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Environmental effects of ozone depletion, UV radiation and interactions with climate change : UNEP Environmental Effects Assessment Panel, update 2017

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3. TERRESTRIAL ECOSYSTEMS, UV RADIATION AND CLIMATE INTERACTIONS

Recent research on the effects of current and future interactions of UV radiation and climate on terrestrial ecosystems is assessed. We also evaluate the way in which changing stratospheric ozone is driving climate in the Southern Hemisphere and the implications of this for ecosystems in terms of precipitation and drying conditions. Rapidly changing climatic conditions extending to other regions may affect agriculture in a number of ways, reducing yield and the quality of some crops, resulting from unseasonal changes together with changing exposure to UV radiation.

Shifts in plant populations to warmer regions are also being reported, which can increase their exposure to UV radiation in a novel environment producing species-specific positive and negative outcomes for plant acclimation and species conservation. UV radiation contributes to global warming through the breakdown of dead plant material, especially in dry areas, causing the release of carbon from terrestrial ecosystems as well as altering the availability of nutrients. Further progress has been made regarding the mechanisms underlying plant response to UV radiation, which aids our understanding of current and future consequences of the multiple interactive effects of climatic conditions and UV radiation.

Finally, in this section we report on some of the improved methodologies for measuring changes in UV radiation, important for increasing the accuracy and reliability of measurements.

3.1 Large ozone-driven changes in climate in the Southern Hemisphere have occurred over the past 3-4 decades and these climate changes are continuing to influence ecosystems in a variety of ways

Ozone depletion has influenced recent temperatures across Antarctica and has also been implicated in changes in precipitation patterns across the Southern Hemisphere and into Asia (Lim et al., 2016b, Lim et al., 2016a, Duc et al., 2017, Bronnimann et al., 2017, Clem et al., 2017, Chaves et al., 2017, Manatsa et al., 2016) (Figure 1; see also section 1). This positive phase has been linked to ozone depletion (see also (Robinson and Erickson III, 2015, Bornman et al., 2015) and section 1).

Since the 1960s, warming and associated desiccation has resulted in an increase in forest fires, measured from tree ring fire scars, at mid and high latitudes on the west of the Andes. (Holz et al., 2017) During the 2016–17 fire season, more than 500,000 hectares burned in central and southern Chile (between ~29 °S and 40 °S) driven by a long-lasting drought that was amplified by concurrent positive phases of SAM and ENSO conditions. Given the predicted continued positive phase of SAM, increased Southern, South American wildfire activity will likely continue for the 21st century. (Holz et al., 2017) Decreased precipitation in this region also has negative implications for Chilean streamflow and ecosystem health as well as production of hydroelectric power. (Munoz et al., 2016)

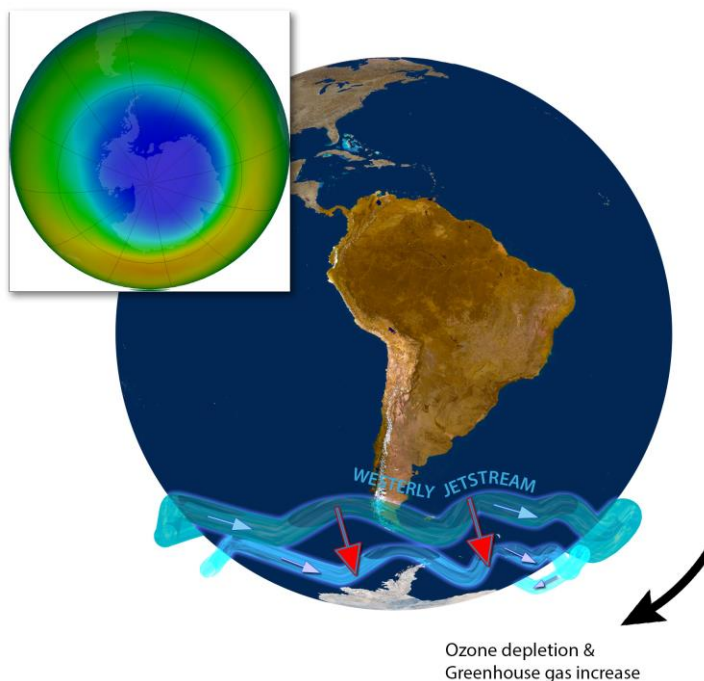
In contrast, the Eastern side of the Andes has experienced wetter conditions. Changes in fauna (ostracods and chironomids) from lake sediments in El Toro Lake (40°S, 70°W) indicate that the lake has become fresher (less saline) as a result of increased precipitation since the middle of the 20th century, associated with the positive phase of SAM. (Coviaga et al., 2017) Ozone depletion and the positive phase of SAM are also associated with more extreme precipitation events in south-eastern South America, (a very important area for food production; (Wu and Polvani, 2017) and SW Madagascar. (Randriamahefasoa and Reason, 2017) The rainfall of the southern Amazon basin has been reconstructed from *Centrolobium microchaete* tree rings (Lopez et al., 2017) and suggests that the extreme wet seasons (from droughts to extremely wet) since 1950 maybe unmatched since 1799.

Along the Antarctic Peninsula and on nearby islands, increasing temperatures, consistent with ozone-depletion and increasing greenhouse gases (Clem et al., 2016), were associated with increased terrestrial productivity (microbial productivity, plant growth rates and carbon accumulation in moss beds) from the

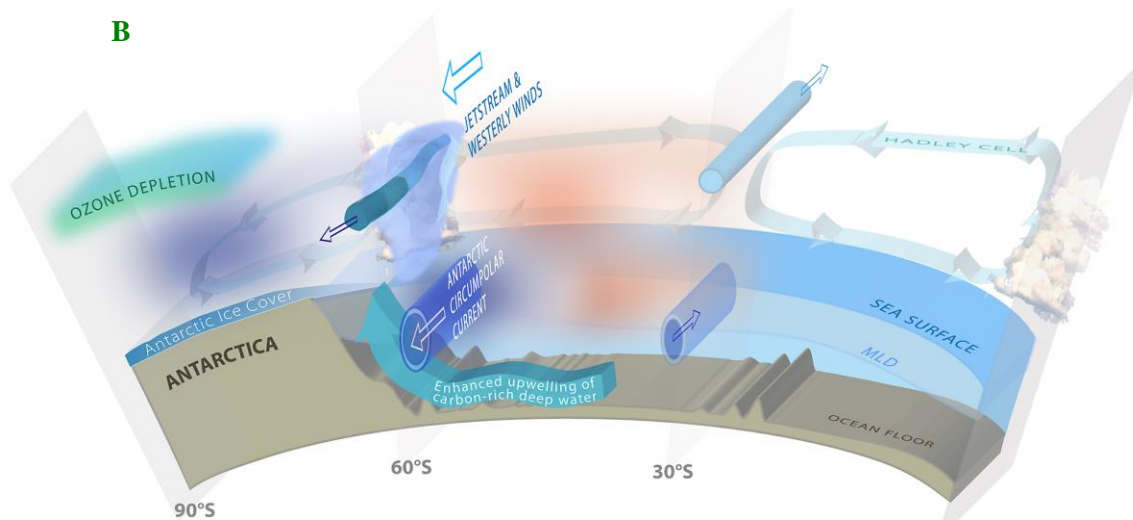
52 1950s to the turn of the century.(Amesbury et al., 2017) There is some evidence that these changes have
53 reversed since 2000, consistent with the recent cooling of this region.(Amesbury et al., 2017)

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55 In the sub-Antarctic islands a positive phase of SAM is associated with better outcomes for some marine
56 animals. A positive relationship between SAM and survival of juvenile wandering albatross has been
57 found on the Crozet Islands.(Fay et al., 2017) The authors speculate that this long-term climatic effect on
58 recruitment age may be related to the progressive increase in weight observed in this species through the
59 juvenile stages (see also (Weimerskirch et al., 2012)). Maternal condition in southern elephant seals on
60 Macquarie Island varied by as much as 59 kg among years, with maternal mass positively associated with
61 the SAM and negatively with sea ice extent.(McMahon et al., 2017) Similarly on the continent, modeling
62 studies suggest that survival of juvenile emperor penguin is positively related to SAM, probably a result
63 of the impacts of SAM on prey availability and sea ice extent (which determines the distance travelled to
64 foraging areas.(Abadi et al., 2017) These findings indicate pervasive and far-reaching effects of ozone-
65 driven climate change on ecosystems across the Southern Hemisphere.(Pecl et al., 2017)

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Figure 3.1. The Antarctic ozone ‘hole’ and its impact on Southern Hemisphere atmospheric and oceanic circulation. Stratospheric ozone depletion and resultant cooling over Antarctica have pulled the polar jet stream towards the South (A). The speed of the jet has also increased (see(Robinson and Erickson III, 2015) for details). The polar shift in the jet and its increased strength have changed atmospheric and oceanic circulation throughout the Southern Hemisphere (B). These changes are manifest in a mode of variability called the Southern Annular Mode (SAM). Imagine that the atmosphere is balanced on a seesaw that is shifting up and down between the polar latitudes (south of 60°S) and a latitude band between 40-55°S. The seesaw moves up and down with mean sea level pressure (MSLP) changes. As it pivots, the large cells that drive the winds and precipitation move towards or away from Antarctica. When MSLP around Antarctica falls, the westerlies are strong and SAM is in its positive mode; when MSLP rises (falls) over those same regions the westerlies weaken and SAM is in its negative mode. Over the past century, increasing greenhouse gases and ozone depletion have both pushed the SAM towards a more positive (black arrows in A). The main effects of the ozone ‘hole’ induced positive phase of the SAM on the Southern Ocean are shown in the lower Figure B. The strengthening of the polar jet enhances the Antarctic Circumpolar Current and the associated overturning circulation (large blue arrows). This drives increased upwelling of deep carbon-rich water and reduces the ability of the Southern Ocean to act as a CO₂ sink.(Le Quééré et al., 2007) South of the polar jet stream, temperatures have decreased (blue), while to the North, temperatures have increased (red). The SAM index is now at its highest level for at least 1000 years.(Abram et al., 2014) As a result, high latitude precipitation has increased and the mid-latitude dry-zone has moved south (see (Robinson and Erickson III, 2015, Bornman et al., 2015)). Clouds indicate areas with increased precipitation (over the equator and at the pole) with the reduced subsistence zone in between. MLD, mixed layer depth. A has been redrawn from(Perlwitz, 2011) and (Robinson and Erickson III, 2015) with the ozone ‘hole’ over Antarctica in September 2017 reproduced from NASA Ozone Watch.(NASA, 2017) B has been reproduced from(Robinson and Erickson III, 2015).

3.2 Climate change alters seasonal weather patterns which then modify how UV radiation interacts with other environmental factors to influence crop ripening and stress tolerance

Understanding how plants respond to changes in UV radiation against a backdrop of other changing environmental factors is important for managing agricultural systems to maintain crop value and productivity under a changing climate. In certain cases, exposure to UV-B radiation can mitigate the negative effects of environmental stress (e.g., drought).(Robson et al., 2015, Alonso et al., 2016b) In other situations, (e.g., supplemental UV-B radiation with increased tropospheric ozone(Alonso et al., 2016b, Mao et al., 2017)) UV-B radiation tends to accentuate the detrimental effects of coincident stresses. There continues to be significant uncertainty about how the combination of multiple environmental factors that change simultaneously, including UV radiation, are affecting food crops.

Complex interactions between climate and UV radiation modify the timing of fruit crop ripening and the quality of harvest, with warmer temperatures and droughts changing the timing of ripening to coincide with the seasonal maximum for UV-B radiation.(van Leeuwen and Darriet, 2016) Drought and high UV-B radiation often co-occur, which can have positive effects on berry quality through changes in their sugar and antioxidant composition.(Del-Castillo-Alonso et al., 2016, Luengo Escobar et al., 2016) In contrast, warmer temperatures may counteract the tendency for increased flavonoid accumulation with UV-B radiation.(Stark et al., 2015)

159 On the other hand, reducing the shade on fruit can increase their carotenoid, xanthophyll and
 160 flavonoid levels in some cases.(Joubert et al., 2016, Zoratti et al., 2014) However, flavonoids are
 161 generally induced by exposure to UV-A and UV-B radiation and ripening of fruits such as berry
 162 crops is hastened.(Carbonell-Bejerano et al., 2014, Zoratti et al., 2014) These potential benefits
 163 are starting to be exploited by manipulating the light conditions (via shading, canopy pruning or
 164 supplemental lighting) during growth and at the time of harvest.(Ordidge et al., 2010, Pastore et
 165 al., 2013) Some investigators are testing how well certain varieties or populations (their origin or
 166 provenances) of crops and trees that are hypothesised to be adapted to novel UV-B radiation and
 167 climate combinations actually perform under various future climate change
 168 scenarios.(Wijewardana et al., 2016)

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170 **3.3 Plants are migrating to higher latitudes and elevations as a consequence of** 171 **climate change and these shifts in geographic ranges are presenting species with** 172 **novel combinations of UV radiation and other environmental conditions**

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174 The tendency towards plant establishment at higher latitudes and elevations is occurring in
 175 response to climate change.(Dainese et al., 2017, Dolezal et al., 2016, IPCC, 2014) In some
 176 cases, non-native, i.e., alien or introduced species, show higher migration potentials than native
 177 (indigenous) species.(Wolf et al., 2016, Dainese et al., 2017) These shifts in geographic ranges
 178 may alter the exposure of plants to UV-B radiation, since UV-B irradiances generally increase
 179 with increasing elevation and decrease with increasing latitude.(Blumthaler et al., 1997, Caldwell
 180 et al., 1980, Bais et al., 2015) As the climate changes, a suite of other environmental conditions
 181 (e.g., diurnal and seasonal temperature patterns, moisture and nutrient availability, and
 182 associated pests, pathogens and competitors) co-occur with changes in exposure to UV radiation
 183 for migrating plants.(IPCC, 2014, Körner, 2007) At present, it is uncertain how the effects of
 184 these changes from exposure to UV radiation interact with unique combinations of effects of
 185 biotic and abiotic factors to influence species' performance and migration patterns. Whether
 186 native and non-native plants differ in their tolerance to UV-B radiation and acclimation to the
 187 changes is unclear.

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Figure 3.2 Plants growing in high elevation tropical alpine locations, such as Mauna Kea, Hawaii, shown here (A), experience some of the highest natural levels of solar UV radiation at the Earth's surface.(Bodhaine et al., 1997) These environments therefore provide excellent field sites for experiments designed to test the effects of extreme UV radiation conditions on plants (B). As plants migrate to higher elevations in response to climate change, they become exposed to increases in solar UV radiation as well as changes in a number of other abiotic and biotic factors. Understanding how plants will respond to UV radiation in the context of multiple environmental changes during migration is critical to assess how UV radiation and climate change will interact to modify the diversity and function of terrestrial ecosystems. Photographs by S. Flint.

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Plants that are native to high elevation environments (i.e., alpine) often show higher levels of UV-screening compounds (flavonoids) and other UV protective mechanisms than plants occurring at lower elevations(Sun et al., 2016, Fu and Shen, 2017, Mejia-Giraldo et al., 2016, Zhang et al., 2017, Wang et al., 2016b) and these differences are likely the result of the combined effects of elevation changes in UV radiation, temperature and other factors.(Albert et al., 2009) For instance, low temperatures induce the production and accumulation of flavonoids, which may then increase levels of UV screening and protection against oxidative stress.(León-Chan et al., 2017, Kohler et al., 2017, Waterman et al., 2017) High- and low-elevation plant populations may also differ in acclimation to changes in UV radiation.(Wang et al., 2016a) In wild potatoes (*Solanum kurtzianum*), populations grown at low elevation have relatively low constitutive (base-line) levels of leaf flavonoids but a high capacity for induction of flavonoids when UV radiation increases. In contrast, plants at high elevations have high constitutive flavonoid levels, but do not necessarily increase their UV-screening in response to supplemental UV-B radiation.(Ibañez et al., 2017)

A study examining UV-screening in plants growing in a tropical alpine environment with high UV radiation in Hawaii,Barnes et al. (2017) found no differences in UV-screening between native and non-native species. In this study, UV-screening increased with increasing elevation and UV-B radiation in a non-native species (*Verbascum thapsus* (mullein)) but did not vary with elevation in the native *Vaccinium reticulatum* (ohelo). Whether these differences in acclimation of native and non-native species to changes in UV-B radiation are widespread is not yet known, although there are studies showing that non-native species acclimate better to environmental change than native species.(Davidson et al., 2011) This has consequences for plant species diversity and ecosystem composition.

For plants expanding their distribution into higher latitudes, it is expected that they would experience less exposure to UV-B radiation that may then lead to a decline in UV-screening compounds, antioxidants and other metabolites involved in photo-protection.(Castagna et al., 2017) The cellular location of UV protective compounds in the same species can also show regional or latitudinal variation.(Waterman et al., 2017) A study of the same moss species from Antarctica and Australia showed that the fast-growing temperate plants maintained high flavonoid concentrations within their cells, whereas the slow growing plants from Antarctica sequestered the same compounds in their cell walls. The latter may represent a more resilient location for plants that experience frequent desiccation and freezing or it could be related to leaf longevity. Similar spatial variation was observed between Arctic species with evergreen *versus* deciduous leaves.(Semerdjieva et al., 2003)

256 Ecosystems, and populations of plant species, including native species have commonly
 257 responded over time to changing environmental conditions. However, the recent rapid rate of
 258 climate change, in particular increasing temperatures, are of concern in terms of the conservation
 259 of species and habitats.(Pecl et al., 2017) These effects may in turn be amplified by the often
 260 associated increased exposure to UV radiation at high elevations. Plant migrations to higher
 261 latitudes may result in decreased tolerance as a consequence of a reduced UV radiation regime,
 262 as well as posing risks of disruption of species diversity and conservation of natural ecosystems
 263 and their services.

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265 **3.4 UV radiation and climate affect food quality and yield in agricultural systems**

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267 Extremes of temperature and low humidity may alter yields in some plants such as peas, while
 268 other changes, e.g., decreased plant growth and flowering, may be more influenced by UV
 269 radiation without significant effects on pea pod production.(Roro et al., 2016) Recent work
 270 confirms earlier findings that direct effects of UV radiation leading to modification of
 271 agricultural production occur through alterations in physiological and biochemical
 272 processes.(Alonso et al., 2016a, Luengo Escobar et al., 2017a) With regard to direct effects, the
 273 prevalence and degree of severity of pathogen and pest attack on crops and other plants may be
 274 reduced by the biochemical reactions of the host plant, mediated through an increase in UV-
 275 induced polyphenolic compounds (see section3.5).(Dillon et al., 2017, Suthaparan et al., 2016)

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277 The way in which food quality can be modified by UV radiation(Wang et al., 2017a, Choudhary
 278 and Agrawal, 2016, Reddy et al., 2016, Tripathi and Agrawal, 2016) has implications for human
 279 health, since quality can be either positively or negatively affected by exposure to UV radiation
 280 and changing climate. Some of the potential health-promoting compounds enhanced by UV
 281 radiation and other environmental conditions include the polyphenolics, flavonoids and
 282 anthocyanins.(Nguyen et al., 2017, Wu et al., 2017) These compounds, found in high amounts in
 283 certain fruits, vegetables and grains, have been implicated in protection against some diseases,
 284 e.g., coronary heart disease and type 2 diabetes, because of their free-radical scavenging
 285 capability (antioxidant activity).(Dykes and Rooney, 2007, Wightman and Heuberger, 2015,
 286 Umeno et al., 2016, Rasines-Perea and Teissedre, 2017)

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288 Response to UV radiation and other stresses is often cultivar- and genotype-dependent,(Luengo
 289 Escobar et al., 2017b, Wu et al., 2017, Waterman et al., 2017, Inostroza-Blancheteau et al., 2016,
 290 Tripathi and Agrawal, 2016, Caldwell and Flint, 1994) findings that can be effectively exploited
 291 for specific crop quality outcomes in stressful environments. Many of these responses result in
 292 an increased accumulation of protective compounds such as the polyphenolics.

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294 UV-B radiation can increase seed oil, while decreasing protein, certain carbohydrates and fatty
 295 acids, depending on the amount of radiation. This was shown in a study on soybean seeds using
 296 realistic levels of biologically effective UV-B radiation ($5-15 \text{ kJ m}^{-2} \text{ day}^{-1}$) in growth chambers
 297 with near ambient visible light.(Reddy et al., 2016) These changes have consequences for food
 298 quality and health. In addition, the effect of UV-B radiation may decrease the desirable
 299 monosaturated oleic acid, and increase the less desirable polysaturated linoleic and linolenic
 300 acids with implications for cardiac disease. However, UV-B radiation also lowered the saturated
 301 palmitic fatty acid and stearic acid (the latter acid at higher levels of UV-B radiation) in the
 302 soybean seeds.(Reddy et al., 2016) These changes in important food nutritional attributes need to
 303 be understood from the perspective of a rapidly changing climate together with potential
 304 interactive effects of different levels of UV radiation on the crops.

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3.5 Agricultural intensification has increased during the course of this century, resulting in increased planting densities and reduced row spacing, which can negatively affect quality and yield of crops by reducing plant exposure to the beneficial effects of solar UV radiation

Solar radiation, including the UV-B radiation component, is often a positive modulator of plant defenses against pathogens and pests. This beneficial role of solar radiation is sometimes caused by increased activity of hormonal pathways responsible for the activation of plant immunity (reviewed in reference (Ballaré, 2014)). In other cases, resistance is conferred by secondary metabolites that the plant accumulates in response to UV radiation, for example, phenolic compounds.(Ballaré, 2014, Escobar-Bravo et al., 2017) The latter has been recently confirmed in field experiments with soybean crops.(Zavala et al., 2015, Dillon et al., 2017)

A common strategy for the management of many crops to enhance biomass production and yield per unit area has been the implementation of practices that increase light interception by the canopy, such as higher planting density, reduced row spacing, and fertilisation. All of these practices can reduce the exposure of individual plants to solar radiation and consequently its beneficial effects on defense responses, thereby making the crops more dependent on synthetic pesticides. Pests and diseases can account for a significant fraction (up to 25 %) of pre-harvest crop losses in modern agricultural systems, and chemical controls are becoming increasingly regulated due to their negative environmental impacts. Manipulation of the molecular links between photoreceptors (see section 3.8) and plant defense responses, may help plant breeders to improve crop health in agricultural and horticultural systems.(Ballaré et al., 2012, Escobar-Bravo et al., 2017, Major et al., 2017, Mawphlang and Kharshiing, 2017)

3.6 Exposure to solar radiation, including UV radiation, can accelerate the decomposition of plant litter by photochemical mineralisation and by facilitating the activity of microorganisms. The balance of these two processes is influenced by environmental conditions and will likely shift as the climate changes

The decomposition of dead plant material (i.e., litter) is a critical process controlling nutrient cycling and carbon storage in terrestrial ecosystems. Photodegradation occurs when UV radiation and short-wavelengths of visible sunlight degrade lignin and other photo-reactive constituents of litter (i.e., photochemical mineralisation) and these changes then facilitate subsequent microbial decomposition. This latter aspect of photodegradation is often called ‘photo-priming’.(Austin et al., 2016, Barnes et al., 2015, King et al., 2012). Under some conditions, UV radiation can also retard decomposition by inhibiting the growth and activity of decomposer microorganisms (bacteria and fungi).(Barnes et al., 2015) The balance of these multiple mechanisms is determined by litter quality and environmental conditions that affect microbial activity.

Photodegradation is thought to be particularly important in arid and semi-arid ecosystems (i.e., drylands) where low moisture availability constrains the activity of decomposing microbes. However, photodegradation varies with species depending on leaf structure and plant chemistry (leaf mass/area, lignin and carbon:nitrogen ratios, C:N). Previous studies have demonstrated that the rate of photodegradation is positively associated with lignin levels.(Austin and Ballaré, 2010) While some experimental and modeling studies often fail to detect this relationship,(Lin et al., 2015, Adair et al., 2017) this discrepancy likely reflects variation among species and litter type

354 (e.g., leaf vs woody litter) in the distribution of lignin with depth in plant tissues that determines
 355 the fraction of the total lignin content exposed to UV radiation. In addition, the litter position
 356 (standing litter vs ground litter), stage of decomposition (i.e., early vs late stages) and level of
 357 mixing of soil with litter will influence the degree of photodegradation.(Pan et al., 2015, Hewins
 358 et al., 2017, Wang et al., 2017b)(Wang et al., 2017c))

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360 Recent studies clarify how variation in environmental conditions and litter quality can modify
 361 the effects of UV radiation on photochemical mineralisation, photo-priming and microbial
 362 activity. For example, a field study conducted at several hyper-arid (annual precipitation < 150
 363 mm) locations in the Gurbantunggut Desert, northern China, showed that solar UV radiation
 364 stimulated the decomposition of litter from all three plant species (grass and shrub) examined,
 365 and that the positive effect of UV on decomposition increased with increasing precipitation in
 366 two of the three species.(Huang et al., 2017) By comparison, a study conducted at two
 367 Mediterranean steppe locations (continental vs maritime climates; annual precipitation = 248 vs
 368 362 mm, respectively) using grass and shrub litter, showed that UV increased rates of
 369 decomposition in both species in the dry continental site but had no effect or a negative effect on
 370 decomposition at the high rainfall maritime site.(Almagro et al., 2017) Studies by Gliksmann et al.
 371 (2016) further indicate that night-time moisture (humidity and dew) can influence the short-term,
 372 diel (daily) balance between day-time abiotic photodegradation and night-time microbial-driven
 373 decomposition in Mediterranean drylands. These findings suggest that in drylands the direct,
 374 abiotic effect of UV radiation on litter (i.e., photochemical mineralisation) dominates under the
 375 driest conditions, whereas the indirect, facilitative effect on microbial decomposition (photo-
 376 facilitation) tends to dominate under slightly moister conditions. However, when moisture levels
 377 and conditions are favourable to support high levels of microbial activity, UV radiation can have
 378 negative effects on decomposition, presumably because of direct inhibitory effects of the
 379 radiation on the decomposing microbes.

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381 Whereas much of the research to date has focused on photodegradation in drylands, some studies
 382 indicate that this process can also occur in moist (e.g., forested) ecosystems.(Austin et al., 2016)
 383 In forested ecosystems, the importance of photodegradation has been linked to canopy cover,
 384 levels of sunlight received by litter, and hence exposure to UV radiation.(Ma et al., 2017) Shifts
 385 in vegetation type (e.g., grassland to shrubland, or loss of woody plant cover due to tree/shrub
 386 dieback) resulting from changes in land-use and climate change have the potential to alter the
 387 importance of photodegradation due to the way in which litter is then exposed to UV radiation
 388 (e.g., increased shade because of encroachment of woody plants into grasslands and changes in
 389 soil-litter mixing). Also, alterations in litter chemistry resulting from changes in plant species
 390 composition (e.g., high C:N grass litter to low C:N shrub/tree litter with the conversion of
 391 grasslands to desert shrublands) will affect the degree of photodegradation and microbial
 392 activity.(Araujo and Austin, 2015, Hewins and Throop, 2016, Bosco et al., 2016) These and
 393 other changes suggest that the role that UV radiation plays in regulating litter decomposition and
 394 carbon cycling in terrestrial ecosystems will likely change in the future as the ozone layer
 395 recovers and the climate continues to change.(Almagro et al., 2015, Chen et al., 2016)

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397 **3.7 UV radiation and other environmental factors, including climate change, are**
 398 **implicated in the production of several greenhouse gases by plants and plant**
 399 **communities**

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401 Methane (CH₄) and nitrous oxide (N₂O) are present in much lower atmospheric concentrations
 402 than CO₂, but the global warming potentials of these gases are much greater (28-36 for CH₄ and

403 265–298 for N₂O over 100 years, with CO₂ normalised to 1; EPA, (Myhre G, 2013, IPCC,
 404 2014)). Plants emit N₂O and a small amount of CH₄. Currently anthropogenic sources of CH₄
 405 exceed natural sources, while for N₂O, natural sources are greater than
 406 anthropogenic.(Mikkelsen et al., 2016)

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408 Aerobic production of CH₄ has been reported from a number of plant sources including leaf
 409 wax(Bruhn et al., 2014b), and the cell wall compounds, cellulose, lignin(Vigano et al., 2008) and
 410 pectin.(Keppler et al., 2006) However, aerobic emissions of CH₄ are small. For example, a
 411 modelling study estimates that just <0.2% of total global CH₄ emissions come from
 412 pectin.(Bloom et al., 2010) A direct effect of UV-B radiation has been found on pectin in plant
 413 foliage. Other environmental factors such as water stress and warmer temperatures can modify
 414 UV-B-radiation-driven methane emissions from certain plants in aerobic
 415 environments.(Abdulmajeed and Qaderi, 2017, Abdulmajeed et al., 2017) A temperature of 28°C
 416 compared with 22°C, at ecologically-relevant UV-B radiation (5 kJ m⁻² day⁻¹ biologically
 417 effective UV radiation) under controlled conditions, resulted in higher emissions of CH₄ from
 418 leaves, stems and roots of pea plants, with the highest emission from the stems
 419 (65.08 ± 4.12 ng (g dry mass)⁻¹ h⁻¹) and lowest for leaves (18.08 ± 0.96 ng (g dry
 420 mass)⁻¹ h⁻¹). (Abdulmajeed et al., 2017) Emission-enhancing interactive effects were found also
 421 for UV radiation and water stress, and higher temperature and water stress for different plant
 422 organs.(Abdulmajeed and Qaderi, 2017). Levels of emissions of CH₄ are broadly consistent with
 423 previous studies(see (Fraser et al., 2015), but with large variations due to plant type, plant organ
 424 and environmental conditions.

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426 Plant leaves and soil bacteria can produce N₂O.(Erickson et al., 2015, Bruhn et al., 2014a) Field
 427 experiments with filtered and unfiltered solar UV-B radiation showed that grasslands and their
 428 soil produced N₂O in the dark, while solar UV radiation increased the N₂O production.(Bruhn et
 429 al., 2014a) Precise data are difficult to obtain, since the N₂O source from plant leaves is often
 430 augmented from natural and anthropogenic sources (e.g., from fertilisers) in addition to
 431 production by leaves. Calculations suggest that emissions of leaf N₂O may be 30% higher than
 432 previous estimates.(Bruhn et al., 2014a) This is important because these radiation-driven
 433 emissions are estimated to comprise between 7 and 24% of all natural production of
 434 N₂O.(Mikkelsen et al., 2016) Another compounding factor for N₂O emissions, is the
 435 environmental feedback effect of increasing temperatures on the emissions from
 436 soil.(Butterbach-Bahl et al., 2013) Additional sources of N₂O have also been reported from
 437 mosses and lichens,(Porada et al., 2017, Lenhart et al., 2015) estimated to contribute up to 4–9%
 438 globally of the natural terrestrial N₂O emissions.(Zhuang et al., 2012, Porada et al., 2017)

439

440 Changes in plant community composition resulting from climate change and its interaction with
 441 UV radiation may also indirectly affect N₂O and CH₄ emissions at ecosystem scales. However,
 442 while anaerobic emissions of CH₄ from peatlands and rice paddies are well researched,(Solomon,
 443 2007) there have been few studies outside of wetlands.(Bruhn et al., 2012, Dinsmore et al., 2017)
 444 A study in a Holm oak (*Quercus ilex*) forest in Italy attempts to estimate CH₄ emissions at plant-
 445 community level based on parallel measurements of canopy and soil gas fluxes.(Savi et al.,
 446 2016) This study found that the highest emissions (37.8 μmol m⁻² h⁻¹) coincided with solar noon
 447 on days when irradiance was highest in summer, but over the whole year the budget was
 448 approximately balanced (i.e., no net emission), switching between a CH₄ source in summer and a
 449 sink in winter.

450

451 Estimating the contribution to the global CH₄ budget by plants is complicated by many factors
 452 including large differences due to species and climate. Recent model calculations range between
 453 1.2 to 24%.(Martel and Qaderi, 2017, Liu et al., 2015, Carmichael et al., 2014) Calculations of
 454 N₂O emissions from plants are also uncertain and vary in different studies depending on whether
 455 soil and plant contributions are quantified together or separately. N₂O and CH₄ are significant
 456 greenhouse gases and also contribute to the dynamics of the stratospheric ozone layer, and thus
 457 their sources and quantification are important in our understanding of UV radiation fluxes and
 458 climate change interactions.

459

460 **3.8 Recent progress in elucidating the molecular mechanisms that mediate plant** 461 **perception of UV radiation can greatly increase our ability to manipulate responses** 462 **to UV radiation in cultivated species**

463

464 The functional characterisation of UV RESISTANCE LOCUS 8 (UVR8)(Rizzini et al., 2011,
 465 Christie et al., 2012, Wu et al., 2012) represented a major step forward in UV photobiology,
 466 defining the first specific photoreceptor for UV-B radiation. Studies in recent years have
 467 endeavoured to establish the functional roles of UVR8 in the control of plant acclimation to UV-
 468 B radiation.

469

470 The central components of the UVR8 photocycle have been elucidated(Jenkins, 2017, Yin and
 471 Ulm, 2017) and the mechanism of action of UVR8 appears to be evolutionary conserved, from
 472 green algae to angiosperms.(Fernández et al., 2016, Tilbrook et al., 2016, Soriano et al., 2017)
 473 Many of the genes regulated by UVR8 are associated with protection against UV-B and repair of
 474 damage by this radiation. Therefore, a major role of UVR8 in protection against UV-B radiation
 475 is often inferred.

476

477 Recent studies have focused on the hormonal signaling pathways that operate downstream of
 478 UVR8 to regulate plant function. The results of these studies suggest that UVR8 modulates
 479 hormonal pathways involved in the regulation of growth (auxin and gibberellins) and defense
 480 responses (jasmonic acid).(Hayes et al., 2014, Mazza and Ballaré, 2015, Hayes et al., 2017)
 481 Based on these advances, it has been postulated that UVR8 is important for regulating plant
 482 growth and immunity in plant canopies.(Mazza and Ballaré, 2015)which might have important
 483 implications for agriculture and crop breeding (See section 3.4).

484

485 Under solar radiation, UVR8 establishes a dimer/monomer photoequilibrium that is regulated by
 486 UV-B radiation and is also influenced by temperature.(Findlay and Jenkins, 2016) Changes in
 487 the dimer/monomer ratio might be used by plants to “measure” UV-B radiation, although UVR8-
 488 independent signaling pathways, e.g., pathways activated by damage to DNA, are likely to play
 489 important roles in UV-B perception under field conditions.(Ballaré and Austin, 2017) Genetic
 490 evidence, obtained using lines of the model plant *Arabidopsis thaliana* with null mutations in the
 491 *UVR8* locus, is contributing to elucidate the roles of UVR8 in nature. Evidence from a limited
 492 number of studies suggests that *uvr8* knock-out mutants are somewhat more sensitive to natural
 493 levels of solar radiation than wild-type plants(Morales et al., 2013, Coffey et al., 2017) and more
 494 sensitive to certain pathogens.(Demkura and Ballaré, 2012) However, additional information
 495 from field studies, measuring fitness components and using a broad array of experimental
 496 conditions and plant species, is needed to establish the adaptive importance of UVR8-mediated
 497 UV-B perception. Thus, more research is needed to link the mechanisms of action of the UV-B
 498 photoreceptor with plant function under field conditions.(Jenkins, 2017, Ballaré and Pierik,
 499 2017)

500
 501 **3.9 Improvements in methods and analytical techniques are reducing the**
 502 **uncertainty associated with reconstructions of solar radiation based on pollen**
 503 **biochemistry that track changes in past UV radiation over geological timescales**
 504

505 Reconstructions of past solar radiation using pollen from sediments and ice cores have the
 506 potential to help us better understand the evolution of the ozone layer and its interaction with
 507 climate change. Spores and pollen grains are made of sporopollenin, which is highly resistant to
 508 degradation over geological timescales and contains the phenolic compounds, *para*-coumaric
 509 acid and ferulic acid. The concentrations of these UV-absorbing compounds are considered to be
 510 proportional to the incident solar UV-B radiation flux received by the pollen.(Rozema et al.,
 511 2002, Fraser et al., 2014, Jardine et al., 2017) However, dose-response curves for the
 512 accumulation of these compounds are yet to be established, and we lack knowledge of the timing
 513 of this process during the production and release of pollen.(Bornman et al., 2015, Seddon et al.,
 514 2017) Until the mechanism of this response is elucidated, and its relationship to incident UV-B
 515 and solar radiation established, the utility of this proxy for inferring changes in the ozone layer
 516 remains limited.(Thomas et al., 2016) Seasonal environmental variability related to weather
 517 patterns and canopy shade also affect incident solar UV-B radiation in ways that are difficult to
 518 retrospectively infer, making some reconstructions from proxies difficult to interpret. These
 519 potentially confounding factors may explain why changes in solar activity or ozone-depletion-
 520 related trends of UV-absorbing compounds in spores and pollen have not always been detected
 521 in the past.(McKenzie et al., 2011) Methodological advances to allow faster and more precise
 522 processing of pollen samples are improving reconstructions.(Seddon et al., 2017, Bağcıoğlu et
 523 al., 2017) For instance, a reconstruction of incident solar radiation at Lake Bosumtwi in Ghana
 524 over a 140 thousand-year period, based on the phenolics from grass pollen contained in
 525 sediments, tracked known variations in the Earth's orbit.(Jardine et al., 2016) One potential
 526 strength of this proxy is that it can be interpreted independently of paleoecological and
 527 paleoclimatological records, in principle allowing solar radiation to be decoupled from climate or
 528 biotic changes.

529
 530 **3.10 Rapid advances in light-emitting diode (LED) technology is enabling more**
 531 **precise replication of the solar spectrum in controlled growth environments**
 532

533 The increasing availability of cost-effective LEDs is providing new opportunities to customise
 534 the light environment of plants grown commercially in greenhouses and controlled
 535 environments. The inclusion of UV (UV-B and UV-A) radiation in artificial lighting systems is
 536 now being considered as a means to improve food plant quality, crop vigour and plant
 537 defense.(Wargent, 2017) While high-power UV-A LEDs are currently available, to date UV-B
 538 LEDs have generally not proven useful in lighting systems because of their low life span and
 539 limited radiant output. However, new generation UV-B LEDs, including some with outputs over
 540 very narrow wavebands, exhibit greater stability and radiant power outputs.(Rass et al., 2015,
 541 Kneissl, 2016)

542
 543 **3.11 Continuing refinement of protocols for the use of field-portable array**
 544 **spectrometers allows for better measurements of solar UV radiation in dynamic**
 545 **light environments with applications in plant science**
 546

547 Improved knowledge of the capacities and limitations of light-weight, field-portable array
 548 spectrometers has permitted their wider use to record dynamic variability in the light
 549 environment. These measurements may have wide utility but are particularly useful for
 550 measurements under clouds and canopies, and in artificial environments for plant growth,
 551 situations where the proportion of UV-B radiation to visible may be very different from that
 552 under clear skies. Those models of array spectrometer intended for measurement in both the
 553 visible and UV regions can capture this part of the solar spectrum with acceptable resolution for
 554 ecological studies provided that certain criteria are fulfilled.(Aphalo et al., 2012, Aphalo, 2015),
 555 To obtain reliable measurements, these devices must be individually calibrated and specific
 556 protocols followed that minimise noise of the UV signal caused by stray visible light and the
 557 instruments' limited dynamic range.(Aphalo, 2017, Aphalo et al., 2016) These spectrometers are
 558 particularly useful for validation of modelled radiative transfer through the canopy layers of
 559 forests and crop fields, although measurements in the early morning and evening when the sun is
 560 low in the sky should be avoided. Parallel applications for plant production are also envisaged
 561 whereby appropriate UV filters and UV-LEDs can be recommended for specific scientific
 562 purposes.

563

564 **3.12 The availability of small, lightweight, cost-effective UV-B dosimeters that can** 565 **be placed on leaves may improve spatial resolution for measuring the UV radiation** 566 **received by the leaves of plants *in situ***

567

568 These sensors will give researchers the opportunity to study the effects of fluctuating UV-B
 569 irradiances caused by variability in the micro-environment; e.g., differences in plant architecture
 570 that could result from changing angle-to-the-sun and canopy heterogeneity. Locating sensors on
 571 leaves would provide greater certainty in the estimation of doses as well as better
 572 characterisation of the environment through measurements at multiple locations. Two major
 573 handicaps to the adoption of dosimeters have been: (1) that they work for too short a time period
 574 to be useful for ecological studies, and (2) they are insufficiently accurate to be reliable. Now,
 575 improved dosimeters are being developed with respect to their longevity(Wainwright et al.,
 576 2015) and wavelength dependence,(Amar and Parisi, 2013) for use with plants as well as for
 577 materials and humans. One such new UV-B dosimeter, made from unstabilised polyvinyl
 578 chloride (PVC),(Parisi et al., 2017) complements an existing UV-A dosimeter manufactured
 579 using 8-methoxypsoralen.(Wainwright et al., 2015) This presents an opportunity to compare in
 580 tandem UV-B and UV-A radiation doses received by leaves at different angles and exposures
 581 within a canopy. Such systems of multiple integrated dosimeters with sensitivity in different
 582 regions of the UV radiation regime have already been designed for use as 'wearable tech' on
 583 human skin (e.g.(Araki et al., 2017)).

584

585 References

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