Implications of Stratospheric Ozone Depletion upon Plant Production

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Scientists have now accumulated sufficient evidence to show that human activity is rapidly changing the chemical composition of trace gases in the earth's atmosphere. These changes are beginning to produce global effects on the earth's ozone layer, climate, and atmospheric chemistry. Gases of primary concern are CO₂, chlorofluorocarbons (CFCs), methane (CH₄) and nitrous oxide (N₂O), and tropospheric ozone (O₃), which is produced as a result of other gases (WMO, 1986). Atmospheric concentrations of all these compounds are increasing at an alarmingly rapid rate. Annual rates of increase in concentrations have been measured at between 5% and 7% for CFCs, 1% for CH₄, 0.2% to 0.3% for N₂O, and 0.5% for CO₂ (WMO, 1986). The concentration of other trace gases is increasing at even a more-rapid rate. With the exception of CFCs, the changes in these gases involve natural processes; however, human activities have greatly accelerated their release into the atmosphere. For example, CH₄ is naturally produced by bacterial activity in water-logged soils and in the digestive tracts of herbivores, but increasing amounts are produced by rice cultivation, cattle raising, burning biomass and mining fossil fuels (WMO, 1986). Nitrous oxide is naturally produced by denitrification and nitrification processes; however, the increased use of ammonia-based fertilizers is also increasing its concentration in the atmosphere (WMO, 1986). Increases in atmospheric CO₂ concentrations are well-known and are primarily associated with the burning of fossil fuels and deforestation. It is anticipated that our atmospheric levels of CO₂ will double to 600 ppm sometime within the next 30 to 75 years (Hansen et al., 1986).

Unlike the other trace gases mentioned above, CFCs are entirely man-made for use as refrigerants, foam-blowing agents, solvents and degreasing agents, and aerosol spray propellants. Historically, use of CFCs has grown roughly twice as fast as economic growth (Gibbs, 1986; Hammitt, 1986; Nordhaus and Yohe, 1986). The United States, Canada, Norway, and Sweden banned nonessential use of CFCs as aerosol propellants in the 1970s. Future growth in CFC use will be reduced by the recently negotiated *Montreal Protocol on Substances that Deplete the Ozone Layer*. Over fifty nations have now signed this landmark environmental agreement, which calls for a 50% reduction in CFC use within 10 years. Despite these restrictions, global CFC concentrations are projected to increase due to their long atmospheric lifetimes, use by countries not party to the Montreal Protocol, and allowed use by Protocol participants (Hoffman and Gibbs, 1988).

An important consequence of this rapid increase in trace gases is that they are projected to have a large impact on global climate. All of these—CO₂, CH₄, N₂O, CFCs, and tropospheric O₃—are greenhouse gases; they warm the earth's surface by allowing short wavelength radiation to pass through relatively unattenuated, but absorb some of the outgoing longwave (terrestrial) radiation and re-emit some of it downward, providing an additional source of heating. It is convenient to combine the radiative effects of all these gases and refer to the effect of "an equivalent doubling of CO₂," which is projected to occur in ~50 years if present emission trends continue. Since CO₂ is projected to provide only about half of the total increased greenhouse effect, the actual concentration of CO₂ will double sometime after that, depending on future policy decisions. Various estimates project this to occur within the next 100 years (Mintzer, 1987).

In addition to their contribution to global warming, CFCs and N₂O may deplete the earth's protective stratospheric ozone layer. CFCs and N₂O are stable compounds with atmospheric lifetimes of up to 150 years (WMO, 1986). Their long lifetimes allow them to

be photodissociated and release NOCl, which catalytically destroys ozone.

Following an 18-month review involving over 100 of the world's leading atmospheric scientists, the International Ozone Trends Panel released its conclusive findings in Mar. 1988 that significant global ozone depletion has already occurred. The panel cited a depletion of between 1.7% and 3.0% from 1969 to 1986 at latitudes between 30 and 64° N (where measurements are most extensive). The panel found that this decrease is conclusively linked to atmospheric chlorine, and is in addition to the natural variation in ozone levels (NASA, 1988). In addition, the Ozone Trends Panel reconfirmed that seasonal concentrations of ozone in Antarctica have fallen by 50% over the past decade, and that the weight of evidence indicates that man-made chlorine species are responsible for the depletion (NASA, 1988).

At this time, it is impossible to project the future ozone losses that will be associated with further inevitable increases in stratospheric chlorine and bromine. Tolbert et al. (1987), for example, have shown that heterogeneous reactions can occur on sulfate aerosols, raising the possibility of nonlinear depletion over parts of the globe. Blake and Rowland (1988) have suggested that CH₄ can transport water vapor to the stratosphere and provide reaction sites for heterogeneous chemistry. Consequently, it would be premature to consider the threat of depletion to be gone, although the Montreal Protocol and announcements about its revision provide a prognosis for ozone layer protection that appears good.

Depletion of the ozone layer is of concern because stratospheric ozone is the primary attenuator of solar ultraviolet-B radiation (UV-B region, between 290 and 320 nm). A decrease in this ozone layer would lead to increases in UV-B reaching the earth's surface. Though representing only a small fraction of the total solar electromagnetic spectrum, UV-B has a disproportionately large photobiological effect.

The reason for concern over stratospheric ozone depletion and the ensuing increase in solar UV radiation is that many important biological macromolecules, including proteins, DNA, and phytohormones, all have appreciable absorption coefficients in the UV region (Giese, 1964). This results in a whole array of physiological and biochemical effects, including direct effects on the primary reactions of photosystem II, dark respiration, stomatal conductance, and the protein, lipid, and carbohydrate composition of plant tissues, etc. (Table 1) (Teramura, 1983; Tevini and Teramura, 1989). These physiological changes produce altered tissues and structures in plants. Among the most characteristic of these alterations are reductions in leaf area and plant stunting resulting from a shortening of internode length. A change in the pattern of biomass allocation can result in proportionately more biomass going into vegetative structures and concomitantly less into reproductive ones, thereby reducing harvestable yield. Under intense solar UV, bronzing, chlorosis, and other direct effects can be observed on sensitive plant tissues, resulting in reduced physiological performance and possibly affecting the quality of fruits and vegetables.

Although economically important crops represent only 10% of global net primary productivity, because of their importance to human nutrition, it is not surprising that >90% of our understanding of UV effects on plants comes from studies on these crops (Table 2). To date, the scientific community has screened >300 species and cultivars of plants, and, alarmingly, over one-half of these showed sensitivity to UV radiation (Teramura, 1986; Tevini and Teramura, 1989). The most sensitive plant families include members of the *Fabaceae* (beans and peas), *Cucurbitaceae* (squash and

Table 1. A summary of the effects of UV-B radiation on plant physiology and growth [adapted from Teramura (1983), see for specific references and details of effects].

A. Physiological/biochemical effects	Relative change ^a
Direct effects on photosynthesis	-
Hill reaction	-
Electron transport	-
RuBP carboxylase	-
PEP carboxylase	-
Dark respiration	+/-
Stomatal conductance	+/-
Photosynthetic pigments	-
Nonphotosynthetic pigments	+
Soluble proteins	+/-
Lipid composition	Δ
Soluble carbohydrates	+/-
Plant hormones	-
Ion transport	-
Cuticular wax composition	Δ
B. Morphological/anatomical effects	
Leaf area	-
Specific leaf wt	+
Bronzing/glazing/chlorosis	+
Seedling growth	-
Dry matter production/allocation	Δ
Yield	-

^aIncrease = +; decrease = -; change in composition or pattern of allocation = Δ.

Table 2. Survey of UV studies by major terrestrial plant ecosystem [after Whittaker, (1975)].

Ecosystem	Global NPP (%)	Included in UV study
Tropical forest	42	No
Temperate forest	13	Yes
Savanna	12	No
Boreal forest	8	No
Agricultural	8	Yes
Woodland and scrubland	5	No
Temperate grassland	5	Yes
Swamp and marsh	4	No
Desert and semidesert	2	No
Tundra and alpine	1	Yes

melons), and *Brassicaceae* (mustard and cabbage).

Only 10 field studies have examined the effects of UV on crop yield in 22 species of plants (Table 3) and yield was reduced in more than half of the crops studied. The range of response shown for each crop species was partially due to differences in experimental treatments and partially due to intraspecific (cultivar) differences in UV sensitivity. A detailed study was conducted at the Univ. of Maryland on soybean, where several soybean varieties were intensively examined for a 6-year period from 1981 to 1986 (Teramura and Sullivan, 1988). Increased levels of UV were artificially supplied from filtered fluorescent sunlamps suspended above plants growing in the field. In a particularly sensitive cultivar, Essex soybean yield was reduced by 19% to 25% in 4 of the 6 years by UV-B radiation levels that simulated a 25% ozone depletion (Table 4). In years with apparently little UV effectiveness (1983 to 1984), all plants experienced a considerable amount of drought stress. Parallel field and greenhouse studies have demonstrated that under water stress, the effects of UV-B radiation are masked (Murali and Teramura, 1986; Sullivan and Teramura, 1989). A similar masking effect was found in studies of UV-B-irradiated, mineral-deficient plants (Murali and Teramura, 1985). These emphasize the importance of understanding the interactions of UV-B with other plant stress factors. Additionally, it suggests that the impacts of UV-B radiation might be greatest under conditions optimal for growth, i.e., irrigated and fertilized regions. Yield quality can also be adversely affected as seen in the protein and oil content of UV-B-

irradiated soybean seed (Table 4). Other investigators have also reported possible UV-induced reductions in quality for potato, tomato, and sugar beet (Teramura, 1986). In addition to these direct effects of UV radiation, yield may be further reduced by indirect effects resulting from increased losses due to weeds (Gold and Caldwell, 1983; Barnes et al., 1988), diseases (Carns et al., 1978; Biggs et al., 1984) and insects. When combined with the direct effects of UV-B radiation these may result in greater overall losses.

Although forest tree species represent up to 80% of global net primary productivity, very little is known of the effects of UV radiation on these species (Table 2). In fact, only 15 temperate forest species have been examined for W sensitivity and nearly half of these were shown to be sensitive. Loblolly pine, red pine, and lodgepole pine were particularly sensitive (Sullivan and Teramura, 1988, 1989). Due to the long lifespan of trees and the lengthy time required for breeding, forests may be particularly vulnerable to increases in UV-B radiation resulting from stratospheric ozone depletion.

Very little is known of the effects of UV on natural, noncultivated ecosystems. To date, only 30 to 40 species of native plants have been screened for UV-B radiation sensitivity. When examining natural plant communities, it appears that plants from naturally high UV environments are more resistant to UV than those from low UV environments (Caldwell et al., 1982). For example, in one study of some native Hawaiian plants collected along an elevational gradient on Mount Haleakala on the island of Maui, it appeared that plants collected near sea level were much more sensitive to UV radiation than those collected from high on the mountain. This increase in UV tolerance with elevation coincides quite well with the increase in UV radiation along the elevational gradient. Due to this differential sensitivity, the biodiversity of natural ecosystems may be significantly altered.

In light of the differences in UV sensitivity found among crop and native plants, it is clear that plants have evolved various protective and repair mechanisms to UV radiation (Beggs et al., 1986). These include specific enzyme-mediated repair mechanisms such as photoreactivation to generalized repair processes mediated through overall growth reduction. One very effective means of protection results from the direct UV-B stimulation of plant pigment production in the upper epidermal cell layers of leaves, the layers that absorb UV radiation, preventing it from penetrating deeper into underlying tissues and causing damage. These pigments include flavonoids, which are colorless, thereby allowing visible radiation to pass into the leaves to drive photosynthesis, but highly absorptive to damaging W radiation. It has been clearly demonstrated that W radiation specifically activates the genes that control the expression of several key enzymes along the phenylpropanoid pathway leading to flavonoid biosynthesis (Hahlbrock and Grisebach, 1979). The degree of flavonoid production has been closely linked with UV sensitivity on several species of plants, including soybean and cucumber (Murali and Teramura, 1986).

CONCLUSIONS

There are 10 major terrestrial plant ecosystems in the world that include > 300 plant families. The effects of enhanced levels of UV-B radiation resulting from stratospheric ozone depletion have been studied in <10% of these families and in only four of these ecosystems. Most of our knowledge of UV-B radiation effects is derived from agricultural crops and little information exists for long-lived perennials such as trees or for noncultivated, natural plant communities.

Plant response to increased levels of UV-B radiation varies markedly both interspecifically and intraspecifically. Presently, the physiological and genetic bases for these inherent differences are not well-understood. However, UV-tolerant plants do possess various types of UV-protective and repair processes, which suggests that increased UV resistance in crops might be achieved via breeding programs. Unfortunately, we currently lack information on the genetic basis and heritability of UV resistance to estimate the feasibility of such crop improvement programs. Furthermore, selective breeding may not be possible in long-lived perennials such as trees

Table 3. Summary of field studies examining the effects of UV-B radiation on crop yields. Values represent percent changes from controls [adapted from Teramura (1986)].

Crop species	Ambler et al. (1978) (1) ^z	Barnes et al. (1988) (2) ^z	Bartholic et al. (1975) (2)	Bccwar et al. (1982) (2)	Biggs and Kossuth (1978) (2)	Biggs et al. (1984) (2)	Eisenstark et al. (1984) (2)	Esser (1980) (1)	Hart et al. (1975) (1)	Teramura and Sullivan (1988) (2)
<i>Cucurbita maxima</i>	0									
<i>Cucurbita pepo</i>					-14 to -90					
<i>Phaseolus vulgaris</i>			+12 to +15					+53 to -75		
<i>Triticum aestivum</i>		0				-5				
<i>Zea mays</i>	0		+29 to +39		0	0	-79 to -87		0	
<i>Spinacia oleracea</i>								+11 to -56		
<i>Sorghum bicolor</i>	0									
<i>Capsicum annum</i>									-(?)	
<i>Glycine max</i>	0					0			0	+22 to -25
<i>Cynodon dactylon</i>										
<i>Beta vulgaris</i>	0									
<i>Brassica oleracea</i>								+19 to -49		
var. <i>capitata</i>										
<i>Brassica oleracea</i>	-24 to -45									
var. <i>botrytis</i>										
<i>Lycopersicon</i>			-5 to -26		-11 to -39				0	
esculentum										
<i>Nicotiana tobaccum</i>									0	
<i>Raphanus sativus</i>				0					0	
<i>Pennisetum glaucum</i>									0	
<i>Solanum tuberosum</i>				0	0			-2 to -41		
<i>Brassica juncea</i>					-9 to -43					
<i>Vigna unguiculata</i>					-18 to -38					
<i>Oryza sativa</i>						0				
<i>Arachis hypogaea</i>					0				0	

^z(1) Unfiltered sunlamps; (2) filtered sunlamps.

Table 4. Summary of UV effects on soybean yield and quality.^z

Year	Change in yield (%)	Change in seed quality (%)	
		Protein	Oils
1981	-25		
1982	-23	-5	-2
1983	+6	-4	+1
1984	-7	0	-2
1985	-20	0	0
1986	-19	0	-1

^zFrom A.H.T. (unpublished) and Teramura and Sullivan (1988)

nor applicable to noncultivated, natural plant communities. UV-B radiation may shift the competitive balance among species, resulting in an alteration of plant biodiversity. Therefore, natural plant communities and forests may be particularly vulnerable to increases in UV radiation resulting from ozone depletion.

In addition to an increase in UV-B radiation, other climatic factors also are anticipated to change concomitantly in the future. These include increases in atmospheric CO₂ concentrations, global warming, changes in the pattern of precipitation, increases in tropospheric (ground level) pollutants such as oxides of N, S, and O₃, etc. Presently, only scant information exists on the effects of UV-B radiation in combination with these other changes. It is clear, however, that interactions with these other factors may greatly modify UV effectiveness. Therefore, it is currently difficult to assess the question of the overall potential impacts of increasing UV-B radiation resulting from stratospheric ozone depletion on global crop production. Much more information is still required to describe and evaluate these effects on plants. Particularly important would be field validation studies using economically important crops and forest species, as well as field tests on natural ecosystems. Also, by understanding the adaptive mechanisms that UV-resistant plants already possess, we may be able to mitigate some of the deleterious impacts of UV-B radiation on agriculturally important crops.

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