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REVIEW ARTICLE

Current and future impacts of ultraviolet radiation on the terrestrial carbon balance

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Abstract One of the most documented effects of human activity on our environment is the reduction of stratospheric ozone resulting in an increase of biologically harmful ultraviolet (UV) radiation. In a less predictable manner, UV radiation incident at the surface of the earth is expected to be further modified in the future as a result of altered cloud condition, atmospheric aerosol concentration, and snow cover. Although UV radiation comprises only a small fraction of the total solar radiation that is incident at the earth's surface, it has the greatest energy per unit wavelength and, thus, the greatest potential to damage the biosphere. Recent investigations have highlighted numerous ways that UV radiation could potentially affect a variety of ecological processes, including nutrient cycling and the terrestrial carbon cycle. The objectives of the following literature review are to summarize and synthesize the available information relevant to the effects of UV radiation and other climate change factors on the terrestrial carbon balance in an effort to highlight current gaps in knowledge and future research directions for UV radiation research.

Keywords climate change, UV-B, ultraviolet radiation, solar radiation, carbon cycle, ozone, photodegradation, nutrient cycling

1 Introduction

UV radiation, and thus changes in UV radiation, can have a substantial impact on ecosystem processes, including some important terrestrial processes such as nutrient cycling and the carbon balance. In terrestrial ecosystems, the carbon balance is determined by the difference between inputs from net primary production and the return of carbon to the atmosphere through heterotrophic respiration (Schlesinger and Lichter, 2001; Nemani et al., 2003). Evidence suggests that UV radiation modifies the terrestrial carbon balance through changes in CO_2 capture (photosynthesis), carbon storage (organic carbon pools), and release (respiration and photodegradation) (Zepp et al., 2007).

Recent investigations have documented several direct effects of UV radiation on the terrestrial carbon cycle. These effects include a reduction in the capture of carbon via decreased photosynthetic carbon gain, as well as an increase in carbon release via accelerated litter decomposition. To date, photosynthesis has been shown to be inhibited by UV radiation through the sensitivity of photosynthetic machinery (Albert et al., 2008) and by the alteration of gene expression, which is critical to photosynthesis (Ballare et al., 1996; Casati and Walbot, 2004; Izaguirre et al., 2003; Savenstrand et al., 2002).

A variety of indirect effects of UV radiation on the terrestrial carbon balance have also been recently elucidated. It is well documented that the chemical composition of plants is altered under UV exposure due to changes in nutrient content and tissue composition (Rozema et al., 1997). Corresponding alterations in plant litter quality indirectly inhibit carbon release by reducing the rate at which microbial communities can access biologically important molecules during the decomposition process (Mazza et al., 1999, 2000; Rousseaux et al., 2004; Milchunas et al., 2004; Pancotto et al., 2005; Ruhland et al., 2007). Furthermore, exposure to UV radiation can also have a selective influence on the species composition of microbial communities resulting in further reduction in carbon release (Gehrke et al., 1995; Moody et al., 2001; Pancotto et al., 2003).

Although UV radiation can affect the terrestrial carbon

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balance by influencing photosynthesis, organic carbon pools, and litter decomposition, the magnitude and, in some cases, the direction of the effect UV radiation imparts on each component of the carbon cycle is poorly understood. Moreover, the combined effect of UV radiation and other climate change factors such as enriched carbon dioxide in the atmosphere, nitrogen deposition, and altered precipitation patterns appear to be non-additive, resulting in complex and possibly synergistic interactions that are difficult to predict. The objectives of the following literature review are to summarize and synthesize (1) the known biological effectiveness of solar UV radiation; (2) the available information relevant to the effects of UV radiation on the terrestrial carbon balance; (3) the available information relevant to the combined effects of UV radiation and other climate change factors on the terrestrial carbon balance; and (4) current gaps in knowledge associated with UV radiation research. This information provides a basis for formulating a strategic plan for predicting the most effective research directions needed to understand future impacts of UV radiation on the global environment.

2 Biological effectiveness of UV radiation

By convention, the UV region of the spectrum is divided into three components: UV-A (320–400 nm), UV-B (280–320 nm), and UV-C (less than 280 nm) (Caldwell and Flint, 1994, 1997). Of these, only UV-B and UV-A have biological importance because the stratospheric ozone layer effectively absorbs UV-C radiation. UV-A and UV-B radiation are only partially absorbed by stratospheric ozone resulting in transmittance of these wavelengths to the surface of the earth. Reductions in stratospheric ozone result in increased UV-A and UV-B radiation incident at the earth's surface with the largest fractional increase occurring in the shorter-wave UV-B region (Caldwell and Flint, 1997). The UV-B region is also comprised of the highest energy wavelengths incident at the earth's surface, making UV-B radiation the dominant contributor to most observed UV radiation effects on the biosphere (Caldwell, 1971). However, UV-A has also been documented to contribute, to a lesser extent, to the observed effects of UV radiation on the biota (Caldwell et al., 2007).

Levels of UV radiation incident at the surface of the earth can also be modified by processes other than changes in stratospheric ozone. Snow cover has been shown to increase levels of UV radiation up to a distance of several kilometers by scattering UV radiation (Mckenzie et al., 1998). Furthermore, decreased snow cover, associated with climate change, will increase soil exposure to UV radiation resulting in modified rhizosphere-level processes. Cloud cover attenuates UV-B radiation by 15–30% (Mckenzie et al., 2003). Therefore, UV exposure in terrestrial ecosystems will be modified by changes in cloud cover. Aerosols scatter up to 50% direct beam UV-B radiation and decrease UV exposure (Sarra et al., 2002). Therefore, changing aerosol concentration will have significant future impacts on UV-B radiation at the earth's surface.

To estimate the impact of increased UV radiation incident at the surface of the earth, spectral sensitivity functions (action spectra) that account for wavelength sensitivity of biological systems must be estimated and applied to spectral irradiance estimates. From action spectra assumed to be relevant for plants, biological weighting functions have been created that appropriately weigh each wavelength with its estimated biological significance (Caldwell, 1971; Caldwell and Flint, 1997). For all UV supplementation studies, biological weighting functions are needed to relate solar UV radiation to UV radiation output from lamps (Caldwell and Flint, 1997; Caldwell et al., 1998).

Currently, UV supplementation studies are difficult to relate to the field because solar radiation cannot be accurately and experimentally represented. Many supplementation studies use square-wave systems (i.e. uniform intensity throughout exposure period) that do not account for the diurnal cycle of UV radiation. For studies that investigate aspects of plant development and growth, careful experimental design is required so that lamps can simulate UV levels that peak at solar noon. This may be important for many aspects of plant development, including germination, growth, and biomass allocation (Caldwell et al., 1998; Bjorn et al., 1999).

Supplementation studies can also be difficult to relate to the field due to the complexity of maintaining accurate proportions of each component of solar radiation experimentally. To accurately simulate solar radiation, the correct proportion of UV-A, UV-B, and PAR (photosynthetically active radiation, 400–700 nm) must be achieved (Caldwell and Flint, 1994). A main challenge associated with the proportionality of solar radiation is generating adequate levels of UV-A radiation experimentally. Because there is approximately 100 times more UV-A than UV-B incident at the surface of the earth, it becomes difficult to design a practical supplementation system capable of generating adequate proportions of UV-A radiation. Therefore, controlled environment studies do not incorporate UV-A radiation into experiments. Ultimately, for a supplementation study to provide insight into the effect of UV radiation, experiments must be carefully designed with special consideration given to the type of supplementation system and, specifically, the composition of radiation generated by the system. Despite these limitations, numerous investigations have recently documented UV radiation as an important component in many global processes including the terrestrial carbon cycle.

3 UV radiation: effects on the terrestrial carbon balance

UV radiation can affect the terrestrial carbon balance both directly and indirectly. In recent studies, several specific impacts have been identified (Fig. 1). Recently elicited direct impacts include the inhibition of photosynthetic carbon gain and the acceleration of decomposition. More indirect impacts of UV exposure include the alteration of the chemical composition of plant material and the inhibition of soil and litter biotic communities. Both direct and indirect effects of UV radiation, as they relate to the terrestrial carbon cycle, have been discussed in more detail below.

3.1 Direct effects of UV radiation

3.1.1 Photosynthesis

UV radiation can inhibit photosynthesis by altering photosynthetic gene expression and by detrimentally affecting UV-sensitive parts of the photosynthesis machinery (Caldwell et al., 2007; Day et al., 2007). Casoti and Walbot (2003) conducted a field experiment on maize plants and documented a significant down-regulation of genes associated with photosynthesis under elevated UV. This decreased expression of genes involved in photosynthesis is consistent with recent laboratory and field studies that have shown similar effects of UV radiation in other species (Ballare et al., 1996; Izaguirre et al., 2003; Savenstrand et al., 2003). Furthermore, Albert et al., (2008) investigated UV-B effects on high arctic *Vaccinium uliginosum* exposed to ambient and 60% reduced UV-B radiation and documented net photosynthesis was an average of 28% lower in treatments of ambient UV-B radiation. This change was attributed to an overall reduction in the ability of plants under ambient UV-B to process light energy. Specifically, photosystem II (PSII) of the photosynthetic machinery has often been documented as particularly sensitive to UV exposure (Bornman, 1989; Teramura and Sullivan, 1994). Ultimately, these results suggest photosynthesis may be reduced substantially as a consequence of changing levels of UV-B radiation which could potentially result in alterations in the plant carbon pool.

3.1.2 Photodegradation

Litter decomposition is a key process in the terrestrial carbon cycle that influences nutrient availability and carbon storage (Schlesinger et al., 2001; Nemani et al., 2003). UV radiation has been identified as a secondary factor influencing litter decomposition rates via photodegradation or the physiochemical transformation of decomposing compounds into smaller compounds caused by the absorption of the high energy UV photons. Austin and Vivanco (2006) documented the effects of UV radiation on litter decomposition by demonstrating exposure to both UV-B and total UV radiation in the semi-arid environment of the Patagonia Steppe resulted in increased aboveground decomposition rates (45% and 60% increases, respectively), despite the absence of microbial activity (i.e. evidence for a direct effect via photodegradation). These findings are further supported by a number of investigations that have documented similar effects of UV radiation in other species (Rozema et al., 1997; Brandt et al., 2007; Day et al., 2007).

Photodegradation has implications for the terrestrial

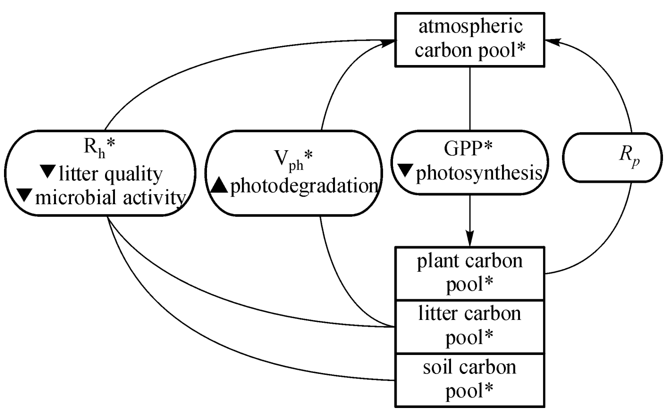

Fig. 1 Schematic of the terrestrial carbon balance as affected by UV radiation
A schematic of the terrestrial carbon balance as affected by UV radiation where R_h, V_{ph}, GPP and R_p represent heterotrophic respiration, photodegradation, gross primary productivity, and plant respiration, respectively. Processes and carbon pools documented to be affected by UV radiation are marked with an asterisk. Mechanisms by which UV radiation affects each process are listed with their directional impact. Processes where the effect of UV radiation is currently unknown are italicized.

carbon balance because the absorption of UV radiation by plant litter is hypothesized to result in the volatilization of a substantial fraction of carbon fixed in plant biomass (Schade et al., 1999; Austin and Vivanco, 2006; Gallo et al., 2006). This photo-mineralization of carbon compounds increases the rate at which CO_2 enters the atmospheric carbon pool and reduces the net carbon available for microbial decomposition. Typically, microbial decomposition results in the storage of a portion of carbon in the microbial carbon pool which is an input of the soil carbon pool. Therefore, photodegradation could impact the terrestrial carbon balance by slowing the transfer of carbon from the microbial to the soil carbon pool and by increasing the rate at which carbon enters the atmospheric carbon pool by volatilization of litter carbon (Fig. 1).

3.2 Indirect effects of UV exposure

3.2.1 Plant chemistry

Plant chemistry influences decomposition indirectly by affecting the rate at which microbial communities can decompose organic material. Enhanced levels of UV radiation have been shown to affect plant chemical composition by promoting an array of protective responses in plants including the production of UV absorbing compounds known as phenolics and other antioxidants. Ruhland et al., (2007) observed that concentrations of bulk-soluble phenolics and ferric reducing antioxidant power (FRAP) were 17% and 24% higher under near-ambient UV-B than under a 71% reduction in UV-B, respectively. Furthermore, Rousseaux et al., (2004) observed that, in oat and lettuce, UV-absorbing compounds responded more to supplemental UV-B radiation (simulating a 30% decrease in ozone) when compared to ambient solar UV-B radiation suggesting elevated UV-B radiation may accelerate changes in plant chemistry. These results are consistent with other recent field studies conducted on a variety of plant species suggesting that solar UV-B radiation increases antioxidant enzyme activity independent of species (Mazza et al., 1999, 2000; Milchunas et al., 2004).

Altered plant litter chemical composition has been shown to indirectly affect decomposition rates by increasing recalcitrant fractions of litter which soil microbes are less able to break down. Pancotto et al., (2005) found that barley plants grown under near-ambient UV-B radiation experienced changes in litter chemical quality that significantly reduced litter decomposition by microbial communities. A reduction in the litter decomposition rate could potentially increase the soil carbon pool therefore increasing carbon storage (Fig. 1). However, the degree to which a plant experiences changes in phenolic and antioxidant composition in response to UV radiation has been observed to be species-specific. Therefore extrapolation to net effects on the global carbon balance is difficult.

3.2.2 Microbial community composition

UV radiation can also impart a selective influence on soil biota resulting in reduced or altered microbial community composition. One investigation in particular, documented litter decomposing under elevated UV-B radiation was less colonized by fungal decomposers, indicating fungal sensitivity to UV-B radiation (Moody et al., 2001). Related studies conducted by Moody et al., (2001) and Pancotto et al., (2003) documented effects of UV-B radiation on bacterial as well as fungal communities suggesting bacteria could also be sensitive to UV radiation. Altered microbial community composition could result in alterations carbon release as a result of alterations in decomposition rates which are a function of microbial activity. However, due to limited research in this area, the effect of UV-B radiation on microbial community composition and the associated impact on the terrestrial carbon balance are poorly understood and require further investigation.

4 UV radiation and other components of climate change

Global climate change factors such as increasing atmospheric CO_2, nitrogen deposition, and changing precipitation regimes have the potential to modify the effect of UV radiation on carbon dynamics by either ameliorating or intensifying ecosystem responses to UV radiation (Caldwell et al., 2007). Evaluation of the interactive effects of increasing UV radiation, in combination with other climate change factors, on the terrestrial carbon balance has just recently been initiated. The results of these experiments are reviewed below.

4.1 UV radiation and CO_2

It is now well-documented that atmospheric CO_2 concentrations are increasing on a global scale (Carter et al., 2007). In addition to the associated increases in global temperatures due to greenhouse warming, enriched atmospheric CO_2 has also been found to enhance photosynthetic rates in certain species (Schulze, 1994). Therefore, a fundamental question is whether increases in atmospheric CO_2 will counteract negative effects of UV radiation on photosynthesis. A series of studies on cotton revealed elevated CO_2 did not completely offset the negative effects of UV-B radiation on photosynthesis (Zhao et al., 2003, 2004). A possible explanation of this observation could be that UV radiation may be affecting the plants' ability to take advantage of enriched atmospheric CO_2. These findings were supported by a similar study conducted on soybean (Koti et al., 2005), indicating plants of contrasting metabolic types (C_3 versus C_4 photosynthesis) may be affected similarly.

Elevated atmospheric CO_2 is also predicted to modify the chemical composition of plants and, thus, litter decomposition rates by increasing the carbon to nitrogen (C:N) ratio of plants. Decomposition rates have been observed to be negatively impacted by increased C:N ratios due to microbial inhibition via nitrogen limitation (Boerner and Rebbeck, 1995; Scherzer et al., 1998). Therefore, the negative impact of UV radiation on microbial activity (i.e. microbial sensitivity to UV radiation) could be intensified either additively or synergistically by the negative impact of elevated CO_2 on microbial activity (i.e. nitrogen limitation). Further research is still required to quantify the potential interactions between UV radiation and elevated CO_2.

4.2 UV radiation and temperature

As a result of the uniform increase in CO_2 and other greenhouse gases, temperature is also expected to continue to increase to various degrees throughout the world (IPCC, 2007). Predicting how temperature increase will interact with other climate change factors is difficult because both detrimental and facilitative effects of elevated temperature on plant growth and development have been recorded. In particular, UV radiation has been shown to enhance, either additively or synergistically, many of the detrimental effects of elevated temperature including reduced fruit and flower production, increased leaf abscission, and increased fruit fall (Caldwell et al., 2007). For example, Zhao et al., (2005) observed that only under conditions of enhanced temperature did UV-B radiation increase fruit fall.

In other cases, elevated temperature has been shown to facilitate plant protective responses ultimately resulting in a higher tolerance to UV radiation (Caldwell et al., 2007). This has been attributed to the heat-induced production of proteins that simultaneously protect the plant from heat stress as well as UV stress (Nedunchezhian and Kulandaivelu, 1996). Adding to the complexity of these interactions, however, the documentation for both UV and temperature effects is specific.

4.3 UV radiation and nitrogen

Biologically available nitrogen (N) is expected to continue to increase substantially as a result of N-deposition and fertilization (Caldwell et al., 2007). N-deposition is the process by which reactive nitrogen species are transferred from the atmosphere to the biosphere, and increases in N-deposition can be attributed to pollution. Fertilization is the anthropogenic application of biologically available nitrogen in agricultural areas. In both cases, increased biologically available nitrogen has the potential to modify plant photosynthesis rates and chemical composition.

Increased biologically available nitrogen can increase photosynthesis rates and therefore counteract the negative effect of UV radiation. Nitrogen regulates photosynthesis by limiting the production of proteins and enzymes which are key to the photosynthesis process. One enzyme in particular, Ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), is a critical catalyst in carbon fixation that occurs during the Calvin cycle of photosynthesis. Therefore, under conditions of increased biologically available nitrogen, the processing of carbon may increase enough to counteract the negative effect of UV radiation on photosynthesis. Chimphango et al., (2004), investigated the interactive effect of UV-B radiation and N deposition on a South American legume species (*Cyclopia maculata*) and found the detrimental UV-B radiation effect on plant biomass production, as a result of decreased photosynthesis rates, was significantly less pronounced when plants were supplied with supplemental nitrate. Hence, the application of biologically available nitrogen to systems has the potential to ameliorate the detrimental effect of elevated UV radiation by countering decreased photosynthesis rates with increased enzyme activity and more efficient processing of captured carbon.

Increased biologically available nitrogen also has the potential to modify the chemical composition of plants by increasing percent nitrogen and, thus, reducing the C:N ratio. This would theoretically increase decomposition rates by removing the inhibition of microbial activity that typically results from low plant nitrogen availability. It would be expected then that UV radiation and nitrogen would have counteracting effects on microbial activity with UV radiation inhibiting microbial activity and increased nitrogen promoting microbial activity. However, limited evidence exists on this potential interaction and the net effect on the terrestrial carbon balance is currently unknown.

4.4 UV radiation and precipitation

Global precipitation regimes are also expected to be significantly altered as a result of climate change; however, it is still unclear how these changes will manifest. One hypothesis suggests climate change will most likely result in extended periods of drought coupled with extreme rain events (IPCC, 2007). This has the potential to alter the response of plants by changing water availability and influencing litter decomposition.

Several controlled environment studies have been conducted to evaluate the effect of drought and UV-B radiation on the chemical composition of different plant species. Hofmann et al., (2003) compared the effect of drought and high UV-B radiation fluxes on several clover varieties and found the treatments interacted synergistically resulting in substantial increases of UV-B absorbing compounds, including phenolics, in treatment of high UV-B flux and drought. Results from this study were similar to results generated by an investigation conducted on soybean (Yang et al., 2005) demonstrating the effect that may occur across species and potentially ecosystems. Consequently, UV radiation and relatively infrequent precipitation could interact to inhibit decomposition by reducing the accessibility of biologically important compounds. However, this interaction has not been quantified and its net effect on the terrestrial carbon balance is currently unknown.

5 Future directions for UV research

Since the documentation of stratospheric ozone depletion resulting from anthropogenic production and release of chlorofluorocarbons (CFCs) (Molina and Rowland, 1974), there have been substantial advances in the understanding of the distribution and effects of UV radiation on the biosphere. More recently, these effects have been linked to impacts on the terrestrial carbon cycle. These effects include direct effects such as reduced photosynthetic carbon gain and photodegradation as well as indirect effects such as altered chemical composition of plant material and reduced microbial activity. In addition, the interactive effects of UV radiation and other climate change factors on the carbon balance have begun to be elicited. For continued advancement of the understanding of UV radiation effects on the carbon balance, areas of future research must emphasize the evaluation of factors that influence UV radiation incident at the earth's surface, the improvement of UV simulation in the field, the determination of the magnitude of direct and indirect effects of UV radiation, and the determination of interactive effects of UV and other climate change factors.

Stratospheric ozone levels have been slowly returning to ambient, pre-industrialization, levels since the initiation of the Montreal protocol and they are expected to fully recover in the distant future. However, recent investigations have begun to elucidate the impact of climate change factors such as cloud conditions, aerosol concentrations, and snow cover on UV flux at the earth's surface. Therefore, to understand how UV incident at the earth's surface will change in the future and to approximate the recovery rate of stratospheric ozone, continued research is needed on climate change factors that impact surface UV flux.

To provide a more comprehensive understanding of future impacts of UV exposure, additional long-term studies, especially under natural field conditions are necessary. This will require improvements in experimentally reproducing a diurnal cycle and improvements in simulating ambient ratios of UV-A, UV-B, and PAR. Also, field supplementation systems need improvement so that long-term field studies can easily incorporate UV supplementation treatments along with UV reduction treatments. This will require systems that use combinations of lamp bank and filters in the field. Inherent difficulties need to be overcome before this is possible. The most notable difficulties include cost of maintaining lamps in the field and problems in maintaining an approximation of natural solar radiation under filter treatments and supplementation treatments.

As UV methodology improves, our ability to determine the effects of UV radiation on processes such as the terrestrial carbon balance will also improve. Long-term field studies will be needed in the future that incorporate treatments specifically designed to quantify the direct and indirect impacts of UV radiation on the terrestrial carbon balance. This review presents compelling evidence that UV radiation is an important factor in determining the terrestrial carbon balance (Fig. 1). Therefore, it will be necessary for accurate predictions of changes in CO_2 flux to incorporate the net impact of UV radiation into future modeling efforts.

Furthermore, additional research is necessary to evaluate the interactions of UV radiation and other abiotic stress factors associated with global climate change. This area should not only be important to the evaluation of the effects of UV radiation on the terrestrial carbon balance, but interaction studies in general will be a critical component for understanding and forecasting more accurately the consequences of global climate change. Integration of future changes in UV radiation in combination with other global change factors, including increased atmospheric carbon dioxide, temperature, nitrogen deposition, and altered precipitation regimes, will be another important challenge of the future.

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