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The Greenhouse Effect: Impacts of Ultraviolet-B (UV-B) Radiation, Carbon Dioxide (CO_2), and Ozone (O_3) on Vegetation

S. V. Krupa

Department of Plant Pathology, University of Minnesota,
St Paul, MN 55108, USA

&

R. N. Kickert

4151 NW Jasmine Place, Corvallis, OR 97330, USA

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ABSTRACT

There is a fast growing and an extremely serious international scientific, public and political concern regarding man's influence on the global climate. The decrease in stratospheric ozone (O_3) and the consequent possible increase in ultraviolet-B (UV-B) is a critical issue. In addition, tropospheric concentrations of 'greenhouse gases' such as carbon dioxide (CO_2), nitrous oxide (N_2O) and methane (CH_4) are increasing. These phenomena, coupled with man's use of chlorofluorocarbons (CFCs), chlorocarbons (CCs), and organo-bromines (OBs) are considered to result in the modification of the earth's O_3 column and altered interactions between the stratosphere and the troposphere. A result of such interactions could be the global warming. As opposed to these processes, tropospheric O_3 concentrations appear to be increasing in some parts of the world (e.g. North America). Such tropospheric increases in O_3 and particulate matter may offset any predicted increases in UV-B at those locations.

Presently most general circulation models (GCMs) used to predict climate change are one- or two-dimensional models. Application of satisfactory three-dimensional models is limited by the available computer power. Recent studies

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on radiative cloud forcing show that clouds may have an excess cooling effect to compensate for a doubling of global CO_2 concentrations.

There is a great deal of geographic patchiness or variability in climate. Use of global level average values fails to account for this variability. For example, in North America:

1. *there may be a decrease in the stratospheric O_3 column (1–3%); however, there appears to be an increase in tropospheric O_3 concentrations (1–2%/year) to compensate up to 20–30% loss in the total O_3 column;*
2. *there appears to be an increase in tropospheric CO_2, N_2O and CH_4 at the rate of roughly 0·8%, 0·3% and 1–2%, respectively, per year;*
3. *there is a decrease in erythemal UV-B; and*
4. *there is a cooling of tropospheric air temperature due to radiative cloud forcing.*

The effects of UV-B, CO_2 and O_3 on plants have been studied under growth chamber, greenhouse and field conditions. Few studies, if any, have examined the joint effects of more than one variable on plant response. There are methodological problems associated with many of these experiments. Thus, while results obtained from these studies can assist in our understanding, they must be viewed with caution in the context of the real world and predictions into the future.

Biomass responses of plants to enhanced UV-B can be negative (adverse effect); positive (stimulatory effect) or no effect (tolerant). Sensitivity rankings have been developed for both crop and tree species. However, such rankings for UV-B do not consider dose–response curves. There are inconsistencies between the results obtained under controlled conditions versus field observations. Some of these inconsistencies appear due to the differences in responses between cultivars and varieties of a given plant species; and differences in the experimental methodology and protocol used. Nevertheless, based on the available literature, listings of sensitive crop and native plant species to UV-B are provided.

Historically, plant biologists have studied the effects of CO_2 on plants for many decades. Experiments have been performed under growth chamber, greenhouse and field conditions. Evidence is presented for various plant species in the form of relative yield increases due to CO_2 enrichment. Sensitivity rankings (biomass response) are again provided for crops and native plant species. However, most publications on the numerical analysis of cause–effect relationships do not consider sensitivity analysis of the models used.

Ozone is considered to be the most phytotoxic regional scale air pollutant. In the pre-occupation of loss in the O_3 column, any increases in tropospheric O_3 concentrations may be undermined relative to vegetation effects. As with the other stress factors, the effects of O_3 have been studied both under controlled and field conditions. The numerical explanation of cause–effect

relationships of O_3 is a much debated subject at the present time. Much of the controversy is directed toward the definition of the highly stochastic, O_3 exposure dynamics in time and space.

Nevertheless, sensitivity rankings (biomass response) are provided for crops and native vegetation.

The joint effects of UV-B, CO_2 and O_3 are poorly understood. Based on the literature of plant response to individual stress factors and chemical and physical climatology of North America, we conclude that nine different crops may be sensitive to the joint effects: three grain and six vegetable crops (sorghum, oat, rice, pea, bean, potato, lettuce, cucumber and tomato). In North America, we consider Ponderosa and loblolly pine as vulnerable among tree species. This conclusion should be moderated by the fact that there are few, if any, data on hardwood species.

In conclusion there is much concern for global climate change and its possible effects on vegetation. While this is necessary, such a concern and any predictions must be tempered by the lack of sufficient knowledge. Experiments must be designed on an integrated and realistic basis to answer the question more definitively. This would require very close co-operation and communication among scientists from multiple disciplines. Decision makers must realize this need.

INTRODUCTION

There is a fast growing and an extremely serious international concern regarding man's influence on the global climate. The issues of concern are: (1) depletion of beneficial stratospheric O_3 and a consequent increase in tropospheric UV-B, (2) the increase in the ground level emissions of 'greenhouse gases', the resulting 'greenhouse effect', and the global warming, and thus, (3) predicted drastic alterations in the terrestrial and aquatic ecosystems.

The popular perception of this subject may be stated, for example, as follows:

> 'Sunlight strikes the earth, heating the rock and water of the surface. The earth then radiates the heat as infrared rays. An equilibrium is thus established between the solar energy received and the heating of the earth and atmosphere. Carbon dioxide and other gases are released into the atmosphere from natural sources, such as plant and animal life, and artificial sources, such as factories and cars. The atmosphere is composed primarily of nitrogen, 78%, and oxygen, 21%, with other trace gases such as carbon dioxide, argon, hydrogen and helium contributing minute amounts.
>
> Gases accumulate in the atmosphere and act like glass in a

greenhouse, letting in the warming rays, but inhibiting the escape of infrared rays.

Scientists know a lot less about the greenhouse effect than the news media may have led you to believe during the long, hot summer.

To be sure, there is no debate among atmospheric scientists that a greenhouse effect exists. It is a fact of nature, it is getting worse and it almost certainly will cause the earth's climate to warm up.

But warm up how much? How fast? With what impact? On those critical questions, scientists disagree.'

(Courtesy of Robert A. Rankin and the *St Paul Pioneer Press Dispatch*, Sunday 4 December 1988).

In the following sections of the analysis, in addition to describing the atmospheric processes governing the 'greenhouse effect', in evaluating the vegetation response research, because of the complexity and the voluminous literature on cause (various parameters of the climate) and effects (plant response) relationships, as a case study we have emphasized the North American literature. The reader should not misinterpret this to mean that there are no studies of similar nature in many other countries.

We request the reader to refer to appropriate additional literature on the subject matter relative to the country of interest and emphasis.

ATMOSPHERIC PROCESSES GOVERNING THE 'GREENHOUSE EFFECT'

The definitions of important terms used in this section are provided in Table 1.

The 'greenhouse effect' and climate modification are governed by the interactions between tropospheric and stratospheric processes (Wuebbles *et al.*, 1989). A key atmospheric constituent participating in these interactions is O_3.

Ozone concentrations vary with altitude above the earth's surface; peak fractions of about 10^{-5} by volume are found between 25 and 35 km (Fig. 1). The vertical column of O_3 is distributed roughly as follows: 0–10 km (troposphere), 10%; 10–35 km, 80%; and above 35 km, 10% (Cicerone, 1987). Ozone concentrations in the troposphere also vary with the latitude (Pruchniewicz, 1973).

In the stratosphere, a series of photochemical reactions involving O_3 and molecular oxygen, O_2, occur. Ozone strongly absorbs solar radiation in the region from ≈ 210 to 290 nm, whereas O_2 absorbs radiation at $\lesssim 200$ nm.

TABLE 1
Definitions of Some Technical Terms used in the Discussion of Atmospheric Processes

Term	*Definition*
Albedo	The ratio of the amount of electro-magnetic radiation reflected by a body to the amount incident upon it, commonly expressed as a percentage. The albedo is to be distinguished from the reflectivity, which refers to one specific wavelength (monochromatic radiation).
Cloud-radiative forcing	A measure of cloud–climate interaction, indicated by the modulation of the short and long wavelength fluxes by clouds.
Dobson Spectrophotometer	A photoelectric spectrophotometer used in the determination of the O_3 content of the atmosphere; compares the solar energy at two wavelengths in the absorption band of O_3 by permitting the radiation of each to fall alternatively upon a photocell.
El Niño	A massive zone of abnormally warm ocean water that from time to time stretches westward along the Equator from South America. This phenomenon produces dramatic effects on the weather in various parts of the world.
Erythema	A redness of the skin, as caused by sunburn.
Free troposphere	The troposphere above the mixed layer.
Planetary boundary layer (PBL)	Also known as atmospheric boundary layer. That layer of the atmosphere from the earth's surface to the geostrophic wind level including, therefore, the surface boundary layer and the Ekman layer (layer of transition between the surface boundary and the free atmosphere).
Stratosphere	Earth's atmosphere between altitudes of 10 km and 50 km where temperature increases with altitude.
Surface boundary layer	That thin layer of air adjacent to the earth's surface extending up to the so-called anemometer level. Within this layer the wind distribution is determined largely by the vertical temperature gradient and the nature and contours of the underlying surface.
Troposphere	Earth's atmosphere for approximately the first 10 km above the surface where temperature decreases with altitude (ignoring localized radiation or subsidence inversions).
UV-B	Ultraviolet radiation in the wavelength band of 280–320 nm.

The absorption of light primarily by O_3 is a major factor causing the increase in temperature with altitude in the stratosphere. Excited O_2 and O_3 photodissociate, initiating a series of reactions in which O_3 is both formed and destroyed leading to a steady state concentration of O_3 (Finlayson-Pitts & Pitts, 1986). This O_3 serves as a shield against biologically harmful solar ultraviolet (UV) radiation, initiates key stratospheric chemical reactions, and transforms solar radiation into heat and the mechanical energy of atmospheric winds. Also, downward intrusions of stratospheric air, supply the troposphere with the O_3 necessary to initiate photochemical processes in the lower atmosphere. The flux of photochemically active UV-B photons

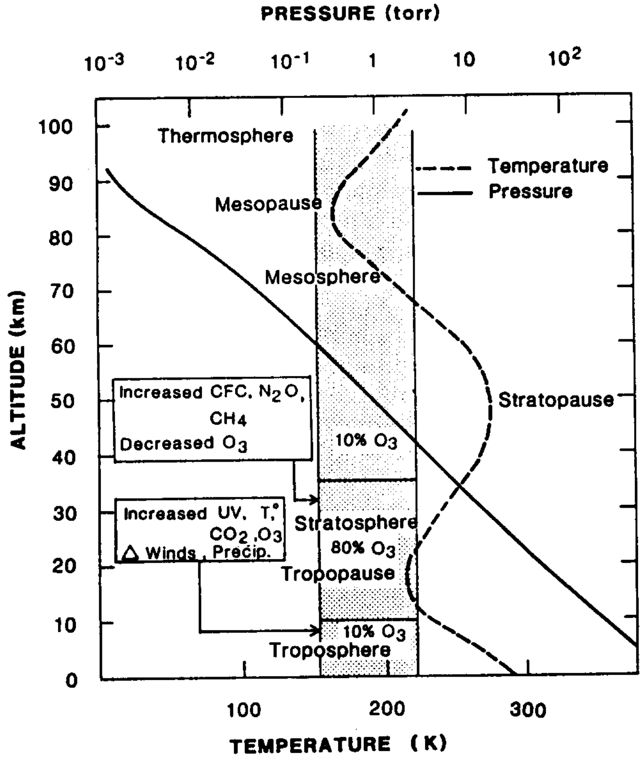


Fig. 1. Relationships between the altitude from the earth's surface, temperature, atmospheric pressure and ozone (O_3). Observed and/or predicted changes in the troposphere and the stratosphere are shown in the boxes to the left.

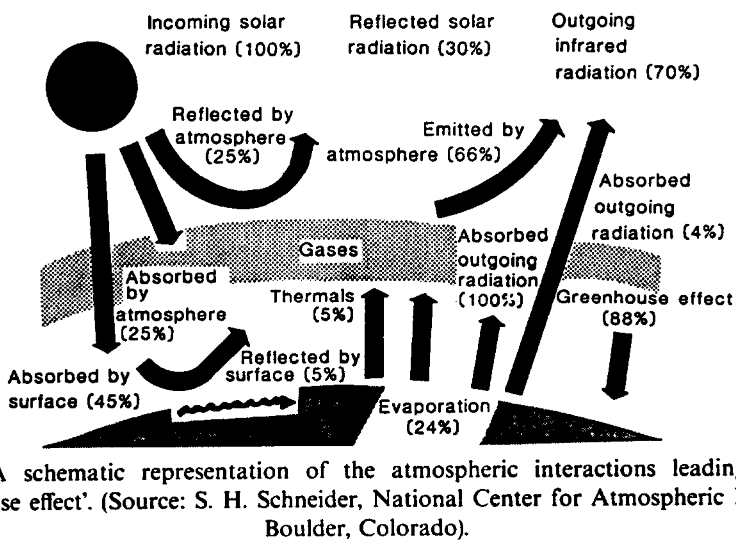


Fig. 2. A schematic representation of the atmospheric interactions leading to the 'greenhouse effect'. (Source: S. H. Schneider, National Center for Atmospheric Research, Boulder, Colorado).

(wavelength, $\lambda < 315$ nm) into the troposphere is limited by the amount of stratospheric O_3 (Cicerone, 1987). In addition to this protective effect of stratospheric O_3 against UV, clouds reflect a large part of the incoming solar radiation, causing the albedo of the entire earth to be about twice what it would be in the absence of clouds (Cess, 1976 as cited by Ramanathan *et al.*, 1989). Clouds cover about one half of the earth's surface, doubling the proportion of sunlight reflected back into space to 30% (Fig. 2).

Ever since the publications of Johnston (1971) and Molina & Rowland (1974) human activities have been projected to substantially deplete the stratospheric O_3 through anthropogenic increases in the global concentrations of key atmospheric chemicals. Cicerone (1987) has provided an excellent treatment of this question. Of concern is the flow into the stratosphere of methane (CH_4), nitrous oxide (N_2O), methyl chloride (CH_3Cl), synthetic chlorofluorocarbons (CFCs), chlorocarbons (CCs) and organo-bromine (OB) compounds.

Many possible stimuli have been proposed for the destruction of stratospheric O_3: NO_x (oxides of nitrogen) from nuclear explosions, hypothetical fleet of supersonic aircraft, solar proton events, increased atmospheric N_2O and chlorine (Cl) from the continued use of CFCs and CCs, volcanoes, and space shuttle rocket exhaust. Also increases in the atmospheric CH_4 can lead to changes in the O_3 layer through interactions with NO_x and ClO_x cycles and through production of HO_x. One of the most definitive experiments to date concerns solar proton events. Observations that followed the large event of August 1972 showed that O_3 concentrations were reduced by about as much as theory predicted, at least in the upper stratosphere (Heath *et al.*, 1977).

Figure 3 (Cicerone, 1987) shows examples of large scale processes that produce and transfer source gases, which undergo irreversible photo-oxidation to yield important gaseous radicals to the stratosphere. The N_2O from soil, oceanic microbial processes and, to some extent, anthropogenic activity enters the lower atmosphere and, through large scale motions (principally in the tropics) is transported upward to the stratosphere. Subsequently, most N_2O is decomposed through:

$$N_2O + h\nu \rightarrow N_2 + O(^1D)$$

and about 5% produces NO through:

$$N_2O + O(^1D) \rightarrow 2NO$$

Similarly, the synthetic CCl_2F_2 and CCl_3F are swept upward into the middle stratosphere, where UV-B photolysis dissociates them to yield chlorine atoms. As with N_2O, there are no known tropospheric sinks for $CClF_2$ and CCl_3F, so that nearly 100% of the molecules released at the

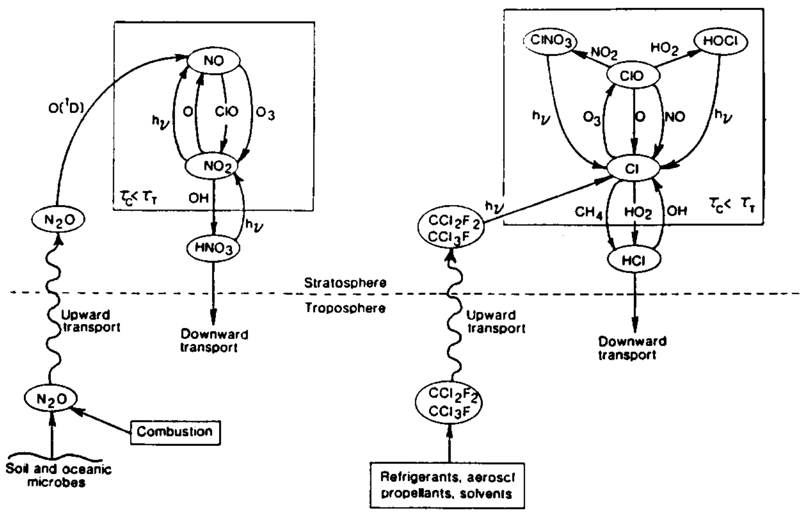


Fig. 3. A schematic depiction of how stratospheric source gases N_2O, CCl_2F_2, and CCl_3F originate at the earth's surface and are transported upward into the stratosphere, where they are irreversibly photo-oxidized to yield key gas-phase radicals. Reactants shown inside the boxes undergo reactions with time constants τ_c that are less than τ_T (the time required for vertical transport). Similarly, some CH_4 reaches the stratosphere, where it gives rise to H_2O, H_2 and HO_x. (From Cicerone (1987). Copyright 1987 by the AAAS).

earth's surface reach the stratosphere. According to Rowland (1989) 'The very lack of chemical reactivity which makes chlorofluorocarbon molecules commercially useful also allows them to persist for many decades in the earth's atmosphere'.

On the other hand, CH_4 is not as inert in the atmosphere as N_2O and CFCs. Perhaps 85% to 90% of the CH_4 released at the earth's surface is consumed in the troposphere. The remaining 10% to 15% reaches the stratosphere (Cicerone, 1987). Stratospheric oxidation of CH_4 gives rise to water vapor and OH and HO_2 radicals. The upper boxes in Fig. 3 show some of the important reactions that control stratospheric O_3 concentrations.

Attempts to predict the future effects of continued increases in stratospheric source gases (e.g. CFCs) have given rise to various mathematical models. Simulated CFC releases lead to decreases in the O_3 column at all latitudes (Isaksen & Stordal, 1986). Larger decreases in the O_3 column were calculated for high latitudes ($>40°$) than for low latitudes.

Reduced amounts of atmospheric O_3 will permit disproportionately large amounts of UV-B radiation to penetrate through the atmosphere. For example, with overhead sun and typical O_3 amounts, a 10% decrease in O_3 was predicted to result in a 20% increase in UV-B penetration at 305 nm, a 250% increase at 290 nm, and 500% increase at 287 nm, all within the UV-B band (Cutchis, 1974).

With or without these predicted changes, the incoming solar radiation to the earth's surface is of short wavelength (Fig. 2). After some absorption, surfaces reradiate heat energy back to the atmosphere at long wavelength, infrared. This energy is trapped by certain atmospheric chemical constituents and by clouds, leading to a warming of the atmosphere above the earth's surface. This is the *natural* 'greenhouse effect'. Without this effect earth would be uninhabitable. The critical concern at this time is whether man's influence has increased and accelerated this 'greenhouse effect' towards progressive global warming leading to disastrous ecological consequences (Houghton & Woodwell, 1989).

Surface emissions and concentrations of globally important trace gases are increasing (Table 2). Many of these gases can have direct effects on the climate through their absorption of infrared radiation. Climate modification, associated with long term changes in weather, is characterized by concerns about trends and variability in surface temperatures, precipitation patterns, cloud cover and other climatic variables. The absorption of surface emitted outgoing infrared radiation in the atmosphere, followed by re-emission at the local atmospheric temperature, can lead to an increase of surface temperature, the *modified* 'greenhouse effect'. There are several recent reviews on this subject (Houghton & Woodwell, 1989; McElroy & Salawitch, 1989; Rowland, 1989; Schneider, 1989; Wuebbles *et al.*, 1989).

As opposed to the primary pollutants listed in Table 2, a major mechanism governing the tropospheric O_3 concentrations is photochemistry. The tropospheric O_3 concentrations across the earth's surface are governed by natural processes and by man's influence. Background concentrations of O_3 observed at a number of locations around the world typically show average daily 1 h maxima of $\approx$20–60 ppb (Singh *et al.*, 1978). An area being classified as remote does not rule out the possibility of long range transport of pollutants to these sites. Nevertheless, long term data at such sites typically show a yearly cycle with a maximum in the late winter or early spring.

Altshuller (1986, 1987) reviewed the processes that can contribute to the surface O_3 concentrations at non-urban locations. These processes consist of: (a) transport of O_3 formed in the stratosphere into the free troposphere and subsequent transport down into the planetary boundary layer (PBL); (b) photochemical O_3 formation within the free troposphere and the clean PBL, (c) photochemical O_3 formation within the polluted PBL; especially during the passage of warm high pressure systems, and (d) O_3 formation within single or superimposed plumes. At some non-urban monitoring locations in the USA, Canada and the UK, during 1978–79, mean and maximum 1 h O_3 concentrations were in the range of 20–57 ppb and 61–200 ppb, respectively (Altshuller, 1986).

TABLE 2
Summary of Important Trace Gases, with Increasing Surface Emissions

Gas	*Common name*	*Surface concentrations*[a]	*Atmospheric trend year*$^{-1}$	*Atmospheric lifetime*	*Primary man-made sources*
CO_2	Carbon dioxide	345 ppmv	~0·4%	~500 years (air–biosphere oceans)	Fossil fuels burning; land use conversion
CH_4	Methane	1·7	~1	~7–10	Domestic animals; rice paddies; biomass burning; gas and mining leaks
CO	Carbon monoxide	0·12	~1–2	~0·4	Energy use; agriculture; forest clearing
N_2O	Nitrous oxide	0·31	~0·3	~150	Fossil fuel burning; cultivation and fertilization of soils
NO_x (= NO + NO_2)	Reactive odd oxides of nitrogen	$1–20 \times 10^{-5}$	unknown	$\lesssim$0·02	Fossil fuel burning; biomass burning
$CFCl_3$	CFC-11	$2·0 \times 10^{-5}$	~5	~75	Chemical industry
CF_2Cl_2	CFC-12	$3·2 \times 10^{-4}$	~5	~110	Chemical industry
$C_2Cl_3F_3$	CFC-113	$3·2 \times 10^{-5}$	~10	~90	Chemical industry
CH_3CCl_3	Methyl chloroform	$1·2 \times 10^{-4}$	~5	~6–9	Chemical industry
CF_2ClBr	Ha-1211	1×10^{-6}	~10–30	~12–15	Fire extinguishers
CF_3Br	Ha-1301	1×10^{-6}	unknown	~110	Fire extinguishers
SO_2	Sulfur dioxide	$1–20 \times 10^{-5}$	unknown	~0·02	Coal and petroleum burning
COS	Carbonyl sulfide	5×10^{-4}	<3	2.2.5	Biomass burning; fossil fuel burning

[a] Corresponds to mid-1980s values.
From Wuebbles *et al.* (1989).

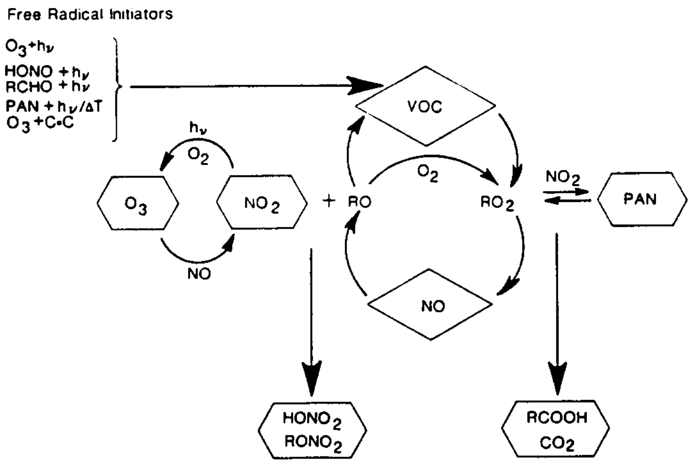


Fig. 4. A schematic diagram of the photochemical oxidation cycle of the polluted atmosphere. (From Demerjian, 1986).

Demerjian (1986), Finlayson-Pitts & Pitts (1986) and Wayne (1987) have reviewed the information relevant to the chemistry of the clean troposphere. Krupa & Manning (1988) provided a summary of the information from these reviews.

Alterations introduced as a result of human activity on the photochemical oxidation cycle within the atmosphere are predominantly due to two classes of compounds, volatile organic carbon (VOC) and oxides of nitrogen (NO_x) (Fig. 4). Seinfeld (1989) has provided an excellent review of urban air pollution and the state of the science. The data on O_3 formation within some urban plumes are summarized in Table 3.

As previously stated, the 'greenhouse effect' and climate modification are governed by the interactions between the stratospheric and tropospheric processes. According to McElroy & Salawitch (1989) a panel of experts convened by NASA (National Aeronautics and Space Administration, USA) concluded that the best current analysis, using mainly data from the ground-based Dobson spectrophotometer network, indicates that the annual averaged column density of O_3 declined between 1·7 and 3·0% in the latitude band 30° to 64° N between 1969 and 1986. The period covered by this analysis occupies less than one solar cycle and includes two significant geophysical events, the eruption of the volcano El Cichon and the unusually large El Niño—southern oscillation. In this context, there are also problems with satellite based instrumentation due to their temporal drift in sensitivity and a need to calibrate such instruments using ground based data. Nevertheless, according to NASA, model calculations are broadly consistent with the observed changes in column O_3, except that the mean values of the observed decreases at mid and high latitudes during the winter

TABLE 3
Ozone Formation Within Urban Plumes

Reference	*Source area*	*Date*	*Receptor area*	*O_3 conc. (ppb)* Within plume	Outside of plume	Distance downwind (km)	Time of day
Spicer *et al.* (1982*b*)	Boston, MA	18 Aug. 1978	Atlantic Ocean	130	60	100	≈1 540 h EDT
		23 Aug. 1978	Atlantic Ocean	154	NA[a]	120	1 600–1 630 h EDT
Siple *et al.* (1977)	S. New York St. Long Island	14 Aug. 1975	Atlantic Ocean	214	NA[a]	200	1 600 h EDT
Spicer *et al.* (1977)	New York City	18 July 1975	NW & W of Boston, MA	150–200	60	400	2 100 h EDT
Spicer *et al.* (1979)	New York and adjacent areas	23 July 1975	S. Connecticut	250–300	70–85	125	1 500 h EST
			NE Connecticut	150–200	80–90	200	2 100 h EST
			NW of Boston, MA	100–150	60–70	300	2 400 h EST
		24 July 1975	NE of Boston, over Atlantic Ocean	130	NA	350	morning
		24 July 1975	Over Atlantic Ocean off Portland, ME	145	NA	450	afternoon
		9 Aug. 1975	Atlantic Ocean	130	NA	160	evening
Wolff *et al.* (1977)	Philadelphia, PA & Camden, NJ	10 Aug. 1975	New Jersey	194	139[b]	45	afternoon
Clark & Clarke (1984)	Washington, DC & Baltimore, MD	14 Aug. 1980	Pennsylvania	140–170	NA[a]	160 km from Baltimore	1 534–1 641 h EST
Sexton & Westberg (1980)	Chicago-N.W. Indiana	15 Aug. 1977	Wisconsin	150	70–80	170	1 450–1 720 h CDT
White *et al.* (1977)	St. Louis, MO	18 July 1975	New Springfield, IL	130	70	140	1 631–1 656 h CDT
		11 Aug. 1975	New Decatur, IL	140	75	60	1 442–1 508 h CDT
Spicer *et al.* (1982*a*)	Springfield, IL	3 Aug. 1977	Illinois	70–80	≤50	70	afternoon

[a] Not available.
[b] Upwind of Philadelphia.
From Altshuller (1986).

are larger than the mean values of the predicted decreases. According to Logan (1985) decreases in the total O_3 column due to the decreases in stratospheric O_3 may partially be compensated by increases in tropospheric O_3. Logan estimated that approximately 20–30% of the decrease in stratospheric O_3 over middle and high latitudes of the northern hemisphere could be compensated for by what appears to be a trend toward increasing O_3 in the troposphere in these geographic areas.

A consequence of the measured or predicted stratospheric O_3 depletion is the increased penetration of radiation in the UV-B band into the lower troposphere. According to Frederick *et al.* (1989), the biologically effective UV-B irradiance at the earth's surface varies with the elevation of the sun, the amount of atmospheric O_3, and with the abundance of atmospheric matter generated by natural and anthropogenic processes, that have scattering and absorbing properties. Taken alone, the reported decrease in the O_3 column over the Northern Hemisphere between 1969 and 1986 implies an increase in erythemal irradiance at the ground of $\leq 4\%$ during the summer. However, an increase in tropospheric absorption, from polluting gases and/or particulate matter over localized areas, could more than offset the predicted enhancement in radiation. Any such extra absorption is likely to be highly regional in nature and does not imply that a decrease in erythemal radiation has occurred on a global basis. A graphic illustration of tropospheric latitudinal UV-B patterns uncorrected for tropospheric absorption/scattering, are presented in Fig. 5.

The Antarctic 'O_3 hole' represents a special case, where a portion of the

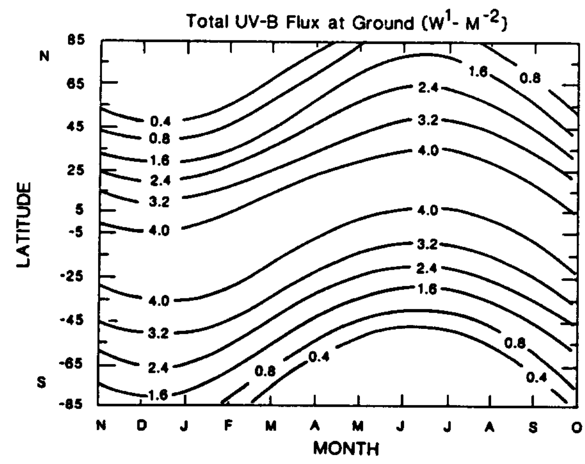


Fig. 5. The latitudinal and monthly distribution of UV-B radiation at the ground computed for clear sky conditions and a local time of 10:00 am. Values include all wavelengths between 280 and 320 nm. (Source: Frederick, 1986).

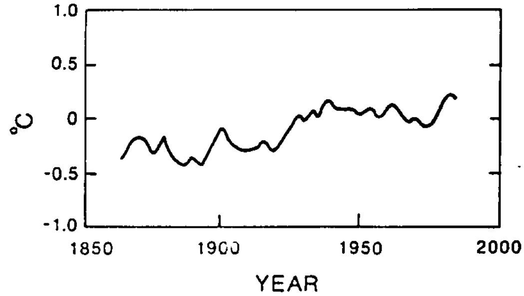


Fig. 6. Relationship between time in years and change in global air temperature after adjusting the marine temperatures for systematic measurement errors. (Source: NASA, Washington, DC 1988).

earth has experienced UV-B radiation levels during spring that are far in excess of levels which prevailed prior to the present decade.

A conclusion that can be derived from the studies of Frederick *et al.* (1989) and from the numerous studies of spatial variability of air pollutants and their deposition patterns is that average values of a stochastic parameter across geographic areas is inappropriate, does not consider spatial variability and the uncertainties attached to masking such variability or geographic patchiness. Nevertheless, changes in global surface temperature have been estimated to be +0·7°C over the past 140 years (Fig. 6) and between +1·5 and +4·5°C from the 19th to the 21st century (Wuebbles *et al.*, 1989). This increase in temperature is considered to be due to increased radiation and/or to increased trapping of the infrared re-radiation from the earth's surface by the increasing concentrations of tropospheric gases, for example, CO_2 (Table 2 and Fig. 7). In this context different tropospheric gases vary in their characteristics relative to climate warming. For example, CH_4 is considered to be 15–30 times more effective than CO_2.

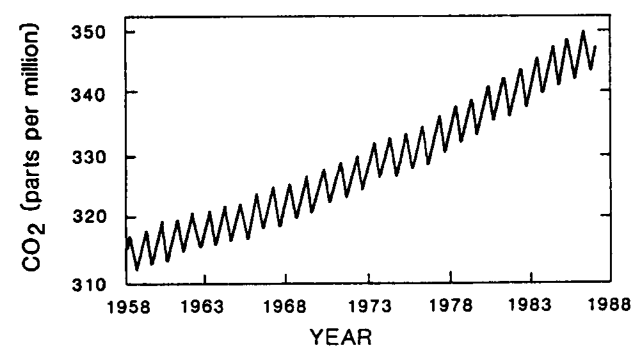


Fig. 7. Observed increase in atmospheric CO_2, resulting largely from human activities. (Source: NASA, Washington, DC 1988).

At the present time, tropospheric CO_2 concentrations are predicted to double (600 ppm) in the 21st century, CH_4 concentrations are increasing at an annual rate of 1–2%, and N_2O by about 0·3% per year (Table 2).

It is most interesting to note that a predominant number of publications, in addition to using average values for most parameters, thus removing geographic patchiness or variability, use the data base for tropospheric CO_2 concentrations, from Mauna Loa, Hawaii. This is because Mauna Loa appears to be the only site where sufficient long term CO_2 data have been gathered. Recent measurements (1985–87) at Fortress Mountain, Alberta, Canada, a background high elevation (2100 m) site, show 345–350 ppm annual, 1 h average CO_2 concentrations (Legge & Krupa, 1989). These data also show daily variability with high CO_2 concentrations at night and lower concentrations during the day. The authors attribute this variation to vegetation acting as a sink during the day. During the day there is vegetational CO_2 uptake through photosynthesis and during night there is CO_2 release through respiration. Thus, global patchiness of vegetation and other sinks must be considered in evaluating global scale tropospheric CO_2 values, for that matter all other air pollutants.

Using average values, global air temperature appears to have increased by roughly 0·7°C over the past 140 years (Fig. 6). Some problems associated with these data include: (a) uncertainties attached to the historical data base of air temperatures over oceans, where measurement methods have changed over the years and the correction factors are in question, and (b) location of many land-based measurement devices in or close to urban centers (heat islands) rather than in rural settings (Watt, 1987, 1989). These types of uncertainties have resulted in controversy concerning global warming. Equally of concern is to separate natural geophysical–chemical cycles, an integral part of the earth, versus any observed and/or perceived changes in the global climate due to anthropogenic influences.

A disturbing aspect to any predictions of global climate change is the use of one, or two, rather than three-dimensional circulation models. Certainly the application of three-dimensional models is limited by the present day availability of computer power. Global change predictions are based on general circulation models (GCMs) of similar geographic magnitude. Of additional concern is the fact that many of these models have not considered cloud forcing. Recent studies on cloud forcing based on the Earth Radiation Budget Experiment (ERB) show atmospheric cooling over North America (Ramanathan *et al.*, 1989). Clouds appear to have a net cooling effect globally of about four times as much energy as would be trapped by doubling CO_2 levels. In mid and high latitudes, the net cooling from clouds is large, but over the tropics, their cooling is nearly cancelled by heating. In fact, Watt (1987) provides evidence that, over the last four decades, the northern hemisphere summer climate has been *cooling* and is strongly correlated with diminished forest growth. Given this evidence, the popular acid precipitation hypothesis, as the causal factor for 'forest decline', does not seem tenable.

The preceding discussion can be summarized as follows, relative to North America:

(a) there might be a *decrease* in the stratospheric O_3 column (1–3%), However, there appears to be an *increase* in tropospheric O_3 concentrations (1–2% per year), this might be sufficient to compensate for up to 20–30% loss in the total O_3 column (Logan, 1985);
(b) there appears to be an *increase* in tropospheric concentrations of CO_2, N_2O, and CH_4 at the rate of roughly 0·8, 0·3 and 1–2%, respectively, per year (Wuebbles *et al.*, 1989);
(c) there is a *decrease* in erythemal UV-B radiation (Frederick *et al.*, 1989); and
(d) there is a *cooling* of tropospheric air temperature due to radiative cloud forcing (Ramanathan *et al.*, 1989).

THE GREENHOUSE EFFECT: AN ASSESSMENT

It is noteworthy that Malone & Roederer (1985) in their book to promote the establishment of an International Geosphere–Biosphere Program, included no sections which identified as important the specific processes involved in: (1) the possible impacts of enhanced ground-level UV-B radiation on vegetation and/or (2) the effects of tropospheric air pollutants *per se* on vegetation. This is a glaring omission in the light of the amount of scientific literature produced in these fields.

In the same book, Clark & Holling (1985) identified the situation which appears to be applicable to the two aforementioned research areas:

> [Most policy studies examine individual environment–development interactions in isolation. One study examines acidic deposition, a second study, greenhouse effects and a third, soil degradation. (To this list we might add: UV-B radiation effects on vegetation.) But it has become abundantly clear that these 'problems' are, in fact, tightly coupled syndromes in need of simultaneous analysis. They are linked through specific development policies and activities (as well as by the connections between the environmental processes) that are the

common cause of a variety of environmental perturbations, for instance the fossil fuel energy policies that affect both greenhouse gases and acidic deposition. In addition, individual 'problems' are linked through subtle ecological, climatic and economic interactions.

...The time is ripe to construct a rigorous synoptic perspective from which these policy and environmental linkages of individual development choices can be better understood, ranked and managed.]

The use of the term 'greenhouse effect' to describe the heating of the atmosphere due to the increasing levels of tropospheric air pollutants might be inappropriate. The term is, in a sense, an implied 'model' pertaining to a specific ground level micrometeorological pattern which is inappropriately applied to the free atmosphere.

To understand this, one should consider the three major processes by which heat can be transferred from one location to another. Heat can be transferred *radiatively* through open space whether or not there is any matter (such as air) in that space. Radiative heat as a portion of the electromagnetic spectrum can be portrayed as being distributed across various wavelengths. In general, the wavelength is dependent upon the temperature of the radiating body. The sun radiates energy at short wavelengths, while the much cooler earth capturing this radiation from the sun re-radiates energy at long wavelengths. Heat can also be transferred *convectively* such as when hot air rises physically and is replaced by cooler air to maintain conservation of matter. *Conduction* is another process by which heat is transferred from a warmer body to a cooler body, and takes place only at the interface between the two bodies. Heat can also be transferred by *phase change* between physical states of matter such as when water evaporates or condenses, but this form of heat transfer, as well as conduction, is not immediately relevant in the present argument.

In a greenhouse, some of the incoming short wavelength solar radiation is absorbed by various surfaces (growth tables, floor, walls, etc.) and is subsequently: (1) re-radiated within the greenhouse as long wavelength radiation, (2) conducted to the air layer immediately adjacent to surfaces within the greenhouse, and (3) convectively circulated in the air within the greenhouse. Of course, if the greenhouse has no open windows or other circulation systems with the outside air, heat transfer by *convection* and *advection* of the moving air within the greenhouse is very limited. As a result, the air temperature and the surface temperatures of objects rise within the greenhouse, compared to the ambient, to a level at which the greenhouse heat is being lost to the outside primarily and relatively slowly through re-radiation of long wavelength radiation and through conduction into the floor and foundation. The key to the heating of the greenhouse by strictly solar radiation is found in the physical barriers of the roof and walls preventing heat transfer (loss) by convection and advection. This is a different set of processes than the heating of the free atmosphere.

In the atmosphere, gases such as O_3 and also water vapor selectively absorb incoming short wavelength solar radiation, and concurrently re-radiate heat energy through long wavelength radiative transfer. There is no physical barrier to prevent convective and advective heat transfer in the atmosphere as there is in a greenhouse. Here, the key to more heating of the atmosphere is a higher concentration of substances that absorb incoming solar radiation and outgoing long wavelength radiation from the earth, and then re-radiate that energy within the atmosphere. The greenhouse gets hotter because of restricted convection and advection; the atmosphere gets warmer because of increased re-radiation of energy. These are two different processes. Therefore, the use of the term 'greenhouse effect' implies the wrong order of importance of heat transfer processes when used to describe the warming of the free atmosphere. If there is an environmental situation which is, or might, present a 'problem', it is inappropriate in the search for a solution, to portray the situation with an incorrect conceptual model. A few years ago, similar criticisms were given by Kimball & Idso (1983), and Walter Orr Roberts (reprinted in Hoffman, 1984).

Although a custom has been established to use the term 'greenhouse effect', for a simple conceptual model that represents the processes, it is perhaps more appropriate to think in terms of an *'atmospheric re-radiative effect'*. Whether in the outside air, or inside a building, as more people huddle closely together, the warmer they will feel up to a point, compared to individuals standing alone, because they are re-radiating heat with each other. The only place where one will find the 'greenhouse effect' is in a greenhouse, or in a parked automobile with windows and doors closed, or some other similarly enclosed space that allows solar radiation to transfer inside while the heated air is unable to escape.

In addition, the so-called 'greenhouse effect' in concept does not include the issue of stratospheric O_3 depletion and consequent predicted increase in the transmission of solar UV-B radiation to the earth surface.

Typically, the 'greenhouse effect' refers only to climatic warming. For the most part, so also does the concept of 'climate change'. The latter concept should be used to refer to more than just the change in air temperature. It ought to also include (1) tropospheric CO_2 increase, (2) the possible increase in UV-B radiation at the ground level as a result of a decrease in stratospheric O_3, and (3) changes in tropospheric trace gases. All of these processes, to the extent that they exist at a given geographic location, are a part of the climate (Fig. 2). Unfortunately, almost always 'climate' is used as an undefined concept by scientists investigating the vegetation effects of some aspect of climate. Far too many authors implicitly seem to think that climate is *only* air temperature and precipitation, when in reality they should use a more dynamic and comprehensive concept of climate such as that described by Terjung (1976). While the criticism of Terjung was directed at geographers, it could just as well be directed toward almost all investigators of today, involved in analyzing the vegetation effects of temperature and moisture conditions, phytotoxic air pollutants, solar radiation, PAR (photosynthetic active radiation), UV-B and CO_2. Many scientists attempting to analyze the expected responses of agricultural and/or native ecosystems to postulated climatic changes have paid little attention to physical climatology and meteorology.

This situation leads to the unfortunate use of concepts such as the Holdridge Life Zones Geographical Model as the basis for studies, for example by Emanuel *et al.* (1985), and then repeated by others (Pollard, 1985; Parry & Carter, 1986; Warrick *et al.*, 1986). Such an approach is misleading because among others, Gates (1962), Terjung (1968), Lowry (1969), Terjung & Louie (1972) and Terjung (1976) have shown that climate must be viewed in terms of the radiation and heat energy balances, as well as the moisture balance, in the context of the earth's surfaces, including vegetation. Air temperature and precipitation are simply atmospheric responses to these energy and mass flow systems.

Another problem is that the concept of 'Global Change' relies heavily on the idea of averaging data. This concept ignores geographic patchiness and spatial variation. It is analogous to the use of long-term average values of air pollutant concentrations to examine vegetation effects, ignoring the temporal episodicity of pollutant exposure. In doing so, this approach ignores much of the information that is important in examining plant response (Krupa & Kickert, 1987; Lefohn & Runeckles, 1987).

The idea of global change in 'climate' is governed by the limitations of computer technology used to run General Circulation Models (GCMs) for projecting possible climatic changes. Current computer technology limits these models to one or two spatial dimensions if many atmospheric processes are included, or to three dimensions at a very crude spatial resolution if certain processes related to the oceans and temporal cloud dynamics are excluded. When GCMs can be run in three-dimensions with all the necessary processes included at a scale approaching the density of first-order weather stations, then we are likely to examine regional geographic variation and not focus so strongly on global change. Modelers of watershed hydrology have gone through this same evolution on a smaller scale. Many watershed models 20 years ago were 'lumped', they considered an entire watershed as a single point, very similar to the implications of the concept of 'global change' today. Subsequently, watershed models were designed on a 'distributed', rather than 'lumped' basis, wherein each slope facet of a watershed was explicitly identified and simulated, with its hydrological processes cascading into streamflow for the watershed as a functioning entity.

Even though at the present time, the GCMs do not generally include certain critical processes such as cloud radiative forcing, the processes included in such models are computed deterministically rather than stochastically. In environmental management today, it is commonly accepted that the best computer simulation models are those designed to show responses probabilistically. This allows the decision makers an opportunity for risk analysis.

For example, daily weather forecasts state: there is a '*x*' % chance of rain in a given geographic area on a given day. In comparison, the results of GCMs *are not* stated as: for example, over the next '*x*' number of years, there is a '*y*' % chance that the global surface air temperature will increase by '*z*'°C. Instead, by implication alone, it is being stated that there is a 100% chance that the global climate is warming. We wonder how many climatologists can make this type of a deterministic statement about the weather several days hence for a typical geographic location.

METHODOLOGY FOR THE ASSESSMENT OF UV-B, O_3, AND CO_2 EFFECTS ON PLANTS

In this section only a very brief discussion of the methods available for studying the effects of UV-B, O_3, and CO_2 on plants is provided. Readers requiring further details should consult the references provided in the appropriate tables or the text in this section.

Ultraviolet-B

The measurement and physical simulation of UV-B radiation in the growth chamber, greenhouse or under ambient field conditions is not a straightforward process. Table 4 provides a summary of methods used for examining the effects of UV-B on plants. The general principle in the experiments to determine the effects of UV-B on plants involves the use of a UV source (a lamp) coupled with different types of filters to exclude bands of UV wavelength not desired in the experiment (Worrest & Caldwell, 1986). The intensity of UV is varied by changing the height distance between the lamp source and the plant canopy.

TABLE 4
Summary of Methods used to Determine the Effects of UV-B on Plants

Methods	*References*
Greenhouse	
UV lamps and selective wavelength filters	Dumpert & Knacker (1985)
Westinghouse FS-40 sun lamp frames with cellulose acetate or Mylar type S filters	Mirecki & Teramura (1984)
Growth chamber	
UV-B lamps, simulated PAR (photosynthetic active radiation) and selective wavelength cut-off filters	Tevini & Iwanzik (1986)
Field exposure	
FS-40 sun lamps coupled with Aclar, Mylar and cellulose acetate filters	Becwar *et al.* (1982) Lydon *et al.* (1986)
Modulated fluorescent lamp system for supplementing natural UV-B	Caldwell *et al.* (1983*a*)

In earlier ambient field studies Robertson-Berger radiation meters (Berger, 1976) were used to monitor UV-B levels. These instruments were designed for measuring wavelengths critical in causing sunburn to human skin, rather than for measuring wavelengths important in plant physiological processes. Further, the Robertson-Berger meters do not provide spectral data for individual wavelengths. Recently, Killick *et al.* (1988) described a polysulphone device for monitoring ambient UV-B at remote field sites, but as with the Robertson-Berger meter, the spectral sensitivity of this device is closer to the erythemal action spectrum of the human skin. In addition, the polysulphone film provides an integrated dose (not the spectral distribution of UV-B) only. Killick *et al.* (1988) did not provide sufficient data of field tests to quantify the measurement uncertainty expected with the use of their method.

Many studies have also used a spectroradiometer (Gamma Corporation, USA) or a double holographic grating spectroradiometer (Optronics, USA) for monitoring the spectral distribution of the incoming UV-B.

Because different biological processes exhibit different degrees of sensitivity to different wavelengths of UV-B, a mathematical response function, the *action spectrum*, must be used as a weighting factor to adjust the measured UV-B flux. Gerstl *et al.* (1981), Caldwell (1982*b*), Rundel (1983), Caldwell *et al.* (1986), and Bjorn *et al.* (1986) have described the various considerations relevant to the use of action spectra. Nachtwey & Rundel (1982) discussed the various problems and sources of uncertainties in calculating biologically effective UV-B flux (UV-B(BE)) and for the concept of dose, refer to de Gruijl *et al.* (1986).

TABLE 5
Summary of Methods used to Determine the Effects of Ozone on Plants

Methods	*References*
Controlled environments	
Modified greenhouses	Darley & Middleton (1961) Menser *et al.* (1966)
Modified growth chambers	Wood *et al.* (1973)
Experimental chambers (used in greenhouses or growth chambers)	
Rectangular chambers	Heagle & Philbeck (1979)
Round chambers e.g., Continuous Stirred Tank Rectors (CSTRs)	Heck *et al.* (1978)
Field exposure systems	
Open-air chamberless systems	
Linear gradient systems	Laurence *et al.* (1982)
Zonal air pollution systems (ZAPS)	Lee & Lewis (1978)
Field chamber systems	
Closed chambers, greenhouses	Thompson & Taylor (1969)
Open-top chambers, up-draft chambers	Heagle *et al.* (1973, 1979), Lee (1985)
Down-draft chambers	Runeckles *et al.* (1978)
Field plots in ambient air	
Natural ozone concentration gradients	Oshima *et al.* (1976)
Cultivar comparisons	Heggestad (1973), Manning *et al.* (1974), Rich & Hawkins (1970)
Protective chemicals	Carnahan *et al.* (1978) Manning *et al.* (1974)
Long-term growth reduction measurements	Miller (1983), Peterson *et al.* (1987), Skelly *et al.* (1983)

(From Krupa & Manning, 1988).

Ozone

The methods used to study the effects of O_3 on plants range from controlled environments to field exposure systems to field plots in ambient air. Information on these methods is summarized in Tables 5 and 6, and reviewed elsewhere (Heagle & Philbeck, 1979; Heagle *et al.*, 1979; Krupa, in Lee, 1985; Hogsett *et al.*, 1987*a,b*; Krupa & Nosal, 1989*a*).

Experimental exposure and ambient O_3 concentrations can be measured by using automated monitors. The most frequently used instruments of today are based on the principle of chemiluminescence or UV-photometry.

TABLE 6
Comparative Advantages and Disadvantages of some Field Assessment Methods of O_3 Exposure and Crop Response

Method	*Advantage*	*Disadvantage*
(1) Open-top chambers (up-draft)	(a) Most widely used system in the US; some 15 years of historical records.	(a) Artificial chamber effect on plant growth and productivity present.
	(b) Many crops can be grown to maturity under conditions somewhat analogous to the ambient.	(b) High cost for including sufficient number of treatments and labor intensive.
	(c) Effects of air pollutants can be evaluated singly or as mixtures.	(c) Complex computer controlled system required to mimic ambient pollutant exposure dynamics within the chamber.
	(d) Comparisons can be made between filtered (80% pollutant removal) and unfiltered ambient air.	(d) Pollutant flow within the chamber artificial and not similar to the ambient.
	(e) Reasonable control on environmental variables within the chamber.	(e) Modifications in the microclimate within the chamber can lead to altered incidence of pathogens and pests.
		(f) Rain shadows present.
		(g) Is subject to weather hazards, including incursion of ambient air into the chamber at times.
(2) Open-top chambers (down-draft)	(a) Same as (b), (c), (d), and (e) of No. (1).	(a) Same as (a), (b), (c), and (e) of No. (1).
	(b) Pollutant flow more realistic, top of the plant canopy downward.	(b) O_3 exclusion from the ambient air entering the chamber varies from 25% to 70%.
		(c) Ambient rain is excluded.
		(d) As with No. (1), is subject to weather hazards.
(3) Open-air, chamberless, artificial field exposure	(a) No chamber effect	(a) Small changes in wind turbulence can cause large changes in O_3 concentrations.
	(b) Large number of plants can be exposed to varying O_3 exposure regimes.	(b) High precision in a feed-back control of O_3 release and intensive and extensive monitoring of O_3 within the study plot required.

(continued)

TABLE 6—*contd.*

Method	*Advantage*	*Disadvantage*
(3) Open-air, chamberless, artificial field exposure *cont.*	(c) Desirable approach if (b), (d), and (e) under the disadvantages are rectified.	(c) Control, study plot difficult to deal with due to the omni-presence of O_3. (d) Intensive and extensive monitoring of other air pollutants and environmental variables required. (e) Powerful, multivariate, time series models required to fully evaluate the results.
(4) Natural gradients of ambient O_3	(a) Evaluation of the real world situation.	(a) Sufficient number of treatments (varying O_3 exposure regimes) within a small geographic area required.
	(b) High degree of replication possible.	(b) O_3 and other pollutants, and environmental variables must be intensively monitored at each site. (c) Variability due to the influence of soil must be accounted, unless standardized soil is used at all study sites. (d) Same as (e) of No. (3). (e) Year to year variability in O_3 exposure and crop response must be accounted.
(5) Chemical protectants (anti-oxidants)	(a) Close to the real world.	(a) Effect of the protectant itself on plant growth and yield possible; thus prior testing required.
	(b) High degree of replication possible.	(b) The amount of protection provided by different chemical doses on different plant species not fully understood. (c) Same as all others listed under No. (4).
(6) Cultivar screening	(a) Closest to the real world	(a) Differences in the chronic responses of cultivars to O_3 exposures must be known.
	(b) No chambers, no chemical protectants.	(b) Same as (b), (d), and (e) listed in No. (4).

From Krupa & Nosal (1989*a*).

Similarly, O_3 can be dispensed in artificial O_3 exposure studies through electric arc or UV-O_3 generators. In these generators either O_2 or dry compressed air is used to produce the O_3. Harris *et al.* (1982) and Kogelschatz & Baessler (1987) have shown that the use of compressed air results in the production of contaminating gases such as N_2O_5, in addition to the O_3. Therefore, it is desirable to use O_2, rather than the compressed air, for the generation of O_3 through either technique.

The ambient O_3 exposure dynamics and flux are inherently stochastic in nature. The frequency distributions of ambient O_3 concentrations appear to be best described by a mathematical function of the Weibull family (Lefohn & Benedict, 1982; Nosal, 1983). Field O_3 exposure studies in general have used exposure patterns which are dissimilar to the ambient characteristics. Thus, results obtained from many field studies (refer to Heck *et al.*, 1988; *Environ. Pollut.*, 1988) have been the subject of much debate (Lefohn *et al.*, 1989). To address this issue, Nystrom *et al.* (1982) developed the first computer controlled field exposure system to simulate the ambient O_3 exposure patterns. This approach, however, has proven to be expensive and labor intensive.

There is little question that this overall issue will continue to be controversial until satisfactory and widely accepted methodologies are developed for: (a) artificial exposures which simulate a variety of ambient scenarios; and (b) models that explain cause and effect relationships under ambient conditions (Krupa & Nosal, 1989*a*,*b*; Runeckles & Wright, 1989). For a general treatment of the subject, the reader is referred to Krupa & Kickert (1987) and Lefohn & Runeckles (1987).

Carbon dioxide

In both controlled and field exposures CO_2 concentrations can be monitored reliably with a non-dispersive infrared analyzer (e.g. Anarad, USA). There are also double beam, differential measurement units (e.g. Analytical Development Company, England) where a dual infrared beam is used to analyze the sample air stream against a reference air stream. There appear to be no detection problems in measuring CO_2 concentrations under ambient conditions.

As with O_3, vegetation exposure studies with CO_2 have been performed in growth chamber, greenhouse and field conditions (Table 7). Rogers *et al.* (1983*c*) described a field technique for the study of plant responses to elevated CO_2 concentrations, using open-top chambers (Table 5) and ambient field plots. In such studies tanks of liquid CO_2 were used to generate large volumes of that gas required for artificial exposures. Shinn & Allen (1985) described a free-air carbon dioxide enrichment (FACE) field method

TABLE 7
Advantages and Disadvantages of the Methods used to Study the Effects of CO_2 on Plants

Method	*Advantage*	*Disadvantage*
Leaf Chamber	Single-leaf gas exchange kinetics obtainable.	No whole plant response such as growth; natural environment difficult to duplicate.
Phytotron	Create and control many desired environments; repeat experiments; many environmental conditions possible; biological factors controlled.	Difficult to extrapolate to natural conditions; environmental factors usually constant; plant size limitations; less than sunlight.
Portable Chambers	Small, inexpensive to build; can be used with either natural sunlight or artificial light.	Same as for most controlled environments.
Sunlit Controlled Environments (e.g., SPAR)	High light, similar to natural irradiance; variable conditions; integrated estimates of carbon and water balance; root zone similar to field; same advantages as phytotron.	Complex control; chamber effects (humidity, temperature, wind gradients); limited replication usually.
Greenhouse	Present data base on CO_2 large; natural sunlight.	Difficult to maintain (CO_2) under some conditions; difficult to extrapolate results to the field.
Field Tracking Chamber	Permits study of natural vegetation; track natural variation in the environment; whole ecosystem effects; integrated estimates of carbon and water balance.	Complexity of control functions in a remote setting; possible chamber effects.
Open Top Chambers	Can be used to study crops and natural vegetation *in situ*; natural sunlight; closely approximates natural environment; ease of establishing elevated CO_2 concentrations.	Gradients in humidity and wind produce chamber effects; growth differs inside from outside; many sample chambers needed to deal with natural variability of ecosystems.
FACE	Closest to natural environmental conditions.	Technical feasibility; strong gradients in CO_2 in windy conditions; large sample areas needed; cost is high for large vegetation.

From Strain & Cure (1985).

for investigating the direct effects of CO_2 on plants. These authors suggested coal gasification facilities as sources for a large supply of CO_2 required in the exposures.

A number of investigators have described process oriented (mechanistic) and statistics oriented (empirical) numerical approaches to relate CO_2 exposures and plant response. Relevant literature on this subject can be found in Kimball (1983*a*), Lemon (1983), Dahlman (1985), Strain & Cure (1985) and Enoch & Kimball (1986).

A summation

With regard to possible warming or cooling of the climate, while the effects of high and low temperatures on plant growth have been studied for many years, such studies have been limited to controlled experiments (growth chambers and greenhouses). Retrospective analyses can be performed on data collected from ambient field sites subjected previously to a season of exceptional heat or cold. However, the ability to design and conduct regulated experiments in the ambient field setting under increased heating or cooling, together with other factors such as enhanced UV-B, CO_2, and O_3, to study their joint effects on plant growth, appears to be technically impossible at the present time. While there are methods to enhance or deplete UV-B, increase CO_2 and O_3 in the atmosphere, we know of no method to do this for heating or cooling the ambient air in regulated steps (to physically simulate 'climate change') and with desired precision, over open-field study plots.

At least in North America, over the past 20 years, with some individual exceptions, scientists investigating the effects of O_3 on plants have neither worked nor held joint technical conferences to exchange information with others who have studied the effects of enhanced UV-B radiation on plants. In addition, neither of these groups has developed sufficient communication with the scientists examining the effects of increased CO_2 concentrations on plants. We know of only one investigator who has addressed all three research areas (Allen *et al.*, 1978*a*,*b*,*c*; Allen, 1989). It is surprising to note the isolationism these three research groups have demonstrated so far. We encourage researchers in each of the study areas to seek ways to come together and perform integrated research.

In the following sections, we discuss the effects of enhanced UV-B radiation, increasing ambient concentrations of CO_2 and O_3 on plants. In the discussion presented in each section, we have attempted to consider the needs of researchers in the other two groups. Scientists reading the section on the topic area of their specialty might not find as much new information as they should, compared to the sections on the other two environmental factors. The main thrust of this paper is to seek comparisons and integration among the three sets of information, particularly in the context of geophysical changes considered to be occurring in the atmosphere.

For the Latin nomenclature of the common names of plants used in the following sections, the reader is referred to the Appendix.

EFFECTS OF UV-B RADIATION ON PLANTS

Much concern has been raised recently about stratospheric O_3 depletion and the possible consequences of enhanced UV-B radiation at the earth's surface on agricultural and wildland ecosystems.

Solar UV-B radiation as a portion of the electromagnetic radiant energy spectrum is often characterized by wavelength. It has become an accepted practice to consider UV-A as the band width between 400–320 nm, UV-B as the band width between 320–280 nm, and UV-C as band width <280 nm. Generally, UV-C does not reach the earth's surface because of the absorption properties of the upper atmosphere, and this is not expected to change regardless of possible alterations in the stratospheric O_3 column. The intensity and temporal patterns of UV-A radiation are also not expected to be altered by possible changes in stratospheric O_3, and plants do not appear to be sensitive to this waveband in the same way as they are to UV-B. Because of the sensitivity of many plant species to UV-B radiation, much research has been directed to this issue in growth chambers, greenhouses and ambient field plots over the past 20 years. Extensive reviews of the relevant research can be found in Caldwell (1968; 1971; 1974; 1977; 1979; 1981; 1982*a*), Nachtwey & Rundel (1982), National Research Council (1982*a*; 1984*a*,*b*), Teramura (1983; 1986*a*,*b*,*c*) and Dudek & Oppenheimer (1986).

Two large and significant research programs were completed in the USA during the early and mid-1970s. Fear of possible climatic effects of emissions from high-flying supersonic aircraft led to the research as reported by the Climatic Impact Assessment Program (CIAP) and summarized by Caldwell (1974). Within a short time thereafter, fear of possible effects of chlorofluorocarbons on stratospheric O_3 led to the research and reports from the Biological and Climatic Effects Research (BACER) Program (Biggs & Kossuth, 1978*a*–*f*).

Types of physiological and morphological responses

Table 8 organized after Teramura (1983), and updated through 1988, lists the physiological and morphological responses which have been studied and by whom. Photosynthesis was found to be sensitive to increased UV-B radiation in many studies. Stomatal resistance for water loss through

TABLE 8
Ecological Effects of Increased UV-B Radiation on Plant Growth
(Partially from Teramura (1983), and updated to 1988)

Photosynthesis
Bartholic *et al.* (1975)
Biggs *et al.* (1975)
Garrard & Brandle (1975)
Sisson & Caldwell (1975)
Thai & Garrard (1975)
Sisson & Caldwell (1976)
Van & Garrard (1976)
Van *et al.* (1976)
Bogenrieder & Klein (1977)
Brandle *et al.* (1977)
Caldwell (1977)
Garrard *et al.* (1977)
Sisson & Caldwell (1977)
Van *et al.* (1977)
Allen *et al.* (1978*b*)
Basiouny *et al.* (1978)
Bennett (1978)
Bogenrieder & Klein (1978)
Sisson (1978)
Teramura *et al.* (1980)
Bennett (1981)
Caldwell (1981)
Sisson (1981)
Teramura (1981)
Teramura & Caldwell (1981)
Tevini *et al.* (1981*b*)
Vu *et al.* (1981)
Bogenrieder (1982)
Bogenrieder & Douté (1982)
Bogenrieder & Klein (1982*b*)
Caldwell (1982*b*)
Caldwell & Warner (1982)
Caldwell *et al.* (1982)
Iwanzik & Tevini (1982)
Renger *et al.* (1982)
Sisson (1982)
Teramura & Perry (1982)
Vu *et al.* (1982*a,b*)
Robberecht & Caldwell (1983)
Rundel (1983)
Warner & Caldwell (1983)
Mirecki & Teramura (1984)
National Research Council (1984*a*)
Teramura *et al.* (1984*c*)
Vu *et al.* (1984)
Flint *et al.* (1985)
Björn *et al.* (1986)
Caldwell *et al.* (1986)
Iwanzik (1986)
Lydon *et al.* (1986)
Murali & Teramura (1986*b*)
Murali & Teramura (1986*c*)
Sisson (1986)
Sullivan & Teramura (1987)
Teramura & Sullivan (1987)
Usmanov *et al.* (1987)

Dark Respiration
Sisson & Caldwell (1976)
Brandle *et al.* (1977)
Biggs & Kossuth (1978*d*)
Teramura *et al.* (1980)
Teramura & Perry (1982)

Stomata (*resistance/conductance*)
Sisson & Caldwell (1975)
Sisson & Caldwell (1976)
Brandle *et al.* (1977)
Bennett (1978)
Biggs & Kossuth (1978*d*)
Teramura *et al.* (1980)
Bennett (1981)
Teramura (1982)
Teramura & Perry (1982)
Teramura *et al.* (1982, 1983, 1984*a*)
Tevini *et al.* (1983*b*)
Mirecki & Teramura (1984)
Flint *et al.* (1985)
Björn *et al.* (1986)
Murali & Teramura (1986*b*)
Negash & Björn (1986)
Tevini & Iwanzik (1986)
Negash (1987)
Sullivan & Teramura (1987)

Leaf area
Ambler *et al.* (1975)
Caldwell *et al.* (1975)
Sisson & Caldwell (1975)

(continued)

TABLE 8—*contd.*

Leaf area cont.	Kossuth & Biggs (1979)
Krizek *et al.* (1976)	Biggs *et al.* (1981)
Sisson & Caldwell (1976)	Teramura & Caldwell (1981)
Caldwell (1977)	Teramura & Perry (1982)
Sisson & Caldwell (1977)	Vu *et al.* (1982*a,b*)
Basiouny *et al.* (1978)	Murali & Teramura (1985*a*)
Biggs & Kossuth (1978*a,b,d*)	Latimer & Mitchell (1987)
Dickson & Caldwell (1978)	Murali *et al.* (1988)
Fox & Caldwell (1978)	
Krizek (1978*a*)	*Leaf discoloring (chlorosis, bronzing, glazing)*
Lindoo & Caldwell (1978)	Krizek & Semeniuk (1974)
Vu *et al.* (1979)	Ambler *et al.* (1975)
Teramura (1980)	Krizek (1975)
Biggs *et al.* (1981)	Wiebe & Caldwell (1975)
Kossuth & Biggs (1981*a,b*)	Krizek *et al.* (1976)
Shomansurov (1981)	Allen *et al.* (1978*a,c*)
Sisson (1981)	Basiouny *et al.* (1978)
Teramura & Caldwell (1981)	Biggs & Kossuth (1978*a,b,d*)
Tevini *et al.* (1981*a,b*)	Krizek (1978*a,b*)
Bogenrieder & Klein (1982*a*)	Robberecht & Caldwell (1978)
Dumpert & Boscher (1982)	Semeniuk (1978)
Teramura & Perry (1982)	Kossuth & Biggs (1979)
Teramura *et al.* (1982)	Semeniuk & Stewart (1979*a,b*)
Tevini *et al.* (1982*a,b,c*)	Vu *et al.* (1979)
Vu *et al.* (1982*a,b*)	Hashimoto & Tajima (1980)
Webb (1982)	Teramura *et al.* (1980)
Teramura *et al.* (1983)	Bennett (1981)
Tevini *et al.* (1983*a,b*)	Biggs *et al.* (1981)
Dumpert & Knacker (1985)	Tevini *et al.* (1981*a*)
Elawad *et al.* (1985)	Basiouny (1982)
Murali & Teramura (1985*a*)	Caldwell *et al.* (1982)
Rumayor (1985)	Semeniuk (1982)
Inagaki *et al.* (1986)	Vu *et al* (1982*a,b*)
Lydon *et al.* (1986)	Teramura *et al.* (1983)
Murali & Teramura (1986*a*)	Dumpert & Knacker (1985)
Murali & Teramura (1986*b*)	Jolley *et al.* (1987)
Murali & Teramura (1986*c*)	Rangarajan & Tibbitts (1988)
Latimer & Mitchell (1987)	
Murali & Teramura (1987)	*Pollen/reproduction potential*
Teramura & Sullivan (1987)	Caldwell (1968)
Barnes *et al.* (1988)	Biggs & Basiouny (1975)
Murali *et al.* (1988)	Campbell *et al.* (1975)
Rangarajan & Tibbitts (1988)	Chang & Campbell (1976)
	Usmanov *et al.* (1980)
Specific leaf weight	Usmanov & Usmanova (1980)
Biggs & Kossuth (1978*a*)	

TABLE 8—*contd.*

Pollen/reproduction potential cont.

Lukina (1983)
Flint & Caldwell (1984)
National Research Council (1984*a*)

Seedling growth/stunting or height growth effects

Brodfuehrer (1956)
Ambler *et al.* (1975)
Biggs & Basiouny (1975)
Biggs *et al.* (1975)
Caldwell *et al.* (1975)
Krizek (1975)
Sisson & Caldwell (1975)
Krizek *et al.* (1976)
Sisson & Caldwell (1976)
Brandle *et al.* (1977)
Basiouny *et al.* (1978)
Biggs & Kossuth (1978*a*)
Fox & Caldwell (1978)
Krizek (1978*a*)
Kossuth & Biggs (1979)
Vu *et al.* (1979)
Hashimoto & Tajima (1980)
Teramura (1980)
Biggs *et al.* (1981)
Kossuth & Biggs (1981*a*)
Shomansurov (1981)
Sisson (1981)
Teramura & Caldwell (1981)
Tevini *et al.* (1981*a,b*)
Vu *et al.* (1981)
Basiouny (1982)
Becwar *et al.* (1982)
Bogenrieder & Klein (1982*a*)
Prudot & Basiouny (1982)
Teramura & Perry (1982)
Tevini *et al.* (1982*b,c*)
Wellmann (1982)
Vu *et al.* (1982*a*)
Teramura *et al.* (1983)
Tevini *et al.* (1983*b*)
Vu *et al.* (1984)
Dumpert & Knacker (1985)
Elawad *et al.* (1985)
Murali & Teramura (1985*a*)
Spalding (1985)
Inagaki *et al.* (1986)
Tevini & Iwanzik (1986)
Teramura & Sullivan (1987)
Usmanov *et al.* (1987)
Barnes *et al.* (1988)
Lercari *et al.* (1988)
Sullivan & Teramura (1988)

Dry matter production, carbon allocation

Brodfuehrer (1956)
Krizek & Semeniuk (1974)
Ambler *et al.* (1975)
Biggs & Basiouny (1975)
Biggs *et al.* (1975)
Caldwell *et al.* (1975)
Hart *et al.* (1975)
Krizek (1975)
Krizek *et al.* (1976)
Sisson & Caldwell (1976)
Van & Garrard (1976)
Van *et al.* (1976)
Nakazawa *et al.* (1977)
Basiouny *et al.* (1978)
Biggs & Kossuth (1978*a,b,d*)
Fox & Caldwell (1978)
Halsey *et al.* (1978)
Krizek (1978*a,b*)
Kossuth & Biggs (1979)
Vu *et al.* (1979)
Hashimoto & Tajima (1980)
Teramura (1980)
Biggs *et al.* (1981)
Kossuth & Biggs (1981*a*)
Tevini *et al.* (1981)
Vu *et al.* (1981)
Basiouny (1982)
Bogenrieder & Klein (1982*a*)
Dumpert & Boscher (1982)
Teramura & Perry (1982)
Tevini *et al.* (1982*a,b,c*)
Webb (1982)
Biggs (1983)
Gold & Caldwell (1983)
Lukina (1983)
Teramura *et al.* (1984*c*)
Vu *et al.* (1984)

(*continued*)

TABLE 8—*contd.*

Dry Matter production, carbon allocation cont.	Semeniuk & Stewart (1979*b*)
Dumpert & Knacker (1985)	Maekawa *et al.* (1980)
Elawad *et al.* (1985)	Teramura (1980)
Murali & Teramura (1985*a*,*b*)	Teramura *et al.* (1980)
Inagaki *et al.* (1986)	Bennett (1981)
Iwanzik (1986)	Biggs *et al.* (1981)
Lydon *et al.* (1986)	Becwar *et al.* (1982)
Murali & Teramura (1986*a*)	Caldwell (1982*b*)
Murali & Teramura (1986*c*)	Caldwell & Warner (1982)
Teramura (1986*c*)	Nachtwey & Rundel (1982)
Tevini & Iwanzik (1986)	National Research Council (1982*a*)
Murali & Teramura (1987)	Teramura (1982)
Teramura & Sullivan (1987)	Tevini *et al.* (1982*b*,*c*)
Murali *et al.* (1988)	Vu *et al.* (1982*a*)
Sullivan & Teramura (1988)	Biggs (1983)
	Caldwell *et al.* (1983*b*)
	Rundel (1983)
Crop yield (incl. quality)	Warner & Caldwell (1983)
Bartholic *et al.* (1975)	Mirecki & Teramura (1984)
Hart *et al.* (1975)	National Research Council (1984*a*)
Lipton (1977)	Beggs *et al.* (1985)
Nakazawa *et al.* (1977)	Beggs *et al.* (1986)
Ambler *et al.* (1978*b*)	Björn *et al.* (1986)
Biggs & Kossuth (1978*c*)	Negash & Björn (1986)
Halsey *et al.* (1978)	Sisson (1986)
Kossuth & Biggs (1978)	Teramura (1986)
Lipton & O'Grady (1980)	Teramura & Murali (1986)
Kossuth & Biggs (1981*b*)	Latimer & Mitchell (1987)
Biggs *et al.* (1982)	
Prudot & Basiouny (1982)	*Interaction—Water Stress*
Webb (1982)	Teramura & Perry (1982)
Elawad *et al.* (1985)	Teramura *et al.* (1982)
Inagaki *et al.* (1986)	Tevini *et al.* (1982*a*)
Lydon *et al.* (1986)	Teramura *et al.* (1983)
Usmanov *et al.* (1987)	Tevini *et al.* (1983*a*)
Teramura & Sullivan (1988)	Teramura *et al.* (1984*a*,*b*,*c*)
	National Research Council (1984*a*)
Interaction—Visible Light (photorepair)	Elawad *et al.* (1985)
Caldwell (1968)	Murali & Teramura (1986*b*)
Caldwell (1971)	Murali & Teramura (1986*c*)
Bartholic *et al.* (1975)	Teramura (1986)
Caldwell (1974)	Sullivan & Teramura (1987)
Hart *et al.* (1975)	Barnes *et al.* (1988)
Sisson & Caldwell (1976)	
Van *et al.* (1976)	*Interaction—Nutrients*
Biggs & Kossuth (1978*d*)	Ambler *et al.* (1975)
Klein (1978)	Bartholic *et al.* (1975)

TABLE 8—*contd.*

Interaction—Nutrients cont.	*Interaction—Herbivory*
Bogenrieder & Douté (1982)	Gold & Caldwell (1983)
Prudot & Basiouny (1982)	National Research Council (1984*a*)
Tevini *et al.* (1982*c*)	
Murali & Teramura (1985*a,b*)	
Teramura (1986)	*Between-Species Sensitivity*
Jolley *et al.* (1987)	Brodfuehrer (1956)
Murali & Teramura (1987)	Caldwell (1968)
	Bartholic *et al.* (1975)
Interaction—Plant Temperature/ Heat/Cold Stress	Biggs & Basiouny (1975)
	Caldwell *et al.* (1975)
Brodfuehrer (1956)	Hart *et al.* (1975)
Lipton & O'Grady (1980)	Krizek (1975)
National Research Council (1984*a*)	Sisson & Caldwell (1975)
Renquist *et al.* (1987)	Thai & Garrard (1975)
	Van & Garrard (1976)
Interaction—Air Pollution	Van *et al.* (1976)
Wiebe & Caldwell (1975)	Bogenrieder & Klein (1977)
National Research Council (1984*a*)	Garrard *et al.* (1977)
	Van *et al.* (1977)
	Allen *et al.* (1978*a,b*)
Interaction—Enhanced CO_2	Ambler *et al.* (1978*a,b*)
(no publications found)	Basiouny *et al.* (1978)
	Bennett (1978)
Interaction—Inter-Species Competition	Biggs & Kossuth (1978*a,c*)
Caldwell & Nachtwey (1975)	Fox & Caldwell (1978)
Caldwell (1977)	Klein (1978)
Fox & Caldwell (1978)	Robberecht & Caldwell (1978)
Caldwell (1979)	Kossuth & Biggs (1979)
Caldwell (1981)	Vu *et al.* (1979)
Bogenrieder & Klein (1982*a*)	Hashimoto & Tajima (1980)
Nachtwey & Rundel (1982)	Teramura (1980)
Gold & Caldwell (1983)	Bennett (1981)
National Research Council (1984*a*)	Kossuth & Biggs (1981*a*)
Teramura (1986*c*)	Tevini *et al.* (1981*a,b*)
Barnes *et al.* (1988)	Basiouny (1982)
	Becwar *et al.* (1982)
Interaction—Plant Disease	Biggs *et al.* (1982)
Carns *et al.* (1978)	Bogenrieder (1982)
Semeniuk & Stewart (1981)	Bogenrieder & Klein (1982*a*)
Gold & Caldwell (1983)	Caldwell *et al.* (1982)
National Research Council (1984*a*)	Dumpert & Boscher (1982)
Biggs & Webb (1986)	Nachtwey & Rundel (1982)
Teramura (1986*c*)	National Research Council (1982*a,b*)
	Teramura *et al.* (1982)
Interaction—Pesticides	Tevini *et al.* (1982*a,b,c*)
Tevini & Steinmüller (1987)	Vu *et al.* (1982*a,b*)

(*continued*)

TABLE 8—*contd.*

Between-Species Sensitivity cont.	Bennett (1981)
Wellmann (1982)	Biggs *et al.* (1981)
Gold & Caldwell (1983)	Teramura (1981)
Teramura (1983)	Teramura & Caldwell (1981)
Tevini *et al.* (1983*a,b*)	Basiouny (1982)
Flint & Caldwell (1984)	Bogenrieder & Klein (1982*a*)
National Research Council (1984*a*)	Caldwell *et al.* (1982)
Dumpert & Knacker (1985)	Dumpert & Boscher (1982)
Steinmüller & Tevini (1985, 1986)	Semeniuk (1982)
Barnes *et al.* (1988)	Lukina (1983)
Sullivan & Teramura (1988)	National Research Council (1984*a*)
	Dumpert & Knacker (1985)
Within-Species Sensitivity	Lydon *et al.* (1986)
Ambler *et al.* (1975)	Murali & Teramura (1986*a*)
Biggs & Basiouny (1975)	Teramura & Murali (1986)
Biggs & Kossuth (1978*a,b*)	Teramura (1986*c*)
Krizek (1978*a,b*)	Usmanov *et al.* (1987)
Semeniuk & Stewart (1979*a,b*)	Murali *et al.* (1988)
Vu *et al.* (1979)	Teramura & Sullivan (1988)
Usmanov *et al.* (1980)	

transpiration and for CO_2 uptake were also found to be affected in a number of studies. There is some evidence that pollen viability, and hence reproduction potential, could be altered by enhanced UV-B. Many studies have shown a decrease in seedling height growth with enhanced UV-B. A number of studies have demonstrated a reduction in leaf area growth under enhanced UV-B. Studies of effects on dry matter production, plant carbon allocation and crop yield have often led to conflicting results depending upon whether the research was performed in a growth chamber, greenhouse or in an ambient field plot.

The most studied interaction of UV-B with another environmental variable, was with visible light, or photosynthetic photon flux density (PPFD). UV-B, whether natural or physically simulated, not only can exhibit different intensities, but also varying spectral composition within the 280–320 nm range. Artificial exposures of plants to some pattern of UV-B alone will often lead to greater negative effects on the plant, as in growth chamber studies, than when the experiment is performed with a simultaneous exposure to realistic intensities of photosynthetically active radiation (PAR) in the 400–600 nm range. PAR has been found to enable photo-repair processes to mitigate against the otherwise accumulating injury in the plant tissue.

Since the early 1980s some research has been conducted on UV-B interaction with plant moisture stress, and some studies have occasionally examined the possible interactions with plant nutrient dynamics.

It is of special interest to note that very little consideration has been given to possible vegetation effects from an interaction between enhanced UV-B radiation and exceptionally warm or cool conditions (e.g. global climate change), or the possible interaction between enhanced UV-B and tropospheric air pollutants. In all the literature reviewed, the only study that examined simultaneously UV-B and an air pollutant used hydrogen fluoride (Wiebe & Caldwell, 1975), not one of the more ubiquitous pollutants such as O_3. To complicate our perspective even more, we could find no studies on vegetation response to enhanced UV-B under increased CO_2. This is a surprising and unfortunate gap in the knowledge base considering the importance that society is attaching to the so-called 'Greenhouse Effect', thought to result in part from an increase in ambient CO_2.

Caldwell and his colleagues have been particularly active in studying the interaction between various plant species in mixed populations (Table 8) as plants compete for resources needed for growth, even when a given species necessarily did not show a reduction in biomass directly from exposure to enhanced UV-B.

The interaction of UV-B with plant diseases induced by biotic pathogens often leads to an advantage for the host plant as the pathogen is affected more than the host, by the exposure. In comparison, there are many reports of increased incidence of facultative parasites and decreased incidence of obligate parasites on plants due to O_3 exposures. It is believed that the effect of O_3 is mainly on the host.

The interaction of enhanced UV-B radiation with pesticide use and herbivory could be significant in agro-ecosystems, but is an almost unexplored research area (Table 8).

While there have been problems with developing the most realistic and reliable technology for physically simulating UV-B radiation under controlled experimental conditions, or altering the ambient natural UV-B radiation to achieve a range of treatments, there is an abundance of reports that show differences in sensitivity to increased UV-B between plant species, and also between cultivars of a given species (Table 8).

Sensitivity rankings of crop species

There is differential sensitivity in plant species exposed to enhanced UV-B. Among plant species there is evidence for a negative response (sensitive), a positive response (stimulation) and no significant difference between treatments and the control (tolerant). While a variety of plant physiological and morphological responses could be used, we choose to *focus on biomass* *accumulation*. Regardless of which response parameter is of greatest interest, and much of the plant physiological research that has been done, still there is no basis by which the sensitivity of a species or a cultivar can be determined without engaging in direct experimental work. We have updated Table 3 in Teramura (1983), and incorporated responses of wildland vegetation (Table 9). We acknowledge that identifying plant species on a simple ordinal scale such as 'sensitive' and 'tolerant' to enhanced UV-B contains much ambiguity because the term 'sensitive' does not explain 'how sensitive' in the sense of using the first derivative (rate of change) of dose–response curves. Investigators in this area of study have not yet presented dose–response curves, thus a massive recomputation of the published data would be required.

What is immediately apparent from Table 9 is that very different UV-B-induced responses were found for the same crop species in different studies. This situation arises due to a variety of reasons: (1) there can be intra-species differences between cultivars; for a given crop in Table 9, we encourage the reader to consult the references given, where there is a need to examine responses among crop cultivars; (2) different UV-B sources, flux densities and action spectra for computing biologically effective UV-B radiation flux densities, were used between various studies; and (3) often, but not always, results of studies with a given crop were observed to be reversed when comparing artificial exposure in growth chambers and greenhouses, to exposures in open, ambient field plots. An example is that of Dumpert & Knacker (1985) where kohlrabi showed tolerance (no response) in the greenhouse, but increased total dry weight (stimulation) under exposure in an open field. Aside from the first two reasons mentioned previously, conflicting results might have been obtained with the same crop under different exposure environments because of differences in microclimatic radiant and heat energy and moisture budgets between the two environments. Very few investigators have measured the leaf temperatures (a result of long wavelength radiant energy at the leaf surface and latent heat flux of evapotranspiration) between the test plants and control plants and between the different exposure environments used.

Only two fiber crops have apparently been examined for UV-B effects on biomass accumulation, and these can be considered as tolerant (Table 9).

Of the C_3 grain crops, barley and oat are sensitive, rice and rye are moderately sensitive, and wheat and sunflower are tolerant. Of the C_4 grain crops, we regard sweet corn as sensitive, and grain sorghum as moderately sensitive. Corn and millet appear to be tolerant to enhanced UV-B with regard to biomass accumulation.

With legume seed crops, soybean is generally sensitive to UV-B, along with pea and cowpea. Bean is moderately sensitive, and peanut exhibited

TABLE 9
Relative Sensitivity of Cultivated Vegetation to *INCREASED* UV-B Radiation Based on Measures of Biomass Accumulation

Sensitivity[a]	*Plant*	*Response effect*	*Exposure environment*[b]	*Reference*
Fiber Crops				
–	Cotton	top dry wt	gh	Ambler *et al.* (1975)
		cotyledon dw	gh	Ambler *et al.* (1975)
		tot dry wt	gh	Bennett (1978)
Tolerant	Cotton	crop yield	field	Hart *et al.* (1975)
		top dry wt	gh	Hart *et al.* (1975)
		tot dry wt	gc	Krizek (1975)
		tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
		tot dry wt	gh	Bennett (1981)
Tolerant	*Cannabis sativa* (drug & fiber)	leaf dry wt	gh	Lydon *et al.* (1987)
C3 Grain Crops				
–	Barley	tot dry wt	field	Caldwell *et al.* (1975)
		tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
		tot dry wt	gh & gc	Hashimoto & Tajima (1980)
		tot dry wt	gh	Dumpert & Boscher (1982)
		tot dry wt	gc	Tevini *et al.* (1982*b*)
+	Barley	tot dry wt	gc	Tevini *et al.* (1981*a*)
		tot dry wt	gh	Dumpert & Knacker (1985)
Tolerant	Barley	tot dry wt	gh & gc	Tevini *et al.* (1981)
		cutic. wax	gc	Steinmüller & Tevini (1985, 1986)
–	Oats	tot dry wt	gh	Thai & Garrard (1975)
		tot dry wt	gh	Van & Garrard (1976)
		tot dry wt	gh	Van *et al.* (1976)
		tot dry wt	gc	Basiouny *et al.* (1978)
+	Oats	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
Tolerant	Oats	tot dry wt	gc & solarium	Biggs & Basiouny (1975)
–	Rice	tot dry wt	solarium	Biggs & Basiouny (1975)
		tot dry wt	gh & gc, field	Biggs & Kossuth (1978*a,c*)
		crop yield	field	Biggs *et al.* (1982)
Tolerant	Rice	tot dry wt	gh	Thai & Garrard (1975)
		tot dry wt	gh	Van *et al.* (1976)
		tot dry wt	gh	Ambler *et al.* (1978*a*)
		tot dry wt	gh, gc, field	Biggs & Kossuth (1978*a*)
		crop yield	field	Biggs & Webb (1986)
–	Rye	tot dry wt	gh	Thai & Garrard (1975)
		tot dry wt	gh	Van *et al.* (1976)
		tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
Tolerant	Rye	tot dry wt	gc	Biggs & Basiouny (1975)

(continued)

TABLE 9—*contd.*

Sensitivity[a]	*Plant*	*Response effect*	*Exposure environment*[b]	*Reference*
–	Wheat	tot dry wt	gc	Hart *et al.* (1975)
		tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
		tot dry wt	gh & gc	Teramura (1980)
		tot dry wt	field	Webb (1982)
		crop yield	field	Webb (1982)
+	Wheat	tot dry wt	gh & gc	Biggs & Kossuth (1978*a,d*)
		tot dry wt	gh & gc	Dumpert & Knacker (1985)
Tolerant	Wheat	tot dry wt	gc	Krizek (1975)
		tot dry wt	gh	Ambler *et al.* (1978*a*)
		grain wt	gh	Ambler *et al.* (1978*a*)
		tot dry wt	gh	Bennett (1978)
		tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
		tot dry wt	field	Moore *et al.* (1978)
		crop yield	field	Moore *et al.* (1978)
		tot dry wt	gh	Teramura (1980)
		tot dry wt	gh	Bennett (1981)
		tot dry wt	field	Becwar *et al.* (1982)
		crop yield	field	Biggs *et al.* (1982)
		shoot biomass	field	Gold & Caldwell (1983)
		crop yield	field	Biggs & Webb (1986)
		shoot biomass	gh & field	Barnes *et al.* (1988)
+	Sunflower	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
C4 Grain Crops				
–	Sweet corn	tot dry wt	gh	Allen *et al.* (1978*a*)
		crop yield	field	Ambler *et al.* (1978*b*)
		plant biomass	field	Halsey *et al.* (1978)
		tot dry wt	gh	Vu *et al.* (1979)
+	Sweet corn	ear size	field	Halsey *et al.* (1978)
–	Sorghum	tot dry wt	gc	Biggs & Basiouny (1975)
		tot dry wt	gh	Thai & Garrard (1975)
		tot dry wt	gh	Van *et al.* (1976)
		tot dry wt	field	Ambler *et al.* (1978*b*)
		tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
Tolerant	Sorghum	tot dry wt	field	Hart *et al.* (1975)
		crop yield	field	Hart *et al.* (1975)
		tot dry wt	gc	Basiouny *et al.* (1978)
–	Corn	tot dry wt	gh, gc, field	Biggs & Kossuth (1978*a,c*)
		crop yield	field	Biggs & Kossuth (1978*c*)
+	Corn	tot dry wt	field	Caldwell *et al.* (1975)
		crop yield	field	Bartholic *et al.* (1975)
		coleoptile dw	gc	Hashimoto & Tajima (1980)
		tot dry wt	gc	Tevini *et al.* (1981*a*)
Tolerant	Corn	tot dry wt	gc	Biggs & Basiouny (1975)
		tot dry wt	field	Hart *et al.* (1975)

TABLE 9—*contd.*

Sensitivity[a]	*Plant*	*Response effect*	*Exposure environment*[b]	*Reference*
		crop yield	field	Hart *et al.* (1975)
		tot dry wt	gh	Thai & Garrard (1975)
		tot dry wt	gh	Van & Garrard (1976)
		tot dry wt	gh	Van *et al.* (1976)
		tot dry wt	gc	Basiouny *et al.* (1978)
		tot dry wt	gh & gc	Tevini *et al.* (1981, 1982*b*)
		crop yield	gh	Pfahler *et al.* (1985)
		crop yield	field	Biggs & Webb (1986)
–	Millet	tot dry wt	gc	Hart *et al.* (1975)
		tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
Tolerant	Millet	tot dry wt	gc	Krizek (1975)
		tot dry wt	field	Hart *et al.* (1975)
		crop yield	field	Hart *et al.* (1975)
		tot dry wt	gh	Thai & Garrard (1975)
		tot dry wt	gh	Van & Garrard (1976)
		tot dry wt	gh	Van *et al.* (1976)
Legume Seed Crops				
–	Soybean	tot dry wt	solarium	Biggs & Basiouny (1975)
		root dry wt	field	Caldwell *et al.* (1975)
		tot dry wt	gh	Thai & Garrard (1975)
		tot dry wt	gh	Van & Garrard (1976)
		tot dry wt	gh	Van *et al.* (1976)
		tot dry wt	gh	Allen *et al.* (1978*a*)
		crop yield	field	Ambler *et al.* (1978*b*)
		tot dry wt	gc	Basiouny *et al.* (1978)
		tot dry wt	gh	Bennett (1978)
		tot dry wt	gh & gc	Biggs & Kossuth (1978*a,b,d*)
		biomass	gc	Kossuth & Biggs (1979)
		tot dry wt	gh	Vu *et al.* (1979)
		tot dry wt	gh	Teramura (1980)
		tot dry wt	gh & gc	Biggs *et al.* (1981)
		tot dry wt	gh	Vu *et al.* (1981)
		tot dry wt	gh & gc	Teramura & Perry (1982)
		tot dry wt	gh & gc	National Research Council (1984*b*)
		tot dry wt	gh	Teramura *et al.* (1984*c*)
		tot dry wt	gh	Murali & Teramura (1985*a*)
		tot dry wt	field	Lydon *et al.* (1986)
		tot dry wt	field	Murali & Teramura (1986*c*)
		crop yield	field	Teramura (1986*c*)
		tot dry wt	gh & field	Teramura & Murali (1986)
		tot dry wt	gh	Murali & Teramura (1987)
		tot dry wt	gh	Teramura & Sullivan (1987)

(*continued*)

TABLE 9—*contd.*

Sensitivity[a]	Plant	Response effect	Exposure environment[b]	Reference
		tot dry wt	gh	Murali *et al.* (1988)
		crop yield	field	Teramura & Sullivan (1988)
+	Soybean	crop yield	field	Teramura & Sullivan (1988)
Tolerant	Soybean	tot dry wt	gc	Biggs & Basiouny (1975)
		tot dry wt	field	Hart *et al.* (1975)
		crop yield	field	Hart *et al.* (1975)
		tot dry wt	gc	Krizek (1975)
		tot dry wt	gh	Bennett (1981)
		crop yield	field	Biggs *et al.* (1982)
		tot biomass	gh	Teramura (1982)
		crop yield	field	Biggs & Webb (1986)
		crop yield	field	Murali & Teramura (1986*b*)
		tot dry wt	field	Murali & Teramura (1986*c*)
		tot dry wt	gh & field	Teramura & Murali (1986)
–	Pea	tot dry wt	gc, solarium	Biggs & Basiouny (1975)
		tot dry wt	gc	Hart *et al.* (1975)
		tot dry wt	gh	Thai & Garrard (1975)
		tot dry wt	gc	Krizek *et al.* (1976)
		tot dry wt	gh	Van & Garrard (1976)
		tot dry wt	gh	Van *et al.* (1976)
		tot dry wt	gh & gc	Brandle *et al.* (1977)
		tot dry wt	gh	Allen *et al.* (1978*a*)
		tot dry wt	gh & gc, field	Biggs & Kossuth (1978*a,c*)
		crop yield	field	Biggs & Kossuth (1978*c*)
		tot dry wt	gh	Vu *et al.* (1979)
		tot dry wt	gc	Basiouny (1982)
		tot dry wt	gh & gc	Vu *et al.* (1984)
+	Pea	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
		biomass	gc	Kossuth & Biggs (1979)
Tolerant	Pea	tot dry wt	gc & gh	Biggs & Basiouny (1975)
		tot dry wt	field	Fox & Caldwell (1978)
		tot dry wt	field	Moore *et al.* (1978)
		tot dry wt	gc	Basiouny (1982)
		tot dry wt	field	Becwar *et al.* (1982)
–	Cowpeas	tot dry wt	gc	Biggs & Basiouny (1975)
		tot dry wt	field	Biggs & Kossuth (1978*a*)
		crop yield	field	Biggs & Kossuth (1978*c*)
		biomass	gc	Kossuth & Biggs (1979)
Tolerant	Cowpeas	tot dry wt	gh	Biggs & Basiouny (1975)
–	Beans	tot dry wt	gc	Biggs & Basiouny (1975)
		tot dry wt	gh	Bennett (1978)
		tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
		biomass	gc	Kossuth & Biggs (1979)
		tot dry wt	gc	Tevini *et al.* (1981*a*)

TABLE 9—*contd.*

Sensitivity[a]	*Plant*	*Response effect*	*Exposure environment*[b]	*Reference*
		tot dry wt	gc	Basiouny (1982)
		tot dry wt	gh	Dumpert & Boscher (1982)
		prim leaf dw	gc	Tevini *et al.* (1982*c*)
		tot dry wt	gh & gc	Dumpert & Knacker (1985)
+	Beans	crop yield	field	Bartholic *et al.* (1975)
Tolerant	Beans	tot dry wt	gh & gc	Biggs & Basiouny (1975)
		crop yield	gh	Hart *et al.* (1975)
		tot dry wt	gc	Krizek (1975)
		tot dry wt	field	Ambler *et al.* (1978*b*)
		crop yield	field	Ambler *et al.* (1978*b*)
		tot dry wt	gh	Bennett (1981)
		tot dry wt	gh & gc	Tevini *et al.* (1982*b*)
–	Peanut	tot dry wt	gc	Hart *et al.* (1975)
		crop yield	field	Biggs & Kossuth (1978*c*)
		tot dry wt	field	Biggs & Kossuth (1978*c*)
+	Peanut	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
		tot dry wt	field	Biggs & Kossuth (1978*c*)
		biomass	gc	Kossuth & Biggs (1979)
Tolerant	Peanut	tot dry wt	gc & solarium	Biggs & Basiouny (1975)
		tot dry wt	field	Hart *et al.* (1975)
		crop yield	field	Hart *et al.* (1975)
		tot dry wt	gh	Thai & Garrard (1975)
		tot dry wt	gh	Van & Garrard (1976)
		tot dry wt	gh	Van *et al.* (1976)
		tot dry wt	gc	Basiouny *et al.* (1978)
Fruit Crops				
–	Tomato	tot dry wt	gh	Biggs & Basiouny (1975)
		tot dry wt	gc	Hart *et al.* (1975)
		tot dry wt	gh	Thai & Garrard (1975)
		tot dry wt	gh	Van *et al.* (1976)
		tot dry wt	gh, gc, field	Biggs & Kossuth (1978*a,c*)
		crop yield	field	Biggs & Kossuth (1978*c*)
		plant biomass	field	Halsey *et al.* (1978)
		crop yield	field	Halsey *et al.* (1978)
		crop yield	field	Nachtwey & Rundel (1982)
+	Tomato	crop yield	gh & gc	Prudot & Basiouny (1982)
Tolerant	Tomato	crop yield	field	Bartholic *et al.* (1975)
		tot dry wt	gc	Biggs & Basiouny (1975)
		tot dry wt	field	Caldwell *et al.* (1975)
		crop yield	field	Hart *et al.* (1975)
		tot dry wt	gc	Krizek (1975)
		tot dry wt	gc	Basiouny (1982)
–	Cucumber	tot dry wt	gc	Biggs & Basiouny (1975)

(continued)

TABLE 9—*contd.*

Sensitivity[a]	*Plant*	*Response effect*	*Exposure environment*[b]	*Reference*
		crop yield	gc	Nakazawa *et al.* (1977)
		leaf dry wt	gh	Ambler *et al.* (1978*a*)
		tot dry wt	gh	Bennett (1978)
		tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
		tot dry wt	gh	Krizek (1978*a,b*)
		cotyledon dw	gc	Hashimoto & Tajima (1980)
		tot dry wt	gh	Bennett (1981)
		tot dry wt	gc	Basiouny (1982)
		cotyledon dw	gc	Tevini *et al.* (1982*c*)
				National Research Council (1984*b*)
		cutic. wax	gc	Steinmüller & Tevini (1985)
		tot dry wt	gh	Murali & Teramura (1986*a*)
		cutic. wax	gc	Steinmüller & Tevini (1986)
		tot dry wt	gc	Tevini & Iwanzik (1986)
Tolerant	Cucumber	tot dry wt	gh	Biggs & Basiouny (1975)
		tot dry wt	gc	Krizek (1975)
		tot dry wt	gh	Murali & Teramura (1986*a*)
–	Squash	tot dry wt	gc	Biggs & Basiouny (1975)
		crop yield	field	Ambler *et al.* (1978*b*)
		tot dry wt	field	Ambler *et al.* (1978*b*)
		tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
		crop yield	field	Biggs & Kossuth (1978*c*)
		tot dry wt	gc	Basiouny (1982)
–	Okra	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
–	Pumpkin	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
–	Watermelon	tot dry wt	gh & gc	Biggs & Kossuth (1978*a,b*)
–	Cantaloupe	crop quality	field	Lipton (1977)
		tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
		crop quality	field	Lipton & O'Grady (1980)
–	Red raspberry	crop yield	gh	Renquist *et al.* (1987)
–	Blueberry	crop yield	gh	Biggs & Kossuth (1978*e*)
		crop yield	gh	Kossuth & Biggs (1978)
		crop yield	gh	Kossuth & Biggs (1981*b*)
–	Pepper	tot dry wt	field	Caldwell *et al.* (1975)
		crop yield	field	Hart *et al.* (1975)
Tolerant	Pepper	crop yield	field	Hart *et al.* (1975)
		tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
–	Eggplant	cotyledon dw	gc	Hashimoto & Tajima (1980)
+	Eggplant	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
Tolerant	Orange	biomass growth	field	Biggs & Kossuth (1978*f*)

TABLE 9—*contd.*

Sensitivity[a]	*Plant*	*Response effect*	*Exposure environment*[b]	*Reference*
Vegetable Flower Crops				
–	Cauliflower	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
–	Broccoli	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
		tot dry wt	field	Ambler *et al.* (1978*b*)
		crop yield	field	Ambler *et al.* (1978*b*)
+	Artichoke	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
Ornamental Flower Crops				
–	Bluebell	tot dry wt	gh	Krizek & Semeniuk (1974)
—	Ivy Geranium	leaf area	gh	Rangarajan & Tibbitts (1988)
Tolerant	Richardson geranium	shoot dry wt	field	Caldwell *et al.* (1975)
–	Marigold	top dry wt	gc	Hart *et al.* (1975)
Tolerant	Marigold	flower number	field	Hart *et al.* (1975)
+	Yellow alyssum	tot dry wt	field	Fox & Caldwell (1978)
		shoot biomass	field	Gold & Caldwell (1983)
Tolerant	Yellow alyssum	tot dry wt	field	Fox & Caldwell (1978)
+	Floribunda rose	petal color	in vitro	Maekawa *et al.* (1980)
Tolerant	Poinsettia	tot dry wt	gh	Semeniuk & Stewart (1979*a*)
–	*Coleus*	leaf discolor	field	Hart *et al.* (1975)
		tot dry wt	gh	Hart *et al.* (1975)
Tolerant	*Coleus*	tot dry wt	gh	Semeniuk & Stewart (1979*b*)
–	Petunia	tot dry wt	gc	Hart *et al.* (1975)
Tolerant	Petunia	flower number	field	Hart *et al.* (1975)
Tolerant	Chrysanthemum	flower number	field	Hart *et al.* (1975)
Leaf Crops				
–	Collards	tot dry wt	gh	Thai & Garrard (1975)
		tot dry wt	gh	Van *et al.* (1976)
		tot dry wt	gc	Basiouny *et al.* (1978)
		tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
		tot dry wt	gc	Basiouny (1982)
Tolerant	Collards	tot dry wt	gc & gh	Biggs & Basiouny (1975)
–	Chard	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
–	Brussels sprouts	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
–	Kale	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
–	Mustard	tot dry wt	gh & gc, field	Biggs & Kossuth (1978*a*)
		crop yield	field	Biggs & Kossuth (1978*c*)
		shoot biomass	gh	Gold & Caldwell (1983)

(*continued*)

TABLE 9—*contd.*

Sensitivity[a]	*Plant*	*Response effect*	*Exposure environment*[b]	*Reference*
—	White mustard	tot dry wt	field	Bogenrieder & Klein (1982*a*)
–	Spinach	tot dry wt	gh	Dumpert & Boscher (1982)
		tot dry wt	gh	Dumpert & Knacker (1985)
		shoot biomass	gh	Gold & Caldwell (1983)
–	Lettuce	tot dry wt	gh & gc	Hart *et al.* (1975)
		tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
		tot dry wt	gh & gc	Bogenrieder & Douté (1982)
		tot dry wt	gh & gc	Dumpert & Knacker (1985)
Tolerant	Lettuce	tot dry wt	solarium	Biggs & Basiouny (1975)
		tot dry wt	gc	Krizek (1975)
–	Cabbage	tot dry wt	gh	Thai & Garrard (1975)
		tot dry wt	gh	Van *et al.* (1976)
		tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
+	Cabbage	tot fresh wt	field	Dumpert & Knacker (1985)
Tolerant	Cabbage	tot dry wt	gh	Biggs & Basiouny (1975)
		tot dry wt	field	Hart *et al.* (1975)
		crop yield	field	Hart *et al.* (1975)
		tot dry wt	gh	Dumpert & Knacker (1985)
–	Kohlrabi	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
+	Kohlrabi	tot dry wt	field	Dumpert & Knacker (1985)
Tolerant	Kohlrabi	tot dry wt	gh	Dumpert & Knacker (1985)
–	Alyce clover	biomass	gc	Kossuth & Biggs (1979)
–	Clover	biomass	gh	Biggs & Kossuth (1978*a*)
Tolerant	Alpine (whiproot) clover	shoot yield	field	Caldwell (1968)
Tolerant	Clover	tot dry wt	gh	Bennett (1978, 1981)
Tolerant	Red clover	tot dry wt	field	Fox & Caldwell (1978)
–	Alfalfa	tot dry wt	gc & gh	Hart *et al.* (1975)
		shoot biomass	field	Fox & Caldwell (1978)
+	Alfalfa	shoot biomass	field	Gold & Caldwell (1983)
Tolerant	Alfalfa	tot dry wt	field	Caldwell *et al.* (1975)
		tot dry wt	gh	Ambler *et al.* (1978*a*)
		tot dry wt	field	Fox & Caldwell (1978)
Tolerant	Kentucky bluegrass	tot dry wt	field	Fox & Caldwell (1978)
Tolerant	Bermuda-grass	crop yield	field	Hart *et al.* (1975)
Tolerant	Orchard grass	crop yield	field	Hart *et al.* (1975)
		tot dry wt	gh	Hart *et al.* (1975)

TABLE 9—*contd.*

Sensitivity[a]	*Plant*	*Response effect*	*Exposure environment*[b]	*Reference*
Tolerant	Digitgrass	tot dry wt	gh	Thai & Garrard (1975)
		tot dry wt	gh	Van & Garrard (1976)
		tot dry wt	gh	Van *et al.* (1976)
Tolerant	Tobacco	tot dry wt	gc & solarium	Biggs & Basiouny (1975)
		tot dry wt	field	Hart *et al.* (1975)
		crop yield	field	Hart *et al.* (1975)
Stem Crops				
—	Rhubarb	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
−	Sugarcane	tot dry wt	gh	Elawad *et al.* (1985)
		crop yield	gh	
+	Celery	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
Tolerant	Celery	tot dry wt	solarium	Biggs & Basiouny (1975)
Tolerant	Asparagus	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
Root, Bulb & Tuber Crops				
−	Sugarbeet	tot dry wt	gc	Hart *et al.* (1975)
		tot dry wt	field	Ambler *et al.* (1978*b*)
		shoot biomass	gh	Gold & Caldwell (1983)
−	Carrot	tot dry wt	gc	Biggs & Basiouny (1975)
		tot dry wt	gc	Hart *et al.* (1975)
		tot dry wt	gc	Basiouny (1982)
+	Carrot	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
Tolerant	Carrot	tot dry wt	gh	Biggs & Basiouny (1975)
−	Rutabaga	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
−	Turnip	tot dry wt	solarium	Biggs & Basiouny (1975)
		tot dry wt	field	Inagaki *et al.* (1986)
		crop yield		
−	Potato	tot dry wt	field	Halsey *et al.* (1978)
		crop yield	field	Halsey *et al.* (1978)
+	Potato	tot dry wt	field	Biggs & Kossuth (1978*c*)
		tot dry wt	field	Halsey *et al.* (1978)
Tolerant	Potato	crop yield	field	Biggs & Kossuth (1978*c*)
		tot dry wt	field	Moore *et al.* (1978)
		crop yield	field	Moore *et al.* (1978)
		tot dry wt	field	Becwar *et al.* (1982)
—	Radish	tot dry wt	gc & gh	Biggs & Basiouny (1975)
		tot dry wt	gh & gc	Hart *et al.* (1975)
		cotyledon dw	gc	Hashimoto & Tajima (1980)
		tot dry wt	gc	Basiouny (1982)
		tot dry wt	gh & gc	Tevini *et al.* (1982*b*, 1983)
		shoot biomass	gh	Gold & Caldwell (1983)
		cotyledon fresh wt	gc	Iwanzik (1986)

(continued)

TABLE 9—*contd.*

Sensitivity[a]	*Plant*	*Response effect*	*Exposure environment*[b]	*Reference*
+	Radish	tot dry wt	gh, gc, field	Biggs & Kossuth (1978*a,c*)
		tot dry wt	gc	Tevini *et al.* (1981*a*)
Tolerant	Radish	tot dry wt	solarium	Biggs & Basiouny (1975)
		tot dry wt	gc	Krizek (1975)
		crop yield	field	Biggs & Kossuth (1978*c*)
		tot dry wt	field	Moore *et al.* (1978)
		crop yield	field	Moore *et al.* (1978)
		tot dry wt	gh & gc	Tevini *et al.* (1981)
		tot dry wt	field	Becwar *et al.* (1982)
		cotyledon dw	gc	Tevini *et al.* (1982*c*)
		tot dry wt	gh & gc	Dumpert & Knacker (1985)
+	Chufa	tot dry wt	gh & gc	Biggs & Kossuth (1987*a*)
−	Onion	tot dry wt	gc	Biggs and Basiouny (1975)
		tot dry wt	field	Fox & Caldwell (1978)
Tolerant	Onion	tot dry wt	gh	Biggs & Basiouny (1975)
		crop yield	gh	Hart *et al.* (1975)
		tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)
		tot dry wt	gc	Basiouny (1982)
Tolerant	Parsnip	tot dry wt	gh & gc	Biggs & Kossuth (1978*a*)

Reference to total dry weight does not necessarily refer to end-of-season, and in many cases, is often after only a few days, or weeks, of growth.
After Table 3 in Teramura (1983) and updated to 1988.
[a] Response showing a decrease under UV-B is '−', showing an increase is '+', and showing relatively little change is 'tolerant'.
[b] gh = greenhouse; gc = growth chamber.

very mixed results with all three types of responses (sensitive or negative; positive or stimulation; no response or tolerance) having been observed in field exposures.

The fruit crops probably exhibit the largest variety of sensitive species: tomato, cucumber, squash, okra, pumpkin, melon, red raspberry and blueberry. Pepper showed mixed results, and we consider eggplant and orange to be tolerant.

Of the few vegetable flower crops for which little, if any, replication of original research has been performed, both cauliflower and broccoli are sensitive to increased UV-B, while artichoke appears to be tolerant.

It can be misleading to list ornamental flower crops in Table 9 where the plant response used as a frame of reference is biomass accumulation. Many of these plants have a market value based upon visual appearance rather than size or weight of the plant. In general, the ornamental plants listed in the table appear to display tolerance to increased UV-B.

TABLE 10
Summary of Relative Sensitivity of Cultivated Vegetation to *INCREASED* UV-B Radiation Based on Measures of Biomass Accumulation

Sensitivity	*Plant*
Fiber Crops	
Tolerant	Cotton
Tolerant	*Cannabis sativa* (drug & fiber)
C3 Grain Crops	
Sensitive	Barley
Sensitive	Oats
Moderately sensitive	Rice
Moderately sensitive	Rye
Tolerant	Wheat
Tolerant	Sunflower
C4 Grain Crops	
Sensitive	Sweet corn
Moderately sensitive	Sorghum
Tolerant	Corn
Tolerant	Millet
Legume Seed Crops	
Sensitive	Soybean
Sensitive	Pea
Sensitive	Cowpeas
Moderately sensitive	Beans
Moderately sensitive	Peanut
Tolerant	
Fruit Crops	
Sensitive	Tomato
Sensitive	Cucumber
Sensitive	Squash
Sensitive	Okra
Sensitive	Pumpkin
Sensitive	Watermelon
Sensitive	Cantaloupe
Sensitive	Red raspberry
Sensitive	Blueberry
Moderately sensitive	Pepper
Tolerant	Eggplant
Tolerant	Orange
Vegetable Flower Crops	
Sensitive	Cauliflower
Sensitive	Broccoli
Tolerant	Artichoke
Ornamental Flower Crops	
Sensitive	Bluebell
Sensitive	*Coleus*
Sensitive	Ivy geranium
Moderately sensitive	Petunia
Tolerant	Richardson geranium
Tolerant	Marigold
Tolerant	Yellow alyssum
Tolerant	Floribunda rose
Tolerant	Poinsettia
Tolerant	Chrysanthemum
Leaf Crops	
Sensitive	Collards
Sensitive	Chard
Sensitive	Brussels sprouts
Sensitive	Kale
Sensitive	Mustard
Sensitive	White mustard
Sensitive	Spinach
Moderately sensitive	Lettuce
Tolerant	Cabbage
Tolerant	Kohlrabi
Sensitive	Alyce clover
Sensitive	Clover
Tolerant	Alpine (whiproot) clover
Tolerant	Clover
Tolerant	Red clover
Tolerant	Alfalfa
Tolerant	Kentucky bluegrass
Tolerant	Bermuda grass
Tolerant	Orchard grass
Tolerant	Digitgrass
Tolerant	Tobacco

(continued)

TABLE 10—*contd.*

Sensitivity	*Plant*	*Sensitivity*	*Plant*
Stem Crops		Sensitive	Rutabaga
Sensitive	Rhubarb	Sensitive	Turnip
Sensitive	Sugarcane	Moderately sensitive	Potato
Tolerant	Celery	Tolerant	
Tolerant	Asparagus	Tolerant	Radish
Root, Bulb & Tuber Crops		Tolerant	Chufa
Sensitive	Sugarbeet	Tolerant	Onion
Sensitive	Carrot	Tolerant	Parsnip

Of the leaf crops, we consider collard, chard, brussels sprout, kale, the mustards and spinach to be sensitive, with lettuce being moderately sensitive. With emphasis on field results, we consider cabbage, kohlrabi, most of the clovers and alfalfa to be tolerant. Several grasses also appear to be tolerant such as Kentucky bluegrass, Bermuda-grass, orchard grass and digit grass. The only evidence available shows tobacco to be tolerant to enhanced UV-B.

Among the stem crops, rhubarb and sugarcane might be sensitive, but there is no field evidence. The only evidence appears to show that celery and asparagus do not respond negatively to enhanced UV-B.

Of the root, bulb and tuber crops, sugar beet, carrot, rutabaga and turnip are considered sensitive. Of all the evidence examined, potato is the only crop for which multiple tests were performed with ambient field exposures. Based on the results obtained, we consider this crop as a whole to range from moderately sensitive to tolerant depending upon the cultivar and weather conditions. Radish, onion and parsnip are considered to be tolerant, although convincing field evidence is lacking for the last two crops. Chufa, the tuberous roots of a sedge consumed by people in southern Europe, did not show a negative response in the one artificial exposure on record.

Table 10 presents a summary of the relative sensitivity of cultivated crops exposed to enhanced UV-B radiation with regard to biomass accumulation.

The UV-B sensitivity of rangeland and non-arboreal wild vegetation is presented in Table 11. It is surprising to find that many investigators generally used either weedy forbs that can create pest problems when mixed with field crops, or species found in disturbed areas, or in mountain meadows. Noticeably missing from this literature are some of the dominant plants of rangelands such as wheatgrass (*Agropyron* sp.), blue grama (*Bouteloua gracilis*), needlegrass (*Stipa* sp.), rabbitbrush (*Chrysothamnus* sp.), bluestem (*Andropogon* sp.), or buffalo grass (*Buchloë dactyloides*).

TABLE 11
Relative Sensitivity of Rangeland and Non-arboreal Wild Vegetation to *INCREASED* UV-B Radiation Based on Measures of Biomass Accumulation

Sensitivity[a]	*Plant*	*Response effect*	*Exposure environment*[b]	*Reference*
−	Tall fescue	top dry wt	gc & gh	Hart *et al.* (1975)
+	Sudan grass	biomass	gh	Biggs & Kossuth (1978*a*)
−	Mouse-ear cress	tot dry wt number plants/ seed crop yield	gh & field Field Field	Brodfuehrer (1956) Usmanov *et al.* (1980) Usmanov *et al.* (1987)
+	Mouse-ear cress	tot dry wt	gh & field	Brodfuehrer (1956)
−	Lesser duckweed	biomass production	gh	Biggs (1983)
+	Duckweed	tot dry wt	gc	Lukina (1983)
−	Foxtail	tot dry wt	Field	Fox & Caldwell (1978)
−	Plantain	tot dry wt	Field	Fox & Caldwell (1978)
−	Dogbane	shoot dry wt	Field	Caldwell *et al.* (1975)
−	Alpine pussytoes	tot dry wt	Field	Brodfuehrer (1956)
+	Alpine pussytoes	tot dry wt	Field	Brodfuehrer (1956)
−	Western yarrow	tot dry wt	Field	Brodfuehrer (1956)
—	Large leaf avens	tot dry wt	Field	Fox & Caldwell (1978)
Tolerant	Yellow avens	shoot yield	Field	Caldwell (1968)
−	Large yellow monkey flower	tot dry wt	gh	Brodfuehrer (1956)
+	Large yellow monkey flower	tot dry wt	gh	Brodfuehrer (1956)
Tolerant	Large yellow monkey flower	tot dry wt	Field	Brodfuehrer (1956)
−	Common-large yellow monkey flower hybrid	tot dry wt	gh	Brodfuehrer (1956)
+	Common-large yellow monkey flower hybrid	tot dry wt	gh	Brodfuehrer (1956)
Tolerant	Common-large yellow monkey flower hybrid	tot dry wt	Field	Brodfuehrer (1956)

(*continued*)

TABLE 11—*contd.*

Sensitivity[a]	*Plant*	*Response effect*	*Exposure environment*[b]	*Reference*
–	Mullein	tot dry wt	Field	Bogenrieder & Klein (1982*a*)
–	Daisy	tot dry wt	Field	Bogenrieder & Klein (1982*a*)
–	Alpine sorrel	tot dry wt	gh	Bogenrieder & Douté (1982)
		tot dry wt	Field	Bogenrieder & Klein (1982*a*)
		shoot biomass	Field	Gold & Caldwell (1983)
–	Patience dock	tot dry wt	gc	Sisson & Caldwell (1976)
Tolerant	Broad-leaved dock	tot dry wt	Field	Bogenrieder & Klein (1982*a*)
–	Tansy	shoot biomass	Field	Gold & Caldwell (1983)
–	Groundsel	tot dry wt	Field	Bogenrieder & Klein (1982*a*)
		shoot biomass	Field	Gold & Caldwell (1983)
–	Pigweed (redroot)	shoot biomass	Field	Fox & Caldwell (1978)
		shoot biomass	Field	Gold & Caldwell (1983)
Tolerant	Pigweed (redroot)	tot dry wt	Field	Fox & Caldwell (1978)
+	Pepper-grass	tot dry wt	Field	Fox & Caldwell (1978)
+	Cheatgrass	tot dry wt	Field	Fox & Caldwell (1978)
+	Pullup muhly	tot dry wt	Field	Brodfuehrer (1956)
+	Dandelion	shoot biomass	Field	Gold & Caldwell (1983)
Tolerant	Dandelion	tot dry wt	Field	Bogenrieder & Klein (1982*a*)
+	English daisy	tot dry wt	Field	Bogenrieder & Klein (1982*a*)
		shoot biomass	Field	Gold & Caldwell (1983)
Tolerant	English daisy	tot dry wt	Field	Bogenrieder & Klein (1982*a*)
Tolerant	Wild oat	shoot biomass	Field	Gold & Caldwell (1983)
		shoot biomass	gh & field	Barnes *et al.* (1988)
Tolerant	Jointed goatgrass	shoot biomass	Field	Gold & Caldwell (1983)
Tolerant	*Kobresia* sedge	shoot yield	Field	Caldwell (1968)
Tolerant	Rock sedge	shoot yield	Field	Caldwell (1968)
Tolerant	*Oreoxis*	shoot yield	Field	Caldwell (1968)
Tolerant	Canada thistle	tot dry wt	Field	Bogenrieder & Klein (1982*a*)

Reference to total dry weight does not necessarily refer to end-of-season, and in many cases, is after only a few days, or weeks, of growth.

[a] Response showing a decrease under UV-B is '–', showing an increase is '+', and showing relatively little change is 'tolerant'.

[b] gc = growth chamber; gh = greenhouse.

TABLE 12
Relative Sensitivity of Forest Vegetation to *INCREASED* UV-B Radiation Based on Measures of Biomass Accumulation

Sensitivity[a]	*Plant*	*Response effect*	*Exposure environment*[b]	*Reference*
–	European beech	tot dry wt	Field	Bogenrieder & Klein (1982*a*)
–	Common hornbeam	tot dry wt	Field	Bogenrieder & Klein (1982*a*)
Tolerant	Common hornbeam	shoot biomass	gh & field	Gold & Caldwell (1983)
–	Sycamore-maple	tot dry wt shoot biomass	Field gh	Bogenrieder & Klein (1982*a*) Gold & Caldwell (1983)
+	Sycamore-maple	tot dry wt	Field	Bogenrieder & Klein (1982*a*)
Tolerant	Sycamore-maple	tot dry wt	Field	Bogenrieder & Klein (1982*a*)
–	Norway maple	tot dry wt	Field	Bogenrieder & Klein (1982*a*)
–	Common ash	tot dry wt shoot biomass	Field gh & field	Bogenrieder & Klein (1982*a*) Gold & Caldwell (1983)
–	Loblolly pine	biomass	gh gh	Biggs & Kossuth (1978*a*) Sullivan & Teramura (1988)
Tolerant	Loblolly pine	tot dry wt	gh	Kossuth & Biggs (1981*a*)
–	Ponderosa pine	biomass tot dry wt	gh gh	Biggs & Kossuth (1978*a*) Kossuth & Biggs (1981*a*)
–	Slash pine	biomass tot dry wt	gh gh	Biggs & Kossuth (1978*a*) Kossuth & Biggs (1981*a*)
–	Scotch pine	root biomass	gh	Sullivan & Teramura (1988)
–	Noble fir	biomass tot dry wt	gh gh	Biggs & Kossuth (1978*a*) Kossuth & Biggs (1981*a*)
+	White fir	biomass tot dry wt	gh gh	Biggs & Kossuth (1978*a*) Kossuth & Biggs (1981*a*)
—	Lodgepole pine	biomass tot dry wt	gh gh	Biggs & Kossuth (1978*a*) Kossuth & Biggs (1981*a*)
Tolerant	Lodgepole pine	branch growth	Field	Kaufmann (1978)
–	Engelmann spruce	root biomass	gh	Sullivan & Teramura (1988)
Tolerant	Engelmann spruce	branch growth	Field	Kaufmann (1978)
Tolerant	Douglas-fir	biomass tot dry wt	gh gh	Biggs & Kossuth (1978*a*) Kossuth & Biggs (1981*a*)
Tolerant	Fraser fir	biomass	gh	Sullivan & Teramura (1988)
Tolerant	White spruce	biomass	gh	Sullivan & Teramura (1988)
Tolerant	Eastern white pine	biomass	gh	Sullivan & Teramura (1988)

(*continued*)

TABLE 12—*contd.*

Sensitivity[a]	*Plant*	*Response effect*	*Exposure environment*[b]	*Reference*
Tolerant	Pinyon pine	biomass	gh	Sullivan & Teramura (1988)
Tolerant	Red pine	biomass	gh	Sullivan & Teramura (1988)
Tolerant	Austrian pine	biomass	gh	Sullivan & Teramura (1988)

Reference to total dry weight does not refer to mature life forms, but is often after only a few weeks, or months, of growth.

[a] Response showing a decrease under UV-B is '−', showing an increase is '+', and showing relatively little change is 'tolerant'.

[b] gh = greenhouse.

Sensitivity rankings of tree species

With respect to forests, Table 12 indicates that a number of European hardwood tree seedlings appear to be sensitive to enhanced UV-B in field exposures. In greenhouse exposures, seedlings of a number of pine species appear to be sensitive to enhanced UV-B, loblolly, Ponderosa, slash and Scots pine. Noble fir was also found to be sensitive, while white fir in two reports 4 years apart showed an increased seedling growth response under enhanced UV-B. Seedlings of several important tree species were found to display tolerance to enhanced UV-B. These include Douglas-fir, Fraser fir, white spruce, eastern white pine, red pine and Austrian pine. If we place greater weight on field, rather than on greenhouse, exposures, seedlings of both lodgepole pine and Engelmann spruce appear to be tolerant to enhanced UV-B radiation.

DIRECT EFFECTS OF INCREASED CO_2 ON PLANTS

Any evaluation of the possible effects of CO_2 on vegetation must consider its direct effects, in addition to the emphasis that has recently been directed to the indirect effects of CO_2 through its role in the context of global warming. Of the three environmental stimuli considered in this paper, many more recent reviews have been published on the direct effects of increased CO_2 on plants, compared to the effects of UV-B radiation or O_3 (Baker & Enoch, 1983; Kimball, 1983*a*,*b*; Kimball & Idso, 1983; Pearcy & Björkman, 1983; Strain & Bazzaz, 1983; Hoffman, 1984; Acock & Allen, 1985; Bazzaz *et al.*, 1985; Cure, 1985; Dahlman, 1985; Kimball, 1985; Oechel & Strain, 1985;

Pollard, 1985; Reynolds & Acock, 1985*a*,*b*; Acock & Pasternak, 1986; Kimball, 1986*a*,*b*; Sionit & Kramer, 1986).

Sensitivity rankings of crop species

Because all higher plants appeared to respond to some extent to an increase in CO_2 if other growth resource requirements were not limiting, rather than indicating which species are sensitive or tolerant, in the following tables we used a slightly more quantitative approach. We present evidence for various plant species (Kimball, 1983, 1986; Cure, 1985; Cure & Acock, 1986), in the form of relative yield increases of plants under CO_2-enrichment versus control conditions. This measure is simply the ratio of yield in CO_2-enriched environment to the control, where the CO_2 concentrations in the control was usually within the range 300–350 ppm, and the CO_2-enriched air was more than the control, but not exceeding, 1200 ppm.

Table 13 shows the species sensitivity ranking for various agricultural crops relative to their entire growth season. With the exception of soybean and corn which were subjected to field exposures (Roger *et al.*, 1983*a*,*b*), the remaining crops were evaluated in artificial environments. As may be noted from the table, cotton, sorghum, eggplant, pea, sweet potato and bean lead the list with greatest response to increased CO_2. Cabbage was found to be very insensitive by comparison.

Although there were no statistical errors or variance measures given for these data, preliminary examination of responses at the early stages of growth only (Table 14), and with crops ranked according to Kimball's (1983) compilation, some interesting patterns emerged in comparison to the results presented in Table 13. Sorghum showed almost no response during its early stages compared to the whole season. Cotton, by contrast, was very responsive in both the early stages and over the whole season. There were no data for the early stages of eggplant and sweet potato. Pea appeared to exhibit increased sensitivity from the immature stage through the whole season, while bean appeared to maintain a relatively constant level of response. Okra, grape and sugarbeet appeared to be sensitive in the immature stage, with no data available for the entire season (Table 13). Sweet pepper, cucumber and radish, while very responsive in the immature stage, showed an apparent dramatic decrease in response over the whole season.

Sensitivity rankings of tree species

Very little screening has been done using non-arboreal wildland plants (Table 15). The degree of sensitivity of forest trees to increased CO_2 is shown

TABLE 13

Mean Relative Yield Increases of CO_2-enriched Versus Control Crops (after Kimball 1983*a,b*; Cure 1985, and Cure & Acock 1986) in Experiments Using Enriched CO_2 Concentrations of 1200 μl/litre[-1] or less (Kimball 1983*a,b*), or 680 ppm (Cure & Acock 1986). *Mature* Agricultural Crops

Crop type	*Crop*[1]	*Mean*[2]	*Crop mean—mean of all crops* (1·36)[3]	*Crop mean—mean of all crops* (1·12)[3]
Fiber crops	Cotton[a]	3·09	1·68[4]	
C4 grain crops	Sorghum	2·98	1·62	
Fiber crops	Cotton[a]	2·59–1·95	1·23	
Fruit crops	Eggplant	2·54–1·88	1·18	
Legume seeds	Peas	1·89–1·84	0·53	
Roots & tubers	Sweet potato	1·83	0·42	
Legume seeds	Beans	1·82–1·61	0·46[4]	
C3 grain crops	Barley[b]	1·70	0·29[4]	
Leaf crops	Swiss chard	1·67	0·31	
Roots & tubers	Potato[c]	1·64–1·44	0·28	
Legume crops	Alfalfa	1·57[4,5]	0·27[6]	
Legume seeds	Soybean[d]	1·55[7]		
C4 grain crops	Corn[e]	1·55		
Roots & tubers	Potato[c]	1·51	0·10[4]	
C3 grain crops	Oats	1·42		
C4 grain crops	Corn[e]	1·40[7]		
C3 grain crops	Wheat[f]	1·37–1·26	0·01	
Leaf crops	Lettuce	1·35	−0·01	
C3 grain crops	Wheat[f]	1·35	−0·06[4]	
Fruit crops	Cucumber	1·30–1·43	−0·06	
Legume seeds	Soybean[d]	1·29	−0·12[4]	
C4 grain crops	Corn[e]	1·29	−0·12[4]	
Roots & tubers	Radish	1·28	−0·08	
Legume seeds	Soybean[d]	1·27–1·20	−0·09	
C3 grain crops	Barley[b]	1·25	−0·11	
C3 grain crops	Rice[g]	1·25	−0·11	
Fruit crops	Strawberry	1·22–1·17	−0·14	
Fruit crops	Sweet pepper	1·20–1·60	−0·16	
Fruit crops	Tomato	1·20–1·17	−0·16	
C3 grain crops	Rice[g]	1·15	−0·26[4]	
Leaf crops	Endive	1·15	−0·21	
Fruit crops	Muskmelon	1·13		
Leaf crops	Clover	1·12		
Leaf crops	Cabbage	1·05		
Flower crops	Nasturtium	1·86		0·74
Flower crops	Cyclamen	1·35		0·23
Flower crops	Rose	1·22		0·10
Flower crops	Carnation	1·09		−0·03
Flower crops	Chrysanthemum	1·06		−0·06
Flower crops	Snapdragon	1·03		−0·09

[1] Crops with superscript have more than one ranking.
[2] From Kimball (1983*a,b*), and, if shown, second value is from Kimball (1986*b*).
[3] From Kimball (1983*a*).
[4] Mean relative yield increase of CO_2-enriched (680 ppm) to control crop (300–350 ppm), after Cure & Acock (1986). Mean of all crops is 1·41.
[5] Based on biomass accumulation; yield not available.
[6] Weighted mean of biomass accumulation for all crops is 1·30.
[7] Field-based result from Rogers *et al.* (1983*a*).

TABLE 14

Mean Relative Yield Increases (Test/Control) of CO_2-Enriched to Control Crops (after Kimball 1983*a*,*b*; 1986*b*) in Experiments using Enriched CO_2 Concentrations of 1200 μl litre^{-1} or less. *Immature* Agricultural Crops (During Growth and Development)

Crop type	*Crop*	(*1986*) *mean*	(*1983*) *mean*	(*1983*) *crop mean— mean of all crops* (*1·75*)
Leaf crops	Okra	2·74	2·96	1·21
Fruit crops	Grape	2·48		
Fruit crops	Sweet pepper	2·41	2·41	0·66
Roots & tubers	Radish	1·79	2·29	0·54
Fiber crops	Cotton	2·16	2·22	0·47
Fruit crops	Cucumber	1·46	1·80	0·05
Roots & tubers	Sugarbeet	1·75	1·71	−0·04
Legume seeds	Beans	1·70	1·70	−0·05
Legume seeds	Peas	1·36	1·68	−0·07
Fruit crops	Tomato	1·52	1·65	−0·10
C3 Grain crops	Barley	1·60	1·61	−0·14
Legume seeds	Soybean	1·65	1·57	−0·18
Leaf crops	Fescue grass	1·51		
C3 Grain crops	Wheat	1·43	1·40	−0·35
Leaf crops	Cabbage	1·28		
C3 Grain crops	Sunflower	1·23	1·29	−0·46
C4 Grain crops	Corn	1·11	1·09	−0·66
Leaf crops	Lettuce	1·68	0·88	−0·87
C4 Grain crops	Sorghum	1·06		

TABLE 15

Mean Relative Yield Increases (Test/Control) of CO_2-Enriched to Control Plants (after Kimball 1983*a*,*b*; 1986*b*) in Experiments using Enriched CO_2 Concentrations of 1200 μl litre^{-1} or Less. *Non-agricultural* Herbaceous Plants

Plant	(*1986*) *mean*	(*1983*) *mean*	(*1983*) *plant mean— mean of all plants* (*1·39*)
Crotalaria	2·53		
Desmodium	1·90		
Jimson weed	1·85	1·85	0·46
Sicklepod	1·55		
Velvetleaf	1·52	1·52	0·13
Pigweed	1·31	1·31	−0·08
Ragweed	1·17	1·17	−0·22
Johnson grass (C4)	1·15		
Itchgrass (C4)	1·09	1·10	−0·29

TABLE 16

Mean Relative Biomass Increases (Test/Control) of CO_2-Enriched to Control-Exposure for Tree Species (after Kimball 1983*a*,*b*; and 1986*b*) in Experiments using Enriched CO_2 Concentrations of 1200 μl litre^{-1} or Less

Type	*Tree species*	*(1986b) mean*	*(1983a) mean*	*(1983b) mean*	*(1983b) tree mean of all species (1·68)*	*Other*[a]
Sensitive						
Coniferous	Eastern white pine			2·24	0·56	
Coniferous	Bristlecone pine					2·06[b]
Deciduous	Black walnut					2·02
Coniferous	Scots pine		1·30	2·00	0·32	
Coniferous	Limber pine					1·80[b]
Deciduous	Silver maple	1·74	1·89	1·75	0·07	
Coniferous	Norway spruce		1·76			
Coniferous	Bristlecone pine					1·73[b]
Deciduous	East. cottonwood	1·69		1·70	0·02	
Deciduous	Sweet gum			1·67[c]		1·56
Coniferous	Douglas-fir	1·18	1·59			
Deciduous	Crabapple			1·57	−0·11	
Coniferous	Ponderosa pine			1·48	−0·20	
Coniferous	White spruce		1·47			
Coniferous	Blue spruce	1·58		1·46	−0·22	
Intermediate						
Coniferous	Jack pine		1·37			
Deciduous	Apple	1·32				
Coniferous	Monterey pine					1·27[d]
Coniferous	Loblolly pine			1·25[c]		
Deciduous	American sycamore	1·21		1·22	−0·46	
Deciduous	New Zld red beech					1·17[d]
Not-sensitive						
Deciduous	Sweet gum	1·10				
Deciduous	Birch	1·06				
Coniferous	Douglas-fir					1·03[d]
Coniferous	Shortleaf pine					1·01[e]
Coniferous	Lodgepole pine[f]					nd
Coniferous	Sitka spruce[f]					nd
Deciduous	Yellow (tulip) poplar[g]					nd
Deciduous	Shagbark hickory[g]					nd
Deciduous	Green ash[g]					nd
Deciduous	American sycamore[g]					nd

[a] From Sionit & Kramer (1986), except as noted.
[b] LaMarche *et al.* (1984); field records of tree rings assumed correlated with rising CO_2.
[c] Field-grown, from Rogers *et al.* (1983*a*,*b*).
[d] Hollinger (1987).
[e] Norby *et al.* (1987).
[f] Canham & McCavish (1981).
[g] Williams *et al.* (1986).

in Table 16. The division of species into categories labeled 'Sensitive', 'Intermediate' and 'Not-Sensitive' is entirely arbitrary and is for the sake of convenience in developing ranks. Relative to biomass response under artificial exposure conditions, eastern white pine, black walnut and Scots pine were the most sensitive. However, the reported studies constitute the evaluation of only a very small number of the major forest tree species even in the USA, without considering those in other countries. There is evidence for possible sub-species differences in sensitivity to increased CO_2, for example Douglas-fir was ranked considerably higher in Kimball's compilations than in Hollinger (1987). The six species shown at the bottom of Table 16 appear to be insensitive based on the reports by Canham & McCavish (1981), and Williams *et al.* (1986), but the numerical data are insufficient to compute their mean relative responses in biomass.

Field studies on the effects of CO_2

Very few field experiments have been performed to evaluate the effects of increased CO_2 on crop growth or native plants (Rogers *et al.*, 1983*a,b*). LaMarche *et al.* (1984) retrospectively invoked the hypothesis of CO_2 increase over the previous two decades as a possible cause for increased growth of limber pine and bristlecone pine, but in their study climatic variables were not monitored on-site. J. H. Shinn (Lawrence-Livermore National Laboratory, California, personal communication) concluded that in general adequate technology is not available to enable CO_2 enrichment experiments to be performed in the field at the plant community or plot-level (Table 7), in contrast to the studies with some air pollutants (Hogsett *et al.*, 1987*a,b*).

VEGETATION RESPONSE TO CLIMATE CHANGE—AIR TEMPERATURE

In the traditional sense, where climate change is viewed only as a change in air temperature, some of the results of Kickert (1984) might serve as a guide for evaluating crop response. After reviewing several hundred papers on crop models, the results of published sensitivity analysis of some of the models were examined. These results show how sensitive the response of a particular crop growth model is, to changes in dynamic environmental conditions, such as air temperature, and to changes in parameter values inherent to the crop species. In several cases, the modeled crop responses were quite sensitive to changes in air temperature.

TABLE 17
Some Crop Parameters Found to be Very Sensitive to Air Temperature Changes in Crop Growth Simulation Models. Only Those Crop Responses having a Sensitivity Index Greater than Those in the Footnotes are Listed Here

Crop response	*Driving variable*	*Sensitivity*	*Source*
Cotton total root wt	Max & Min daily temperature	18·8[a]	Bar-Yosef *et al.* (1982)
Daily alfalfa herbage growth rate	Air temperature	4·64[b]	Schreiber *et al.* (1978)
Root wt of annual semi-arid pasture	Air & dew point temperature	3·40[a]	van Keulen *et al.* (1980–81)
Sorghum grain wt yield	Air temperature	1·95[c]	Maas & Arkin (1980)
Apple fruit yield	Overwinter & early season temperature	1·90[c]	Landsberg *et al.* (1980*a*,*b*)
Soybean fruit dry wt	Air temperature	1·73[c]	Acock *et al.* (1982, 1984, 1985)

[a] Only sensitivity values greater than 2·00 were considered.
[b] Only sensitivity values greater than 3·00 were considered.
[c] Only sensitivity values greater than 1·00 were considered.
After Kickert (1984).

The sensitivity index was defined as the ratio of:

> [the absolute value of the percent change in the crop response with a change in the environmental parameter (in this case, air temperature) relative to the control] *to* [the absolute value of the percent change in the environmental parameter under the test condition compared to the control].

The cases for which a modeled crop response was found to be very sensitive to air temperature are shown in Table 17. Most of these models, however, have not been adequately field tested to evaluate their behavior. In addition, most of the modeling papers reviewed, beyond those mentioned here, provided no data on sensitivity analysis. However, these limited results might still give some indication of the crop responses which could be severely impacted by global, long-term change in air temperature (whether warming or cooling), if it were the only context in which 'climate change' is examined.

EFFECTS OF O_3 ON PLANTS

Ozone in the earth's boundary layer is regarded as one of the most phytotoxic air pollutants. Information on the responses of plant species to

O_3 exposure should be of interest to scientists investigating the plant effects of enhanced UV-B radiation, and increased CO_2 concentrations. Scientists in those fields should realize that there is considerable debate and controversy over how to define and analyze the O_3 exposure time series to which the vegetation is subjected (Krupa & Kickert, 1987; Krupa & Kickert, in preparation). In contrast, researchers analyzing UV-B effects on plants have generally designed their studies only to test for differences between treatments and controls. So far in general, they have not attempted to quantify the relationship between a variable, realistic time series of the biologically effective UV-B flux density, and the time series of some plant response. When this type of study is attempted, researchers in plant photobiology should review the literature on quantifying air pollutant exposure and plant response for time-varying concentrations. This could be a fruitful area for information exchange between these two subjects. Many reviews (descriptive and explanatory narratives) are available on vegetation response to O_3 exposure (Ashmore, 1984; Heggestad & Bennett, 1984; Guderian, 1984; Heck *et al.*, 1984, 1988; Tingey, 1984; Roberts, 1984; McLaughlin, 1985; Cooley & Manning, 1987; Torn *et al.*, 1987; Krupa & Manning, 1988; Pye, 1988).

For exploratory, experimental and predictive purposes, researchers investigating the effects of O_3 on plants have produced a number of quantitative models of O_3 exposure and vegetation response (Kickert *et al.*, in preparation; Schaefer *et al.*, 1989). Only brief mention of these is provided here, without our necessarily giving endorsement, to alert scientists studying UV-B radiation and CO_2 effects on plants. A critical review of these models can be found in Krupa & Kickert (1987) and Kickert *et al.* (in preparation). Some of these models were designed principally for the objective of evaluating ambient air quality standards, while others were aimed instead at achieving a better understanding of the relationships between the processes involved in pollutant exposure and the resulting plant responses. This distinction is quite important when considering the approaches that have been used.

Statistical models for plant response to short-term, acute and long-term, chronic exposures include the Larsen & Heck (1984) model of 'effective mean' O_3 concentration. The Larsen and Heck model, aimed at air quality standards-evaluation, is a statistical relationship in which the percent crop yield reduction is a function of the hourly average O_3 concentration during the daytime hours over the growing season, the number of such hours, and an 'exposure time–concentration' parameter.

Mechanistic process models for plant response to acute exposure include those of Schut (1985), Taylor *et al.* (1982), and the model of Lieth & Reynolds (described in Heck *et al.*, 1984) based on the Richards function for relative growth rate. Schut's ecophysiological model is based on foliar resistances and fluxes of O_3, carbon dioxide, and water vapor between the atmosphere and the leaf interior. It handles cumulative O_3 effects, threshold effects, recovery and repair in which repair processes are examined for constant rate, O_3 concentration-dependence, and/or net photosynthesis-dependence. There are strong parallels to the processes of interest of those investigators examining short term effects of UV-B irradiance on plant physiology, although Schut does not consider UV-B in his model. Taylor *et al.* (1982) also attempted to relate plant response to O_3 uptake (effective dose of Runeckles, 1974) rather than to the concentration of O_3 to which the plants are exposed (ambient or exposure dose).

The Lieth & Reynolds model (Heck *et al.*, 1984) describes the relative growth rate of a plant using a modified form of the Richards growth function with a stress effect from a single O_3 exposure applied to the growth rate, but with parameters for percent recovery and the recovery rate following the exposure event (or between sequential exposures, i.e. respite time).

Statistical models of plant response to whole-season chronic exposure include: the Rawlings & Cure (1985) hypothesis based on the Weibull function, an O_3 dose–response model for the evaluation of air quality standards in an agricultural context; and the Krupa & Nosal (1989*a*,*b*) time series model aimed at understanding how crops respond to variable sequences of O_3 exposures in relation to crop growth stages.

A mechanistic process model for chronic exposure and response is found

TABLE 18

Guide to Table Numbers on Vegetation Sensitivity to Ozone, by Vegetation Type, Stage of Growth, and Exposure Environment[a]

Sensitivity ranking and comparison of biomass production for several species:	*Exposure environment*			
	Greenhouses, growth chambers, and artificial field chambers		*Chamber-less ambient field exposures*	
	Crops	*Wildlands*	*Crops*	*Wildlands*
Seedlings	19	25 26		27
Whole-season annuals or mature perennials	20 21 22 23		24	

[a] Values in the table reflect table numbers.

in Reich (1987). This is actually a series of simple exposure–response models expressed graphically where net photosynthesis and growth for crops, hardwoods, and pine are shown as functions of ambient O_3 dose and, alternatively, O_3 uptake (effective dose) by foliage. The approach is based on extensive use of published literature.

Models of the air pollutant uptake process and subsequent plant response are found in Amiro *et al.* (1984), King (1987), and King *et al.* (1988). Amiro found the time required for visual foliar injury on bean plants to be a negative power function of the O_3 flux density, rather than to be directly related to O_3 concentration or ambient dose. King's model is a simulation of soybean growth in which the daily sum of daytime hourly mean concentrations (ambient dose) above a threshold is modified by an O_3

TABLE 19
Sensitivity Indices for Agricultural Crops under Acute (One to Eight Hour Exposures) Ozone Exposures. Sensitivity Index is the Ratio of Response to Dose

Agricultural crop	*Sensitivity index*
Sensitive	
Bean	127·57
Tomato	115·07
Grasses[a]	83·72
Legumes[a]	83·54
Oat	65·79
Intermediate	
Vegetables[b]	62·97
Wheat	52·45
Grasses[a]	49·60
Clover	38·66
Legumes[a]	38·94
Resistant	
Cucumber	22·90
Perennials[c]	22·21
Vegetables[b]	16·98
Legumes[a]	16·90
Grasses[a]	9·92
Woody species[c]	8·62

[a] Found in all three sensitivity classes; not discriminated in Torn *et al.* (1987).
[b] Found both in Intermediate and Resistant Sensitivity Classes; not discriminated by Torn *et al.* (1987).
[c] Not classified by species in Torn *et al.* (1987).
Source: Table 28 in Torn *et al.* (1987).

TABLE 20

Maximum Sensitivity Indices for Agricultural Crops under *Acute* (One to Eight Hour Exposures) Ozone Exposures. Sensitivity Index is the Ratio of Response to Dose

Agricultural crop	*Maximum sensitivity index*
Sensitive	
Grapevine (shoot growth)	187·5
Radish (root dry wt)	61·7
Intermediate	
Tomato (plant dry wt)	30·0
White clover (shoot dry wt)	28·3
Cucumber (top dry wt)	19·0
Onion (plant dry wt)	19·0
Resistant	
Snap bean (plant dry wt)	13·9
Tall fescue grass (shoot dry wt)	12·2
Potato (tuber dry wt)	2·5
Soybean (shoot growth)	2·2

Source: Table 20 in Torn *et al.* (1987).

TABLE 21

Maximum Sensitivity Indices for Agricultural Crops under Whole-season Ozone Exposures. Sensitivity Index is the Ratio of Response to Dose

Agricultural crop	*Maximum sensitivity index*
Sensitive	
Pinto bean (leaf dry wt)	9·5
Italian ryegrass (dry wt)	8·3
Potato (Kennebec; tuber wt)	7·5
Crimson clover (dry wt)	6·9
Intermediate	
Radish (root fresh wt)	5·4
Wheat (anthesis exposure; yield)	5·4
Alfalfa (top dry wt)	4·4
Resistant	
Perennial ryegrass (shoot dry wt)	2·3
Orchard grass (shoot dry wt)	2·3
Beet (top dry wt)	2·2
Spinach (fresh wt)	2·0
Tomato (top dry wt)	1·96
Soybean (seed dry wt)	1·2
Golden sweet corn (top dry wt)	0·61
Tall fescue grass (leaf & shoot dry wt)	0·18

Source: Table 21 in Torn *et al.* (1987).

TABLE 22

Sensitivity of Agricultural Crop Yield Reduction to Ozone Exposures. Sensitivity Index is the Per cent Yield Reduction to a *Seasonal 7-h daily mean* Concentration of 100 $\mu g\ m^{-3}$ [a]

Agricultural crop	*Sensitivity index*
Sensitive	
Legumes	12·3
Alfalfa	12·3
Potato	8·3
Corn	8·3
Onion	8·3
Lettuce	8·3
Spinach	8·3
Intermediate	
Cucumber	4·8
Tomato	4·8
Grass	3·6
Endive	3·6
Carrot	3·6
Cabbage	3·6
Carnation	3·6
Chrysanthemum	3·6
Cereals	2·5

[a] 1960 $\mu g\ m^3$ O_3 = 1 ppm at 25°C and 1 atmos. pressure.
Source: van der Eerden *et al.* (1988).

damage reduction factor. Transpiration is partly a function of this quantity, and the relative crop yield is a function of seasonal transpiration and transpiration efficiency.

While King, and Larsen & Heck, applied their models to the regional level, the other models mentioned were designed for local site application. A regional forest assessment model for pollutant effects was described by Grossman & Schaller (1986), and Grossman (1988). This model was found to give the best fit to regional observations in Austria when conifer tree needle injury and the viability of trees was partially a response to a more than additive pollution effect. The definition of this effect consists of a Weibull-weighted function of O_3 concentration, multiplied by a Weibull function-weighted sum of primary (SO_2, NO_x) and secondary pollutants (formic acid, acetic acid, formaldehyde, hydrogen peroxide, and nitric acid).

Sensitivity rankings of crop species

There is no single literature source that lists the relative sensitivities of cultivated and wildland plants to O_3 exposure in screening studies. As a result, we present several tables which are organized according to the overview shown in Table 18. We have compiled species tables showing relative sensitivities of crop seedlings, and over the whole-season for annuals or mature perennials, separately by artificial exposure methods, and for chamber-less ambient field exposures. In addition, three tables are given for wildland plant seedling sensitivities to O_3, separately by artificial exposure methods, and for chamber-less ambient field exposures.

TABLE 23
Sensitivity of Agricultural Crop Yield Reduction to Ozone Exposures

Agricultural crop	*Sensitivity index*
Sensitive	
Onions	−9·90
Lemons	−8·09[a]
Grapes	−6·90[b]
Spinach	−6·07
Oranges	−5·92
Cotton	−4·466
Alfalfa	−3·83
Sweet corn	−2·82
Intermediate	
Dry beans	−0·21 to −0·28[c]
Wheat	−0·220 to −0·20
Tomato (processing)	−0·0184 to −0·1004
Rice	−0·031 to −0·091
Lettuce	−0·000 38 to −0·0234
Tomatoes (fresh)	−0·0232[d]
Grain sorghum	−0·004 to −0·017
Resistant	
Barley	
Strawberries	
Sugar beet	

The sensitivity index is the rate of change of per cent of yield under ozone exposure (compared to control) with respect to the *seasonal 7-h or 12-h daily mean* concentration (ppm) (computed from equations given in Olszyk *et al.*, 1988).

[a] Provided 7·4 is used rather than 74 in the equation given in Olszyk *et al.* (1988). Apparent mistake in original paper.

[b] Provided 6·6 is used rather than 66 in the equation given in Olszyk *et al.* (1988). Apparent mistake in original paper.

[c] Dose response function is exponential so rate of change depends on the ozone concentration value used; values given here are for 0·05 and 0·08 ppm.

[d] Based on seasonal dose for concentrations greater than 0·10 ppm.

Bean, tomato and oat are among the leading sensitive crops to acute O_3 exposure (Torn *et al.*, 1987) (Table 19). Grapevine and radish are also reported to be highly sensitive to O_3 (Table 20) if maximum ratios of response to acute exposures are considered. For the entire growth season, using cumulative O_3 dose, Torn *et al.* indicate that pinto bean, Italian ryegrass, potato and crimson clover are quite sensitive to O_3 (Table 21). In contrast, van der Eerden *et al.* (1988) used a seasonal 7-h daily mean O_3 concentration and showed that alfalfa and other legumes were highly sensitive in terms of yield responses (Table 22). With a different approach,

TABLE 24
Sensitivity Indices for California Agricultural Crop Yield to Field Ozone Exposures

Agricultural crop	*Sensitivity index*
Sensitive	
Green onion	$5{\cdot}97 \times 10^{-2}$
Leaf lettuce	$5{\cdot}19 \times 10^{-2}$
Parsley	$4{\cdot}8 \times 10^{-2}$
Spinach	$4{\cdot}006 \times 10^{-2}$
Red beet	$2{\cdot}59 \times 10^{-2}$
Red kidney bean[a]	$2{\cdot}40 \times 10^{-2}$
Pole tomato (6718 VF)[b]	$2{\cdot}327 \times 10^{-2}$
Processing tomato (5 cvs)	$2{\cdot}29 \times 10^{-2}$
Potato (Centennial)[a]	$1{\cdot}03 \times 10^{-2}$
Alfalfa (Moapa 69; 3 other cvs)[a]	$9{\cdot}258 \times 10^{-3}$
Cotton (3 cvs)	$6{\cdot}947 \times 10^{-3}$
Intermediate	
Red kidney bean[a] (3 cvs)	not given
Potato[a] (3 cvs)	not given
Alfalfa[a] (3 cvs)	not given
Resistant	
Red kidney bean (Limas-Fordhook)	not applicable
Pole tomato (2 cvs)	not applicable
Potato[a] (3 cvs)	not applicable
Alfalfa[a] (3 cvs)	not applicable
Cotton (Acala SJ-4)	not applicable
Sugarbeet (4 cvs)	not applicable
Strawberry (7 cvs)	not applicable
Turnip (Tokyo Cross hybrid)	not applicable

Sensitivity index is the rate of change of percent yield reduction to dose (i.e., slope in regression equation). (Source: Musselman *et al.*, 1987).
[a] Cultivars in all three sensitivity classes.
[b] Other examined cultivars were resistant.

Olszyk *et al.* (1988) indicated that the yields of onion, lemon, grape, spinach and orange were very sensitive to O_3 (Table 23). Similarly, Musselman *et al.* (1987) showed that green onion, lettuce, parsley and spinach yields were very sensitive to O_3 (Table 24).

Sensitivity rankings of tree species

With tree seedlings exposed in chambers to O_3, Miller *et al.* (1983) found Jeffrey pine × Coulter pine hybrid, western white pine, Ponderosa pine, Jeffrey pine, white fir, and Coulter pine to exhibit highest visible foliar injury scores when the means of the logarithms of the scores were ranked (Table 25). Visible foliar injury data alone cannot be directly converted into changes in tree biomass because other ecophysiological processes not measured are also involved. The data of Miller *et al.*, however, provide supporting evidence for biomass changes in Ponderosa pine, although not in Jeffrey pine (Table 26). Such decreases in biomass are for tree seedlings generally observed under artificial exposure conditions, with the exception of field data from mature trees at the San Bernardino National Forest in California

TABLE 25

Sensitivity of Conifer Tree Seedlings to Ozone Exposure of 0·36 ppm, 12 h day^{-1}, over 25 Days in Field Chambers, where Sensitivity is Rated in Terms of the Mean of the Log of Visible Foliage Injury Index as Used and Reported in Miller *et al.* (1983)

Tree species	*Mean log injury score*
Sensitive	
Jeffrey pine × Coulter pine hybrid	1·24
Western white pine	1·24
Ponderosa pine	1·00
Jeffrey pine	0·97
White fir	0·91
Coulter pine	0·87
Intermediate	
Red fir	0·69
Monterey pine × knobcone pine hybrid	0·69
Knobcone pine	0·51
Incense cedar	0·51
Resistant	
Big cone Douglas-fir	0·41
Sugar pine	0·38
Inland ponderosa pine	0·28

TABLE 26

Maximum of Response/Dose Ratios for Controlled Ozone Exposures of Tree Seedlings Based on Weight Growth (After Pye, 1988). Some Species Appear in More than One Sensitivity Category

Species	*Dose* (μl *litre* h^{-1})	*Decreased biomass change* (%)	*Maximum observed response/dose*
Sensitive			
Pitch pine	2·4	−18	−7·71[a]
American sycamore	17	−61	−3·59
Loblolly pine	7	−21	−3·00
Eastern cottonwood	6	−14	−2·33
Shortleaf pine	7	−15	−2·14
Red ash	8	−14	−1·75
Sweet gum	25	−42	−1·67[b]
Sugar maple	25	−41	−1·64
White ash	11	−17	−1·55
White ash[c]			
Green ash[c]	17	−24	−1·43
Sweet gum[c]			
Honey locust[c]			
Pin oak[c]			
Yellow (tulip) poplar[c]			
American sycamore[c]			
Quaking aspen[c]			
White oak[c]			
Ailanthus[c]			
Intermediate			
Pitch pine	25	−24	−0·96
Sweet gum	25	−24	−0·96
Yellow (tulip) poplar	12	−9	−0·75
Willow oak	25	−19	−0·75
Willow oak	17	−11	−0·65
Virginia pine	25	−13	−0·52
Ponderosa pine	146	−65	−0·45[d]
Silver maple	144	−64	−0·44
Red maple	84	−37	−0·44
Slash pine	155	−50	−0·32
Ponderosa pine	76	−21	−0·28
Resistant			
Douglas-fir	76	−15	−0·20
Sitka spruce	76	−14	−0·18
White fir	146	−24	−0·16[d]
Black cherry	14	−2	−0·14
Western white pine	76	−9	−0·12

(*continued*)

TABLE 26—*contd.*

Species	*Dose* (*μl litre h*$^{-1}$)	*Decreased biomass change* (%)	*Maximum observed response/ dose*
Lodgepole pine	76	−8	−0·11
Quaking aspen	297	−17	−0·06
Jeffrey pine	76	−2	−0·03
Monterey pine	76	0	0·00
Sugar pine	76	0	0·00
Green ash	25	0	0·00[b]
Yellow (tulip) poplar	25	0	0·00[b]
Flowering dogwood[c]			
Northern white cedar[c]			
Sugar maple[c]			
Red maple[c]			
Red oak[c]			
Black gum[c]			
Eastern hemlock[c]			
Black walnut[c]			
American linden[c]			
Black locust[c]			
Incense cedar[d]			
Sugar pine[d]			
Jeffrey pine[d]			

[a] Scherzer & McClenahen (1989).
[b] Kress & Skelly (1982).
[c] Harkov & Brennan (1979); no order implied other than 'sensitive' versus 'resistant'.
[d] Kickert *et al.* (1980); calculated for average total summer oxidant over 1968–77 at Rim Forest/Sky Forest; annual average mature tree ring growth in the field at Camp O-Ongo plot: the average for 1956–65 is taken as the 'control', and the average for 1966–75 is taken as the 'treatment'.

(Kickert *et al.*, 1980). The most sensitive tree species listed in Table 26 are pitch pine, American sycamore and loblolly pine. Those species for which numerical data are available, have been sorted into 'Sensitive', 'Intermediate' and 'Resistant' categories using arbitrary values of separation. Since the availability of this type of data from ambient field plots is rare, seedling height growth decreases from Duchelle *et al.* (1982) are displayed in Table 27 for eastern deciduous forest species in the USA. Green ash and yellow tulip poplar seedlings were found to be sensitive to O_3 under ambient exposures. While differing growth response parameters were used, and

TABLE 27

Sensitivity of Eastern Deciduous Forest Tree Seedlings in Open Ambient Plots to Ozone Exposure of about 15·19 ppm-h from 9 May, 1979, through October 1980, where Sensitivity is Rated in Terms of the Fractional Decrease in Average Height Growth over the Time Period as Reported in Duchelle *et al.*, (1982)

Tree species	*Fractional decrease in average height growth compared to adjusted controls*[a]	*Response/dose*
Sensitive		
Green ash	0·65	−4·28
Yellow-tulip poplar	0·56	−3·69
Intermediate		
Black locust	0·37	−2·44
Eastern hemlock	0·37	−2·44
Virginia pine	0·24	−1·58
Eastern white pine	0·22	−1·45
Table mountain pine	0·17	−1·12

[a] Fractional decrease was calculated as height growth in charcoal filtered chambers adjusted for chamber effect, minus height growth in open plots, divided by height growth in charcoal filtered chambers adjusted for chamber effect, where height growth in charcoal filtered chambers adjusted for chamber effect is the difference between average height growth in charcoal filtered chambers less the difference between average height growth in non-filtered chambers and in open plots.

consequently the numerical values were different between species, these data nevertheless corroborate the results presented in Table 26.

JOINT EFFECTS OF UV-B, CO_2 AND O_3 ON PLANTS

Although CO_2 might not continue to increase because of the constraints on human population dynamics (Watt, 1989; Watt, 1990; in press), we assume that, for sometime yet before these constraints become active, CO_2 will increase. Such increases in the atmosphere will tend to stimulate photosynthesis primarily in those plants possessing a C_3 pathway. In Table 28, modified from Teramura (1986*b*), the third column shows the other plant responses expected from increased atmospheric CO_2.

Since there is already some enhancement in the concentrations of ambient CO_2, when possible interactions with enhanced UV-B radiation, and

TABLE 28
Overview of the Effects of UV-B, CO_2 and O_3 on Plants in Single-Stress Mode

Plant characteristic	*Plant response to environmental change*		
	(Stratospheric O_3 depletion) increased UV-B only	*(Direct effect) doubling of CO_2 only*	*Increased tropospheric O_3 only*
Photosynthesis	Decreases in many C3 and C4 plants	C3 plants increase up to 100%, but C4 plants show only a small increase	Decreases in many plants
Leaf conductance	Not affected in many plants	Decreases in C3 and C4 plants	Decreases in sensitive species and cultivars
Water use efficiency	Decreases in most plants	Increases in C3 and C4 plants	Decreases in sensitive plants
Leaf area	Decreases in many plants	C3 plants increase more than C4 plants	Decreases in sensitive plants
Specific leaf weight	Increases in many plants	Increases	Increases in sensitive plants
Crop maturation rate	Not affected	Increases	Decreases
Flowering	Inhibits or stimulates flowering in some plants	Earlier flowering	Decreased floral yield, number and yield of fruits, and delayed fruit setting
Dry matter production and yield	Decreases in many plants	C3 plants nearly double, but C4 plants show only small increases	Decreases in many plants
Sensitivity between species	Large variability in response among species	Major differences between C3 and C4 plants	Large variability in sensitivity between species
Sensitivity within species (cultivars)	Response differs between cultivars of a species	Can vary among cultivars	Response differs between cultivars of a species
Drought stress sensitivity	Plants become less sensitive to UV-B, but sensitive to lack of water	Plants become less sensitive to drought	Plants become less sensitive to ozone but sensitive to lack of water
Mineral stress sensitivity	Some plants become less while others more sensitive to UV-B	Plants become less responsive to elevated CO_2	Plants become more susceptible to ozone injury

Modified from Teramura (1986*b*).

TABLE 29

Various Possible Patterns of Environmental Stress for Field Vegetation with Respect to O_3 and UV-B Depending upon Stratospheric O_3 Status and Ground Level O_3 Pollution

Surface boundary layer status	*Mid-latitudes stratospheric O_3 status*	
	No O_3 depletion	*O_3 depletion occurring*
Background O_3 only	(1) 'Normal' UV-B plant effects with no pollution effects	(3) Enhanced UV-B plant effects only with no pollution effects
Elevated O_3 pollution	(2) 'Normal' UV-B plant effects and O_3 effects on plants	(4a) *Enhanced* incoming UV-B might be *depleted in boundary layer* with no net effect of UV-B on plants, BUT with O_3 effects on plants (similar to case at left) (4b) Enhanced UV-B effects on plants *co-occuring or intermittent with* O_3 effects on plants

ground-level O_3 are considered, it may be necessary to examine the plant responses shown in Table 29.

At those geographic locations where there is no predicted or observed stratospheric O_3 depletion, no increase in UV-B radiation, and no increase in the tropospheric O_3 concentrations, we would only expect 'normal' UV-B effects on plants. This means that we would expect no effects demonstrable from either UV-B reduction or enhancement (Case 1, Table 29).

At those geographic locations where there is no predicted or observed stratospheric O_3 depletion and no increase in UV-B, but continued increase in the tropospheric O_3 concentrations, we expect a situation comparable to that observed in geographic locations such as southern California (Case 2, Table 29). This is the type of situation that air pollution–plant effects scientists have addressed for several years. By way of synopsis, Table 28, column 4, lists the various effects on plants due to tropospheric O_3. However, as CO_2 appears to be still increasing, such studies should begin to identify the possible joint quantitative effects of CO_2 (Table 28, Column 3) and O_3 (Column 4).

In those geographic areas where stratospheric O_3 depletion might occur, if spring–summer cloud conditions are not significantly increased, one might expect an increase in UV-B. At those geographic areas not under boundary layer O_3 concentrations significantly above the background (Case 3, Table 29), we might expect some plants to respond to an interaction of enhanced UV-B and some increased ambient CO_2. The responses to each of these environmental stimuli taken separately are shown in columns 2 and 3 in Table 28. Although the effects of increased CO_2 were not examined, most of the photobiology research cited in this paper, and especially in the reports of CIAP and BACER projects in the early and mid-1970s, used this type of situation (Case 3) as a frame of reference.

The most complex situation is what some people think the future might hold for some geographic regions: (1) continued increase in CO_2, (2) mid-latitude stratospheric O_3 depletion with increased UV-B, and (3) continued increases in O_3 within the boundary layer. In Table 29, two different scenarios are shown which we envision as possibilities. In one case (4a), the timing and geography could lead to high boundary layer O_3 concentrations along with enhanced UV-B, but with the high O_3 concentrations off-setting (by absorption) the UV-B enhancement. The net result would simply be the effects of O_3 on the vegetation. This situation is slightly different from the case where, there is no stratospheric O_3 depletion, but increase in the tropospheric O_3 (Case 2, Table 29).

In the other case (4b in Table 29), we can envision situations where, there is an increase in CO_2, there is also a net enhancement in UV-B during the growing season, occurring intermittently and inversely with O_3 episodes in the boundary layer, or, when ground-level O_3 concentrations are not high enough to absorb the enhanced UV-B, then all three stress factors would confront the vegetation. In this situation, the three potential factors of stress, as shown in Table 28 would compete with or enhance each other in affecting a particular plant response process. There are no studies to show how plant responses would behave under such a situation.

In those geographic areas where the two aforementioned situations (Cases 3 and 4b, Table 29) might be found in the future, it would be helpful to identify the crop and tree species in terms of their sensitivity to increased CO_2, enhanced UV-B and O_3. From Tables 9, 13 and 20 through 24, we have derived Table 30 for agricultural crops. Since sensitivity ratings are available at least for increased CO_2, we have used that factor as the basis for the contents of the table. If we had used the sensitivity to UV-B, or O_3 as the basis, there would be many more crops, but with no sensitivity rating to increased CO_2.

From Table 30, it is evident that sorghum apparently has the highest sensitivity to increased CO_2 while also being sensitive to enhanced UV-B and having an intermediate response rating to O_3. Other crops showing sensitivity to all three factors, but in a decreasing order of sensitivity to

TABLE 30

Comparison of Sensitivities of Agricultural Crops to Enhanced CO_2 (Mean Relative Yield Increases of CO_2-Enriched to Control) (after Kimball 1983*a,b*; 1986*b*, Cure 1985, and Cure & Acock 1986) for CO_2 Concentrations of 1200 μl $litre^{-1}$ or Less (Kimball 1983*a,b*), or 680 ppm (Cure & Acock 1986)); to Enhanced UV-B Radiation; and to Ground-Level O_3

Crop type	*Crop*[1]	*Enhanced CO_2 mean relative yield increase*[2]	*Sensitivity to enhanced UV-B*	*Sensitivity to O_3*
Fiber crops	Cotton[a]	3·09	Tolerant	Sensitive
C4 grain crops	Sorghum	2·98	Sensitive	Intermediate
Fiber crops	Cotton[a]	2·59–1·95		
Fruit crops	Eggplant	2·54–1·88	Tolerant	Unknown
Legume seeds	Peas	1·89–1·84	Sensitive	Sensitive
Roots & tubers	Sweet potato	1·83	Unknown	Unknown
Legume seeds	Beans	1·82–1·61	Sensitive	Sens/intermed.
C3 grain crops	Barley[b]	1·70	Sensitive	Tolerant
Leaf crops	Swiss chard	1·67	Sensitive	Unknown
Roots & tubers	Potato[c]	1·64–1·44	Sens/toler.	Sensitive
Legume crops	Alfalfa	1·57[3,4]	Tolerant	Sensitive
Legume seeds	Soybean[d]	1·55[5]	Sensitive	Tolerant
C4 grain crops	Corn[e]	1·55	Tolerant	Sensitive
Roots & tubers	Potato[c]	1·51		
C3 grain crops	Oats	1·42	Sensitive	Sensitive
C4 grain crops	Corn[e]	1·40[5]		
C3 grain crops	Wheat[f]	1·37–1·26	Tolerant	Intermediate
Leaf crops	Lettuce	1·35	Sensitive	Sensitive
C3 grain crops	Wheat[f]	1·35		
Fruit crops	Cucumber	1·30–1·43	Sensitive	Intermediate
Legume seeds	Soybean[a]	1·29		
C4 grain crops	Corn[e]	1·29		
Roots & tubers	Radish	1·28	Tolerant	Intermediate
Legume seeds	Soybean[d]	1·27–1·20		
C3 grain crops	Barley[b]	1·25		
C3 grain crops	Rice[g]	1·25	Sensitive	Intermediate
Fruit crops	Strawberry	1·22–1·17	Unknown	Tolerant
Fruit crops	Sweet pepper	1·20–1·60	Sens/toler.	Unknown
Fruit crops	Tomato	1·20–1·17	Sensitive	Sens/intermed.
C3 grain crops	Rice[g]	1·15		
Leaf crops	Endive	1·15	Unknown	Intermediate
Fruit crops	Muskmelon	1·13	Sensitive	Unknown
Leaf crops	Clover	1·12	Tolerant	Sensitive
Leaf crops	Cabbage	1·05	Tolerant	Intermediate
Flower crops	Nasturtium	1·86		
Flower crops	Cyclamen	1·35		
Flower crops	Rose	1·22	Tolerant	
Flower crops	Carnation	1·09		Intermediate
Flower crops	Chrysanthemum	1·06	Tolerant	Intermediate
Flower crops	Snapdragon	1·03		

[1] Crops with superscript have more than one ranking.
[2] From Kimball (1983*a,b*), and, if shown, the second value is from Kimball (1986*b*).
[3] Mean relative yield increase of CO_2-enriched (680 ppm) to control crop (300–350 ppm), after Cure & Acock (1986).
[4] Based on biomass accumulation; yield not available.
[5] Field-based result from Rogers *et al.* (1983*a,b*).

TABLE 31
Forest Tree Species by Major Forest Type in the United States

Inter-species comparative weight growth sensitivity available for: CO_2	*UV-B*	O_3	*Tree species*	*Western hemlock–sitka spruce*	*Coastal Douglas-fir*	*SW Oregon mixed conifer*	*True Fir-Mtn. hemlock*	*East OR & WA mixed pine-fir*	*NW Ponderosa pine*	*Redwood*
			Western hemlock	xxxxxxx	xxxxxxx	xxxxxxx	xxxxxxx			xxxxxxx
T		T	Sitka spruce	xxxxxxx		xxxxxxx				xxxxxxx
			Redwood	xxxxxxx						xxxxxxx
S	T	T	Coastal Douglas-fir	xxxxxxx	xxxxxxx	xxxxxxx	xxxxxxx	xxxxxxx	xxxxxxx	xxxxxxx
			Red alder	xxxxxxx						xxxxxxx
			Western red cedar	xxxxxxx	xxxxxxx					
			Pacific silver fir	xxxxxxx			xxxxxxx			
T	–, T	T	Lodgepole pine	xxxxxxx				xxxxxxx	xxxxxxx	
			Mountain hemlock	xxxxxxx	xxxxxxx		xxxxxxx			
S	–	I	Ponderosa pine			xxxxxxx		xxxxxxx	xxxxxxx	

	T	Sugar pine	xxxxxxx				
	T	Incense cedar	xxxxxxx				
		Grand fir	xxxxxxx		xxxxxxx	xxxxxxx	xxxxxxx
+	T	White fir	xxxxxxx			xxxxxxx	
	T	Jeffrey pine	xxxxxxx			xxxxxxx	
		Knobcone pine	xxxxxxx				
		Calif. black oak	xxxxxxx				
		Canyon live oak	xxxxxxx				
		Oregon white oak	xxxxxxx				
		Tan oak	xxxxxxx				xxxxxxx
		Pacific madrone	xxxxxxx				
		Port-Orford-cedar	xxxxxxx				xxxxxxx
–		Noble fir		xxxxxxx			
	T	Western white pine		xxxxxxx			
		Southwest white pine					
		Shasta red fir		xxxxxxx			
		Calif. red fir					
		Subalpine fir		xxxxxxx			
–, T		Engelmann spruce		xxxxxxx			
		Western larch			xxxxxxx	xxxxxxx	

(continued)

TABLE 31—*contd.*

Inter-species comparative weight growth sensitivity available for: CO_2	*UV-B*	O_3	*Tree species*	*Red fir-white fir*	*Calif. mixed conifer*	*Pacific Ponderosa pine*	*Ponderosa pine Rocky mtn. Douglas-fir*	*Western larch*	*West white pine & associates*
			Western hemlock					xxxxxxx	xxxxxxx
T		T	Sitka spruce						
			Redwood						
S	T	T	Coastal Douglas-fir		xxxxxxx	xxxxxxx			
			Red alder						
			Western red cedar					xxxxxxx	xxxxxxx
			Pacific silver fir						
T	–, T	T	Lodgepole pine	xxxxxxx			xxxxxxx		xxxxxxx
			Mountain hemlock	xxxxxxx					
S	–	I	Ponderosa pine		xxxxxxx	xxxxxxx	xxxxxxx		
		T	Sugar pine		xxxxxxx	xxxxxxx			
		T	Incense cedar		xxxxxxx	xxxxxxx			
			Grand fir				xxxxxxx	xxxxxxx	xxxxxxx
	+	T	White fir	xxxxxxx	xxxxxxx	xxxxxxx			
		T	Jeffrey pine	xxxxxxx	xxxxxxx				
			Knobcone pine						
			Calif. black oak		xxxxxxx	xxxxxxx			
		T	Western white pine	xxxxxxx					xxxxxxx
			California red fir	xxxxxxx					
			Subalpine fir					xxxxxxx	xxxxxxx
	–, T		Engelmann spruce						xxxxxxx
			Western larch				xxxxxxx	xxxxxxx	xxxxxxx
			Digger pine			xxxxxxx			
	T	T	Rocky Mtn. Douglas-fir				xxxxxxx	xxxxxxx	xxxxxxx
S ?			Limber pine				xxxxxxx		
S ?			Bristlecone pine				xxxxxxx		
	T		[illegible]						

TABLE 31—*contd.*

Inter-species comparative weight growth sensitivity available for: CO_2	UV-B	O_3	*Tree species*	*Englemann spruce-subalpine fir*	*Lodgepole pine*	*SW Ponderosa pine*	*SW mixed conifer*	*Pinyon-juniper*	*Rocky mtn. aspen*	*Black Hills Ponderosa pine*
			Western hemlock		xxxxxxx					
			Western red cedar		xxxxxxx					
			Pacific silver fir							
T	–, T	T	Lodgepole pine	xxxxxxx	xxxxxxx					
			Mountain hemlock		xxxxxxx					
S	–	I	Ponderosa pine			xxxxxxx	xxxxxxx			xxxxxxx
			Grand fir		xxxxxxx					
	+	T	White fir				xxxxxxx			
		T	Western white pine		xxxxxxx					
			Southwest white pine				xxxxxxx			
			Subalpine fir	xxxxxxx	xxxxxxx					
	–, T		Engelmann spruce	xxxxxxx	xxxxxxx		xxxxxxx			
			Western larch		xxxxxxx					
	T	T	Rocky Mtn. Douglas-fir		xxxxxxx		xxxxxxx			
		S	Aspen	xxxxxxx			xxxxxxx		xxxxxxx	
S			Blue spruce				xxxxxxx			
			Corkbark fir				xxxxxxx			
			Gambel oak				xxxxxxx			
S ?			Limber pine	xxxxxxx		xxxxxxx		xxxxxxx		
S ?			Bristlecone pine	xxxxxxx						
	T		Pinyon pine					xxxxxxx		

Tree species and forest types partially from US Dept. of Agriculture, Forest Service, 1973.
S, –, or + = sensitive; I = intermediate sensitivity; T = tolerant.

(continued)

TABLE 32
Forest Tree Species by Major Forest Type in the United States

Inter-species comparative weight growth sensitivity available for: CO_2	UV-B	O_3	Tree species	Lake states northern hardwood	Red pine	Jack pine	Black spruce	Lake states aspen	Oak-hickory
		S	Aspen		xxxxxxx	xxxxxxx	xxxxxxx	xxxxxxx	xxxxxxx
		S	Sugar maple	xxxxxxx				xxxxxxx	xxxxxxx
			Yellow birch	xxxxxxx					
		I	Eastern hemlock	xxxxxxx					
			American beech	xxxxxxx					xxxxxxx
			Mountain maple	xxxxxxx				xxxxxxx	
			American basswood	xxxxxxx				xxxxxxx	
			Balsam fir	xxxxxxx	xxxxxxx	xxxxxxx	xxxxxxx	xxxxxxx	
			American elm	xxxxxxx					xxxxxxx
		T	Red maple	xxxxxxx	xxxxxxx		xxxxxxx	xxxxxxx	xxxxxxx
S		I	Silver maple					xxxxxxx	xxxxxxx
S	T	I	Eastern white pine	xxxxxxx	xxxxxxx	xxxxxxx		xxxxxxx	xxxxxxx
		S	White ash	xxxxxxx					xxxxxxx
			Paper birch	xxxxxxx	xxxxxxx	xxxxxxx	xxxxxxx		
			Black ash	xxxxxxx			xxxxxxx		xxxxxxx
	T		Red pine		xxxxxxx	xxxxxxx	xxxxxxx	xxxxxxx	
I			Jack pine		xxxxxxx	xxxxxxx	xxxxxxx	xxxxxxx	
		S	Northern pin oak		xxxxxxx	xxxxxxx			xxxxxxx
		T	Northern red oak		xxxxxxx	xxxxxxx		xxxxxxx	xxxxxxx
S	T		White spruce		xxxxxxx	xxxxxxx	xxxxxxx	xxxxxxx	
			American hazel			xxxxxxx			
			Beaked hazel			xxxxxxx			

		Alder	xxxxxxx			
		Red-osier dogwood	xxxxxxx			xxxxxxx
		Willow	xxxxxxx			
		Black spruce		xxxxxxx	xxxxxxx	
		Tamarak		xxxxxxx		
	T	Northern white-cedar		xxxxxxx	xxxxxxx	
		Balsam poplar			xxxxxxx	
	S	White oak				xxxxxxx
		Black oak				xxxxxxx
		Scarlet oak				xxxxxxx
		Chestnut oak				xxxxxxx
		Burr oak				xxxxxxx
		Post oak				xxxxxxx
		Blackjack oak				xxxxxxx
		Southern red oak				xxxxxxx
T		Shagbark hickory				xxxxxxx
		Pignut hickory				xxxxxxx
		Mockernut hickory				xxxxxxx
		Bitternut hickory				xxxxxxx
	T	Blackgum				xxxxxxx
T	S	Yellow (tulip) poplar				xxxxxxx
		Sassafras				xxxxxxx
	T	Black cherry				xxxxxxx
	I	Black locust				xxxxxxx
S	T	Black walnut				xxxxxxx
		Eastern redcedar				xxxxxxx
T	S	Shortleaf pine				xxxxxxx
	S	Pitch pine				xxxxxxx
	I	Virginia pine				xxxxxxx

(continued)

TABLE 32—*contd.*

Inter-species comparative weight growth sensitivity available for: CO_2	*UV-B*	O_3	*Tree species*	*NE spruce-fir*	*East white pine*	*NE northern hardwoods*	*Cherry-maple*	*Appalach. mixed hardwoods*	*Oak-pine*
		S	Aspen	xxxxxxx					
		S	Sugar maple	xxxxxxx		xxxxxxx	xxxxxxx	xxxxxxx	
			Yellow birch	xxxxxxx		xxxxxxx	xxxxxxx	xxxxxxx	
		I	Eastern hemlock	xxxxxxx		xxxxxxx	xxxxxxx	xxxxxxx	
			American beech	xxxxxxx		xxxxxxx	xxxxxxx	xxxxxxx	
			Mountain maple	xxxxxxx		xxxxxxx			
			American basswood					xxxxxxx	
			Balsam fir	xxxxxxx		xxxxxxx			
	T		Fraser fir					xxxxxxx	
		T	Red maple	xxxxxxx		xxxxxxx	xxxxxxx	xxxxxxx	
S		I	Silver maple	xxxxxxx		xxxxxxx		xxxxxxx	
S	T	I	Eastern white pine	xxxxxxx	xxxxxxx			xxxxxxx	
		S	White ash	xxxxxxx		xxxxxxx	xxxxxxx	xxxxxxx	
			Paper birch	xxxxxxx		xxxxxxx			
		T	Northern red oak					xxxxxxx	xxxxxxx

S	T		White spruce	xxxxxxx					
			Black spruce	xxxxxxx					
			Tamarak	xxxxxxx					
		T	Northern white-cedar	xxxxxxx					
		S	White oak					xxxxxxx	xxxxxxx
			Black oak						xxxxxxx
			Scarlet oak						xxxxxxx
			Chestnut oak						xxxxxxx
			Southern red oak						xxxxxxx
T			Shagbark hickory					xxxxxxx	
			Pignut hickory					xxxxxxx	
			Mockernut hickory					xxxxxxx	
			Bitternut hickory					xxxxxxx	
T		S	Yellow (tulip) poplar					xxxxxxx	xxxxxxx
		T	Black cherry				xxxxxxx	xxxxxxx	
		I	Black locust					xxxxxxx	
T		S	Shortleaf pine						xxxxxxx
		I	Virginia pine						xxxxxxx
			Red spruce	xxxxxxx		xxxxxxx		xxxxxxx	
			Sweet birch				xxxxxxx	xxxxxxx	
			Cucumbertree					xxxxxxx	
			Yellow buckeye					xxxxxxx	
S		S	Sweetgum						xxxxxxx
I	–	S	Loblolly pine						xxxxxxx

(continued)

TABLE 32—*contd.*

Inter-species comparative weight growth sensitivity available for: CO_2	*UV-B*	O_3	*Tree species*	*Longleaf & slash pine*	*Atlantic oak gum-cypress*	*Loblolly-shortleaf pine*	*Midsouth oak gum-cypress*
			American beech		xxxxxxx		
			American elm		xxxxxxx		xxxxxxx
		T	Red maple		xxxxxxx		
		S	White ash		xxxxxxx		
		S	White oak		xxxxxxx		
T		S	Yellow (tulip) poplar		xxxxxxx		xxxxxxx
T		S	Shortleaf pine			xxxxxxx	
S		S	Sweetgum		xxxxxxx		xxxxxxx
I	–	S	Loblolly pine		xxxxxxx	xxxxxxx	
			Longleak pine	xxxxxxx			
	–	I	Slash pine	xxxxxxx			
			Water tupelo		xxxxxxx		xxxxxxx
			Swamp tupelo		xxxxxxx		xxxxxxx
			Baldcypress		xxxxxxx		xxxxxxx
			Swamp cottonwood		xxxxxxx		

T	S	Green ash–red ash	xxxxxxx	
		Sweetbay	xxxxxxx	
		Redbay	xxxxxxx	
		Carolina ash	xxxxxxx	
		Overcup oak	xxxxxxx	xxxxxxx
		Water oak	xxxxxxx	
		Laurel oak	xxxxxxx	
	I	Willow oak	xxxxxxx	
		Water hickory	xxxxxxx	
		Sugarberry	xxxxxxx	xxxxxxx
		River birch	xxxxxxx	
I	S	American sycamore	xxxxxxx	xxxxxxx
		Cherrybark oak	xxxxxxx	xxxxxxx
		Swamp chestnut oak	xxxxxxx	
		Winged elm	xxxxxxx	
		Boxelder	xxxxxxx	xxxxxxx
		American holly	xxxxxxx	
S	S	Eastern cottonwood		xxxxxxx
		Black willow		xxxxxxx
		Sweet pecan		xxxxxxx
		Swamp privet		xxxxxxx
		Nuttall oak		xxxxxxx
		Shumard oak		xxxxxxx

Tree species and forest types from US Dept. of Agriculture, Forest Service, 1973.
S, or – = sensitive; I = intermediate sensitivity; T = tolerant.

increased CO_2 are: pea, bean, potato, oat, lettuce, cucumber, rice and tomato. Although they are not major crops, sweet potato and Swiss chard cannot be evaluated at this time because, while they have a high sensitivity to increased CO_2, their sensitivity to enhanced UV-B (sweet potato) and O_3 (both crops) is unknown. However, they should be considered as candidates for further research.

Several crops shown in Table 30 are tolerant to either enhanced UV-B or O_3, but this insensitivity has not been satisfactorily tested for the combined effects. This situation appears simply due to incomplete information on response screening when cross-correlating crop sensitivity to CO_2, UV-B and O_3. Similarly, we do not know how 'protected' eggplant, sweet potato and strawberry might be since the needed information is unknown for either enhanced UV-B or O_3.

There is much less information for tree species. Table 31 gives sensitivity ratings for western tree species in the USA and the respective forest types in which they are found. We used the forest classification of the US Department of Agriculture (1973) to relate tree species to forest types in the USA. Table 31 is a synthesis of data in Tables 12, 16 and 26 for enhanced UV-B, elevated CO_2 and O_3. A major limitation is that these sensitivity ratings are for each stress factor individually and in the absence of any other stress. Also, it must be noted that this information was obtained only for seedlings, not for saplings, or mature trees. Therefore, the more conservative application is to consider this information as relevant only to regeneration, and not to established forest stands.

Table 31 shows that only about one fourth of the western USA tree species have been evaluated for biomass responses to O_3, and even fewer species have been examined for their responses to UV-B enhancement or increased CO_2. Information is available on only three species, Douglas-fir, lodgepole pine and ponderosa pine, concerning their sensitivity to all three potential stress factors. Of these, ponderosa pine should be used as an example for further research on possible interactions between the three factors and biomass response. In terms of seedling biomass response, this species (or at least certain varieties of the species) was reported to be sensitive to increased CO_2, enhanced UV-B, and at least intermediately sensitive to O_3. Only future research designed to analyze the possible interactions between these stress factors simultaneously, and/or sequentially in various exposure patterns, will be able to determine the nature of response of ponderosa pine in the integrative sense. There is the possibility that some combination of this set of interactions could alter species composition in almost half of the western forest types because ponderosa pine is a component of the following forests: Southwestern Oregon Mixed Conifer; Eastern Oregon and Washington Mixed Pine–Fir; Northwestern Ponderosa Pine; California Mixed Conifer;

Pacific Ponderosa Pine; Ponderosa Pine–Rocky Mountain Douglas Fir; Southwestern Ponderosa Pine; Southwestern Mixed Conifer; and Black Hills Ponderosa Pine.

Only slightly more than one-fourth of the tree species in the eastern USA have been evaluated for sensitivity to O_3 and biomass response, and only half as many have been evaluated for responses to increased CO_2 (Table 32). Very few species have been examined for their sensitivity to enhanced UV-B, and only two species, loblolly and slash pine, showed significant growth reductions to the exposures used. Information is available for only two species, eastern white and loblolly pine, concerning their sensitivity to all three potential stress factors. However, eastern white pine was reported to be tolerant to the enhanced UV-B dose used. For this reason, we conclude that the tree species that should be used for further research on possible interactions under field conditions is loblolly pine. In terms of seedling biomass growth, this species is reported to be intermediately sensitive to increased CO_2, sensitive to enhanced UV-B, and O_3. More evaluation of the responses of eastern forest tree species is obviously needed to enhanced UV-B and increased CO_2 especially since the effects of UV-B enhancement have only been examined for the conifers and not for any deciduous hardwood species. Of the 16 eastern USA forest types, loblolly pine is found in three: Oak–Pine; Atlantic Oak–Gum Cypress; and the Loblolly–Shortleaf Pine type. It is noteworthy that Table 12 shows several European hardwoods to be sensitive to enhanced UV-B (beech, Norway maple and common ash) with mixed results for hornbeam and sycamore–maple.

AN ASSESSMENT: ANALYSIS AND ESTIMATION OF INTERACTIONS

Of the nine crops identified in this analysis as being sensitive to increased CO_2, enhanced UV-B and tropospheric O_3, three are grain crops (sorghum, oat and rice) having international importance. Of the remaining six vegetable crops, potato, has international significance. The five remaining vegetable crops are of major significance primarily in North America and Western Europe.

One way to assess the possible interactions between the stress factors discussed in this paper is on a geographic basis. We considered the international distribution of sorghum, potato, oat and rice. For the remaining vegetable crops and sorghum, we considered the spatial variation of production within the United States based on the 1982 Census of Agriculture (United States Department of Commerce, 1985).

According to the world map of the distribution of sorghum, this crop is

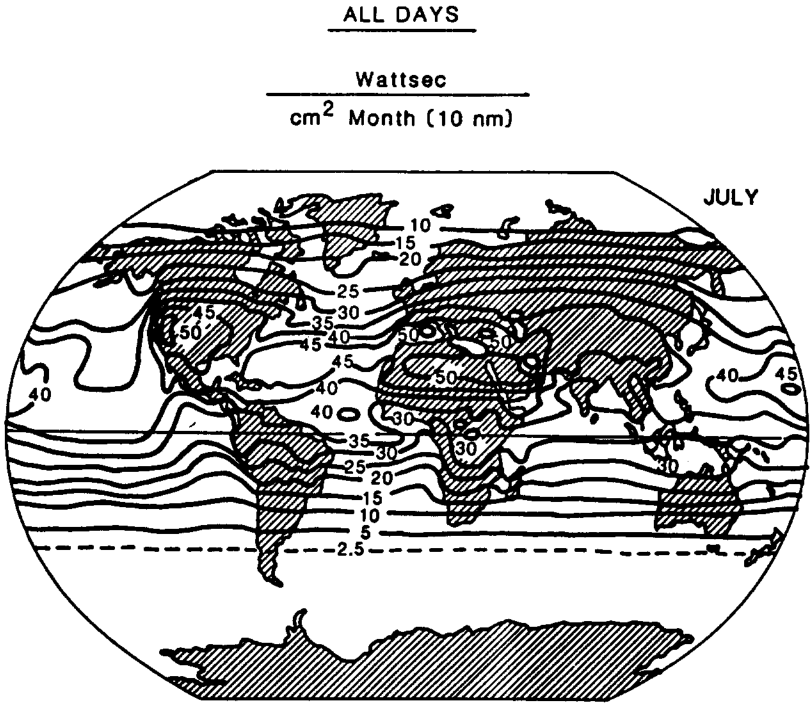


Fig. 8. Global patterns of UV radiation (Source: Schulze & Gräfe, 1969).

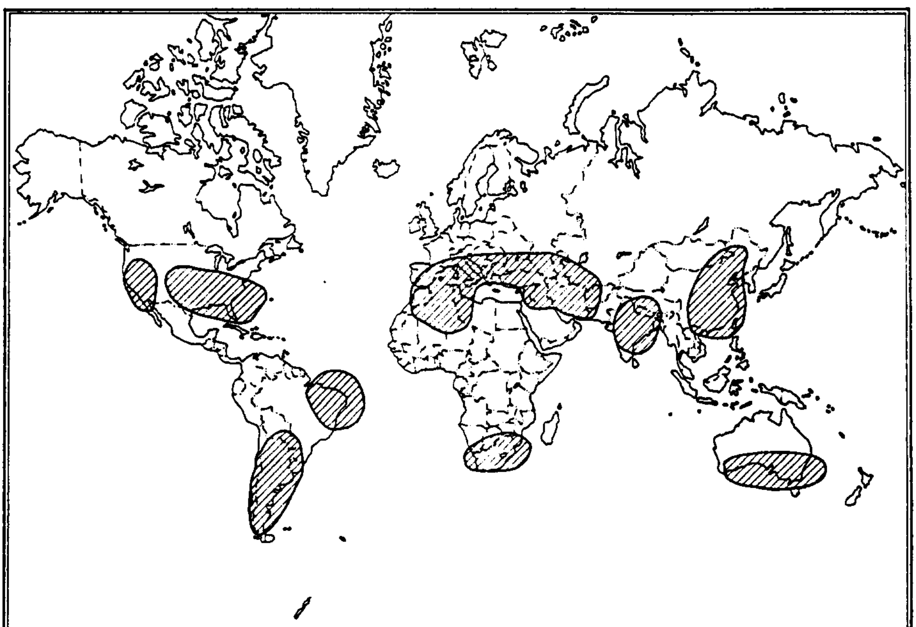


Fig. 9. Regions of high susceptibility to photochemical smog. (Source: Hidy *et al.*, 1978).

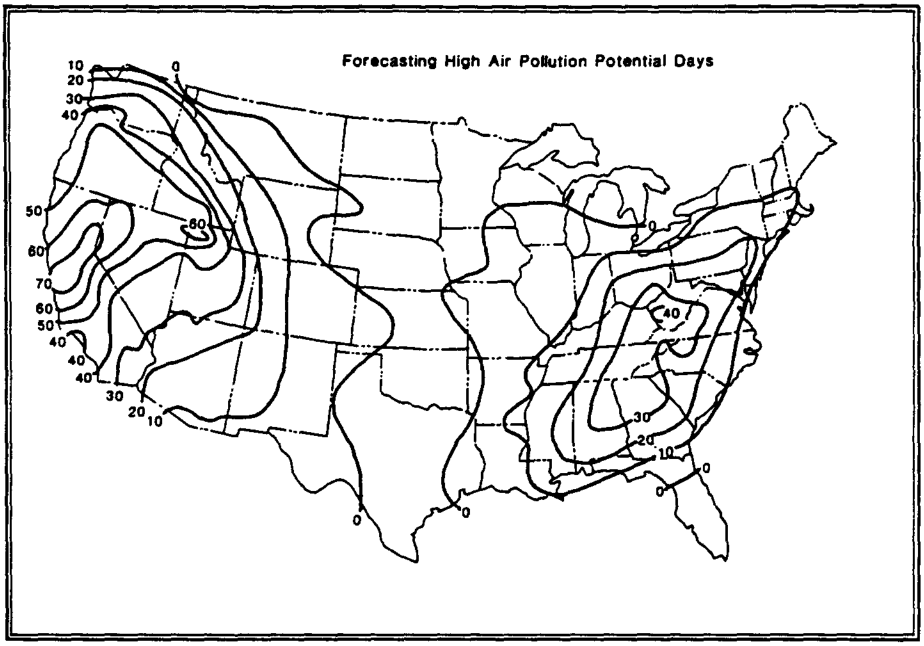
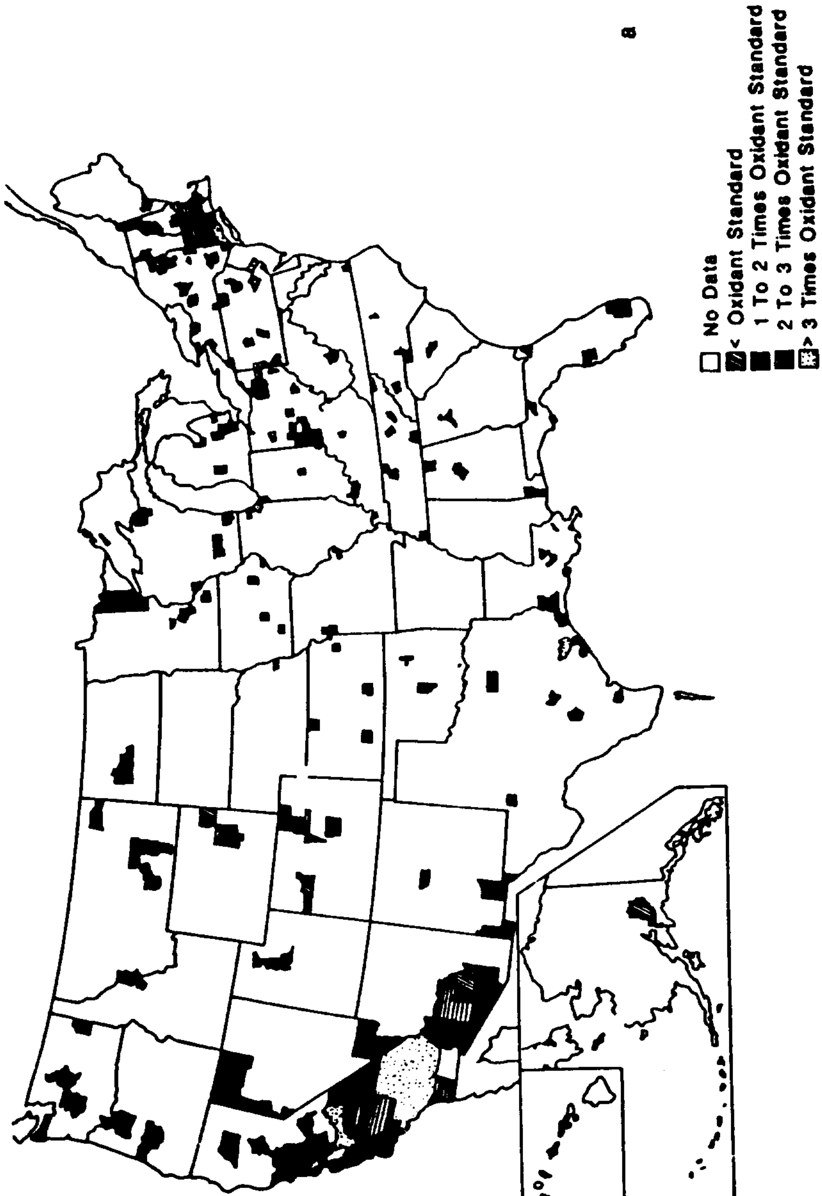


Fig. 10. Isopleths of total numbers of forecast-days of high meteorological potential for air pollution in a five year period. (Source: Holzworth, 1972).

grown in the central and southern Great Plains in the USA, northern China, and to some extent in southern Bolivia and far northern Argentina. During the growing season, UV-B radiation of 45 to 50 W s cm^{-2} $month^{-1}$ is indicated in this portion of the USA (Fig. 8). Somewhat less (approximately 40 W s cm^{-2} $month^{-1}$) is shown for northern China in July, and the South American countries growing sorghum in January. According to Hidy *et al.* (1978) these three regions are highly susceptible to photochemical smog (Fig. 9).

For the USA, if one considers the map of Holzworth (1972), for high meteorological air pollution potential (Fig. 10), and that of King (1988) (Fig. 11b), as being indicative of the spatial distribution of O_3 in the troposphere and capable of absorbing any enhanced UV-B radiation, then these maps could be considered in a very rough sense as a negative image of UV-B radiation flux density with an increasing geophysical north to south gradient.

A closer look at the USA situation using Holzworth's map (Fig. 10) and the USA map for sorghum harvested (Fig. 12) shows that region as being more vulnerable in the future if increased UV-B should occur, while being relatively free of air pollution on a regional scale. Sorghum production in the Mississippi River basin and the southeastern states, however, could be


a
No Data
< Oxidant Standard
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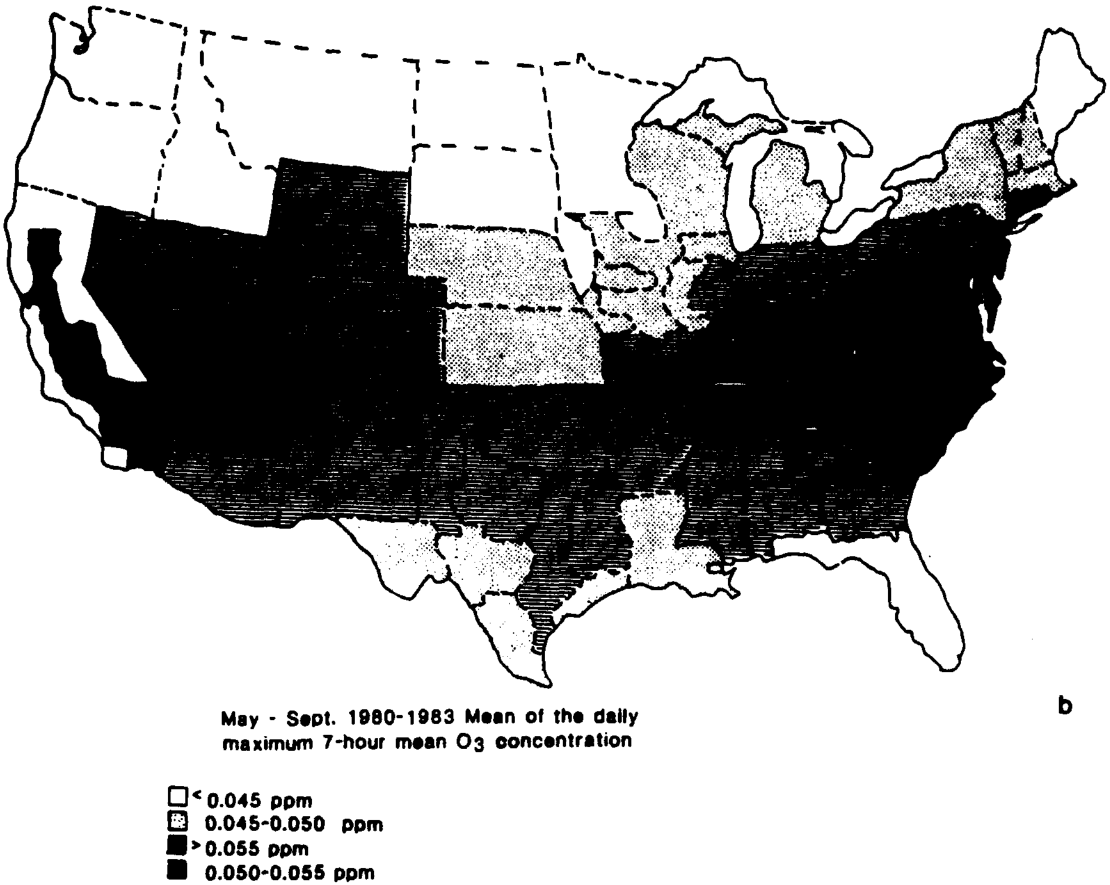

Fig. 11. a: Photochemical oxidants, second daily one hour average, 1974–1976. The 1-h primary and secondary national ambient air quality standards were 0·08 ppm (160 $\mu g\ m^{-3}$), not to be exceeded more than once per year. (Source: EPA, 1977). b: Mean O_3 concentrations for 68 crop production areas in the US determined by A. S. Lefohn (unpublished). No estimates were made for blank areas. (Source: King, D. A., 1988).

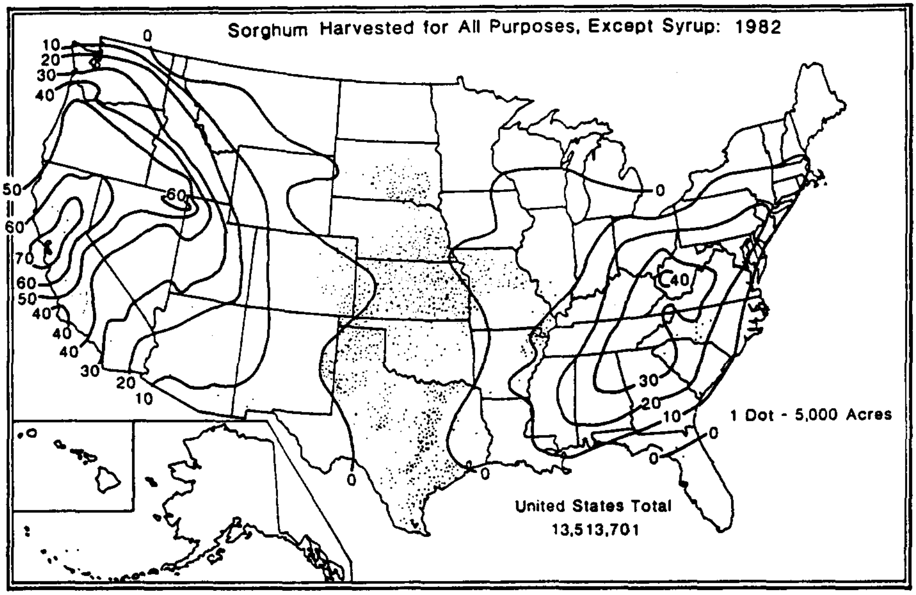

Fig. 12. Distribution of sorghum growing areas in the US and area under cultivation. 2·47 acres = 1 hectare. (Source: US Dept. of Commerce, 1985). Isopleths from Fig. 10 are overlayed on the crop data.

subjected to an interaction between periods of low pollution and increased UV-B, and periods of increased tropospheric air pollution.

On a global scale potato production is highest in Europe. The map of global UV-B shows a north–south range of 25 to 45 $W s cm^{-2} month^{-1}$ during July. The southern portion of Europe is also known to have a high susceptibility to photochemical oxidant pollution.

Oats are grown in the southern Canadian plains, the north central USA, northern Europe and western USSR. These areas are outside of the regions of high susceptibility to O_3 pollution (Fig. 9) according to Hidy *et al.* (1978). They also correlate spatially with areas of lower UV-B radiation during July (Fig. 8).

Rice production is highly concentrated in southern China, Japan and Bangladesh. Figure 8 shows that all three regions exhibit UV-B radiation during July of roughly 35 to 40 $W s cm^{-2}$. Southern China and Bangladesh may also be highly susceptible to O_3 pollution according to Hidy *et al.* (1978) (Fig. 9).

The remaining crops identified as sensitive to CO_2, UV-B and O_3 are vegetables for which we considered the USA distribution. Commercial pea and snap bean production is shown in Figs 13 and 14. The Pacific Northwest region might have a slightly higher UV-B radiation load in July when compared to the North Central states, but the prominent production

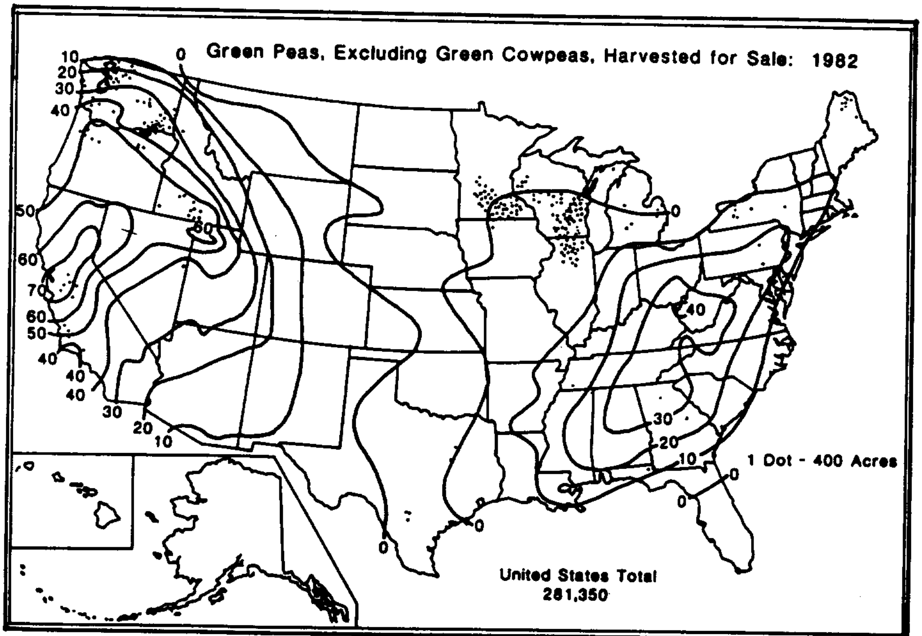

Fig. 13. Distribution of pea growing areas in the US and area under cultivation. 2·47 acres = 1 hectare. (Source: US Dept. of Commerce, 1985). Isopleths from Fig. 10 are overlayed on the crop data.

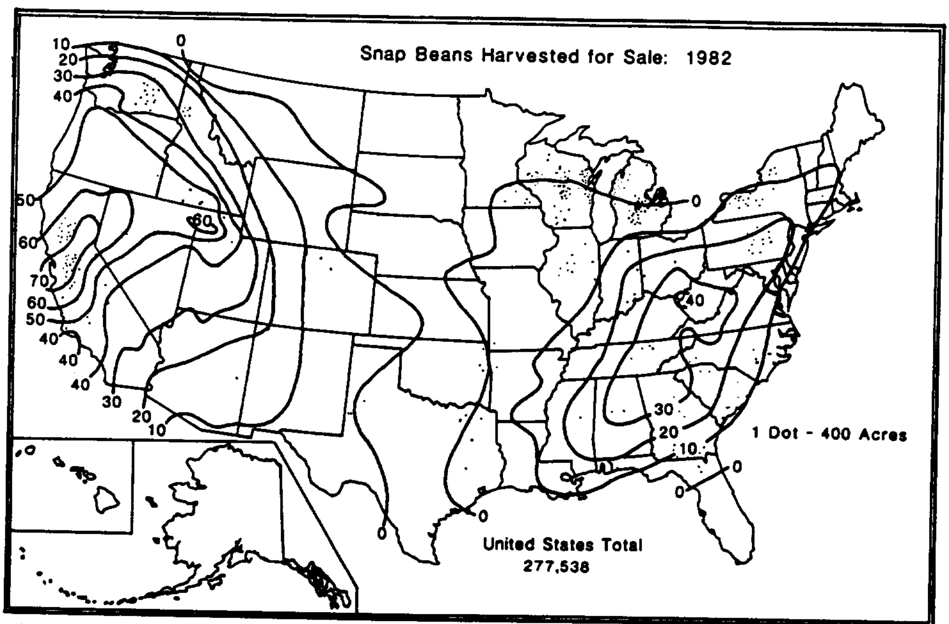

Fig. 14. Distribution of snap bean growing areas in the US and area under cultivation. 2·47 acres = 1 hectare. (Source: US Dept. of Commerce, 1985). Isopleths from Fig. 10 are overlayed on the crop data.

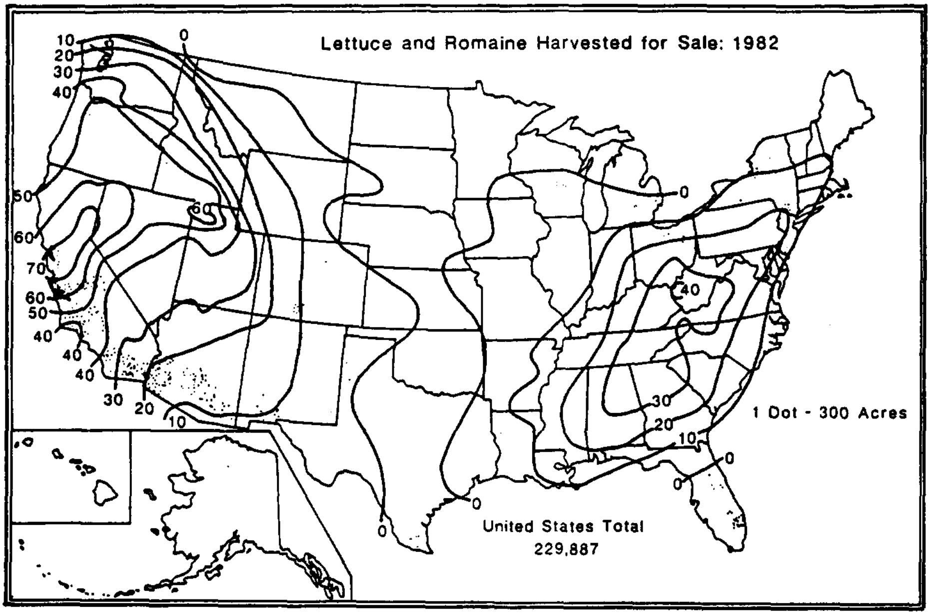

Fig. 15. Distribution of lettuce growing areas in the US and area under cultivation. 2·47 acres = 1 hectare. (Source: US Dept. of Commerce, 1985). Isopleths from Fig. 10 are overlayed on the crop data.

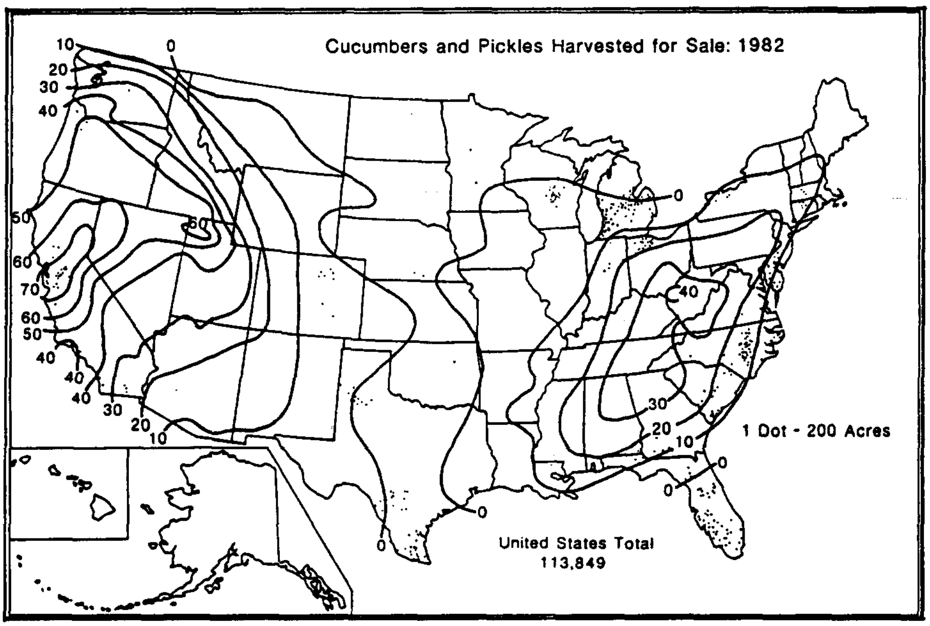

Fig. 16. Distribution of cucumber growing areas in the US and area under cultivation. 2·47 acres = 1 hectare. (Source: US Dept. of Commerce, 1985). Isopleths from Fig. 10 are overlayed on the crop data.

nationwide is at least in the 40 to 45 W s cm^{-2} $month^{-1}$ range. Holzworth's map (Fig. 10) would indicate that the Pacific Northwest would have more air pollution days, but King's map (Fig. 11b) shows the North Central states as having a higher mean O_3 concentration.

Lettuce is commercially important in central and southern California, and southern Arizona (Fig. 15). These are areas of 40 to 45 W s cm^{-2} $month^{-1}$ UV-B in July (Fig. 8). They are also areas of high measured and potential (Fig. 10) air pollution.

Commercial cucumber production is largely a 'coastal' crop (including the Great Lakes) around the contiguous 48 states (Fig. 16). As a result, with the exception of Florida and extreme coastal California (Fig. 11b), most of the production areas have at least some air pollution well exceeding a background level during the growing season. The maps of both Hidy *et al.* (Fig. 9), and Holzworth (Fig. 10), indicate the southern Great Lakes area should be more pollution-free than indicated in the map of King (Fig. 11b). The global UV-B map for July (Fig. 8) shows the southern Great Lakes area as exhibiting a value of around 45 W s cm^{-2}, but generally less than that value for the circum-continental cucumber growing areas.

Tomatoes are commercially harvested to a great extent in interior California, southwest Florida, eastern Maryland–central Pennsylvania and

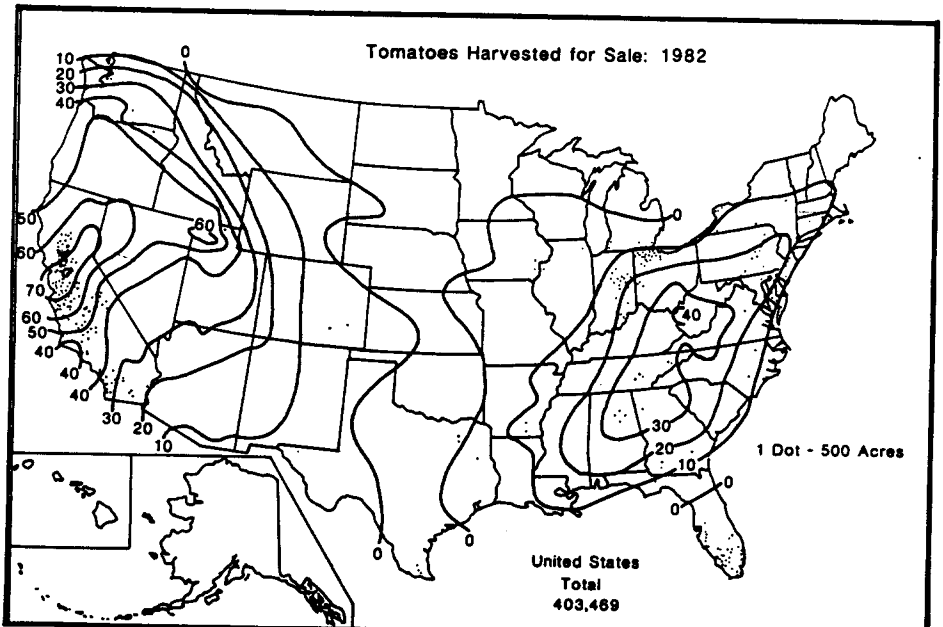

Fig. 17. Distribution of tomato growing areas in the US and area under cultivation. 2·47 acres = 1 hectare. (Source: US Dept. of Commerce, 1985). Isopleths from Fig. 10 are overlayed on the crop data.

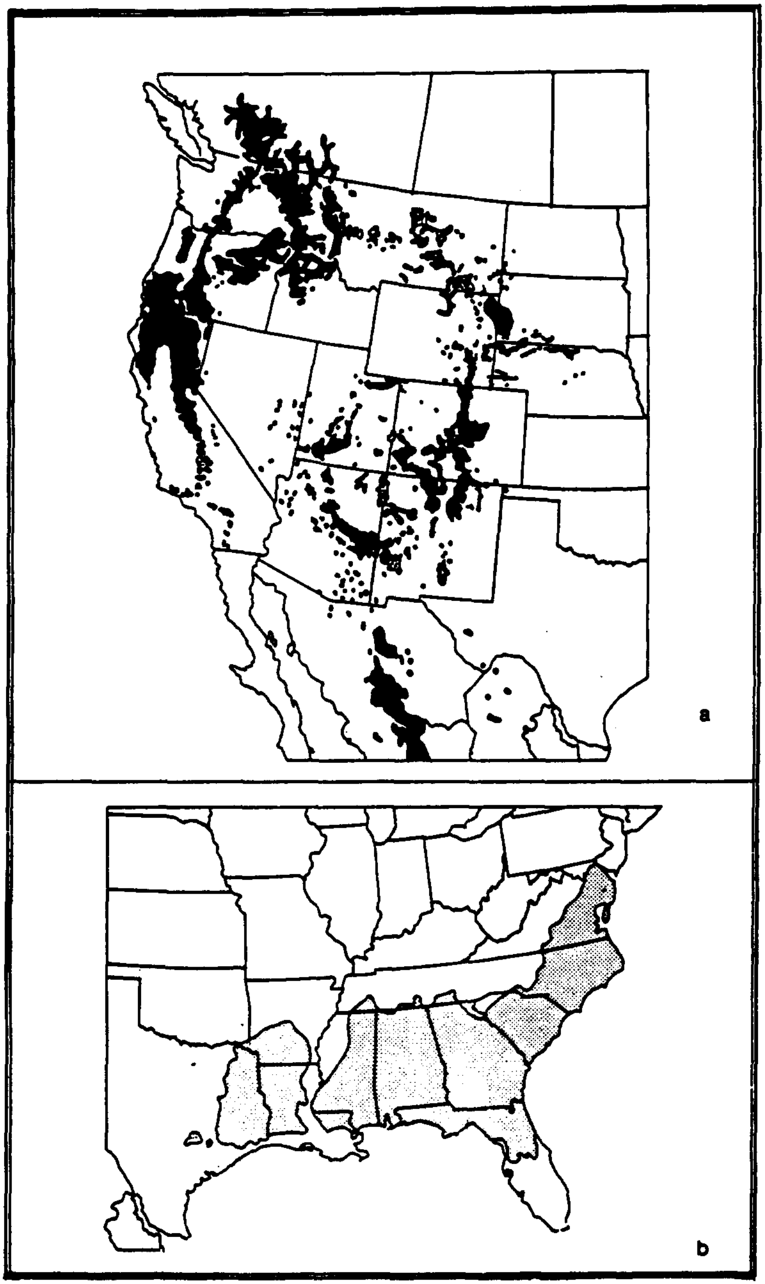

Fig. 18. a & b: Geographic distribution of Ponderosa (dark areas in a) and lobolly (dotted areas in b) pine in the US. (Source: Fowells, 1965).

Indiana–Ohio (Fig. 17). All of these areas are shown to have a July UV-B level of 40 to 45 W s cm^{-2} (Fig. 8). Florida is the only one of these production areas shown to be relatively free of potential (Fig. 10), or measured (Fig. 11a), O_3 pollution. The other three areas can have days of relatively high O_3 concentration during the growing season.

Similarly the possibility of increased UV-B effects on ponderosa pine can be seen by comparing the species geographic distribution (Fig. 18a) to the map of July global solar UV-B radiation (Fig. 8). The latter shows a high region of 50 W s cm^{-2} (10 nm) at wavelength 307·5 nm (within the UV-B band) over the far western United States approximately over the northern Sierre Nevada portion of California. This intensity of radiation is found elsewhere only over North Africa and the Arabian Peninsula. In addition, Holzworth's map of days of high meteorological potential for air pollution (Fig. 10) shows a high number of such days over the geographic extent of ponderosa pine.

The geographic range of loblolly pine (Fig. 18b), when compared to the map of July global solar UV-B radiation, is found to range from between 40 to 45 W s cm^{-2} (10 nm) on the southeast coast of the US to over 45 W s cm^{-2} (10 nm) on the far western end of its range in eastern Texas. The range of loblolly pine also extends along and then down the gradient of the southern portion of the geographic area with high number of potential days of air pollution in Holzworth's map (Fig. 10). Based on the sensitivity of this species, and the geographic distributions for UV-B and air pollution potential, we conclude that there is a possibility for interaction over the growing season between enhanced UV-B and tropospheric O_3 relative to effects on loblolly pine.

After we consider the sequence of agricultural crop sensitivity to CO_2, UV-B and O_3 (sorghum, pea, bean, potato, oat, lettuce, cucumber, rice and tomato), and the two tree species, ponderosa and loblolly pine, one of the next steps should be to incorporate, for each of the potential stress factors and plant species, realistic quantitative exposure–response equations into suitable growth simulation models. There is an existing knowledge base of such growth models (McLeod, 1989) that can provide the foundation upon which to incorporate the additional processes to study plant responses to the complex set of potential climatic stress factors discussed in this paper. The result of this work should provide sets of dynamic alternative working hypotheses which could be used to guide further experimental field research under multiple stress conditions in agricultural and forest ecosystems.

In terms of the types of interactions between surface O_3 and a possible future increase in UV-B flux, we envision two model situations. Figure 19 characterizes a temporal pattern of sequential exposures over relative time. Ozone episodes are interspersed between episodes of enhanced UV-B at the

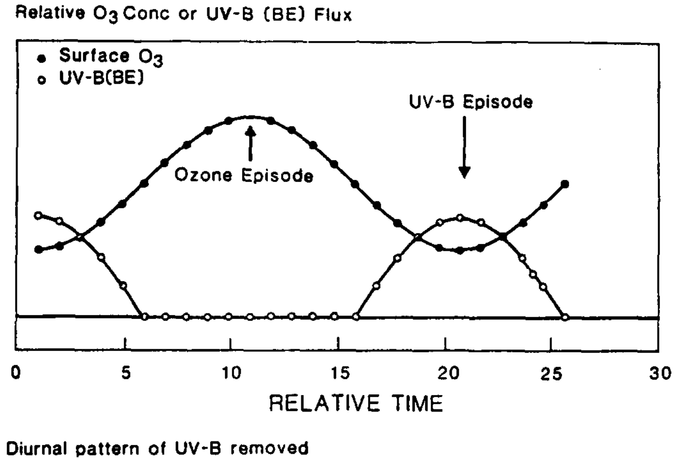

Fig. 19. A model situation showing a pattern of sequential exposure to surface O_3 and UV-B.

surface, where the latter depletes surface O_3 pollution to some extent. Alternatively the lower O_3 concentrations during respite periods allows enhanced UV-B. This could take place downwind of northern mid-latitude cities and metropolitan areas. In latitudes closer to the sub-tropics, enhanced UV-B would be higher as shown in Fig. 20. When surface O_3 episodes occur in this situation, it would decrease the concurrent UV-B flux, but vegetation would still be exposed to simultaneous stimuli from still-increased UV-B and surface O_3.

The question then arises: What might be the nature of the multiple stress effect on crops and forests? In the sense of Platt's (1964) philosophy, we suggest three alternative working hypotheses:

1. There might be no interaction between the stress factors. The 'Law of Limiting Factors' might prevail in which the most severe stress overrides plant response.
2. There might be a cumulative effect in which the net plant response is simply the sum of stress effects from O_3 and increased UV-B regardless of the temporal patterns of exposure.
3. There might be a more than additive effect where the plant response is more severe than would be found from either stress singly. There is also the possibility of a less than additive interaction in the sense that high ambient CO_2 might allow sufficient repair processes to proceed in some plants so that sensitivity to increased UV-B and /or ambient O_3 may be reduced.

If one conceives of mathematical functions, or graphs, where the 'UV-B effect' and 'Ozone effect' on net photosynthesis (P_{NA}) as an example are

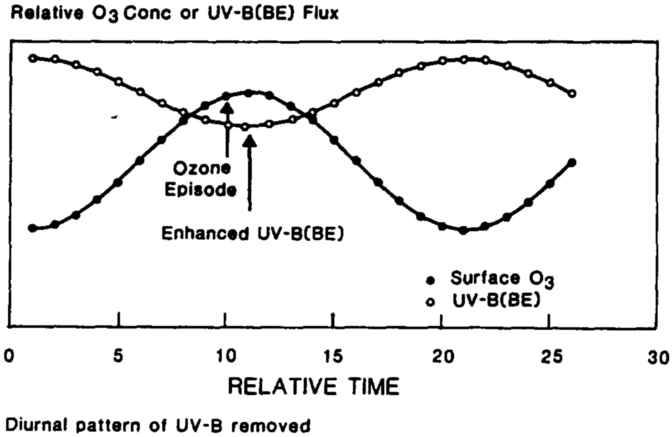

Fig. 20. A model situation showing a pattern of simultaneous exposure to surface O_3 and UV-B.

scaled between 0·0 to 1·0 as functions of UV-B(BE) and ambient O_3 exposure respectively, then, as a first approximation to mathematical model development, we consider the following counterparts to the three hypotheses stated above:

1. $P_{NA} = P_{NCO2} \times$ AMIN (UV-B effect, O_3 effect)
   where P_{NCO2} is the net photosynthesis modeled as a response to increased CO_2, P_{NA} is net photosynthesis after adjustment for UV-B and/or O_3, and AMIN is a computer program function than means 'use the minimum value of the variables in parenthesis' which actually represent the most severe stress;
2. $P_{NA} = P_{NCO2} \times (1 -$ AMIN[1 − UV-B effect) + (1 − O_3 effect), 1])
3. $P_{NA} = P_{NCO2} \times C \times$ (UV-B effect × O_3 effect)
   where C is a coefficient of proportionality. This set of alternative hypotheses could be imbedded within a larger, comprehensive crop growth model run day-by-day over the growth season for the purpose of conducting computer simulation experiments.

For those plant species that show sensitivity to any two of the environmental stimuli, O_3, enhanced UV-B radiation, or increased CO_2, or especially for those species that are sensitive to all of these stimuli, serious questions must be raised about the results of ambient field exposures of such plants to either O_3, enhanced UV-B, or increased CO_2 alone. We know of no ambient field exposures of plants to O_3 in which the study also included measurements of natural UV-B and ambient CO_2 concentrations. Any plant effects not attributable to O_3, which might have occurred in such studies would be unidentified and masked in the error terms of any quantitative analyses. Likewise, none of the open field experiments of enhanced UV-B radiation on plants have included the measurements of ambient O_3, or any other air pollutant, or CO_2. Accordingly, results of such studies could be confounded by the effects of pollutants and/or the increase in CO_2, in addition to failing to describe microclimatic flows of radiant and heat energy and moisture, for comparison to analogue studies in artificial exposure environments. However, if any increase in CO_2 in the field is a very stable long-term process without a high frequency of variability, it simply means that the *relative* level of effects between plant species and cultivars under experimentally enhanced UV-B radiation might not be affected by the long-term increase in CO_2. The *absolute* level of effects would, however, be unknown because we do not know the 'normal' concentration of CO_2 in a given ambient environment to which plant species and cultivars have become adapted over time.

The only way out of this dilemma in the future is for field experiments to include monitoring and analysis of all three potential stress factors, in addition to the more common considerations generally given to soil and meteorological constraints, as well as the effects of biotic pathogens and pests, on plant growth. First order numerical time series models which can accommodate such measurements in evaluating cause–effects relationships are presently available (Krupa & Nosal, 1989*a*,*b*). However, such models must be integrated with approaches to plant disease epidemiology and would require the use of main-frame computers.

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APPENDIX

Nomenclature of Common and Latin Names of Plant Species

Common name	*Latin name*
Alder	*Alnus* sp.
Alfalfa	*Medicago sativa*
Alpine (whiproot) clover	*Trifolium dasyphyllum*
Alpine pussytoe	*Antennaria alpina* var. *media*
Alpine sorrel	*Rumex alpinus*
Alyce clover	*Alysicarpus vaginalis*
American basswood	*Tilia americana*
American beech	*Fagus grandifolia*
American elm	*Ulmus americana*
American hazel	*Corylus americana*
American holly	*Ilex opaca*
American linden	*Tilia americana*
American sycamore	*Platanus occidentalis*
Apple	*Malus pumila*
Artichoke	*Cynara scolymus*
Asparagus	*Asparagus officinalis*
Austrian pine	*Pinus nigra*
Baldcypress	*Taxodium distichum*
Balsam fir	*Abies balsamea*
Balsam poplar	*Populus balsamifera*
Barley	*Hordeum vulgare*
Beaked hazel	*Corylus cornuta*
Bean	*Phaseolus* sp.
Beet	*Beta* sp.
Bermudagrass	*Cynodon dactylon*
Big cone Douglas-fir	*Pseudotsuga macrocarpa*
Birch	*Betula* sp.
Bitternut hickory	*Carya cordiformis*
Black ash	*Fraxinus nigra*
Black cherry	*Prunus serotina*
Black locust	*Robinia pseudoacacia*
Black oak	*Quercus velutina*
Black spruce	*Picea mariana*
Black walnut	*Juglans nigra*
Black willow	*Salix nigra*

(continued)

Common name	*Latin name*
Blackgum	*Nyssa sylvatica*
Blackjack oak	*Quercus marilandica*
Blue spruce	*Picea pungens*
Bluebell	*Browallia speciosa*
Blueberry	*Vaccinium* sp.
Boxelder	*Ader negundo*
Bristlecone pine	*Pinus longaeva*; *Pinus aristata*
Broad-leaved dock	*Rumex obtusifolius*
Broccoli	*Brassica oleracea* var. *botrytis*
Brussels sprout	*Brassica oleracea* var. *gemmifera*
Bur oak	*Quercus macrocarpa*
Cabbage	*Brassica oleracea* var. *capitata*
California black oak	*Quercus kelloggii*
California red fir	*Abies magnifica*
Canada thistle	*Cirsium arvense*
Cantaloupe	*Cucumis melo* var. *cantalupensis*
Canyon live oak	*Quercus chrysolepsis*
Carnation	*Dianthus caryophyllus*
Carolina ash	*Fraxinus caroliniana*
Carrot	*Daucus carota*
Cauliflower	*Brassica oleracea* var. *botrytis*
Celery	*Apium graveolens*
Chard	*Beta vulgaris* var. *cicla*
Cheatgrass	*Bromus tectorum*
Cherrybark oak	*Quercus falcata* var. *pagodaefolia*
Chestnut oak	*Quercus prinus*
Chrysanthemum	*Chrysanthemum morifolium*
Chufa	*Cyperus esculentus*
Clover	*Trifolium* sp.
Coastal Douglas-fir	*Pseudotsuga menziesii* var. *menziesii*
Collard	*Brassica oleracea* var. *acephala*
Common ash	*Fraxinus excelsior*
Common hornbeam	*Carpinus betulus*
Common monkey flower	*Mimulus guttatus*
Corkbark fir	*Abies lasiocarpa* var. *arizonica*
Corn	*Zea mays*
Cotton	*Gossypium hirsutum*
Coulter pine	*Pinus coulteri*

Common name	Latin name
Cowpea	*Vigna sinensis*
Crabapple	*Malus toringoides*
Crimson clover	*Trifolium incarnatum*
Crotalaria	*Crotalaria spectabilis*
Cucumber	*Cucumis sativus*
Cucumbertree	*Magnolia acuminata*
Cyclamen	*Cyclamen* sp.
Daisy	*Chrysanthemum vulgare*
Dandelion	*Taraxacum officinale*
Desmodium	*Desmodium paniculatum*
Digger pine	*Pinus sabiniana*
Digitgrass	*Digitaria decumbens*
Dogbane	*Apocynum pumilum*
Douglas-fir	*Pseudotsuga menziesii*
Duckweed	*Lemna* sp.
Eastern cottonwood	*Populus deltoides* var. *deltoides*
Eastern hemlock	*Tsuga canadensis*
Eastern red cedar	*Juniperus virginiana*
Eastern white pine	*Pinus strobus*
Eggplant	*Solanum melongena*
Endive	*Cichorium endivia*
Engelmann spruce	*Picea engelmannii*
English daisy	*Bellis perennis*
European beech	*Fagus sylvatica*
Fescue grass	*Festuca* sp.
Floribunda rose	*Rosa* sp.
Flowering dogwood	*Cornus florida*
Foxtail	*Setaria glauca*
Fraser fir	*Abies fraseri*
Gambel oak	*Quercus gambelii*
Grand fir	*Abies grandis*
Grape	*Vitis* sp.
Green ash	*Fraxinus pennsylvanica*
Groundsel	*Senecio sylvaticus*
Hemp	*Cannabis sativa*
Honey locust	*Gleditsia triacanthos*
Incense cedar	*Callocedrus decurrens*
Inland ponderosa pine	*Pinus ponderosa* var. *scopulorum*
Italian ryegrass	*Lolium multiflorum*

(continued)

Common name	*Latin name*
Itchgrass	*Rottboellia exaltata*
Ivy geranium	*Geranium* sp.
Jack pine	*Pinus banksiana*
Jeffrey pine	*Pinus jeffreyi*
Jimson weed	*Datura stramonium*
Johnson grass	*Sorghum halepense*
Jointed goatgrass	*Aegilops cylindrica*
Kale	*Brassica oleracea* var. *acephala*
Kentucky bluegrass	*Poa pratensis*
Knobcone pine	*Pinus attenuata*
Kobresia sedge	*Kobresia myosuroides*
Kohlrabi	*Brassica oleracea* var. *gongylodes*
Large yellow monkey flower	*Mimulus tilingi*
Largeleaf avens	*Geum macrophyllum*
Laurel oak	*Quercus laurifolia*
Lemon	*Citrus limon*
Lesser duckweed	*Lemna minor*
Lettuce	*Lactuca sativa*
Limber pine	*Pinus flexilis*
Loblolly pine	*Pinus taeda*
Lodgepole pine	*Pinus contorta*
Longleaf pine	*Pinus palustris*
Marigold	*Tagetes* sp.
Millet	*Setaria italica*
Mockernut hickory	*Carya tomentosa*
Monterey pine	*Pinus radiata*
Mountain hemlock	*Thuja mertensiana*
Mountain maple	*Acer spicatum*
Mouse-ear cress	*Arabidopsis* sp.
Mullein	*Verbascum phlomoides*
Muskmelon	*Cucumis melo*
Mustard	*Brassica* sp.
Nasturtium	*Tropaeolum* sp.
New Zealand red beech	*Nothofagus fusca*
Noble fir	*Abies procera*
Northern pin oak	*Quercus ellipsoidalis*
Northern red oak	*Quercus rubra*
Northern white cedar	*Thuja occidentalis*
Norway maple	*Acer platanoides*

Common name	Latin name
Norway spruce	*Picea abies*
Nuttall oak	*Quercus nuttallii*
Oat	*Avena sativa*
Okra	*Hibiscus esculentus*
Onion	*Allium cepa*
Orange	*Citrus* sp.
Orchard grass	*Dactylis glomerata*
Oregon white oak	*Quercus garryana*
Overcup oak	*Quercus lyrata*
Pacific madrone	*Arbutus menziesii*
Pacific silver fir	*Abies amabilis*
Paper birch	*Betula papyrifera*
Parsley	*Petroselinum crispum*
Parsnip	*Pastinaca sativa*
Patience dock	*Rumex patientia*
Pea	*Pisum sativum*
Peanut	*Arachis hypogaea*
Pepper	*Capsicum frutescens*
Peppergrass	*Lepidium perfoliatum*
Perennial ryegrass	*Lolium perenne*
Petunia	*Petunia* sp.
Pignut hickory	*Carya glabra*
Pigweed	*Amaranthus retroflexus*
Pin oak	*Quercus palustris*
Pinto bean	*Phaseolus vulgaris*
Pinyon pine	*Pinus edulis*
Pitch pine	*Pinus rigida*
Plantain	*Plantago patagonica*
Poinsettia	*Euphorbia pulcherrima*
Ponderosa pine	*Pinus ponderosa*
Port-Orford-cedar	*Chamaecyparis lawsoniana*
Post oak	*Quercus stellata*
Potato	*Solanum tuberosum*
Pullup muhly	*Muehlenbergia filiformis*
Pumpkin	*Cucurbita pepo*
Quaking aspen	*Populus tremuloides*
Radish	*Raphanus sativus*
Ragweed	*Ambrosia artemisiifolia*
Red alder	*Alnus rubra*

(*continued*)

Common name	Latin name
Red ash	*Fraxinus pennsylvanica*
Red beet	*Beta* sp.
Red clover	*Trifolium pratense*
Red fir	*Abies magnifica*
Red kidney bean	*Phaseolus vulgaris*
Red maple	*Acer rubrum*
Red oak	*Quercus rubra*
Red pine	*Pinus resinosa*
Red raspberry	*Rubus strigosus*
Red spruce	*Picea rubens*
Red-osier dogwood	*Cornus stolonifera*
Redbay	*Percea borbonia*
Redroot pigweed	*Amaranthus retroflexus*
Redwood	*Sequoia sempervirens*
Rhubarb	*Rheum rhaponticum*
Rice	*Oryza sativa*
Richardson geranium	*Geranium richardsonii*
River birch	*Betula nigra*
Rock sedge	*Carex rupestris*
Rocky Mountain Douglas-fir	*Pseudotsuga menziesii* var. *glauca*
Rose	*Rosa* sp.
Rutabaga	*Brassica napobrassica*
Rye	*Secale cereale*
Sassafras	*Sassafras albidum*
Scarlet oak	*Quercus coccinea*
Scotch pine	*Pinus silvestris*
Scots pine	*Pinus silvestris*
Shagbark hickory	*Carya ovata*
Shasta red fir	*Abies magnifica* var. *shastensis*
Shortleaf pine	*Pinus echinata*
Shumard oak	*Quercus shumardii*
Sicklepod	*Cassia obtusifolia*
Silver maple	*Acer saccharinum*
Sitka spruce	*Picea sitchensis*
Slash pine	*Pinus elliottii*
Snap bean	*Phaseolus vulgaris*
Snapdragon	*Antirrhinum majus*
Sorghum	*Sorghum vulgare*
Southern red oak	*Quercus falcata* var. *falcata*

Common name	Latin name
Southwestern white pine	*Pinus strobiformis*
Soybean	*Glycine max*
Spinach	*Spinacia oleracea*
Squash	*Cucurbita* sp.
Strawberry	*Fragaria* sp.
Subalpine fir	*Abies lasiocarpa*
Sudan grass	*Sorghum sudanense*
Sugar beet	*Beta vulgaris*
Sugar maple	*Acer saccharum*
Sugar pine	*Pinus lambertiana*
Sugarberry	*Celtis laevigata*
Sugarcane	*Saccharum officinarum*
Sunflower	*Helianthus annuus*
Swamp chestnut oak	*Quercus michauxii*
Swamp cottonwood	*Populus heterophylla*
Swamp tupelo	*Nyssa sylvatica* var. *biflora*
Swamp-privet	*Forestiera acuminata*
Sweet birch	*Betula lenta*
Sweet corn	*Zea mays* var. *saccharata*
Sweet pecan	*Carya illinoensis*
Sweet pepper	*Capsicum frutescens*
Sweet potato	*Ipomoea batatas*
Sweetbay	*Magnolia virginiana*
Sweetgum	*Liquidambar styraciflua*
Swiss chard	*Beta vulgaris* var. *cicla*
Sycamore-maple	*Acer pseudoplatanus*
Table mountain pine	*Pinus pungens*
Tall fescue	*Festuca* sp.
Tamarack	*Larix laricina*
Tanoak	*Lithocarpus densiflorus*
Tansy	*Tanacetum vulgare*
Tobacco	*Nicotiana tabacum*
Tomato	*Lycopersicon esculentum*
Turnip	*Brassica rapa*
Velvetleaf	*Abutilon theophrasti*
Virginia pine	*Pinus virginiana*
Water hickory	*Carya aquatica*
Water oak	*Quercus nigra*
Water tupelo	*Nyssa aquatica*

(continued)

Common name	Latin name
Watermelon	*Citrullus vulgaris*
Western hemlock	*Tsuga heterophylla*
Western larch	*Larix occidentalis*
Western redcedar	*Thuja plicata*
Western white pine	*Pinus monticola*
Western yarrow	*Achillea lanulosa*
Wheat	*Triticum aestivum*
White ash	*Fraxinus americana*
White clover	*Trifolium repens*
White fir	*Abies concolor*
White mustard	*Sinapis alba*
White oak	*Quercus alba*
White spruce	*Picea glauca*
Wild oat	*Avena fatua*
Willow	*Salix* sp.
Willow oak	*Quercus phellos*
Winged elm	*Ulmus alata*
Yellow alyssum	*Alyssum alyssoides*
Yellow avens	*Geum rossii*
Yellow birch	*Betula alleghaniensis*
Yellow buckeye	*Aesculus octandra*
Yellow-(tulip) poplar	*Liriodendron tulipifera*

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