PLANT RESPONSES TO NEAR-ULTRAVIOLET LIGHT

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Although man has effectively accelerated genetic alteration among crop plants in the direction of greater suitability for intensive culture, this has been a comparatively recent and minor genotypic rearrangement as compared to the accumulated contribution of millions of years of prior evolutionary selection. Man's concern with plants has from the beginning been based on their unique photosynthetic capability through which light energy, the ultimate source of life-sustaining free energy, is converted to biologically available chemical energy. In addition, light has been a primary environmental factor within the total regime of selection pressures which have shaped the morphogenic character of plants. It is permissable to anticipate terrestrial plants as responsive in a variety of ways (many yet undescribed) to all wavelength regions of the earth-impinging solar irradiance spectrum. This could be especially true within the shorter wavelength regions (ultraviolet) due to greater photon energies enabling greater possible photochemical and thus greater photobiological activity (39). With the foregoing in mind, how do common light sources vary and is this of any consequence?

LIGHT SOURCES

Technically, light is radiant energy in that portion of the transverse electromagnetic spectrum to which the human eye responds for vision. However, terminology directly implying that ultraviolet, visible and infrared are factions of the overall light regime has fallen into general use when referring to radiant energy in the wavelength regions from 10 to 380 nanometers (nm)[2], 380 to 760 nm, and 760 to approximately 40,000 nm respectively (23, 8). In addition to wavelength, radiant energy is frequently described in units of frequency or wave number. Measurement of intensity is accomplished either photometrically or radiometrically (32). Spectroradiometric measurement enables a complete and graphic assessment of intensity or irradiant power throughout the wide range of plant-responsive wavelengths, whereas the commonly employed photometric measurement yields only an approximate singular assessment of the integrated intensity between 450 and 650 nm (39). When dealing with plants, radiant energy is more appropriately referred to as irradiant energy and measured radiometrically in watts per square meter (W/m^2) in lieu of the photometric units of lux, footcandles, etc. (4, 32). This discussion is primarily concerned with the near-ultraviolet (300 to 380 nm) which necessitates a radiometric presentation. This is done in accordance with the international units for light measurement (SI units) as adopted in 1964 by the United States Bureau of Standards.

In anticipating or evaluating plant responses to any wavelength region, it is particularly instructive to examine the solar irradiance spectrum incident on the earth's surface as positionally, diurnally and seasonally attenuated by the earth's atmosphere. To this end, Fig. 1 represents a compilation of data (13, 14, 15, 39, 16, 35, 41) revealing the shape and intensity of the solar irradiance spectrum before and after atmospheric filtration. In terms of intensity, the solar irradiance spectrum is reduced from 1400 W/m^2 (the solar constant) at the outer fringes of the atmosphere to 865 W/m^2 at sea level when the sun is directly overhead (zenith distance = 0^{o} and optical air mass = 1.0) and the atmosphere is clear. At sea level intensity, approximately 450 W/m^2 (50 + % of total expressed above) are delivered within the bounds of the near-ultraviolet plus visible (300 to 760 nm) with the near-ultraviolet comprising approximately 10% of this total (39, 16). Overall spectral attenuation is due to Rayleigh and Mie scattering which is further augmented by the more spectrally localized band absorptions of atmospheric oxygen, carbon dioxide and water vapor. Whereas these 3 atmospheric constituents affect primarily the visible and infrared regions, it is ozone (approximately 0.4 ppm in an unpolluted atmosphere) which attenuates and determines the limit transmission in the near-ultraviolet (13, 39, 41). Filtration by these atmospheric constituents establishes an "atmospheric window" permitting only transmittance of solar radiation with wavelengths greater than 290 nm. The elimination of these shorter wavelengths by

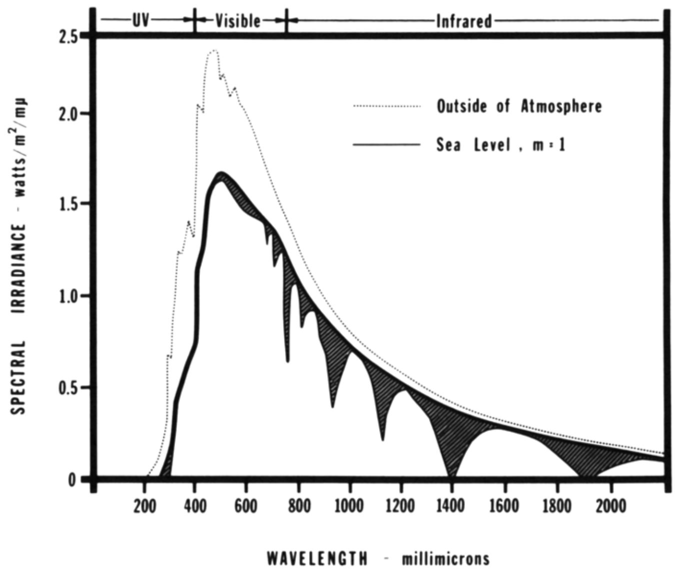

Fig. 1. Solar irradiance spectra. The uppermost, dotted line represents the solar irradiance at the outer fringes of the earth's atmosphere where the optical air mass equals 0. The uppermost solid line represents solar irradiance at sea level as attenuated by atmospheric scattering (Rayleigh and Mie). Optical air mass in this case equals 1.0 indicating the sun as directly overhead (zenith angle = 0^{o}) and the atmosphere as clear. The lowest solid line represents solar irradiance as additionally attenuated by atmospheric ozone, oxygen, carbon dioxide, and water vapor (shaded areas). As the concn of these constituents vary due to weather or atmospheric polution, the ultimate final shape of solar irradiance for any given optical air mass will concomittantly vary. Adapted from (13).

ozone retains special significance for this feature has permitted life on earth to evolve to the present level. Wavelengths less than 290 nm become increasingly lethal (germicidal) due principally to the strong absorption by nucleic acids and proteins which can result in molecular dissociation (23, 39).

Concerning the solar near-ultraviolet, the general attenuation by air mass plus the specific absorption by ozone results in "positionally increased" near-ultraviolet irradiance near the equator and at higher elevations, "diurnally increased" near-ultraviolet irradiance approaching mid-day and "seasonally increased" near-ultraviolet irradiance during summer and fall (27, 13, 28, 16, 35, 2). The later is especially evident within the mid-lattitudes. Even with the foregoing discussed disparities in solar near-ultraviolet irradiance, this irradiance region appears to fluctuate less diurnally and seasonally than does the visible (27). This is due to the offsetting influence of skylight (most intense at 330 and 410 nm) during increased zenith distances (decreasing solar altitudes) plus the greater comparative transmission through water vapor (especially evident with cloud cover) at the shorter wavelengths (16, 17, 43). Thus, from the first indication of dawn, throughout the photoperiod (16) until the last glimpse of dusk (24), regardless of the presence or absence of clouds, the near-ultraviolet represents the most stable portion of the solar irradiance spectrum between 300 and 760 nm. It is of interest to speculate on the possible mediatory significance of this phenomenon on the regulation of plant growth and development.

Artificial light sources are being increasingly used for both experimental and production purposes. Extent of use varies from mere supplemental lighting in greenhouses to total artificial illumination of controlled environment rooms. The variability commonly associated with such efforts is not so surprising when comparisons are made of the spectral irradiance delivered by flourescent or incandescent sources (Fig. 2) with that from the sun (Fig. 1). Flourescent sources are characterized by a

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[2]1 nanometer = 1 millimicron = 10 Angstroms = 1 X 10^{-9} meter.

wavelength-continuous emission from the phosphor (27) upon which is superimposed the intense mercury line emissions. The latter contribute to an exceptionally irregular irradiance spectrum, especially in the near-ultraviolet where irradiance is wavelength-discontinuous due to discrete mercury line emissions at 297, 303, 313, 334, and 366 nm (23). These lines are the only radiant emission in this portion of the spectrum and jointly represent approximately 1 to 3%[3] of the total radiant output.

The typical tungsten incandescent source (Fig. 2) is also characterized by a unique radiant energy distribution. Although emission in this case is continuous (typical 2300°K blackbody peaking at 900 nm), the resulting irradiance is disproportionately intense in the longer wavelength regions of the visible and virtually non-existent in the near-ultraviolet[4]. Obviously, both light sources represent substantial departures from the solar irradiance spectrum. This is true for total intensity as well as irradiant wavelength distribution for it is presently difficult to achieve greater than 125 W/m^2 between 300 and 760 nm, even within the most modern controlled environment rooms as commonly equipped with a combination of flourescent plus incandescent lamps[5]. By comparison, solar intensities (taken near noon) range at 250 to 450 W/m^2 (sea level) during the growing seasons common to the United States. In order for the experimental results obtained in these facilities to be more applicable to field conditions, much improved light sources are needed.

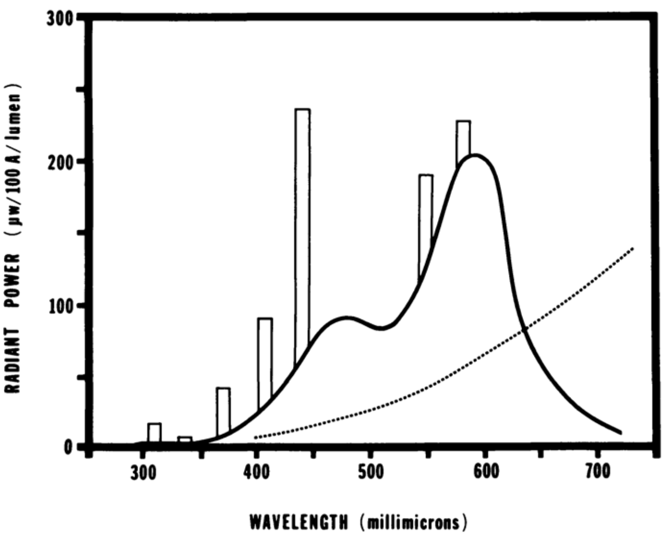

Fig. 2. Radient energy spectra from artificial light sources. The solid lines describe the radiant energy distribution of a "Cool White" flourescent lamp with a luminous efficacy of 62.2 lumes/watt. The mercury emission lines have been equivalently lowered and broadened so that their discernible areas more graphically indicate their individual contribution to total radiant power (intensity). The dotted line indicates the relative radiant emission of a tungsten incandescent lamp of equal consumptive wattage. The ordinate description is not applicable to this comparison because the luminous efficacy of a typical tungsten incandescent source (17.5 lumens/watt) is considerably below that of a flourescent lamp. Adapted from data of The General Electric Company and The Instrumentation Specialties Company.

PLANT RESPONSES TO LIGHT

A cursory examination of plant responses to light (3, 20, 29, 22, 18, 30, 31, 39, 12, 21, 36, 40) suggests that the growth and development of higher plants is controlled by at least 4 distinct photochemical reaction systems, namely:

1. The photochemical system related to photosynthesis.
2. The photochemical system related to phototropism.
3. The photochemical system involving phytochrome.
4. The high-energy reaction system of photomorphogenesis.

The system involving phytochrome is presently considered photomorphogenically dominant within all potentially green plants. In fact, phytochrome is regarded as important to photomorphogenesis as chlorophyll is to photosynthesis (31). The dramatic morphogenic consequences of the reversibility of this pigments structure by low-energy red (660 nm) and far-red (730 nm) have firmly implicated this irradiance region in an overwhelmingly wide range of responses including photoperiodism, seed germination, seedling and vegetative growth, etc. (11). Whereas the blue region of the irradiance spectrum is considered additionally contributory to such "high-energy" photomorphogenic responses as elongation, pigmentation, etc., the near-ultraviolet is comparatively uninfluential as plant photomorphogenesis is presently viewed. Such a conclusion would be unexpected in view of the higher photon energies of this region and the nearly complete absorption by plant leaves of near-ultraviolet irradiance (28, 17). The only plant response uncontested as a sole function of the near-ultraviolet is the base curvature of *Avena* coleoptiles (31, 39), a response closely related, if not identical, to daylight phototropism. Consequently, the remaining discussion concerns a restricted selection of less firmly established near-ultraviolet responses which are presented in hopes of encouraging a reassessment of this irradiance region with regards to horticultural potential.

PLANT RESPONSES TO NEAR-ULTRAVIOLET

Certain consequences of near-ultraviolet absorption by various organisms are well recognized. They are clearly expressed in animals by such low dosage responses as vitamin D synthesis and melanin pigmentation (suntanning) as contrasted to such high dosage effects as erythema (sunburning) and the development of epidermal cancers (27, 23, 5). Whereas the foregoing responses are prompted by short wavelength near-ultraviolet, articles implicating all regions of the near-ultraviolet as diversely involved in altered growth of bacteria, fungi, algae and higher plants are in evidence (25, 28, 33, 34). Even the *in vitro* repression of the growth of plant (Ginkgo pollen) and animal (Hela) cell cultures in response to the near-ultraviolet from flourescent lamps has been established (25).

In agriculture, there is an embryonic resurgence of interest in the benefits derived from the presence of low intensity near-ultraviolet as part of a "balanced" irradiance spectrum. Tomato plants appear less susceptible to viral attack (33) and agricultural animals display increased immunobiological responsiveness and thus greater vitality and productivity when supplemental near-ultraviolet (approximately 50% of erythemal dose) is included within normal lighting regimes (6). Similar immunobiological responsiveness is also apparent when human beings are subjected to such near-ultraviolet supplementation, especially under conditions where little solar irradiance exposure is possible (6, 33, 34).

All available evidence suggests that the diverse plant responses to near-ultraviolet irradiance are strongly intensity-dependent (28). As suggested by Ott (33, 34), the near-ultraviolet may be likened to trace elements in biochemistry wherein small amounts are essential but as concentrations increase, toxicity may occur.

With the foregoing as a prelude, three morphogenic responses to near-ultraviolet irradiance of particular interest to the author will be briefly discussed. Each is of possible significance to crop production and together they present a cross-sectional glimpse depicting the diversity of influence attributable to this environmental factor.

Vegetative growth

The influence of the near-ultraviolet upon inhibition or promotion of vegetative growth is perhaps the most widely recognized response. Inhibition of growth under solar irradiance is increasingly evident at higher elevations (28). Plants so inhibited appear smaller and thicker (alpine-like) and are retarded in growth and delayed in flowering. As altitudes increase, temperatures decrease (1°C/640 ft) and solar near-ultraviolet irradiance increases. These two environmental factors have long been considered dominant to the "alpine-effect". Similar plant morphology has been observed with such crop plants as tomato, snap beans, lima beans, lettuce, cabbage and cucurbits when grown in the high intermountain arid regions of southern Idaho (9). This growth retardation as well as an associated leaf abnormality is alleviated by either reducing the intensity of, or removing completely, the short wavelength near-ultraviolet. This was accomplished by

[3]Data from The General Electric Co., Sylvania Lighting Products, Inc., and The Instrumentation Specialties Co.

[4]Data from The Instrumentation Specialties Co. and author's measurements using an ISCO Model SR spectroradiometer.

[5]See chapter 16 of the ASHRAE 1968 Guide and Data Book.

filtering the solar irradiance through polyethylene, saran shade cloth or glass. The effect is most discernible with plants possessing exposed growing points (10). Noticeable vegetative growth increases have also been observed when potatoes are grown under polyethylene canopies (7). Utilizing either solar or fluorescent-incandescent derived irradiance, the author of this paper has made similar observations while culturing a diploid selection (PI 5279.15) of potato. When solar irradiance is filtered by polyethylene, polyvinyl chloride (PVC) or Mylar (see Fig. 4 for transmission features), this potato clone responds with a very obvious increase in vegetative growth (Fig. 3). An identical response is achieved in a controlled environment room[6] when the near-ultraviolet is filtered from a flourescent source inherently rich in the red and far-red (specifically, Sylvania's Gro-Lux Wide Spectrum). A similar, but much reduced, response results with the restriction of the near-ultraviolet from the irradiance derived from Cool White, Sylvania's Gro-Lux, etc. which represent flourescent lamps delivering little radiant energy above 680 nm. The foregoing correlates nicely with the results obtained outdoors as solar irradiance is also rich in wavelengths from 680 to 760 nm (see Fig. 1). Because there is also an increase in tuber yield with near-ultraviolet restriction (author's unpublished data), it is interesting to speculate on the importance of this environmental factor to potato production. Eastern Idaho potato producing areas (4,000 to 5,000 ft elevations) experience high solar near-ultraviolet irradiance and yield substantially less per acre than does Washington's Columbia Basin (1,000 to 1,300 ft elevations) which receives substantially less near-ultraviolet irradiance.

Similar vegetative growth responses have been obtained with marigold, tomato, corn, *Impatiens* plants, *Chlamydomonas* cells and the mycelium of *Sordaria* (26) when all irradiance below 385 nm is filtered from a flourescent (Cool White) plus incandescent source.

Pigmentation

The current surge of information surrounding the phytochrome system and it's relation to anthocyanin synthesis (31, 37, 38, 42) has all but buried older reports which implicate the short wavelength near-ultraviolet as a dominant influence on such pigmentation. Specific reference is made to the convincing work of Arthur (1). Using whole 'McIntosh' apples, he demonstrated that a mercury lamp filtered to deliver ultraviolet irradiance from 290 to 312 nm proved the most effective wavelength region in the induction of anthocyanin pigmentation (coloring). This author has also observed increased red pigmentation (assumed to be anthocyanin) on 'McIntosh' apples and the undersurfaces of potato leaves when all wavelengths emitted by a 1:1:1 mixture of Cool White, Gro-Lux, and Gro-Lux Wide Spectrum lamps (delivering approximately $75 W/m^2$)[7] are permitted to reach the leaves or fruit. Restriction of near-ultraviolet transmission by thin films of PVC and Mylar resulted in depressed pigmentation. Outdoors, apples remaining attached to a tree have been observed to remain green and continue to increase in size when solar irradiation is filtered through window glass (33, 34). When this glass (which restricts short wavelength near-ultraviolet) is removed, pigmentation commences.

When band-pass filter systems are used to isolate the various wavelength regions of a flourescent (Cool White plus Gro-Lux Wide Spectrum) derived irradiance spectrum, pigmentation of apples is evident only in the blue (410 to 460 nm). The unavoidable concomittant reduction in intensity (10% of initial) within each band-pass region is likely contributory to such a limited response for anthocyanin synthesis is presently regarded as a "high-energy reaction system" response (30, 31). Such responses have been recently linked directly to phytochrome (19). Therefore, when one examines the absorption spectra of the interconvertible phytochrome forms P_{fr} and P_r discovering substantial absorption in the near-ultraviolet, this awareness prompts speculation suggesting that under high irradiance intensities the observed near-ultraviolet influence is yet another manifestation of the phytochrome system.

Leaf morphology

When this author attempted to culture the diploid potato selection (PI 5279.15) in a controlled environment room[5] there appeared (7 days after emergence) chlorotic, hypertrophical leaflet lesions positioned predominantly near the leaflet veins and evident only on the upper surfaces of the individual leaflets (Fig. 5). Extensive lesion development caused leaflet curling and consequently an obvious departure from normal leaf morphology (Fig. 5). Exploratory examination of many possible causes led ultimately to the involvement of the near-ultraviolet. Widespread alterations in composition of basic flourescent-incandescent light regimes (of approx. $75 W/m^2$)[7] yielded no detectable alleviation, however, when the controlled environment room was compartmentized into either 4 or 6 equivalent sections and various thin films positioned as irradiance filters between the lamps and plants, the cause became apparent.

Fig. 3. The influence of solar near ultraviolet screening on vegetative growth of a diploid potato selection (PI 5279.15) grown during July, August and September (1969) at Pullman, Washington (elev. 2600 ft.). Filters employed from left to right are: none, polyethylene, polyvinyl chloride (PVC), and Mylar (all films of 8 mil thickness). See Fig. 4 for transmission characteristics of each film. Note that the short wavelength near ultraviolet is evidently most influential to these results.

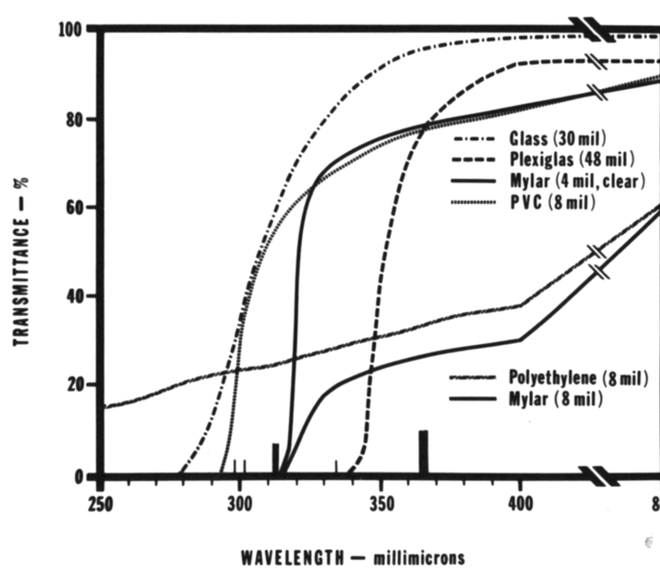

Fig. 4. Radiant energy transmittance of various filter materials. The vertical lines on the baseline represent the position and relative intensities of the mercury emission lines from a flourescent lamp. The glass (30 mil) curve reflects the transmissability of the flourescent lamp glass envelope. The two diffuse films of polyethylene and Mylar reveal low transmittance in comparison to the clear films due to instrument limitations in the measurement of their optical density. Direct comparison with the clear films is therefore not appropriate. Plexiglas is a trade name given a methyl methacrylate polymer by the Rohm and Haas Company, whereas Mylar is the trademark for a polyester film developed by E. I. Dupony de Nemours and Company (23).

[6]Hotpack Model 1750-1 (a walk-in model).

[7]Measured by ISCO Model SR spectroradiometer.

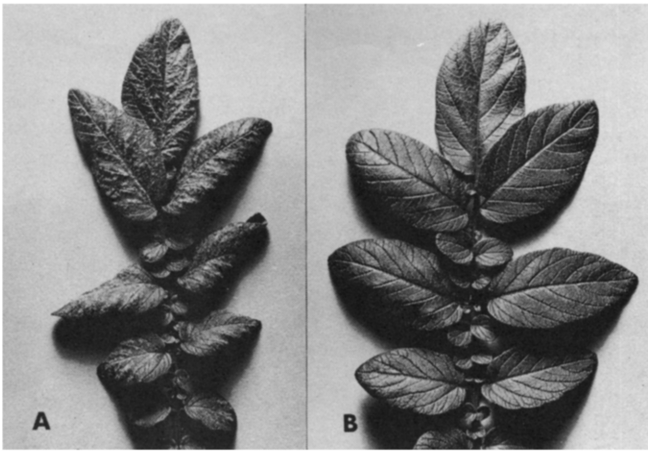

Fig. 5. A. Lesion-afflicted leaf of diploid potato selection PI 5279.15. Note particularly the elevating of veinal regions and curling of leaflets. B. Normal, healthy leaf of diploid potato selection PI 5279.15.

Whereas the films used are nearly equivalent transmitters throughout the visible (determined by spectroradiometric measurement of each section), they present individual uniqueness as sharp-cut filters in the near-ultraviolet (Fig. 4). Plants grown in sections filtered by Mylar (duplicating the room as originally equipped) or Plexiglas were consequently denied exposure to flourescent lamp emission lines of wavelengths shorter than 315 nm and in response developed leaf lesions as in Fig. 5 (left). However, those plants grown in sections filtered by PVC or polyethylene received irradiance including the 313 nm emission lines and in response were free of leaf lesions (Fig. 5 right). When near-ultraviolet irradiance within a Mylar-filtered section is supplemented by two 15 W BL flourescent lamps delivering peak irradiance of only 0.2 W/m^2 (23), lesion development is prevented. The obvious requirement for near-ultraviolet by this clone can be demonstrated under solar irradiance as well, however, total solar global irradiance (direct incident plus skylight) must be appropriately filtered or lesion development is not apparent.

Finally, a second diploid potato selection (PI 5293.2) of nearly identical genotype to PI 5279.15 does not develop leaf lesions with similar treatment but instead exhibits a more subtly discernible lack of vigor.

Plant responses to the near-ultraviolet may thus be dramatic yet illusive. Although this research area presents unique technical difficulties, it looms with promising horticultural relevance -- especially to crop plants of high altitude origin.

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