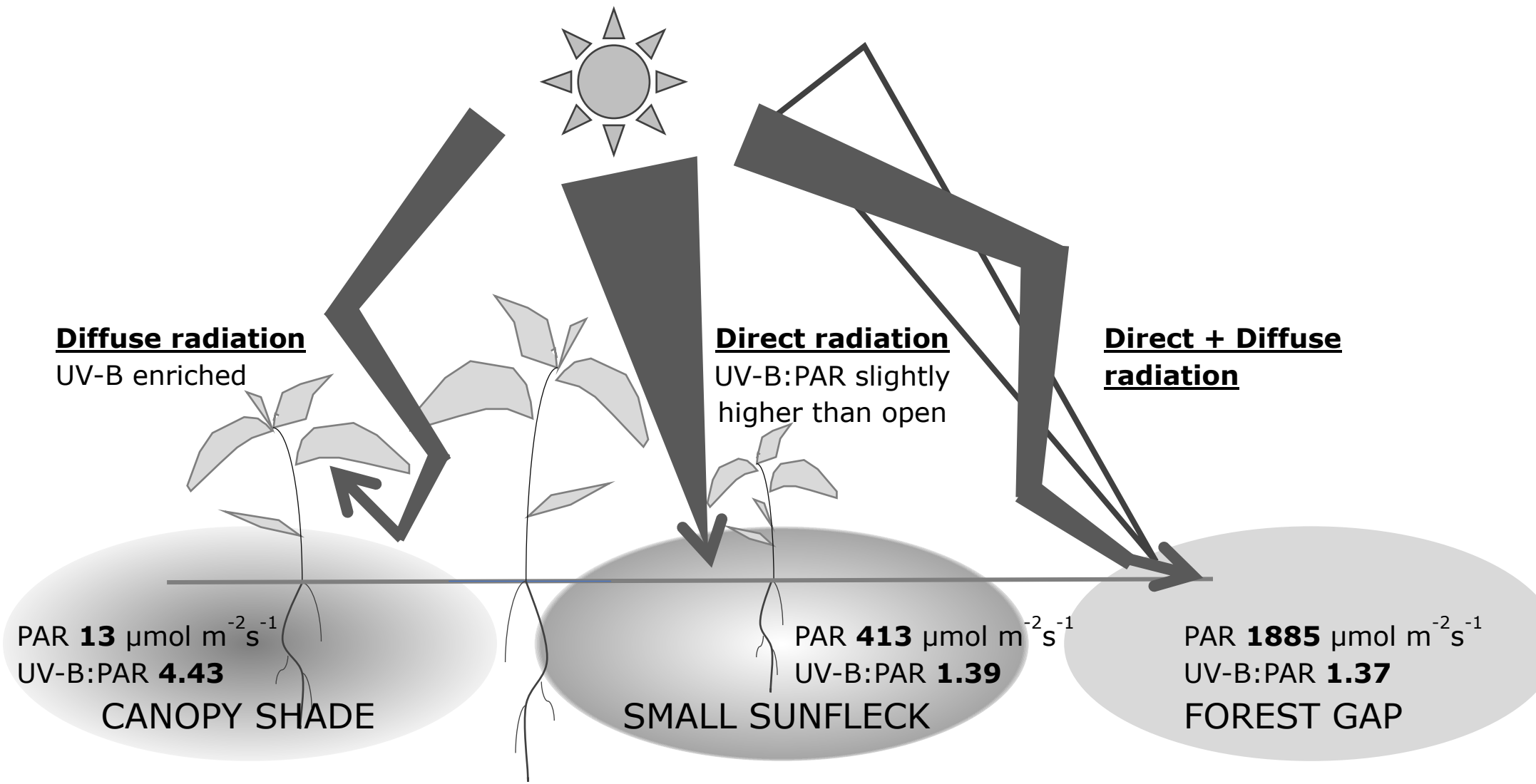
Diffuse radiation
UV-B enriched
Direct radiation
UV-B:PAR slightly higher than open
Direct + Diffuse radiation
PAR 13 µmol m-2s-1
UV-B:PAR 4.43
CANOPY SHADE
PAR 413 µmol m-2s-1
UV-B:PAR 1.39
SMALL SUNFLECK
PAR 1885 µmol m-2s-1
UV-B:PAR 1.37
FOREST GAP

Figure 2: The influence of a plant canopy of spectral irradiance. Values are calculated from spectral photon irradiance measured with a diode array spectroradiometer (Ocean Optics Maya Pro2000+). Photosynthetically Active Radiation (PAR: µmol m-2s-1) and the ratio of UV-B to PAR ×104 are given. Measurements represent points in canopy shade, in a sunfleck, and in a 10-m diameter gap on the floor of an old-growth Fagus sylvatica forest (el Hayedo de Montejo), central Spain on the 17th May 2014 at solar noon.