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Sunlight and Plants, Some Pursuits in Physiological Ecology

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SUNLIGHT AND PLANTS
Some Pursuits in Physiological Ecology

by
Martyn M. Caldwell

SIXTY-NINTH HONOR LECTURE
DELIVERED AT THE UNIVERSITY

A basic objective of the Faculty Association of Utah State University is, in the words of its constitution:

> to encourage intellectual growth and development of its members by sponsoring and arranging for the publication of two annual faculty research lectures in the fields of (1) the biological and exact sciences, including engineering, called the Annual Faculty Honor Lecture in the Natural Sciences; and (2) the humanities and social sciences, including education and business administration, called the Annual Faculty Honor Lecture in the Humanities.

The administration of the University is sympathetic with these aims and shares, through the Scholarly Publications Committee, the costs of publishing and distributing these lectures.

Lecturers are chosen by a standing committee of the Faculty Association. Among the factors considered by the committee in choosing lecturers are, in the words of the constitution:

> (1) creative activity in the field of the proposed lecture; (2) publication of research through recognized channels in the field of the proposed lecture; (3) outstanding teaching over an extended period of years; (4) personal influence in developing the character of the students.

Martyn M. Caldwell was selected by the committee to deliver the Annual Faculty Honor Lecture in the Natural Sciences. On behalf of the members of the Association, we are happy to present Professor Caldwell's paper.

Committee on Faculty Honor Lecture

SUNLIGHT AND PLANTS

Some Pursuits in Physiological Ecology

by
Martyn M. Caldwell
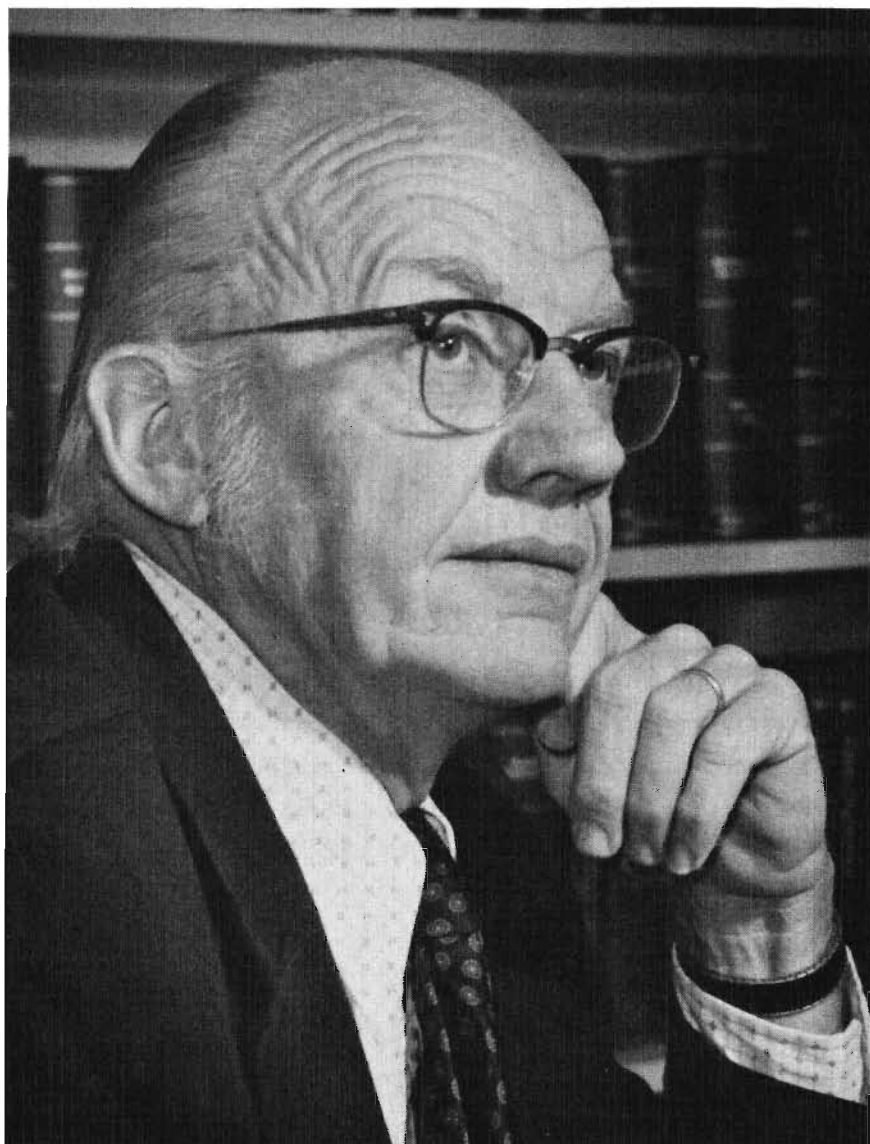
Herman Henry Wiebe, 1921-1984

In Honor

This lecture is dedicated to Herman Henry Wiebe, former Professor of Botany at Utah State University. An academician and professor in the classic and most respected sense. An independent and original thinker. An innovative experimenter. A perceptive and incisive critic. A naturalist by devotion and innate curiosity. A person who respected and cherished tradition, but who could take considerable delight in being nontraditional. A zealous traveler. A pursuer of the offbeat. A person of unbending principles. And, despite sardonic expressions and a sometimes-disapproving countenance — often contrived, I felt — a person of immense warmth, humor, and charity.

SUNLIGHT AND PLANTS:
Some Pursuits in Physiological Ecology

by
Martyn M. Caldwell*

Die Wirkungen des Lichtes auf die Pflanze sind je nach der Intensität desselben und jenach der einzelnen physiologischen Function fördernd oder hemmend, schaffend oder zerstörend.

A. F. W. Schimper, 1898

Since its inception some 34 years ago, each person chosen to present the Honor Lecture has viewed this opportunity somewhat differently. This lecture presents the opportunity to explain something about the academic niche one occupies in this time of increasing specialization. For lectures in the Natural Sciences, this involves how one approaches science, both philosophically and technically, and something about the object of study — in my case, plants and their immediate environment, as I am a physiological ecologist of plants.

Physiological Ecology: Working in the Middle Ground

A physiological ecologist, as the name suggests, focuses on the interface between plant physiology and the ecology of individual organisms. Yet, one in this field should know something about disciplines ranging from physiology, or in the case of the subject of this lecture, even photochemistry, to the study of entire ecosystems.

Accompanying this breadth of subject matter is also a considerable difference in how one may practice science. As one moves from the highly reductionist approach of the photochemist through levels of integration to the study of entire ecosystems, one deals with much less exactness, with complexities that increase by orders of magnitude, and with generalizations that are much less powerful. One also more frequently encounters the compromise between experiments that are most desirable and those that are simply tractable. Although there are basic precepts to the scientific method that all must respect and follow, no single formula can be so comprehensive as to adequately and explicitly guide research at all levels of integration. When

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working with complex systems, it is difficult, and often impossible, to devise the pivotal hypothesis that can be cleanly tested without tenuous assumptions and involved statistics in order to sort through the variability that characterizes complex systems.

Though the opportunity to do absolutely "clean," clearly interpretable experiments becomes rarer at higher levels of integration, the questions are no less pressing. They cannot be adequately addressed by working exclusively with reduced systems anymore than a metallurgist specializing in aircraft alloys can predict how an aircraft flies. In addition to studying the components, the system itself must be studied. Despite the ambiguities inherent in investigating the behavior of complex systems, clear distinctions exist between those who conduct incisive experiments and those who simply take comfort that the complexity of the system being studied will forgive muddled thinking.

Although the physiological ecologist is fortunate in having many more experimental approaches at hand than the ecosystem scientist, each approach has its limitations either in control, on the one hand, or in ecological meaningfulness on the other. Physiological ecology ranges from studies of individual plant organs under controlled laboratory conditions (still an abhorrently complex system when viewed by the biochemist) to studies involving manipulation and measurement of the microenvironment and physiological processes of vegetation in nature. The former are of limited import in understanding how entire plants function in the real world and the latter are limited by the degree of control and simplification that can be imposed on such experiments in the field. Furthermore, when a sufficiently comprehensive set of measurements cannot be made, or if the measurement itself unduly perturbs what is being measured, simulation modelling must be used (usually by computer). Such mathematical models attempt to simulate the real system. These models vary in their effectiveness and are almost always a substantial abstraction from reality. Nevertheless, these can be very instructive as long as one remains skeptical and considers the simulations a tool rather than an answer.

The most effective physiological ecology obtains when several of these approaches are brought to bear on a given question. In this sense, this subdiscipline differs from many other scientific fields in that an unusually broad array of experimental approaches can, and should, be used to address the questions at hand. In the course of this lecture, I hope to illustrate a few of these. To limit the scope, I have selected a single environmental factor, sunlight, and a single type of organism, higher plants, to illustrate some applications of physiological ecology. First, a few general words about the nature of sunlight reaching the Earth's surface and some general perspectives on higher plant photobiology are in order.

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Sunlight and Photobiology

Sunlight. The sun presents a relatively constant source of radiation for the Earth. In fact, changes in solar output are much less than 1% and have only been measurable in recent years with the NIMBUS 6 and NIMBUS 7 satellites (Smith et al. 1983). Like the solar intensity, the solar spectral composition, i.e., the mix of radiation at different wavelengths, is also, for practical purposes, constant. Wavelength is that characteristic of radiation that dictates to what degree radiation will be absorbed by different molecules and also how effective it will be in driving photochemical reactions. Photobiology pertains to photochemical reactions in living organisms. Because photobiological reactions are highly wavelength specific, the spectral characteristics of sunlight in nature must be considered.

The spectral irradiance from the sun (the intensity of radiation at different wavelengths) received outside the Earth's atmosphere is shown in Figure 1. Only about half of the sun's energy is important for photochemical reactions in plants since radiation at wavelengths greater than approximately 800 nanometers (nm) are not effective in driving these reactions. For radiation at wavelengths shorter than 800 nm, the Earth's atmosphere is generally transparent to sunlight. This, of course, includes the part of the spectrum termed "visible light" (400-700 nm). This "window" through our atmosphere is also the waveband (wavelength range) where most photochemical reactions of plants occur. There is, however, a distinct curtain on this window in the ultraviolet (UV) at about 290 nm due to the very effective absorption by ozone in the upper atmosphere.

Although the intensity of sunlight obviously changes considerably at the Earth's surface, the spectral composition varies little except for brief periods near sunrise and sunset. There can, however, be large spectral changes in certain habitats such as under the shade of green foliage.

In order to depict briefly some facets of plant photobiology, a few vignettes follow.

Plants conduct handsome photochemistry. The most famous example of plant photochemistry is photosynthesis. Two distinct photosystems participate in series to push electrons to a higher "chemical potential" and these electrons ultimately drive the chemistry of photosynthesis. There are "antenna" chlorophyll pigments that harvest light and pass it on to so-called "trap" chlorophyll pigments, where the flow of electrons actually starts. This system is beautifully organized and proportioned (about 300 antennae for each trap)
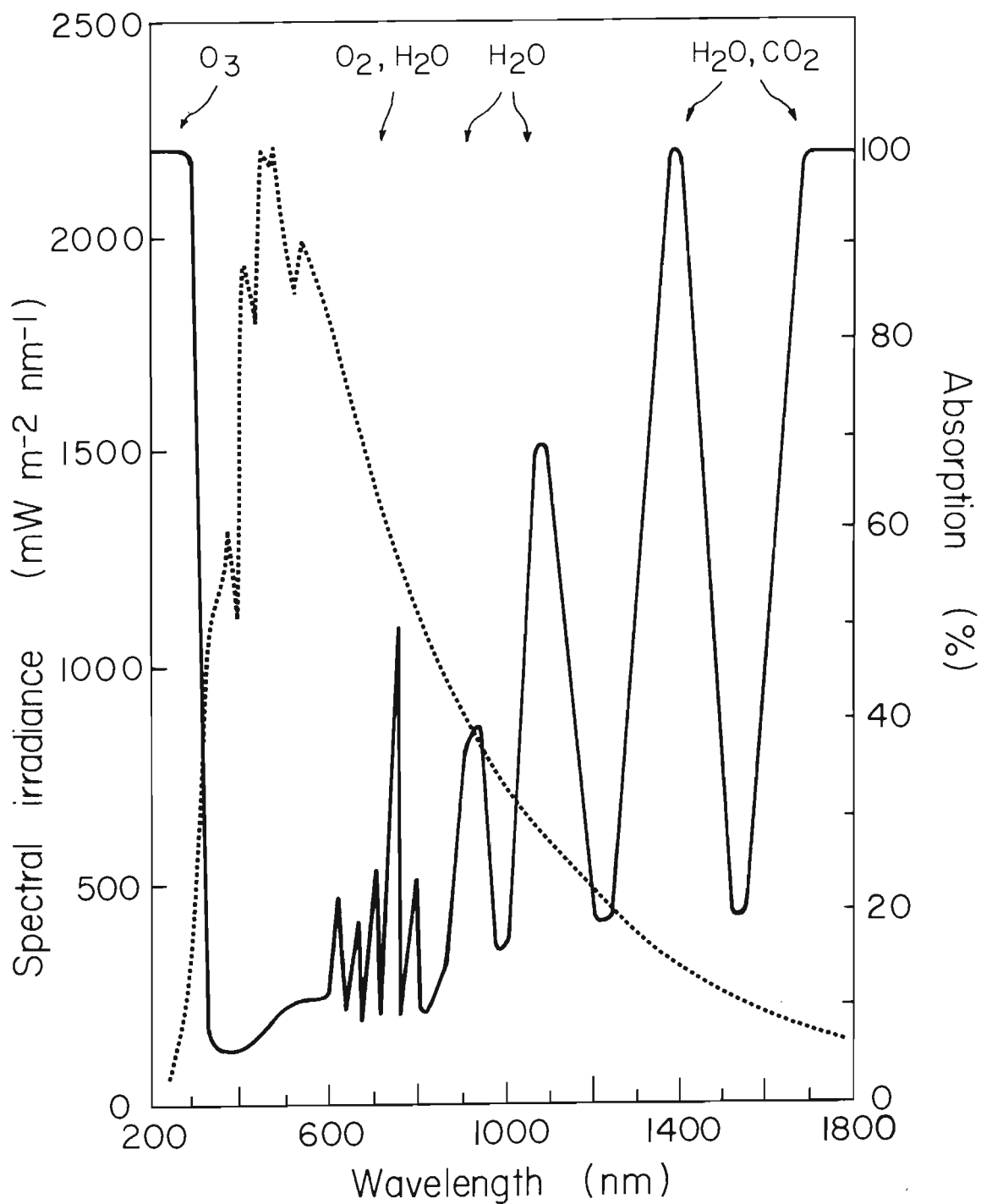
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Figure 1. Solar spectral irradiance reaching the Earth's atmosphere (dashed line) and relative absorption of radiation at different wavelengths by gases of the atmosphere (solid line). The gases responsible for major absorption peaks are indicated (O_2, oxygen, O_3, ozone, H_2O, water vapor, CO_2, carbon dioxide).

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to process light efficiently so that each trap sends an electron on its way about every 1/300th of a second under average light conditions, approximately the rate at which the chemistry of the system can handle them efficiently. Under ideal conditions, the photosynthetic system is so efficient that as much as 33% of the light absorbed can actually be converted to chemical energy. Conditions in nature are never so ideal, but this potential for energy conversion is impressive.

There are many responses of plants to light by nonphotosynthetic pigment systems—these, too, are photochemical and can be extremely sensitive. It has been recently discovered that seedlings of oat plants, germinated in total darkness and physiologically sensitized, can detect the amount of light in a single flash of a firefly, which is roughly equivalent to a one-second exposure to 1/1000th of the intensity of full moonlight (Shinkle and Briggs 1983). These recent studies make it quite clear that there is no such thing as a "safe light" (analogous to those used in photographic darkrooms) that can be used in such experiments—a setback for those who have depended on such lights in their work for many years. Seeds of some species can have this extreme light sensitivity under certain conditions. There is even the suggestion that some roots may have this heightened light sensitivity, and the response to gravity may be first induced by a very small amount of light that penetrates the very upper layers of the soil (Mandoli et al. 1982).

Plants can pipe light. A fiber optic even when bent at sharp angles conducts light very efficiently. Light is trapped in the fiber and moves only along its length, much like water in a pipe. It has been convincingly demonstrated that certain plant tissues also have such fibers (Mandoli and Briggs 1982). These properties are causing much rethinking about where light might be received in a plant and where it might be sensed by a particular pigment system—they need not be in the same location. This has implications for light reactions in plant organs, such as roots, usually not thought to experience light in nature.

Plants can detect color. Color is, after all, what the eye perceives as light of a certain wavelength. Plants, too, can detect changes in the spectral composition of light in their environment. This enables plants to use light quality as a cue to certain features of their environment. A small plant, or even a seed, can detect whether it is exposed to different qualities of low light, e.g., resulting from cloud cover or from shading by living vegetation. Even if both situations result in the same light intensity, the spectral quality is quite different. In the shade of green plants, the light is quite enriched in what is called "far red," i.e., the light of wavelength just beyond the longwave

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threshold for the human eye (700 nm). The balance between far red and shorter wavelength light is detected by the pigment system known as phytochrome. (This is the same pigment that participates in the measurement of daylength—within 5-10 minutes in some plants.) The quality of such shade light stimulates many plant species to invest heavily in stem growth at the expense of producing leaves and branches. Thus, they grow rapidly above the shade of neighboring plants, after which they return to producing leaves (Holmes 1983). Shade from dead leaves does not possess this light quality and plants do not respond to such shade by rapid stem growth. This is a useful mechanism in the competition for light. The shade of living foliage will also inhibit the germination of many seeds—an environmental cue to wait until the vegetation overhead is disturbed, until normal daylight penetrates to the soil, and, therefore, conditions are more favorable for seedling survival.

Plants also possess primary receptors for blue light and for ultraviolet in the region of 280-320 nm (UV-B). These receptors can direct a wide variety of physiological responses in plants.

Plants can track the sun. Just as solar collectors at the solar energy plant in Barstow, California, orient themselves perpendicularly to the sun's rays, so the leaves of many species track the sun with amazing precision. As the sun courses through the sky, leaves of a solar-tracking plant will remain within a few degrees of a right angle to the solar beam. This greatly facilitates the harvesting of solar energy in photosynthesis, especially during times of day when other environmental conditions are particularly favorable for photosynthesis (Forseth and Ehleringer 1982). The pigment system known as the "blue light receptor" directs this activity.

Plants are plastic. Plants exhibit immense plasticity under different environmental conditions of water, salinity, mineral nutrients, and temperature. But, it is light of different intensity and quality that has by far the greatest influence on the development of different plant structures and physiological traits. For example, the light environment causes changes in virtually every aspect of plant leaf structure ranging from a substantial change in leaf thickness, to the organization of membranes in the photosynthetic organelles of the leaf interior and the molecular organization of the light-harvesting and electron-processing apparatus. And for good reason. A "sun" leaf, one grown and developed in high-light intensities, will literally starve to death in the shade and a "shade" leaf will be very inefficient in harvesting high-light intensities under full sun conditions and can even be severely damaged by light. Plant species vary in their plasticity when grown in different light environments, but most species do exhibit some of these changes.

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Plants can be photoinhibited. Destructive photochemistry may also occur in plant tissues. This may operate in several pathways. As discussed earlier, the photosynthetic system is very efficient in light capture. Under some circumstances, this can lead to damage if the captured energy cannot be appropriately used or dissipated. A "shade" leaf may suffer such photochemical damage in high light because it cannot adequately dissipate the excess solar energy—a phenomenon often experienced by the houseplant enthusiast who likes to allow the plants that were standing in dark corners of the living room to bask in the sun. But even some "sun" leaves may experience such photoinhibition under conditions of water stress or chilling temperatures (Björkman 1981).

A very different type of photoinhibition can be effected by ultraviolet radiation of certain wavelengths. Fortunately, the most destructive UV is absorbed by ozone in the atmosphere before this radiation reaches the Earth's surface. The UV can attack the photosynthetic system (apparently in a different manner than the excess light of the 400-700 nm waveband that normally drives photosynthesis) and can also cause photochemical damage to proteins and nucleic acids, just as it does in our skin. Plants, microorganisms, and mammals are all equipped with molecular repair systems that can literally undo some of the damage to nucleic acids. One repair system known as photoreactivation, is itself driven by light (longwave UV and blue). What becomes important is the balance between the destructive photochemistry and the rate and effectiveness of repair.

Specific Questions

A stated purpose of this lecture is to illustrate how different questions in physiological ecology are approached—in this case concentrating on the subject of sunlight and plants. Three questions will be addressed. (1) How effectively do bunchgrasses harvest sunlight? (2) How important is leaf orientation for light capture and water loss in a Portuguese oak tree? (3) How might a change in the atmospheric ozone layer and the consequent increase in solar UV radiation affect the Earth's plant life? These questions vary in scope and have both theoretical and practical importance. Although physiological ecology is a basic, rather than an applied, discipline, it is particularly satisfying for me to pursue problems that have direct implications for natural resource management and agriculture.

Light capture by bunchgrasses. Many prominent grass species in several parts of the world grow in distinct tussocks or bunches. These grasses constitute

important components of the forage resource in the rangelands of several continents. The specific question regarding light harvesting is a small component of a major study presently underway that concerns two species of bunchgrass prominent in the rangelands of the Intermountain West — one very grazing tolerant and the other very grazing sensitive. This study involves everything from root tips and belowground competition to leaf photosynthesis and flower bud development.

A consequence of the bunchgrass growth form is that the tight clustering of foliage in distinct tussocks, as opposed to a more even turf-like arrangement, may result in a substantial amount of self-shading. This raises the question of how efficiently this growth form intercepts and captures sunlight in photosynthesis. This is of both theoretical and practical interest. Much of the progress that has been made in breeding more productive crops and pasture grasses has not come about by selecting individual plants that have higher photosynthetic rates (per amount of leaf material) but by selecting plants that display their foliage in certain ways — a characteristic that is referred to as canopy architecture. Races of a species that arrange their foliage to most effectively capture sunlight for photosynthesis are capable of higher productivity, and this single trait is usually of much greater importance than high rates of photosynthesis, per se. The practical significance of understanding canopy architecture and light harvesting is readily apparent.

Within a bunchgrass there is considerable light attenuation. As shown in Figure 2, a special light sensor, whose sensitivity to light of different wavelengths is very similar to the sensitivity of photosynthesis, records light in the tussock interior, always less than 5% of that reaching the top of the bunchgrass. Thus, the interior of the tussock is quite light limited. This has also been shown by measurements of individual leaf photosynthesis in the tussock interior in the field (measured as carbon dioxide uptake in a small cuvette). Yet, in order to assess light harvesting by the entire tussock, a quite different approach is necessary. Light capture by the entire plant depends on the arrangement and inclination of both the green living foliage as well as the dead leaves and stems that remain in the tussock from past years' growth. This needs to be considered with respect to how the solar beam strikes the plant at different times of day. This all results in a rather complex geometry that is not so easily calculated. It can, however, be measured in the field. Sunlight rays can be simulated in the field by a device that passes a fiber optic probe through the tussock in the same path that solar radiation would penetrate at different times of day. The fiber optic system detects contacts with foliage elements. When the sampling is complete, an analysis of light interception can be pieced together which, together with measurements of direct solar radiation, shows that despite the light-limited condition in the interior of the tussock that the bunchgrass as a whole is able to capture light
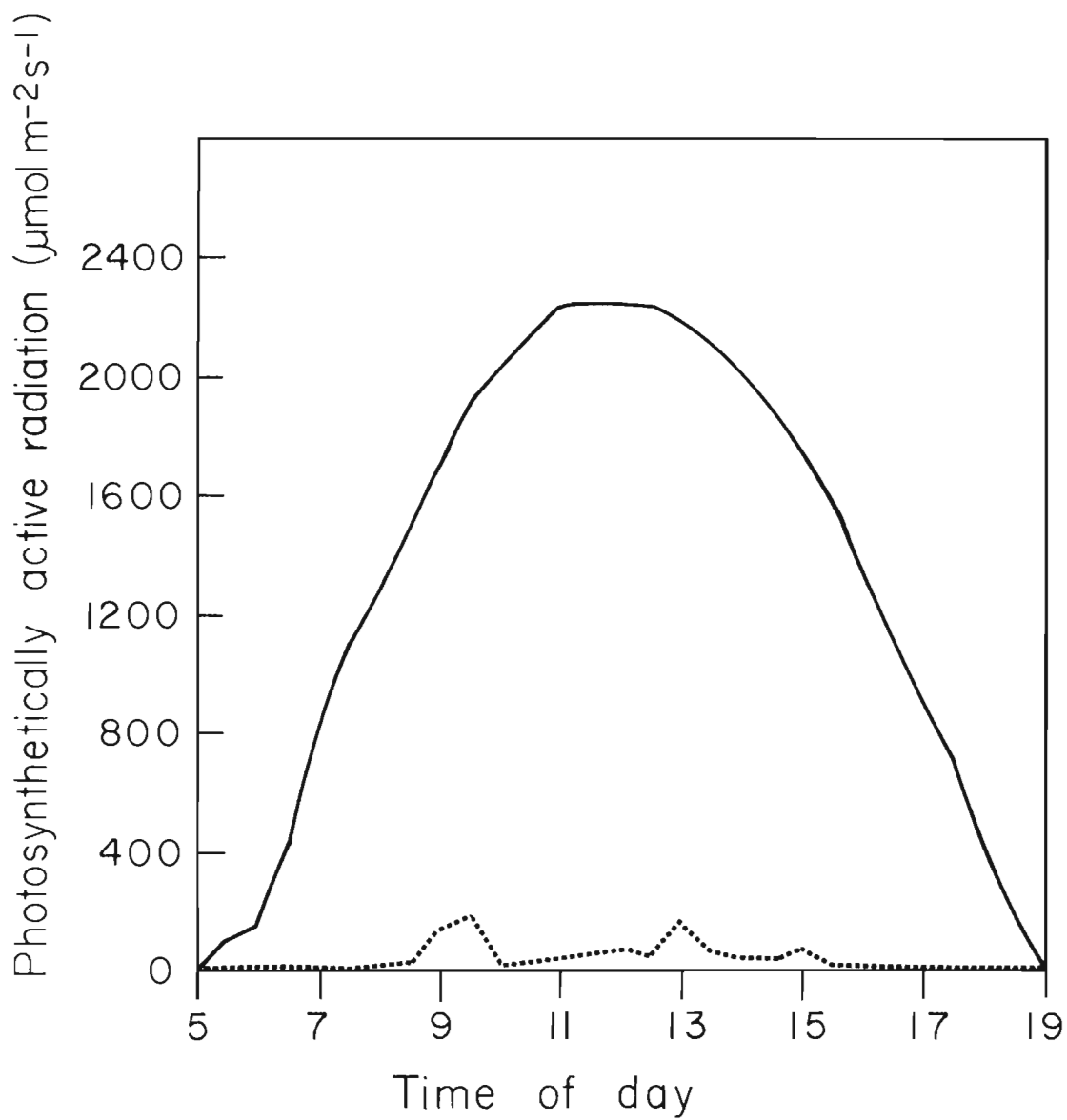
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Figure 2. Light capable of driving photosynthesis that reaches the top (solid line) and the interior (dashed line) of a bunchgrass, *Agropyron desertorum*, during a clear day in May. (Adapted from Caldwell et al., 1983.)

quite adequately. Such a tussock intercepts just as much light as a turf grass of the same amount of foliage spread over a ground area in excess of six times the ground area underneath the canopy of this tussock (Figure 3).

But, how does sunlight interception translate into the efficiency of photosynthetic energy capture? In a water-limited environment such as the Intermountain West, one measure of efficiency is the amount of light captured in photosynthetic carbon gain relative to the amount of water lost from the foliage. Plants can evaporate immense quantities of water from their leaves (a process called transpiration) and when foliage is active in photosynthesis it is necessarily transpiring. Thus, the efficiency with which it is capturing light energy in photosynthesis is quite important. Using large climatized, transparent cuvettes, which can enclose an entire bunchgrass, photosynthesis and water vapor loss from foliage have been measured in the field. These show the bunchgrass to have water-use efficiency (photosynthesis relative to transpiration) as high as any plants that have ever been measured in arid or semiarid environments. Thus, bunchgrasses are certainly not as ill-suited for light capture as one might at first think. But, only by studying the intact plant does this become apparent.

Leaf orientation in a Portuguese oak. This second question concerning the influence of leaf orientation on photosynthesis and transpiration of an oak tree is briefly addressed as an example of the use of simulation modelling. Although measurement of individual plant leaves of an oak tree is similar to the approach taken with bunchgrass leaves, an entire oak tree cannot be studied in the manner described for intact tussock grasses. The oak trees are simply too large. There are other complicating factors as well. The oak leaves are much larger than a grass blade and when sunlight strikes them they can heat above air temperature, unlike the blade of grass. This in turn causes them to lose water at a faster rate which, of course, influences the water-use efficiency. Thus, the entire energy budget (the processes of heat exchange between the leaf and its environment) must be taken into account. The individual leaf energy budgets, light penetration into the tree canopy, and processes of photosynthesis and transpiration can all be simulated by a computer model to address questions concerning characteristics of the entire tree. Part of the model is simply borrowed from heat exchange engineering and other parts of the model have been devised to simulate physiological processes. Of course, the model must be compared to actual measurements of leaf temperatures, photosynthetic rates, etc., in the tree canopy even though processes of the whole tree cannot be measured.

The question of leaf orientation and light capture is an example of issues the model can address. Leaf orientation, i.e., the angles at which various leaves on the tree are positioned, is certainly not random. The upper leaves
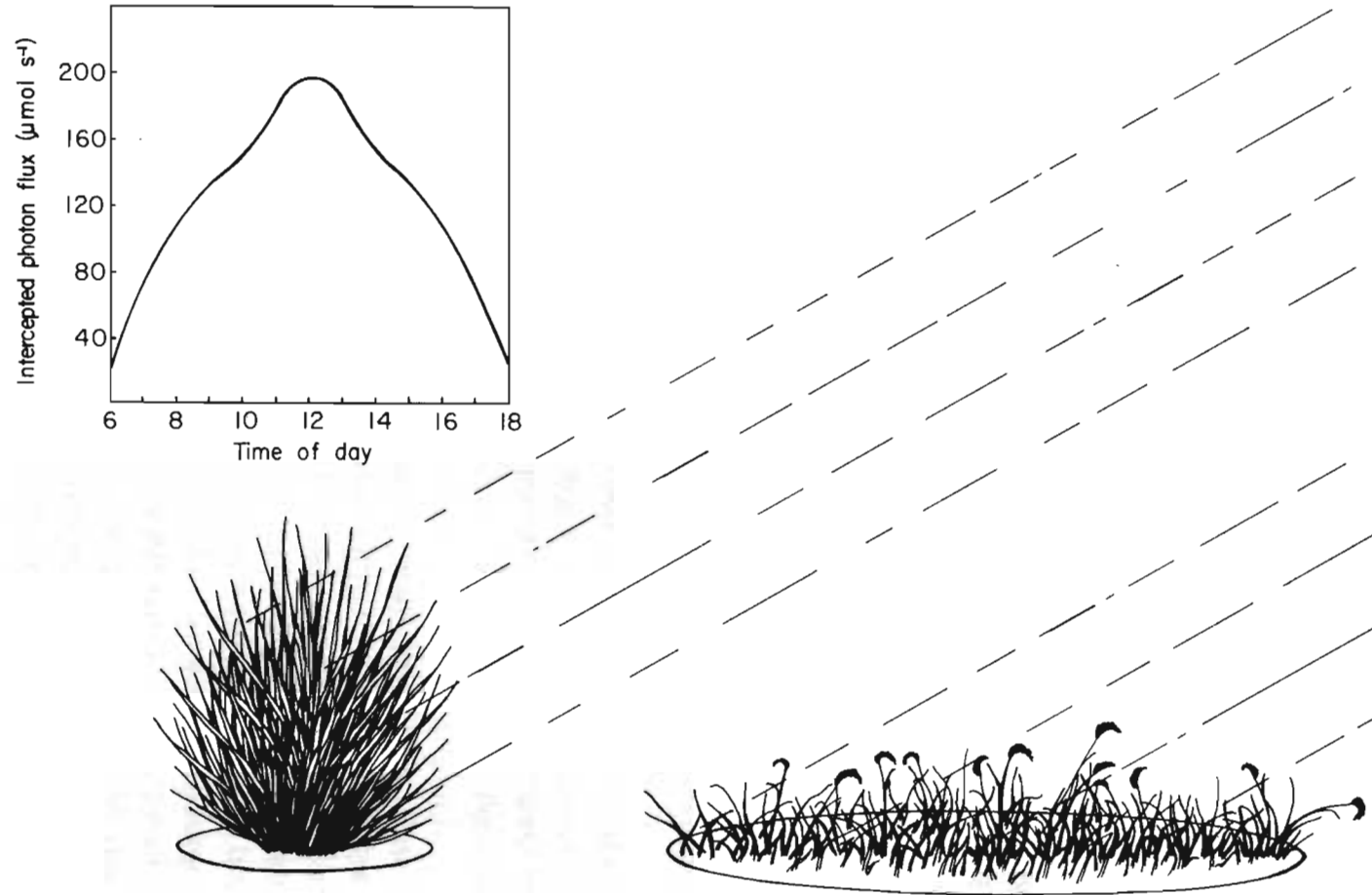
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Figure 3.   Daily course of total light (total photons in the photosynthetically active waveband, 400-700 nm) intercepted by green foliage of a bunchgrass, *Agropyron desertorum*, on a clear day in May. Also depicted is the bunchgrass and a grass of equivalent foliage area (and comparable foliage angles) randomly distributed over an area 6.4 times the ground area beneath the canopy of the bunchgrass. Both grasses theoretically intercept the same amount of radiation during the course of a day. (Adapted from Caldwell et al., 1983.)

tend to be more steeply inclined than those in the lower canopy. This arrangement of leaves influences the effectiveness of sunlight penetration in the canopy, the energy budgets of individual leaves, photosynthesis, and transpiration.

These simulations were computed for days during the dry season for three hypothetical canopies each with a different distribution of leaf angles. As with the real canopy in nature, these ranged from steeply inclined leaves near the top of the canopy to lesser inclinations near the bottom. The three distributions were (a) 40° to 10°, (b) 60° to 30°, and (c) 80° to 50°. The results of the simulations indicated that photosynthesis and water-use efficiency were greater for each canopy at different times of the day. As the angle of the sun and the canopy microclimate changed during the course of the day, each of the different canopies was superior at a particular time. However, when water-use efficiency was computed for the entire day, the canopy (b) with leaves at 60° near the top of the canopy progressing to 30° at the bottom was the most efficient in the simulations. This is indeed the closest of the three hypothetical canopies to leaf inclination angles actually measured in Portugal. A nice result. This may, of course, be coincidental, and this simulation does not necessarily prove what is the optimal arrangement of the leaves. However, it would certainly discourage a forester from attempting to breed a better oak tree with leaf inclinations different from those currently existing in nature.

Simulations can also serve a useful purpose in setting priorities for experimental work and in posing questions that might not otherwise come to mind. Even though such models do not yield definitive answers, they are very useful tools in physiological ecology.

Ozone, UV, and plants. The third question of this set concerns the consequences of global, atmospheric ozone reduction for the Earth's plant life — a comprehensive question of obvious pragmatic relevance, but certainly not as easily addressed as the first two questions.

Some background is in order. Please return to Figure 1 and consider the absorption of short-wavelength solar radiation by ozone in the atmosphere. It is this gas, though in very small concentrations in the atmosphere, that is almost entirely responsible for the absorption of solar UV. At the time when the Earth's atmosphere was almost completely devoid of oxygen, from which ozone is formed, the absence of ozone permitted solar UV radiation to stream freely to the Earth's surface. It may well have been a major constraint on the evolution of plant and animal life. Nothing so dramatic is envisaged for the case of ozone reduction by man-made pollutants. Instead, only a modest reduction is anticipated — less than 10% according to present estimates.

If the graph of radiation absorption in Figure 1 were modified to account

for a modest (10%) ozone layer reduction, one would scarcely notice the difference in this Figure. The additional UV radiation reaching the Earth's surface as a result of a 10% ozone reduction amounts to less than a 0.05% increase of the total sunlight energy and less than a 1% increase of the UV component. What is critical is the wavelength distribution of the intensified radiation. Ozone reduction becomes a serious biological problem if the particular spectral changes of solar UV coincide precisely with the spectral characteristics of biologically damaging reactions. That is, even though only a small amount of additional solar energy reaches the Earth, if this radiation is of wavelength composition that is particularly damaging with respect to other wavelengths, this small amount of energy can be important.

A partial ozone reduction would affect various parts of the UV spectrum quite differently since radiation absorption by ozone is a pronounced function of wavelength. The absorption coefficient of ozone increases by a factor of more than 1,000,000 with decreasing wavelength in the UV spectrum. This means that a moderate change in the total ozone layer is manifested only in a rather small waveband—approximately 290-315 nm. At shorter wavelengths, the absorption coefficient is so great that even an ozone layer depleted by some 90% would still be effectively opaque to this solar radiation. At wavelengths longer than 315 nm, the absorption coefficient of ozone is so small that a change of the ozone layer would be of little consequence for solar radiation.

A link between ozone reduction and agricultural productivity can be easily envisaged. If ozone is reduced, an increase of solar UV in the waveband 290-315 nm is quite predictable. That UV of this 290-315 nm waveband can be damaging to higher plants, and especially to the photosynthetic apparatus, has also been clearly demonstrated. Because this appears to be a rather simple chain of reactions from ozone reduction to plant photosynthetic damage, estimates of reduced crop yields might follow. A federal agency might use these yield estimates along with estimates of increases in skin cancer incidence, to undertake an economic analysis of the costs and benefits of reducing the release of pollutants such as chlorofluoromethanes. At the present time, however, such a scenario is most unworkable. The problem falls into several categories. There are spectral considerations, questions of plant optical properties and acclimation to UV, and subtle processes such as changes in the balance of competition between neighboring plants that considerably complicate the problem.

Spectral considerations. There is simply no ozone reduction problem for biological organisms (including man) unless the biologically damaging reaction, such as damage to nucleic acids, is specifically restricted to UV radiation of wavelengths short enough to be influenced by ozone reduction. This is

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illustrated in the next two figures, which show action spectra for damage to plants and the application of these spectra in evaluating solar radiation change. An action spectrum is the relative effectiveness of radiation of the same intensity at different wavelengths to elicit a biological effect. The spectra shown in Figure 4 are similar in many respects and certainly appear so if plotted on a graph with linear axes (in the left side of this Figure). With a logarithmic scale (as shown in the right side of this Figure), the differences in the spectra are more apparent. As with so many damaging photochemical reactions in biological tissues, the effectiveness of the radiation increases dramatically with decreasing wavelength in both spectra.

What becomes critical for the ozone reduction problem is that just in the waveband where the ozone absorption coefficient becomes so small as to have little influence on solar UV (with or without ozone reduction) the action spectrum of the damaging photoreaction also drops to a very low level. In Figure 5, at the top, the change in solar radiation resulting from an ozone reduction of 16% is shown. Note that there is no difference in radiation at wavelengths greater than approximately 315 nm. The increment of radiation becomes relatively greater at shorter wavelengths, but the absolute intensity in either case drops abruptly at shorter wavelengths due to the rapidly increasing absorption by atmospheric ozone. To evaluate what the change in solar UV might mean biologically, the action spectra may be used as weighting functions, i.e., to weight, or count, radiation at each wavelength according to how effective it is in causing damage. This has been done in the middle and lower frames of Figure 5. The total weighted radiation at each wavelength is then integrated (summed) over all wavelengths in the solar UV to provide an expression of what can be called "biologically effective solar UV." (This is analogous to using the action spectrum of the human eye to weight radiation in the visible spectrum to express illumination, as a lighting engineer might do in assessing the light available in a classroom.) The relative change in the integrated weighted irradiance before and after ozone reduction is a critical assessment of whether or not ozone reduction may be of biological significance. This relative change is what we have defined as a radiation amplification factor, RAF.

In the case of radiation weighted by the first action spectrum (Figure 5, middle frame) the RAF is trivial, i.e., for the 16% ozone reduction represented, the solar UV would be increased by only 2% under these conditions. However, for the second spectrum (Figure 5, lower frame), this amplification is considerable; the 16% ozone reduction would result in a 47% increase in effective UV radiation. Thus, the importance of relatively small differences in the action spectra can be decisive for the potential of ozone reduction to result in increasing biologically effective solar UV.

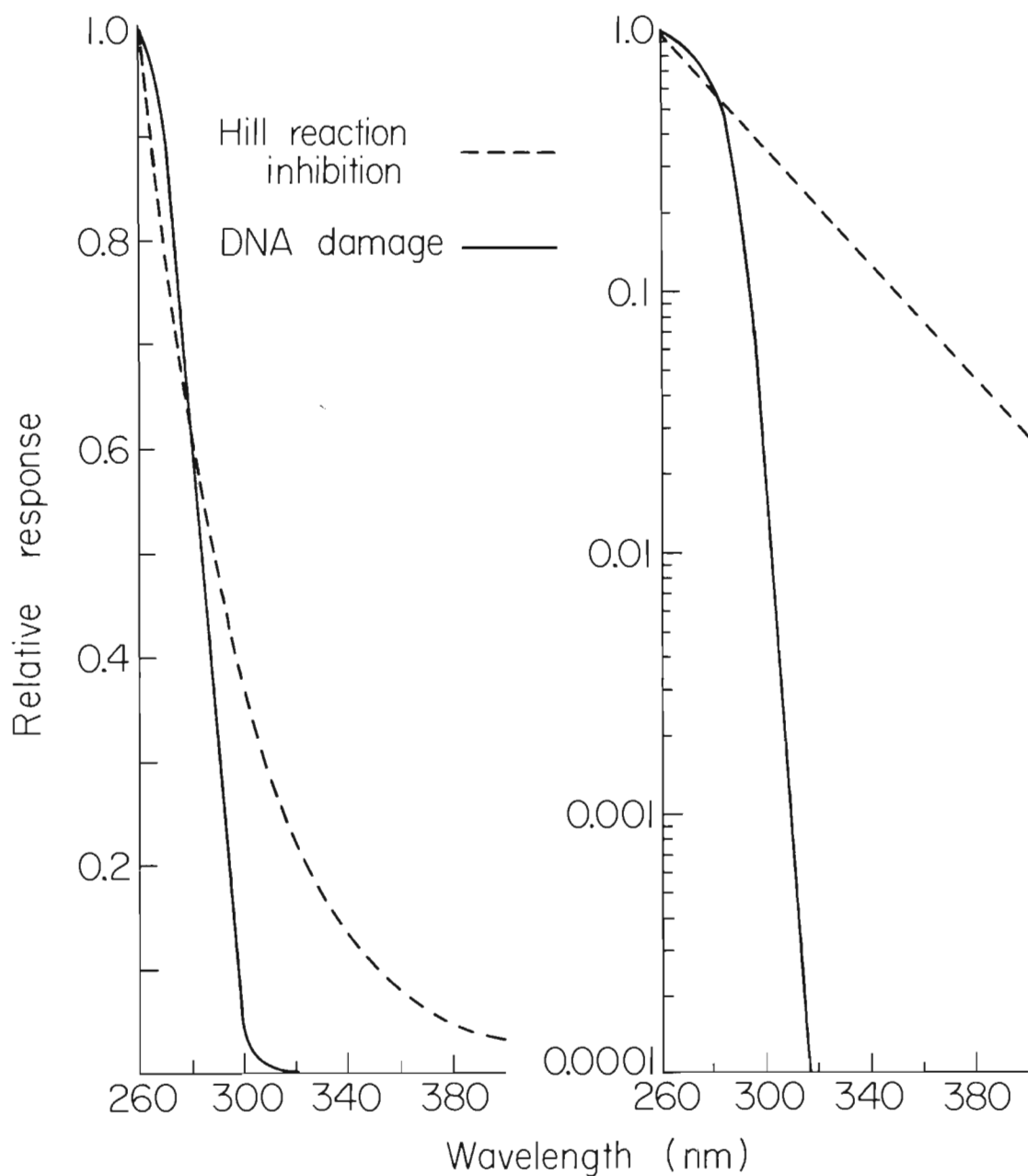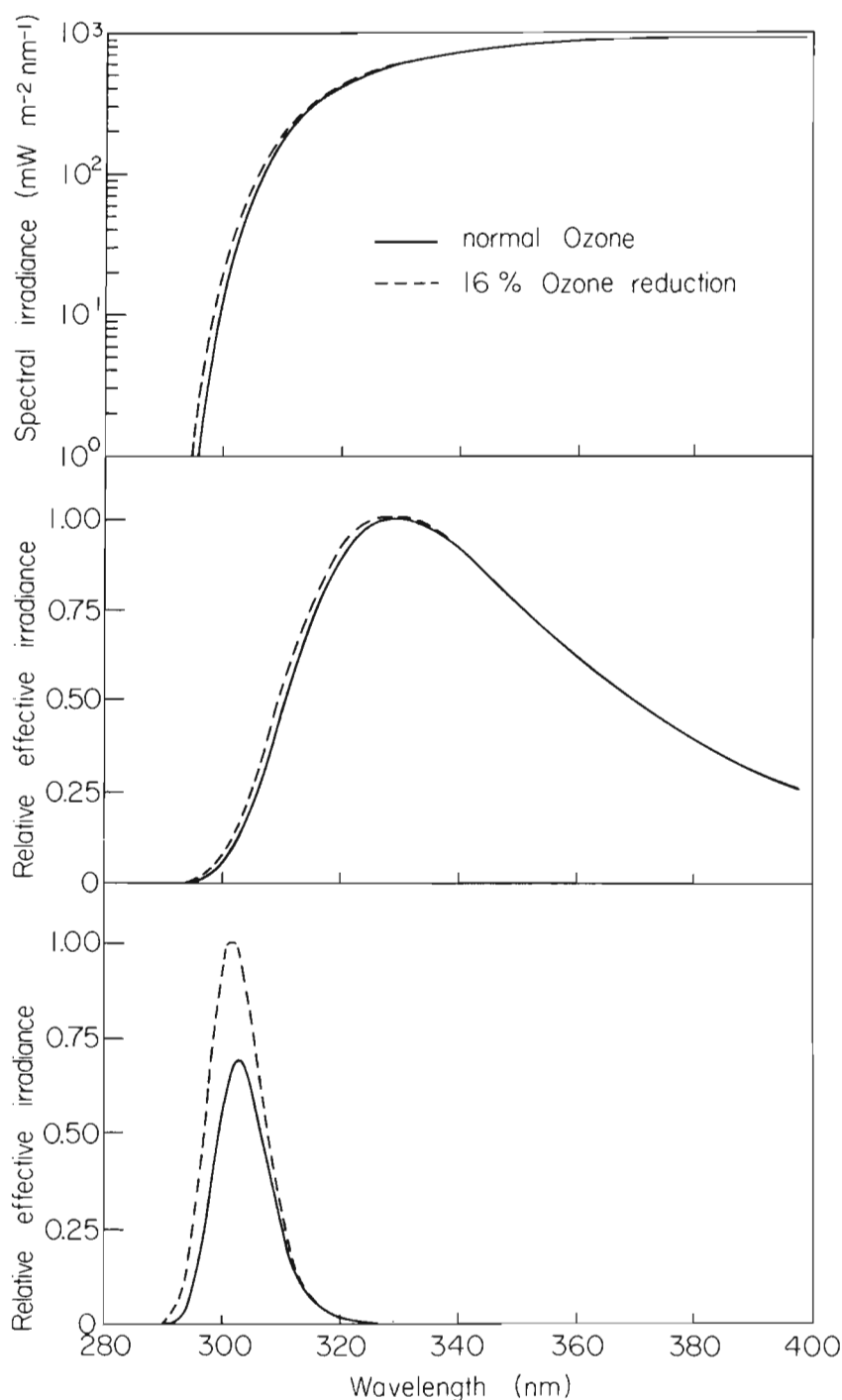The uncertainties in predicting solar UV spectral irradiance (the UV

Figure 4.   Action spectra for UV damage plotted with a linear (left side) and a logarithmic (right side) ordinate scale. One spectrum is for inhibition of a partial photosynthetic reaction (the Hill reaction) with isolated chloroplasts and the other spectrum is a composite of spectra developed with microorganisms where UV damaged the nucleic acids (primarily DNA). (From Caldwell 1981.)

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Figure 5. Midday solar spectral irradiance during the summer at temperate latitudes under clear skies under normal atmospheric ozone conditions and with 16% ozone reduction (top frame). The spectral irradiance is weighted with action spectra for Hill reaction inhibition (middle frame) and DNA damage (lower frame) to calculate relative effective irradiance under normal and reduced ozone conditions. See Figure 4 for action spectra. (From Caldwell 1981.)

intensity at each wavelength) under any particular atmospheric condition are considerably smaller than the uncertainties of the appropriate action spectrum for UV damage to plants, especially higher plants. The first action spectrum used in Figure 5, was one developed for inhibition of a partial photosynthetic reaction (Hill reaction) using chloroplasts extracted from spinach leaves (Figure 4). (Chloroplasts are the organelles of the leaf cells where photosynthesis occurs.) The second action spectrum, the one that resulted in the large RAF, was compiled from spectra for damage to bacteria and other microorganisms where injury was associated with nucleic acid damage. There is no indication that either is an appropriate spectrum for the primary damage to intact higher plants.

Since action spectra are pivotal in the assessment of the ozone reduction problem for the Earth's vegetation and few are available, we have devoted considerable effort in our laboratory to developing action spectra for damage to photosynthesis of intact higher plant leaves. The work has been slow and tedious but is showing quite different results than the earlier spectra with isolated chloroplasts or recent work in Sweden with isolated thylakoid membranes (the membranes in the chloroplasts where much of the photosynthetic light capture takes place). The spectrum for damage to the entire photosynthetic process of an intact leaf drops off much more abruptly with increasing wavelength than the chloroplast spectrum shown in Figure 4.

Another difference in the development of these intact leaf spectra is that polychromatic (radiation of mixed wavelengths) instead of monochromatic (radiation of a single wavelength) radiation is being used. Normally, in the development of biological action spectra, the biological system is exposed to radiation at only one wavelength at a time (monochromatic), and a relationship between exposure and biological effect is developed for each wavelength. These so-called dose-response relationships form the basis of the action spectrum. In the polychromatic approach, which we feel to be more ecologically sound because plants are exposed to polychromatic radiation in nature, different configurations of polychromatic radiation are presented to the leaf and dose-response relationships developed. The action spectrum is then extracted from these data by a mathematical procedure known as deconvolution.

This approach with intact leaves and polychromatic radiation is a rather inefficient way to develop an action spectrum and is certainly fraught with much more variability—to be expected with more complex systems. Yet, for the ecological purpose at hand, this seems to be the preferable outcome of the trade-off and is certainly yielding very different results. The spectra developed with intact leaves and polychromatic radiation will result in a significant RAF unlike the earlier monochromatic spectra with chloroplasts. This, of course, has far-reaching implications for the potential effects of ozone reduction on higher plants.

Although working with intact leaves and polychromatic radiation comes closer to the situation of plants in nature than the study of simpler systems, extrapolating results of such laboratory studies to the Earth's vegetation is tenuous. The spectral distribution of the polychromatic radiation is different than sunlight and much more intense—a necessary compromise to conduct these experiments. Questions can also be raised about how representative the results of the studied species are for other plant species. Furthermore, the environmental conditions such as the temperature and water status of the leaves in these laboratory experiments are not necessarily representative for plants growing in nature.

The importance of these action spectra for the ozone reduction problem is clear, yet are the action spectra developed in the laboratory necessarily appropriate? One might simply wait until ozone reduction is a fact rather than a prediction of atmospheric computer models and see if plant photosynthesis under field conditions is detrimentally affected. But the time frame is intimidating. Unlike increasing carbon dioxide in the Earth's atmosphere, which is now occurring, the reduction of the ozone layer is not, and should not be, yet detectable. This is a consequence of the very slow vertical circulation of the stratosphere (the upper atmosphere, which contains most of the ozone), the long time involved for the stratosphere to exchange materials with the lower atmosphere, and the decades involved until the chemistry of the entire stratosphere adjusts to the steady release of pollutants, such as chlorofluoromethanes, into the lower atmosphere. If the release of pollutants remains constant, a new equilibrium ozone layer would be approached finally in about a century. If, in the future after ozone reduction is well established, society decides that ozone reduction is unacceptable and the release of offending pollutants is halted, the reversal of ozone reduction would take even longer than it took to develop. Thus, a prior knowledge of possible consequences is critical.

This wait-and-see alternative is undesirable. Thus, a search for independent evidence that could corroborate the action spectra is needed, and this involves leaving the laboratory and moving to a different level of study.

We can take advantage of differences in solar UV that exist presently on the Earth's surface. A few years ago, we sought a large natural solar UV gradient on the Earth's surface. It was also desirable to seek locations where other factors of the environment and vegetation were not too dissimilar. Physical models of the atmosphere's optical properties predicted that a large gradient might exist in the arctic-alpine life zone extending from the arctic tundra in northern Alaska (70° N latitude) at sea level to the alpine zone of the high Andes at equatorial latitudes (Figure 6). There are three basic reasons for this. The first and most important reason is the prevailing angles of the sun. At equatorial latitudes, the sun can be high in the sky, in fact, directly
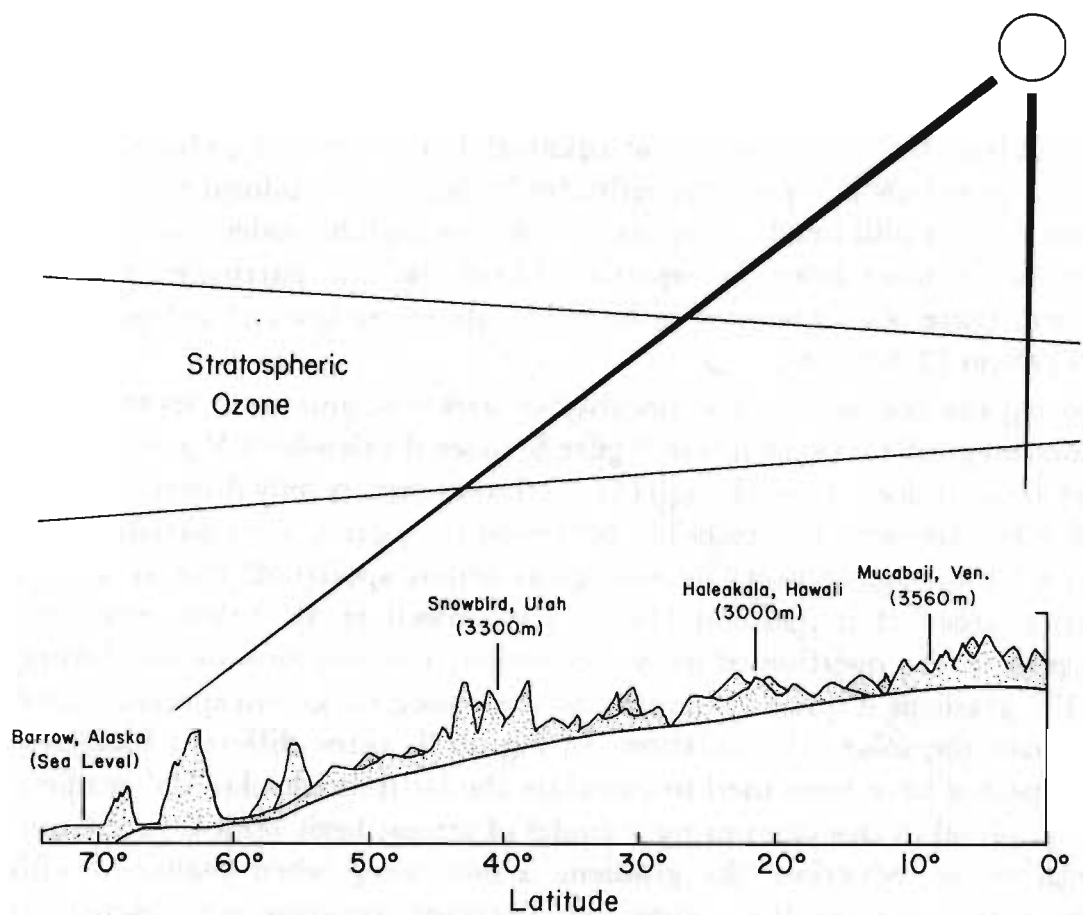
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Figure 6.   Depiction of latitudinal arctic-alpine life zone gradient. The stippled area represents this life zone, which progresses from sea level in the Arctic to high elevations at low latitudes. Some of the sites where research was conducted are indicated. The change in effective solar UV-B irradiance is due to differences in prevailing solar angles which result in different pathlengths in the atmosphere, differences in elevation above sea level, and a difference in the stratospheric ozone layer thickness at different latitudes. (From Caldwell et al., 1980.)

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overhead at times and, thus, the sun's rays can penetrate almost vertically through the atmosphere. At high latitudes, the sun is never very high in the sky (at 70° N latitude, never above 45° in the sky) and the sun's rays must travel obliquely through the atmosphere, therefore, the effective pathlength through the atmosphere is much greater. This means more attenuation of radiation. A second reason is that the amount of ozone in the atmosphere is greater at high latitudes than it is at equatorial latitudes. Even though ozone is formed primarily at equatorial latitudes in the upper atmosphere, the circulation systems pull much of this ozone towards high latitudes resulting in a thinner ozone layer near the equator. Third, for the particular gradient described, there is a difference in elevation above sea level of at least 3,500 meters (about 11,500 feet).

During the course of a few months, we took instruments to several locations on this gradient (as shown in Figure 6) to see if this solar UV gradient did indeed exist. It does. Even though the total solar energy only differs by a factor of 40% between the ends of the gradient, solar UV radiation, when evaluated with the appropriate biological action spectrum, can vary by a complete order of magnitude (1000%) (Caldwell et al. 1980). However, analogous to the question of ozone reduction, the steepness of the natural solar UV gradient is quite dependent on the biological action spectrum used to evaluate the solar UV radiation. In Figure 7, three different biological action spectra have been used to calculate the latitudinal solar UV gradient (all at sea level in this case) using a model of atmospheric optical properties. As with ozone reduction, the gradient is only steep when evaluated with steeper action spectra (i.e., ones that decrease abruptly with increasing wavelength).

The question then becomes whether the plants occurring along the latitudinal gradient provide clues that would indicate whether a steep gradient of biologically effective UV indeed exists. There are three clues.

First, we have measured the UV optical properties of plant leaves in the field at several locations along this gradient. Specifically, this was a measure of how well the epidermis (the outer single-cell layer of the leaf) absorbs UV and thus shields the leaf interior. Although there is considerable variability among plant species, there were distinct trends in that plants growing in the Andes (3,000-4,000 m elevation) and on the Haleakala Crater (3,000 m elevation) in Hawaii all had consistently very high UV absorption in this epidermal tissue while those at high latitudes did not. This UV filter in the epidermis is quite important in protecting photosynthesizing cells in the leaf interior and it is apparent that plants growing in these low-latitude, high-elevation areas have developed this filtration ability much more consistently than plants at higher latitudes (Robberecht et al. 1980). If solar UV in these areas were not more of a stress than at higher latitudes (as would be calculated by a less-steep
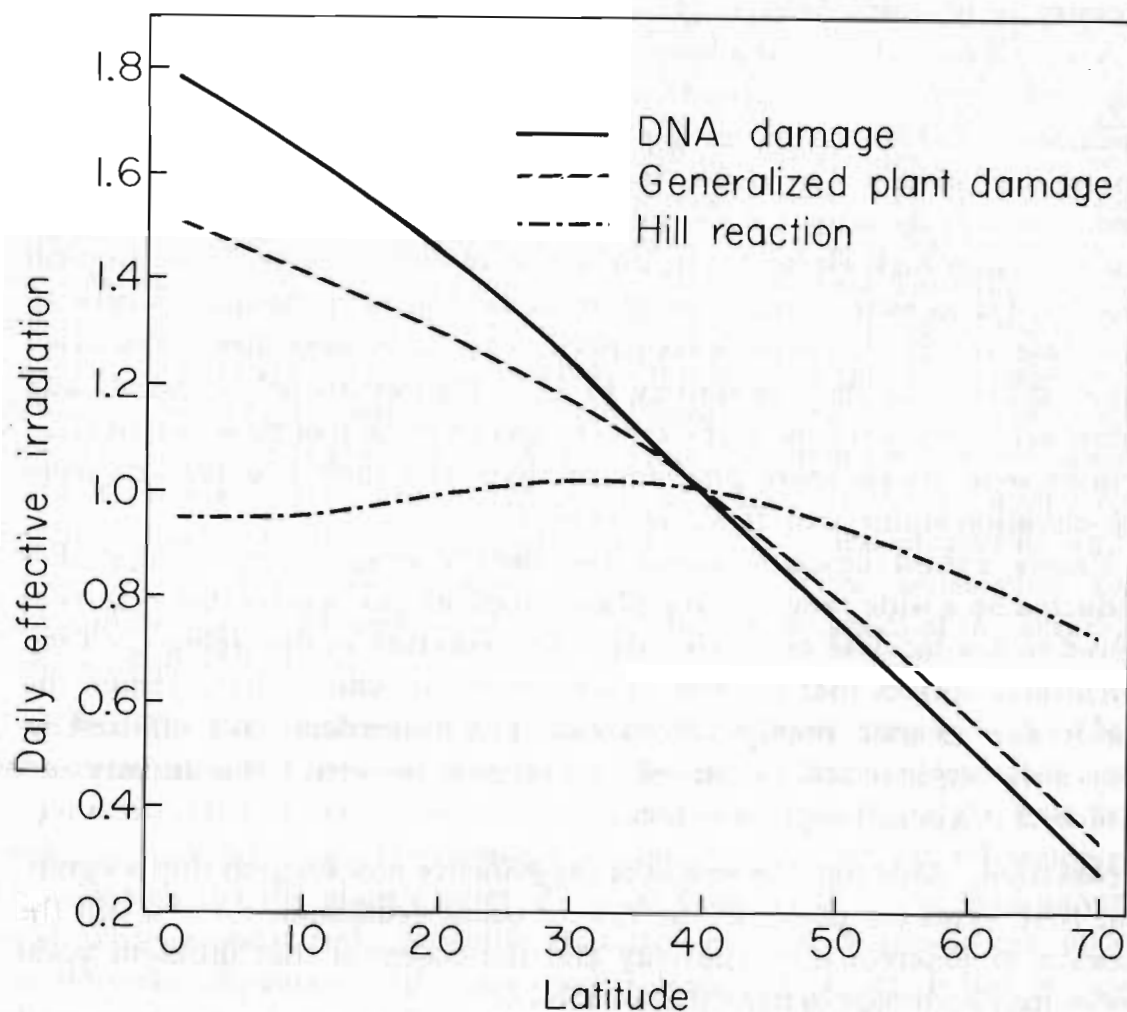
Figure 7. Latitudinal gradient of effective solar UV-B at sea level calculated using three action spectra. The values are for total daily UV at the time of year of maximum irradiation. The DNA damage and Hill reaction inhibition spectra are shown in Figure 4 and the generalized plant damage spectrum has characteristics intermediate between those of the DNA and Hill reaction spectra.

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action spectrum), one would expect that plants in these low-latitude areas would not be so consistent in exhibiting this intense UV absorption.

This filtration in the epidermis must be very selective with respect to wavelength. If the epidermis absorbed radiation at all wavelengths, then light necessary for photosynthesis could not penetrate to the leaf interior.

A second indication that a latitudinal UV gradient does exist and, thus, a steep action spectrum is appropriate, comes from studies under controlled conditions in the laboratory using plants that have evolved at different locations on this latitudinal gradient. Seeds of plants of the same genus, or of difference races of the same species, were collected from the Arctic at low elevations and from high elevations in the alpine of either temperate or tropical latitudes. Plants were grown from these seeds in growth chambers where all environmental factors could be controlled. The plants were then tested to see if they differed in their sensitivity to UV. Photosynthetic inhibition and nucleic acid damage of the arctic races or species of each of these paired comparisons were always more pronounced than with their counterparts from high-elevation alpine areas (Caldwell et al. 1982).

Finally, a third indication comes from the UV sensitivity-screening studies conducted on a wide range of crop plants. Agricultural species that originally evolved in low-latitude areas are more often resistant to damaging UV than agricultural species that evolved in temperate latitudes. Thus, despite the considerable genetic manipulations that plant breeders have effected in modern-day agricultural species, this correlation between UV sensitivity and latitude of origin still appears to hold.

Acclimation. Although the weight of the evidence now suggests that a significant RAF exists for plants in the case of ozone reduction, there is still the question of inherent UV sensitivity and the potential that different plant species may acclimate to more intense solar UV.

Plant species vary considerably in sensitivity to UV radiation. This has been known for some time as a result of simple experiments where a variety of plant species have been exposed to UV from lamps and injury or growth inhibition rated. The environmental conditions to which a plant has been previously exposed also greatly influences the basic UV sensitivity. Much, though not all, of this difference in sensitivity is apparently the result of different leaf optical properties. An important component of these optical properties is UV-absorbing pigments of the general flavonoid group. This group of pigments is a very diverse family of compounds whose quantity and composition vary considerably among plant species, and even among tissues of the same plant organ. Most flavonoids are colorless which, together with their pronounced UV absorption, renders them as very effective wavelength-selective filtering agents. These pigments can fluctuate considerably through time and much of this is influenced by environmental factors, including UV.

Though structural properties and variations in UV damage-repair systems (such as photoreactivation) are also important, flavonoids constitute the most readily adjustable manner of accommodating more intense UV radiation.

Flavonoid synthesis can be induced in certain plants by UV in the waveband 290-315 nm. This could, of course, be very convenient for plants facing potentially injurious solar UV. However, light at longer wavelengths also influences flavonoid synthesis and many of the flavonoid compounds can also be induced without light exposure. The question of ecological relevance is whether or not the small amount of additional UV that would occur with ozone reduction would induce still more flavonoids in plants that have already been exposed to a complete solar spectrum. Will still more flavonoids be synthesized and will they be of sufficient quantity to adequately adjust the plant's capacity to filter UV? We are currently addressing these questions under field conditions where electronically modulated lamp systems provide a small UV supplement that changes continually according to current atmospheric conditions. Early results from these field studies indicate that at least with a test species, broad bean, that an adequate adjustment in optical properties can be made if the UV intensification is moderate. How widespread this phenomenon is among higher plant species and the dynamics of this acclimation remain to be studied.

Competition. Economists and decision makers focus on crop yield as a key parameter in their analyses. Yet, other changes in both agricultural and nonagricultural ecosystems may be of greater consequence. In the past few years, we have addressed the question of change in competitive relationships between neighboring plant species. This has been tested in the field in very small plots of wheat and commonly associated weeds such as wild oat under the electronically modulated lamp systems described earlier. It has become apparent that the balance of the competitive advantage of two species growing in a mixture can be shifted from one to the other even though the UV supplement is so mild that there is no reduction in yield of the mixture or yield of either species when grown by itself (Gold and Caldwell 1983). Although extrapolating expansively to plant assemblages in nature is imprudent, the evidence is sufficiently convincing that such alterations may be more important than reductions of crop yield.

Whether ozone reduction would indeed be a problem for the Earth's vegetation is difficult to assess. There is certainly evidence that the action spectrum characteristics are appropriate and that a potential for changes in the competition balance of plants exists. What we see as subtle changes in features such as the competition between plant species could be reflected in large-scale alterations of some ecosystems. The answers are certainly not yet in and physiological ecologists still have much to do.

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Appreciation