Historical account

Understanding the ecological role of solar ultraviolet radiation in the life (and death) of terrestrial plants: an historical perspective

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One of the over-arching goals of ecology is to understand how abiotic and biotic environmental factors influence the performance (evolutionary fitness), distribution and abundance of organisms in nature. Because there is a myriad of direct and indirect avenues by which environmental factors can potentially impact organisms, ecologists tend to focus their studies on a select few factors that are deemed to be most important in a particular habitat (i.e., they apply the concept of limiting factors to direct their research questions). Thus, plant ecologists give great attention to studying how water availability influences desert plants, how understorey forest plants have adapted to low light conditions, and how grazers impact grassland plants, etc. Perhaps because ultraviolet-B (UV-B; 280–315 nm) and ultraviolet-A (UV-A; 315–400 nm) radiation (hereafter collectively referred to as UV radiation) makeup seemingly minor parts of the solar spectrum at the earth's surface, ecologists have generally assumed that this radiation plays a rather minor role in the ecology of land plants. Indeed, even today UV is typically ignored in most introductory ecology and plant ecology textbooks, and if it does appear it is usually treated as a harmful environmental factor that plants must protect themselves against (e.g. Gurevitch et al. 2006). Consequently, most ecologists have a rather limited knowledge of UV photobiology and the techniques, instrumentation and literature specific to this field.

Consistent with the approach described above, early ecological studies on UV and plants examined UV effects in places where solar UV levels are naturally high, such as high elevation locations in Europe and North America (e.g. Brodführer 1955; Caldwell 1968). This research occurred during a time when physiological ecologists were keen to study plant adaptations in harsh environments, including the arctic and alpine tundra. There was also a push, under the auspices of the International Biological Program (IBP; 1964–1974), to understand factors controlling primary production in the major biomes of the world. However, even though alpine plants experience relatively high UV exposures, the earliest UV-exclusion experiments conducted in these habitats often revealed little if any detectable effect of ambient UV on the growth, morphology or reproduction of resident species (but see Caldwell 1968, for some effects on flowering in certain species). These findings pointed to a rather minor ecological role of UV in such systems and even raised questions about the value of these types of field filter experiments (i.e., if one can't detect effects of attenuating ambient UV in high UV environments is it likely that UV would elicit detectable ef-

fects in environments with much lower levels of UV?). And yet, comparative studies of ecotypes or closely related taxa that were distributed across a natural latitudinal/elevation UV gradient spanning low-elevation Arctic tundra in Alaska (low UV) to high-elevation tropical alpine tundra in Venezuela (high UV) revealed measurable differences in leaf optical properties, UV-absorbing compounds and physiological sensitivity to UV (Caldwell et al. 1982; Robberecht et al. 1980). These findings implied that UV, and in particular UV-B, was an important selective force in the evolution of these taxa and, moreover, that a relatively steep action spectrum was appropriate for plant responses to UV (Barnes et al. 1987). To be sure, elevation/latitudinal gradients differ in a number of environmental factors, including UV, so isolating the effects of UV on plants along these complex gradients is challenging. Nonetheless, these 'natural' UV experiments have continued to draw the attention of plant ecophysiologists interested in probing mechanisms of UV adaptation and acclimation (Nybakken et al. 2004; Ruhland et al. 2013; Sullivan et al. 1992). These types of studies are especially relevant today as plants are on the move in response to climate change (i.e., migrating to higher elevations and latitudes) and will likely occupy habitats in the future where they will be exposed to novel combinations of biotic and abiotic environmental factors, including UV. Understanding how UV influences plant performance and distribution in the context of a changing climate is thus an important area of research for ecologists today and into the future.

Concerns in the 1970–90's over the potential ecological effects of stratospheric ozone depletion and the associated increase in UV-B lead to a substantial increase in the level of UV research activities on plants during this time (Björn 2015) and also shifted the emphasis to specifically probe plant responses to enhanced UV-B. For obvious reasons, much, but not all, of this early ozone-depletion-related research examined the potential consequences of increased UV-B on economically important crop species (e.g. Biggs and Bartholic 1972; Caldwell 1972). The primary concern at this time was that enhanced UV-B might depress crop yield via partial inhibition of photosynthesis (i.e., increased UV-B→decreased photosynthesis→decreased plant yield), and results from many early laboratory studies generally supported this hypothesis (Brandle et al. 1977; Teramura 1983; Tevini et al. 1981). Improvements in the instruments used to measure UV-B (e.g., temperature-regulated scanning UV spectroradiometers), the development of sophisticated modulated UV lamp/filter supplementation systems (Caldwell et al. 1983) and refinements in action spectra/weighting functions (Flint and Caldwell 1996; Quaite et al. 1992) all improved our ability to provide for more realistic UV exposures to plants. In addition, the recognition that plant responses to UV were highly dependent on background levels of visible light (i.e., PAR; Mirecki and Teramura 1984; Warner and Caldwell 1983) lead some to question the ecological validity of findings obtained solely from greenhouse or growth chamber experiments (Caldwell and Flint 1994). Indeed, with some notable exceptions (e.g. Murali and Teramura 1986), results from field experiments have generally shown no pronounced negative effect of UV-B enhancement on photosynthesis and primary productivity (Ballaré et al. 2011). By comparison, exposure to enhanced UV-B consistently stimulated the production and accumulation of UV-absorbing compounds, and had subtle, but detectable, effects on shoot morphology without any apparent reductions in biomass production (Searles et al. 2001). These findings, and others, suggested that UV-B elicited specific photomorphogenic responses in plants that were distinct from more general "damage" responses (Ballaré et al. 1991). Over time, attention thus began to shift away from a focus on the negative

effects of enhanced UV-B on productivity to understanding how these photomorphogenic effects of UV-B mediated species interactions (e.g., plant-plant competition; Barnes et al. 1995; and herbivory; McCloud and Berenbaum 1994). In addition, there was a growing recognition that plant responses to enhanced UV-B may well be influenced by other ongoing climate change factors (e.g., increased atmospheric CO_2). Thus, some began to explore the interactive effects of UV-B, CO_2, temperature, tropospheric ozone and other factors on both agronomic and wild species (e.g. Moody et al. 1997; Sullivan and Teramura 1994; Ziska and Teramura 1992).

Because ozone depletion was most acute at high latitudes there was a particular interest in evaluating the influence of altered UV-B (alone and with other climate change factors) on the plants and ecosystems of the Arctic, Antarctic and adjacent regions. Field studies at these locations utilized both UV-B-exclusion and UV-B-enhancement (i.e., lamps) approaches with the most extensive field efforts conducted on species occupying the Antarctic peninsula (Day et al. 2001), the sub-Antarctic vegetation of Tierra del Fuego, Argentina (Ballaré et al. 2001), and Arctic and sub-arctic ecosystems of northern Sweden (Björn et al. 1999). These studies not only examined plant responses to altered UV-B (Callaghan et al. 2004; Day et al. 1999; Searles et al. 1999), but also explored important ecosystem processes such as litter decomposition, herbivory and plant-microbe interactions (Gehrke et al. 1995; Robson et al. 2004; Rousseaux et al. 1998). Results from these and many subsequent studies conducted in a wide range of environments and UV-B exposures have shown that even ambient UV-B can influence plant performance, species interactions and litter decomposition though effects are often subtle and vary considerably with species and ecosystem type (e.g., Grammatikopoulos et al. 2001; Kotilainen et al. 2009; Rousseaux et al. 2004). It should be noted that the existence of seemingly small UV effects on plants does not necessarily imply minor ecological effects as small changes can accumulate over time (Robson et al. 2004) and be amplified via non-linear mechanisms (e.g., competition for light; Barnes et al. 2005). Having said this, well-designed experiments with high replication continue to be required for statistical detection of UV effects under field conditions—a caveat voiced nearly 50 years ago by Martyn Caldwell (1968).

With the implementation and subsequent strengthening of the Montreal Protocol, large-scale stratospheric ozone losses were avoided (Garcia et al. 2012) and research over the past several decades has returned to focus more on the fundamental roles of UV-B (and UV-A; e.g., Verdaguer et al. 2017) in influencing the growth and development of plants. An increased appreciation for beneficial effects of UV on plants (Schreiner et al. 2012; Wargent et al. 2011) has caused ecologists (as well as plant physiologists and horticulturalists) to re-examine and, in some cases reinterpret, plant responses to UV (Mazza et al. 2012; Wargent and Jordan 2013). The discovery and characterization of a specific UV-B photoreceptor (UVR8; Rizzini et al. 2011) and elucidation of other aspects of UV-B-signal transduction (Favory et al. 2009) has greatly increased our mechanistic understandings of the nature of UV perception and UV-induced photomorphogenesis (Jenkins 2014). This line of research has further prompted ecologists to examine how UVR8 interacts with other photoreceptors (e.g., cryptochromes and phytochromes) to mediate plant behavior and defense against pests and pathogens in natural settings (Mazza and Ballaré 2015). Increasingly, plant ecologists are recognizing that UV serves as a source of information for plants, which influences various aspects of their behavior and defense (Ballaré 2014; Barnes, Tobler, et al. 2015). Thus, these findings have expanded the field of plant photosensory ecology to include the study of UV as well as visible light signals.

Figure 4.1: Living and dead saguaro cacti (*Carnegiea gigantea*) plants in the Sonoran Desert, Arizona, USA. Solar UV radiation (280–400 nm) can influence the growth and development of living plants as well as the decomposition of dead plant material (litter). Photo by Steve Archer, University of Arizona, USA.

In addition to these molecular advances, research conducted by ecosystem ecologists has identified UV as an important driver in the decomposition of dead plant material (i.e., litter). While ecologists have known for some time that UV can influence decomposition (e.g., via effects on decomposing microbes and litter chemistry), the report by Austin and Vivanco (2006) was the first to convincingly demonstrate that UV could have a strong, positive effect on litter decomposition via the process of photodegradation. This study was conducted on grass litter in Patagonia, Argentina, and sparked further investigation by a number of other researchers to examine UV-driven photodegradation in arid and semi-arid ecosystems in North America, Africa and the Mediterranean region (e.g., Almagro et al. 2016; Brandt et al. 2010). More recent studies suggest that photodegradation interacts with microbial processes in ways to influence litter decomposition in moist as well as dry ecosystems (Austin and Vivanco 2006). Thus, it now clear that UV can play an integral ecological role throughout the life and death cycles of terrestrial plants (Fig. 4.1, Bornman et al. 2015).

At the present time, there is a renewed interest in the study of UV effects on plants and terrestrial ecosystems. No doubt this "mini-renaissance" has been fueled, at least in part, by the discovery of the UV-B photoreceptor and the heightened appreciation for the role that UV plays in governing litter decomposition and biogeochemistry. Advances in UV measurement and dosimetry (Aphalo et al. 2012), artificial UV lighting (LEDs; Wargent 2016) and field-portable instruments that enable ecologists to non-invasively measure UV protection in plants (Barnes, Flint, Ryel, et al. 2015) have also contributed to this renewal. The European Union-sponsored COST Action FA0906 'UV4Growth' program has been instrumental in fostering the growth of UV plant research by sponsoring UV conferences, training sessions for students, and facilitating collaborative research among ecologists, plant physiologists, photobiologists and plant molecular biologists (Aphalo et al. 2015; Jansen et al. 2015). These activities have been crucial for the development of young ecologists who have little formal training in UV photobiology. This program has not only kept ecologists abreast of the latest findings in molecular biology but has also encouraged molecular biologists to address ecologically relevant questions. As a result of this COST program a new scientific society (International Society for Plant UV Research) has emerged that will continue to foster these cross cutting activities. These collaborations will no doubt lead to new insights into what role UV plays in influencing the fitness, distribution and abundance of

plants in nature. And who knows, perhaps someday soon all ecology textbooks will include UV as an important ecological factor in the life (and death) of plants.

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