ARTIFICIAL LIGHT SPECTRA AND PLANT GROWTH.

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SUMMARY

This study was undertaken to investigate the suitability of various commercially available high-pressure discharge lamp systems for controlled environment use. Two main experiments were carried out. The Spectral Balance experiment consisted of three treatments each at a similar total visible irradiance (160 W m^{-2}) based on high-pressure discharge lamps (HPLR, HPI and "Metal-arc" types) supplemented with blue-fluorescent and tungsten lamps, and three subsequent treatments based on the "Metal-arc" lamp with varying supplemtation and different irradiance levels (105, 200, 250 W m^{-2}). The Spectral Bias experiment consisted of blue-biased, balanced and red-biased spectral treatments obtained by varying the proportions of different artificial lamp types (viz. "Metal-arc", Blue HPI and Quartz Halogen). Each spectral bias treatment was studied at two irradiance levels (130 and 200 W m^{-2}). Four species (*Sorghum bicolor* L., *Glycine max* L., *Lolium perenne* L., *Trifolium repens* L.) were used as test plants at day and night regimes of 22.5/17.5°C and 60/90% R.H. with a 12 h photoperiod for all treatments. The two experiments were carried out in Climate Rooms and Growth Cabinets of the Plant Physiology Division, D.S.I.R., Palmerston North.

Results from the Spectral Balance experiment showed that either of the three lamp types with adequate blue and red wavelength supplementation could be used for plant studies in controlled environments, but on an efficiency basis the order of selection was "Metal-arc", HPI, HPLR. Results from the Spectral Bias experiment showed marked changes in shoot dry-weight increases, leaf area formation, dry-weight per unit area of leaf, stem length, tiller number, main stem angle, root/shoot ratio, proportions of plant parts, relative growth rates, relative rates of leaf area expansion, net assimilation rates and leaf area ratios in response to the biased spectral treatments. Biochemical changes were also recorded which showed short-wave enhancement of total amino-acids, proteins, aspartic and glutamic and other amino acids, and a long-wave enhancement of soluble sugars, starch and total carbohydrates. A scheme is presented incorporating the observed responses with those recorded in the literature. Total leaf chlorophyll was

increased under short-wave conditions but chloroplast structure was found to be unaffected by the spectral treatments.

Calculations were made of the relationships between leaf area, the number of absorbed quanta and the total dry-matter accumulation for each Spectral Bias treatment and results indicated that the spectral influence on the distribution of the assimilated carbon within the plant (i.e. to leaf or to non-leaf tissue) primarily influenced the subsequent plant dry-weight increase.

The implications of the present studies are discussed in relation to providing a standardized artificial light spectrum for controlled environment work. This consideration includes a study of natural sunlight spectra under various environmental conditions and a discussion of the technical difficulties encountered when using these particular lamp systems.

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"If at any time I speak of Light and Rays as coloured or endued with colours, I would be understood to speak not philosophically and properly, but grossly, and according to such Conceptions as vulgar People in seeing all these experiments would be apt to frame. For the Rays to speak properly are not coloured. In them there is nothing else than a certain Power and Disposition to stir up a Sensation of this or that Colour".

"OPTICKS"
NEWTON.

I. INTRODUCTION.

The growth, development and differentiation of plants growing in natural environments is determined by biotic, genetic and physical factors. Within each plant species the absolute limits of any growth response is established by inherent genetic information and the delineation of that response is, in turn, determined by the physiology of the plant.

Among the most important physical factors in any natural environment are light quality, quantity and duration. Plant growth depends on a very narrow bandwidth of the electromagnetic spectrum which usually includes the near ultraviolet (down to 320 nm), the visible, and the near infra-red (up to 800 nm) regions. The radiation of this spectral range not only supplies the necessary energy for photosynthesis on which plant metabolism is based, but also by way of various photomorphogenetic processes, it controls, independently of photosynthesis, the way in which this captured energy is directed along the various metabolic pathways. Since for most processes other than photosynthesis, the amount of radiant energy initially absorbed is low, in relation to the response effect, these light reactions can be considered to belong to a group of photostimulus processes which are characterised by dose-effect relationships. These are exothermic in that they ultimately release, or direct an amount of stored energy, which may be very large as compared with the energy content of the radiation initially responsible for the stimulus (Wassink and Stolwijk, 1956).

In addition to this group of low-energy photomorphogenic responses there are those responses related to the so-called "high energy reaction" of photomorphogenesis, (Mohr, 1964) where a photoreactive system appears to depend to some extent on short-wave visible radiation for controlling morphogenesis.

The influence exercised by the environment on growing plants is exceedingly complex, not only because of many climatic variables, but also because of the constant interaction between them. As a consequence of this complexity the

usual experimental approach is to vary only one factor at a time and to examine the corresponding plant response under that isolated factor - this technique is not simplified in the field or glasshouse, however, because of the non-homogeneity of the natural environment during growth. In relation to these problems, controlled environment facilities (sometimes called "phytotrons") have been constructed in recent years in order that environmental factors may be controlled independently in the study of plant growth.

The first large-scale facilities for growing plants under partially controlled conditions were the Clark Greenhouse in 1939 and the Earhart Plant Research Laboratory in 1949 (both at the California Institute of Technology). These units were basically air-conditioned glasshouses as opposed to completely controlled facilities and a main contribution to physiology from these units was the demonstration of the potential of a large-scale controlled environment operation. Such controlled facilities are now a common feature of present day research equipment although larger laboratories are found only in a few major centres.

Among the most significant problems in the use of completely controlled facilities, in comparison to air-conditioned glasshouses, is the implied requirement to replace sunlight with some form of artificial lighting. This implication is important with respect to the performance of the plant, the physical porperties of the artificial spectra being used and the technical complexities of the manufactured light sources currently available.

Despite the widespread use of controlled cabinets or rooms, however, there is still surprisingly little published information, of a quantitative character, on the varying effects of different artificial light sources on the growth and development of higher plants. It is true that many papers have been published on the influence of spectral composition of light on growth and morphogenesis, but in the earlier investigations it was not feasible to ensure that comparisons between spectral bands were made on the basis of equal energy,

or equal quanta, nor were actual irradiance values quoted in each case. In addition, where comparisons were made on such a basis as equal energy, in general, the levels of energy involved were much below those encountered under outdoor conditions.

The requirement in this investigation then was to study lamp types and lamp combinations which would be capable of giving adequate plant growth and development under controlled environment conditions and which would provide the energy levels desirable in physiological studies. To this end two major studies were entertained. In one of these, potentially suitable high-pressure discharge lamps were tested under controlled environment growth-cabinet conditions in an attempt to select the most suitable lamp of this type for plant studies. The second major study was designed to examine the effects of biased-artificial light spectra on plant growth.

The objectives were to examine both the effects of spectral composition on plant growth and the degree of operating flexibility within these lamp types and their resultant combined spectra. Lamp ageing, and the effect of more than one radiation source possibly creating a considerably heterogeneous radiant flux at the level of the highest leaves as regards density, spectral composition and direction of individual rays means, that for systems to be acceptable, some knowledge of these factors is required.

The aim of the studies recorded then was to test various artificial lamp combinations with respect to their suitability in providing light sources for plant growth in climate rooms and growth cabinets. The criteria of judgement on the light systems were:

(a) Their spectral output in the 380-800 nm range in relation to that of sunlight; and

(b) the plant responses under the systems used as indicated by the rate of growth, the form of growth, the carbohydrate, protein and pigment composition of the laminae, and the visible appearance of the plants with particular reference to any deleterious symptoms.

II. LITERATURE REVIEW

1. The influence of Light Spectra on Plant Growth and Development.

1.1. General.

The influence of spectral quality on the growth and development of plants is manifest in two significant ways. Firstly, light supplies the energy required for the assimilation of carbon dioxide in the photosynthetic process. Secondly, it is responsible for the outward appearance of plants, it determines plant height, the dimensions of leaves, the length of the internodes, and many of the other features which together constitute the "normal" appearance of a plant, as opposed to the "etiolated appearance" acquired in the absence of light. These light functions can be broadly divided into two groups in relation to the functions of the processes involved and may be regarded as either photoenergetic or photostimulus processes.

Photosynthesis belongs to the photoenergetic group. This process requires a comparatively high light irradiance for a significant response, and at irradiances below the saturation level the photosynthetic rate increases linearly with irradiance. The compounds in which the chemical energy from photosynthesis is stored supply the energy for the remainder of the metabolic activities and are used as raw materials in the growth and expansion of the plant.

The second group contains a large number of processes, such as phototropism, photoperiodism, internode inhibition, leaf growth promotion, seed germination and many others. These processes are characterised by relatively low (light) energy requirements, in general by a non-linear relation between irradiance and effect, and by the fact that the overall process is endothermic. The amount of energy released or directed typically exceeds greatly the energy input by the light.

1.2. Wavelength Dependence of Photomorphogenesis.

Many controversies in the literature on photostimulus processes can possibly be ascribed to differences in methods, and inadequate control of the environments used. It is clear from the literature reports that several methods have been used in studying the spectral effects on plant growth and development. These include:

(a) the study of formative effects of light of restricted spectral regions under the complete exclusion of white light,

(b) the study of the effect of restricted spectral regions following pre-treatment with white light under which the plant has reached a certain seedling stage,

(c) a similar study on dark pre-treated (etiolated) material,

(d) the study of narrow spectral bandwidths given as supplementary irradiation to normal daylight, and

(e) the study under broad bandwidth conditions which often include the entire visible spectrum and are typified by artificial light source experiments.

Each of these treatment types can produce a response which may or may not bear relation to the response under any other treatment even where the same wavelength of radiation is being considered. In this respect some effort is made here to keep these sections separate and to consider these possible differences when discussing the results.

Stolwijk (1954) from a series of experiments in the Wageningen Laboratories characterised the morphogenetic action of light as follows: the absence of the wavelength region 400-500 nm results in a strong elongation of stems, petioles and in some cases, of leaves. Evidence from cell counts showed that cell elongation was a much more important factor than cell division in accounting for the increases in length shown. The wavelength region around 400 nm was found to be much more effective in inhibiting elongation than the region around 460 nm.

On the whole, the results presented by Stolwijk (1954)

bearing on the morphogenetic action of various wavelength regions, are in close agreement with the results of previous investigators. For example, Schanz (1919) and Popp (1926) used day-light from which various parts in the short wavelength regions were absorbed by glass filters, in comparison to the Wageningen Laboratory where various fluorescent tube types and filters were used. From this work Popp (1926) reported that when plants were grown in daylight from which all wavelengths shorter than 529 nm were eliminated, they developed the following characteristics as compared with plants grown in "normal" daylight:-

(a) an increased rate of elongation of the stem of all species during the first 2 or 3 weeks growth; a greater final height in soybeans, tomatoes, and coleus, but a marked decrease in height in sunflowers, petunia, buckwheat, and Sudan grass.

(b) a considerable decrease in thickness of stems.

(c) A reduction in the number of branches or side shoots.

(d) A general rolling or curling of leaves.

(e) Good development of chlorophyll, but a reduction in anthocyanin of leaves and flowers.

(f) Less differentiation of stem and leaf tissues, less compact and thinner walled cells, and a reduction of strengthening tissues.

(g) A considerable delay in time of flowering and a reduction in the number of flowers produced.

(h) A very weak development of seeds, fruits, and general storage organs.

(i) A decrease in fresh weight and dry weight and an increase in percentage of moisture.

(j) A considerable decrease in starch and total carbohydrates, generally an increase in total nitrogen and often an increase in soluble nitrogen compounds.

The degree to which these different effects were produced varied with different species, but all species, apart from the presence of chlorophyll, had an etiolated appearance. When all wavelengths shorter than 472 nm were removed, the same effects were produced as listed above, but to a somewhat lesser degree and in general, there was very little difference between plants

that received all the wavelengths of the daylight spectrum and those from which only ultraviolet rays were eliminated.

The results obtained with plants from which all wavelengths shorter than 529 or 427 nm were eliminated were somewhat similar to those obtained when plants were grown under greatly reduced light.

Although the results of this work demonstrated very aptly the effects of various wavelengths of light on plant growth, a direct comparison of treatments is not completely valid due to light irradiance differences encountered. However, some effort was made in the experiment to compensate for these differences and the qualitative comparisons, at least, are valid and are supported by more recent studies.

Earlier, Shanz (1919) had shown for a range of species (cucumber, fuchsia, chrysanthemum, lobelia, begonia and oxalis) that maximum plant height was attained under red light conditions and minimum height under blue light conditions. With potato and red beet, largest plants were found under blue-violet light with green and yellow light giving respectively small plants. With beans, soybean and potato, chlorophyll development was found to be most rapid in red light, whereas with lettuce, chlorophyll development occurred only with blue and violet light but not with yellow or green. Schanz unfortunately presents no temperature or light irradiance records.

The formative effects of light of restricted spectral regions on the growth of plants under complete exclusion of "white light" was intensively studied by Wassink and Stolwijk (1956). Most plants showed short growth in white light (daylight fluorescent tubes) which was even more evident in blue and violet light. In green light, and still more in yellow and red, plants showed marked stem elongation. In tomato (var. Vetomold 121), the plants in the yellow and red cabinets showed conspicuous epinasty of the mid-ribs and lateral veins of the leaves, in addition to stem elongation. This is in strong contrast to plants of the same variety, exposed to a short day in white light, supplemented by some hours of fairly

low intensity radiation in narrow spectral regions.

1.2.1. Leaf Growth Response to Specific Wavelength Regions.

A number of studies have dealt specifically with the effect of light quality on leaf growth.

Vince and Stoughton (1957) report data for the wavelength effect on leaf length of tomato, calendula and pea. In all cases the shortest leaves resulted under the blue light treatment and the longest under red light. A green light treatment gave intermediate values.

These responses were considered in relation to stem growth but it was found that the expansion of veins in light of different wavelengths was not related to the behaviour of the internodes since maximum leaf length occurred in red light in all the species they studied, even where internode expansion was reduced by red light. These authors found also that mesophyll expansion was more variable. Normally-expanded leaves developed in any wavelength region in calendula, cucumber and lettuce, with maximum expansion occurring in red light. In pea, maximum expansion of the mesophyll occurred in red light, but the leaflets were reflexed from the petioles. In tomato, mesophyll expansion was reduced, compared with vein extension, in red light and to a lesser extent in green light, and the mesophyll tissue was curved downward from the veins. The main vein also showed epinasty.

Went (1941) also presents wavelength response data for pea. Larger and more normal leaves resulted under red light than under either blue or green (see also van der Veen and Meijer, 1959).

Van der Veen and Meijer (1959) found that seedlings of Mirabilis jalapa produced only small leaves when grown in red or green light but normal sized leaves were produced in blue light. The larger leaves are those normally grown in shade. Higher light irradiances produced smaller, thicker leaves which was mainly an effect of blue, violet and near ultraviolet radiation. In extreme shade, the thinness and folding

of leaves was attributed to the failure of mesophyll cells to divide and enlarge (Cormack, 1955). Some plants needed blue light for normal leaf development (van der Veen and Meijer, 1959); red light alone produced small curved leaves. Plants of Coleus grown in white light with ultraviolet radiation had smaller, more hairy, leaves with a thicker cuticle than plants grown in white light alone.

1.2.2. Stem Growth Responses to Specific Wavelength Regions.

Many investigations have been carried out on the subject of plant stem elongation in relation to light of different spectral regions but consideration must be given to the fact that many of the results have included the possible contamination of the isolated wavelength regions with unwanted radiation, especially in the infra-red region; the possibility that the results may differ at different irradiances; and the suggestion (Wassink & Stolwijk, 1956) that dark-grown material irradiated for short periods of time may respond differently from material raised under monochromatic light and irradiated for long periods during each day. It is likely also that the differences in behaviour are related to species as well as to these other factors.

Vince and Stoughton (1957) present data where two types of response have been observed in plants grown in identical wavelength regions. Tomato and lettuce show significantly greater internode extension under red as compared to blue light whereas with calendula and pea the inverse response was shown. In all species a green light treatment produced intermediate values to the red and blue light treatments. These authors also report that in pea the relative response to wavelength was the same in seedlings irradiated for 15 minutes, 1 hour and 16 hours per day, and that for tomato and pea the relative response was not affected by irradiance in the range of 1.3 to 7.4 W m^{-2}.

In the Philips Laboratories, Meijer (see van der Veen and Meijer 1959) studied stem elongation in a large number of

plants either previously raised in white light or exclusively grown in coloured light. The spectral treatments consisted of coloured fluorescent tubes and suitable filters producing blue, green, red or infra-red bandwidths. In the first three of these the irradiance was approximatedly 10 W m^{-2}. The spectral response of three species, tomato, Mirabilis and petunia, germinated in white light were reported.

Young tomato plants (var "Victory") treated with light of different colours varied in the extent of their growth. In red light they were of average height, in green light they were somewhat taller and in blue light shorter. With a small amount of infra-red added to blue considerable elongation, greater than green light, was reported. The same amount of infra-red added to red light had no effect at all; the plants then attained the same length as those grown in red light only. Successive 8 hour spectral treatments also produced interesting results. Red light after blue (8RD) and blue after red (R8D) resulted in each case in short, compact plants, no larger than those exposed to 8 or 16 hours of blue light alone.

In this combination of colours it appeared, then that the influence of blue light prevailed over that of red. Red light was also shown to render the plant more sensitive to infra-red. The particular feature of these results is that weak infra-red did not stimulate the elongation when given simultaneously with strong red light, but it did when strong blue and weak infra-red were given at the same time. On the other hand, infra-red had a marked effect if given after strong red light, but no such effect after strong blue.

Mirabilis jalapa showed very different behaviour to spectral treatments from that of tomato. In red light the plants became extremely tall, but with very small leaves. Green light had a similar effect and the addition of both small and large amounts of infra-red did not influence the results from these spectral treatments. Blue raised plants were short with normal leaves and infra-red added to blue

only marginally increased elongation. From successive spectral treatments it was apparent that elongation reached a maximum in red or green light and that additions of, or later irradiation with near infra-red did not affect the response.

In petunia, the normal development of the plant in white light is a rosette after which elongation occurs and a leafy stem is formed. Young plants exposed to light of various colours were found to differ appreciably in their response. In red and in green light the plants continued to grow in a rosette form but in blue light the rosette stage was omitted altogether. With near infra-red added to the blue light the elongation was even more pronounced, although the general form was the same as with blue light alone. A small amount of infra-red given together with red light produced no visible effect. However, the results of giving a little infra-red after exposure to red light were much the same as those obtained in blue light. On the other hand, if the young plants were exposed to infra-red after irradiation with blue light the former did little or nothing to alter the elongation that had already taken place in the blue light.

Other species have also been examined by Meijer and resemble two main response types. Calendula (marigold), Perilla and gherkin seedlings resemble Petunia on the one hand, whereas on the other, Mentha (mint), Bryophyllum and potato behave more like Mirabilis. The response was found to be independent of both daylength and irradiance.

This author distinguished these two types as follows:

1. the "Mirabilis type"; inhibition by blue light more pronounced than by red light.
2. the "Gherkin type"; red light more inhibitive than blue light.

With seedlings exposed exclusively to coloured light van der Veen and Meijer (1959) report that irradiance experiments indicate that it does not simply depend on the plant species or on the pre-treatment which spectral region is the most effective one in inhibiting elongation. It was found,

with plants of the two types mentioned above, that at relatively low light irradiance blue light was always less active than red light, whereas at relatively high irradiances the situation was reversed. At a certain "critical intensity" the elongation of the internodes of plants exposed to red, and of those exposed to blue light, were inhibited to the same extent, i.e. the internodes were the same length. The value of this "critical intensity" depended on the plant species: with plants of the "Mirabilis type" it was reached at a low irradiance, but in the case of the "Gherkin-type" it was found at much higher irradiances. These authors suggest that as blue light is less inhibitive than red light at low, but more so at high irradiances, two different photoreactions are involved in the process of elongation inhibition.

Wassink and Stolwijk (1956) introduce a further situation where the spectral response of stem growth depends on pre-treatment conditions. This is in etiolated (dark-grown) plant material where the inhibition of elongation is most effective in the red spectral region, whereas in light-grown plants, and at high irradiances, the blue-violet region of the spectrum is especially effective.

Clearly the implications of these studies have been in part resolved by the discovery and elucidation of the phytochrome system and the associated red-far-red photomorphogenetic responses. The earlier work in this field was reviewed by Parker and Borthwick (1950) and subsequently many reviews and papers have been published.

1.2.3. Growth Analysis Components Response to Specific Wavelength Regions.

Hughes and Evans (1964, 1965a, 1965b) in a series of papers on the effects of environment on the growth of Impatiens parviflora, included in the study blue and red light (from fluorescent tubes) treatments in comparison with a standard daylight/white combination as a reference. Although the temperature and irradiance levels varied between treatments several valid comparisons are possible.

In both spectral treatments there was no response of this species to the distribution of leaf dry weight to total dry weight. Blue light decreased the dry-matter percentage of the leaves whereas the red light treatment produced the opposite response. Red light increased the proportion of stem but decreased the root proportion in comparison with the daylight/white control. Blue light on a quantum basis did not appear to affect the net assimilation rate (NAR) but decreased NAR logically on an energy basis. Red light, on the other hand, on an incident energy/apparent assimilation basis increased rates by 20% over the daylight/white comparison. Under both treatments the leaf area ratio showed a characteristic fall with time and increasing dry weight which was due largely to a similar decline in specific leaf area. The red light treatment leaf area ratio was similar to the daylight/white values but in comparison the blue treatment values were consistently lower.

Rajan et al (1971) present data for leaf area per plant for Gossypium, Helianthus, Phaseolus and Zea which show an increase in values which correspond to an increase in red bias (increase in tungsten content) including an increase in the red:far-red ratio. More detailed data was presented for Phaseolus which was the most responsive species and it is evident that between 10 and 25°C the total leaf area was increased as the proportion of tungsten lamps was raised but at 30°C and more particularly at 35°C there was a dramatic decrease. These interacting relationships for total leaf area were more dependent on changes in leaf size rather than leaf number since the magnitude of the changes induced in leaf area by the nature of the light source were much greater. Furthermore, for leaf number the inclusion of tungsten lamps caused no depression at 35°C. The pattern for the changes in the ratio of leaf area to leaf weight was somewhat different. Between 10 and 20°C the ratio was little affected by light quality but as the temperature was raised above 20°C the ratio was progressively favoured by fluorescent lighting.

1.3. Phytochrome and High Energy Response Systems.

The study of the response of a plant to the quality of

the light environment has, particularly in the past two decades, predominantly centred around the role of phytochrome and its chemical and physical properties. Hendricks and Borthwick (1963) list four distinct ways in which phytochrome can link the plant to the environment. Firstly, it changes with light quality independently of irradiance above low values. Secondly, it reverts in darkness from the P_{730} form to P_{660} and in doing so regulates photoperiodism. Thirdly, the substrates upon which it acts, and the products that it forms, depend upon photosynthetic and reserve metabolic activity. Fourthly, the rates of the main reactions in which P_{730} is involved, including its own dark transformation, but not its photoconversion, are temperature dependent.

The reversible photochemical change $P_{660} \leftrightarrows P_{730}$ depends upon the energy distribution in the spectrum. In a given wavelength region the reaction is driven towards an equilibrium at a rate depending on the irradiance and, on the product of the molar absorptivity and the quantum efficiency for conversion, of the two forms. Equilibrium is approached within short time periods (minutes) at irradiances as low as one per cent of sunlight in 10 nm bands through the range of 400-780 nm (Hendricks and Borthwick, 1963). Evidence is now well established for the role of phytochrome in a number of higher plant systems which include: flower initiation, flower development, leaf enlargement, internode elongation, seed germination, leaf epinasty and development and differentiation of plastids of etiolated leaves.

The position of the phytochrome equilibrium becomes a significant factor when the light quality for use in controlled environments is considered. Where, for example, only fluorescent tubes are used as the main source of radiation, irradiance in the 700-800 nm region is very low relative to that in the 600-700 nm region which results in very predominant P_{730}. Addition of radiation from incandescent filament lamps displaces the equilibrium towards the level reached in sunlight, which is probably near 50 per cent P_{730}. Radiation in the blue part of the spectrum is also important because of the combination of absorptivities of P_{730} and P_{660}, quantum

efficiencies for conversion, and screening absorption of chlorophyll led to intermediate levels of P_{730}. Hence although the plant may be in a light regime in controlled environments it is important to consider how far removed this may be from similating sunlight and to what extent any deficiency, if it does exist, can be influencing the plant.

Phytochrome has, without doubt, been established as the primary receptor in many higher plant physiological processes. However, in order to account for the observed responses recorded to date, several theories have been advanced for intermediate stages in the phytochrome reversion processes, and this can now include as many as three photoreactions and five dark reactions (Borthwick et al, 1969). These accepted, however, there are still several processes which are exceptions to the normal phytochrome responses and which include considerations of high energy-requiring processes and the involvement of wavelength regions other than those in the red and far-red wavelength regions.

Mohr (1962, 1964) emphasized the importance of a photoreaction which could be unrelated to phytochrome. A number of plant response are controlled, many of which are also controlled by phytochrome.

The pigment system was considered to be different, however, since

(a) high irradiation was required for relatively long periods of time,

(b) no signs of reversibility were detected, and furthermore,

(c) the action spectra showed fairly sharp peaks in the blue (440 nm) and the far-red (725 nm) regions.

Mohr contended that the response under these conditions occurs through the action of a pigment system which circumvented phytochrome control. Further explanations are that phytochrome might also initiate the process in the absence of Mohr's pigment system, or that the two could also act synergistically with

each other.

Phytochrome proponents, on the other hand, have felt that Mohr's High Energy Reactions are exclusively phytochrome controlled, but that they come about while phytochrome conversion is taking place in both directions under the steady-state conditions which might be expected in high irradiance light (both forms of phytochrome absorb some light at all wavelengths in the visible spectrum).

Absorption spectra of purified preparations show that both the red-absorbing form, and the far-red-absorbing form, of phytochrome have substantial and only slightly differing absorbancy in the blue and long-ultraviolet regions (Butler et al, 1964). Action spectra for *in vivo* conversion of the two phytochrome forms confirmed the results of the absorption spectra showing that blue light near 400 nm will drive the pigment from either form to an intermediate mixture. These results, then partly resolve the often contradictory reports concerning photomorphogenic and photoperiodic actions of blue light (Sigelman and Butler, 1965).

Similarly, Mohr (1969) was able to interpret the "high energy responses" of the mustard seedling (*Sinapis alba* L.) on the basis of phytochrome, at least as far as wavelengths above 550 nm were concerned. Consequently, he adheres to the conception that photomorphogenesis in the wavelength range above 550 nm is exclusively due to the formation of P_{730}. However, although P_{730} is formed under the influence of blue and near ultraviolet light, there are on Mohr's evidence, a considerable number of blue-light dependent photoresponses where an explanation on the basis of phytochrome seems to be excluded. The action spectra of these responses (for example, the light-dependent carotenoid synthesis in the fungus *Fusarium aquaeductuum*, polartropism in germlings of the fern *Dryopteris filix-mas*), point to a flavoprotein as the active photoreceptor and other action spectra of blue-light-dependent photoresponses (e.g. phototropic responses in higher plants) can be interpreted in the same way. Therefore, it seems possible that the same photoreceptor might be acting in all cases

in which development and movement are mediated by light from short wavelength regions (Mohr, 1969). If indeed the physiologically effective short-wavelength light is absorbed in all systems by the same photoreceptor, the situation would be somewhat analogous to what has been the basis for phytochrome : one and the same photoreceptor with a diversity of photoresponses.

Clearly in both flowering and other photostimulus responses whatever the final agreement in these theories, the basic observations are most interesting and important. Obviously plants in natural environments are exposed to long periods of high irradiance light containing various proportions of blue, red and far-red radiation depending on the time of day (sun angle and air mass considerations), weather conditions, filtering of plant canopy leaves, and so on. It is clear that study of these factors is as important in natural environments as it is in controlled environments in order to describe and understand plant responses and development under these conditions.

2. Effects of Light Quality on Photosynthesis in Higher Plants.

Photosynthesis takes part in the over-all growth processes of green plants. Both in fundamental studies, and in comparative studies of the efficiency of different light sources in artificial lighting, it is important to know to what extent light quality has an indirect effect on growth via photosynthesis.

The dependence of the net photosynthetic rate on light irradiance is described by the so-called "light curve" of photosynthesis. The shape of this curve may be influenced by a number of internal and environmental factors among which the quality of incident radiation is important. According to the Einstein law of photochemical equivalence, there is a simple integral relationship between the number of molecules changed photochemically and the number of photons (quanta) absorbed (Rabinowitch, 1951). This applies regardless of the energy of the photon, provided that, for photosynthesis, it falls

within the requisite 400-700 nm waveband. Any excess energy is dissipated as heat. When plant tissue is light-saturated the maximum rate of photosynthesis is determined by the rate of the dark reactions and CO_2 diffusion processes, and should therefore be independent of the quality of irradiation. Therefore if saturating monochromatic light at any wavelength is used, the photosynthetic rate should be the same at each wavelength. At irradiances below the saturation value, differences in rate in differing spectral regions will become apparent and will be related in part to the pigment complement of the plant.

Significant reviews of literature on spectral effects in photosynthesis have been made by Rabinowitch (1951, pp 1142-1168) and Gabrielson (1960). Almost all of the quantum yield measurements reviewed in these papers centre on the role of the carotenoids and other accessory pigments, and they have been made on algae, which provide a more interesting range of pigment systems for physiological research than higher plants (Emerson and Lewis,1943; Haxo and Blinks, 1950;Tanada, 1951; Haxo, 1960; Blinks, 1964; Krinsky, 1968).

Action spectra[1] for photosynthesis in higher plants have been obtained for wheat (Hoover, 1937), for radish and corn (Bulley et al, 1969), and for bean (Balegh and Biddulph, 1970). Some more limited measurements were made on Sinapis alba, Corylus maxima and Fraxinus excelsior by Gabrielson (1940), and on wheat, pine and spruce by Burns (1942), both using three broadband coloured filters.

The action spectra from these studies are quite diverse. The Hoover curve for wheat has two very pronounced peaks, one in the red and the other in the blue. Burns obtained roughly the same result for wheat, but not for pine and spruce, which showed much lower rates in the blue than in the red. The leaves tested by Gabrielson, by Bulley et al and by Balegh and Biddulph also gave a lower response in the blue. As Gabrielson pointed out, differences of this type could be caused

1. (i.e. the rate at which carbon dioxide is taken up, or oxygyn evolved, divided by the rate at which energy is received by the leaf).

by differences in spectral absorptance between a dark green and a pale green leaf. The absorptance was not measured in these studies.

Spectral quantum yields[2] have been measured for Solidago virgaurea L., Mimulus cardinalis and Plantago lanceolata (Bjorkman, 1966, 1968; Bjorkman et al, 1965). These three species showed very similar responses. Quantum yield was relatively constant from 650 nm to the limit of measurement at 450 nm (a fact used by Tanner (1968) as a basis for his proposal that "photosynthetically active radiation" be measured with a quantum counter). There was a sharp fall at 700 nm, which could be modified by simultaneous irradiation with shorter wavelengths (Emerson enhancement).

McCree (1972) has recently provided some very detailed data for the action spectrum, absorptance and spectral quantum yield of CO_2 uptake for leaves of 22 species of crop plants, over the wavelength range 350 to 750 nm. The following factors were varied : species, variety, age of leaf, growth conditions (field or growth chamber), test conditions such as temperature, CO_2 concentration, flux of monochromatic radiation, flux of supplementary white radiation, orientation of the leaf (adaxial or abaxial surface exposed). For all species and conditions the quantum yield curve had two broad maxima, centred at 620 and 440 nm, with a shoulder at 670 nm, where the average height of the blue peak was 70% of that of the red peak. The shortwave cutoff wavelength and the height of the blue peak varied slightly with the growth conditions and with the direction of illumination. In this respect, the use of the flux of absorbed quanta directly as a measure of "photosynthetically active radiation" will give a small systematic overestimation of the effectiveness of blue light relative to red, although for practical purposes these differences are probably insignificant.

Generally, these results refer to rather short term experiments where the plant tissue has been grown in white light

2. (i.e. the rate of photosynthesis per unit rate of absorption of quanta).

prior to the spectral treatment study. In controlled environment studies two further complicating factors must be taken into account. Firsty, the pigment components of the leaf may be affected by the wavelength in which it is grown, although Stolwijk (1954) has shown for tomato that the absorption spectra of methanol extracts from leaves of plants grown in red and in violet light do not differ appreciably. Secondly, since the growth rate of plants is a product of net assimilation per unit leaf area and the total leaf area, the differing effect of wavelength on leaf expansion, leaf shape, or the ratio of leaf area to non-photosynthetic tissue are factors determining the total growth which will be made under various light sources.

In growth experiments with tomatoes, Stolwijk (1954) found that the dry-weight formed over long periods in different spectral regions of equal irradiance was related directly to the number of incident quanta. This indicates that under his experimental conditions, green and yellow light were just as effective as red and blue in photosynthesis.

Vince and Stoughton (1957) using broad spectral regions showed that the relative dry weight gain for equal irradiance had a minimum value in blue light and maximum in red for tomato, calendula and pea; wheat demonstrated a different type of response with a minimum dry-weight in green. The relative position of white light was apparently related to the pattern of leaf expansion in red light; in tomato, dry weight increased faster in white than in red light as leaf expansion became progressively more reduced in the latter. In calendula, where leaf expansion occurred normally in red light, dry-weight production was greater in red than in white light. Determinations of net assimilation rates for tomato gave values of 53.1 mg dm^{-2} wk^{-1} in blue, 65.1 in green, 140.7 in red and 124.4 in white light. The first three figures represent a ratio of 0.35: 0.50: 1.00 which is similar to the ratio of the mean values for relative photosynthesis determined by Gabrielson (0.37:0.62:1.00).

3. Wavelength Effects on Metabolism.

3.1. Influence of Specific Wavelengths on Metabolism.

Several investigators have reported that the quality of photosynthetically active radiation affects the metabolic distribution of absorbed carbon in plant biosynthetic systems. Although this reported work presents some well defined responses, there are some large interpretational difficulties in rationalizing some of the short-term intermediary-metabolism based studies with the complexities of an integrated plant metabolism. This interpretation centres around the time course of a number of studies and whether pool values, intermediary product turnover rates, or end product accumulation were measured. These difficulties considered, generally the results reported indicate a short-wave radiation enhancement of amino acid and protein metabolism, whereas red light (visible long-wave radiation) enhances sugar and general carbohydrate metabolism.

Raghavan and De Maggio (1971) found that blue light increased ^{14}C-amino acid incorporation into proteins nearly five-fold compared to red light in isolated Pteridium chloroplasts. Voskresenskaya et al (1970) with Pisium sativum, Pirson and Kowallik (1964) studying Chlorella and Horvath and Szasz (1969) with soybean each reported that blue light grown plants had higher protein contents than red light grown samples. Mohr (1964), Ohlenroth and Mohr (1963) and Bergfeld (1968) with fern chloroplasts found enhanced rates of protein synthesis under blue light conditions. Kowallik (1965) with Chlorella showed clearly that there was a blue light requirement for protein synthesis which could show an effect at low energy levels (0.2 W m^{-2}) and was maximal at 4-5 W m^{-2}. The action spectrum for the response peaked at 450-490 nm.

Similarly, the evidence for enhanced carbohydrate biosynthesis under red light conditions is established. Horvath and Szasz (1969) found that compared to blue light, red light grown soybean plants had relatively high carbohydrate contents and Bergfeld (1968) with a fern chloroplast system found that red light enhanced mainly carbohydrate bio-synthesis.

Several extensive papers report specific wavelength effects on amino acids and individual carbohydrate compounds. Voskresenskaya (1953, 1967), Nichiporovich et al (1957) and Voskresenskaya and Grishina (1958, 1959), working with bean and Chlorella, reported that blue light favoured synthesis of N-containing organic substances, increased total and protein-N content and decreased ^{14}C incorporation into sugar-phosphates and free carbohydrates. Blue light specifically accelerated alanine, aspartic acid, glycine and organic acid (malic) synthesis. Protein synthesis and the glycolate cycle reactions were activated by short wave radiation whereas red light increased ^{14}C uptake in sugars. Das and Raju (1965) with rice, Zak (1965) and Ogasawara and Miyachi (1969, 1970) reported similar red and blue light effects with Chlorella.

More specifically, Miyachi and Hogetsu (1970) with Chlorella showed a two-to three-fold increase under blue light of ^{14}C uptake into aspartate compared with red light treatments and Szasz and Barsi (1971) with Vicia faba reported that red light increased glucose, fructose, sucrose and starch compared with blue light.

Krotkov (1964), Hauschild, Nelson and Krotkov (1962a, 1962b), Tregunna, Krotkov and Nelson (1962) in a series of experiments with unicellular algae and tobacco reported similar results. Blue light stimulated accumulation of ^{14}C into aspartic, glutamic, malic and fumaric acids and also increased the turnover of aspartic and glutamic acids. Red light increased ^{14}C accumulation in serine, glycine and sugars. The ^{14}C label distribution in glucose changed under blue compared with red light. All Studies reported were carried out under equal photosynthesis conditions.

Andreeva and Korozheva (1964), in a study of spectral and intensity effects on amino acid content of sunflower leaves, reported a blue light effect of increased asparate, glycine and serine formation but a suppression of alanine synthesis. There was no effect, however, at low irradiances (26 W m^{-2} for red light, 40 W m^{-2} for blue light) as well as during short term cultivation of the plants under light of

various spectral compositions (also low irradiance light however).

There appears to be a conflict in this result with the amino acids serine and glycine with the trends shown in the other papers. Similarly, Hess and Tolbert (1967) studying Chlamydomonas and Chlorella found that after growth in red light ^{14}C accumulated in malate, aspartate, glutamate and alanine whereas blue light accumulation was mainly in glycolate. In their discussion, Hess and Tolbert suggest that dark pre-treatment, spectra pre-treatment and quality of irradiation could account for these differences in the various responses.

These differences aside, the general trend of these investigations has been that blue light stimulates the synthesis of the amino acids alanine, aspartic acid, glutamic acid and perhaps glycine and the synthesis of protein. It also appears to accelerate the synthesis of organic acids (malic and fumaric) and increases the rates of reactions in the glycolate cycle. In addition, blue light leads to the suppression of carbon incorporation into free carbohydrates, phosphorylated sugars, phosphate esters and serine whereas red light appears to increase incorporation of carbon into these compounds.

These responses are not considered to be related to a new series of metabolic pathways but merely reflect the dynamics of alternative sinks of assimilated carbon.

3.2. Mechanisms of Wavelength Action.

From the evidence presented on light quality effects it is clear that the wavelength of incident light affects the quantitative distribution of assimilated carbon among various products of photosynthesis, their turnover, and their relative rates of synthesis. Hence, the problem is to define by what mechanism or mechanisms the light quality influences these events.

Clearly, there are several reactions and light systems which could respond to the wavelength of incident light and

so change the pattern of metabolism within the cell. These can be grouped into three categories, viz;

(a) wavelength effects on pigment systems and the responses through increased reducing power and incresed photophosphorylation,

(b) wavelength effects on the genetic status of the cell, particularly with respect to changes in the DNA and RNA types relating to cell regulation and specifically protein and enzyme synthesis,

(c) wavelength activation of various enzymes controlling each metabolic pathway.

Each of these alternatives has been discussed by various workers in an attempt to account for their results and an outline of these discussions follows.

(a) Wavelength effects on pigment systems, reducing power and photophosphorylation.

For an explanation of the red light stimulated polysaccharide accumulation Szasz and Barsi (1971) combined the energy requirement for the synthesis of these compounds on the one hand and the wavelength dependence of the energy converting processes of photosynthesis (photophosphorylation) on the other. In the synthesis of polysaccharides nucleotide-bound sugars are the initial compounds (Hassid, 1969) and the energy required for their formation may be supplied, in addition to non-cyclic photophosphorylation in which ATP and NADPH are produced in a 1:1 ratio, by ATP production in the cyclic processes related to photosystem I. (Tagawa, Tsujimoto and Arnon 1963a, b). From this Szasz and Barsi argue that there is specific excitation of cyclic photophosphorylation in red light and hence a greater ATP production. There is more chlorophyll (chl) a (higher a/b ratio) in photosystem I than in photosystem II and the higher absorption of red light by chl a is the result of

(i) the higher specific absorption coefficient of chl a than that of chl b in the red wavelength region, and

(ii) the higher amount of chl a than of chl b in the

leaves which increases the absorption difference.

In the blue wavelength region the specific absorption coefficient of chl b is somewhat higher but this is counter-balanced by the higher amount of chl a.

Hence the stimulatory effect of red light on the polysaccharide accumulation may be explained by an "extra" ATP production in cyclic photophosphorylation, via preferential activation of photosystem I.

This general interpretation is in line with a suggestion of Metzner (1969) that the effects of red and blue light are probably connected with a change of the ATP:NADPH ratio. Similarly, Horvath and Szasz (1969) had earlier suggested that the stimulatory effect of red light on carbohydrate accumulation might be in connection with the light absorption of chl a, and of blue light on nitrogen compound accumulation, attributed to chl b absorption.

It is interesting that earlier, Krotkov (1964) hypothesized that the difference in the nature of metabolic products produced in blue and red light was due to the presence of two photochemical (reactions) systems. Since these reactions would be coupled to different reactants with different oxidation-reduction potentials, carbon absorbed in photosynthesis could be preferentially directed along alternative pathways.

(b) Wavelength effects on the genetic status of the cell (incl. DNA, RNA, protein and enzyme synthesis).

Differences characterized mainly by morphological and biochemical criteria in fern gametophyte systems have stimulated some investigations in these species at the subcellular level. Mohr (1964) reported that the size of the chloroplasts in the sporelings (basal cell) of Dryopteris was determined by the wavelength of light; in blue light the chloroplasts were much larger than under red light. Bergfeld (1963a) showed that this process of plastid growth was reversible and directly related to the light treatment.

Bergfeld (1963b) has also demonstrated marked changes in nuclei volume; the volume of the nuclei increased rapidly up to a certain level if the Dryopteris sporelings were placed under blue instead of red light. Again, this shift was shown to be reversible. This change in nuclear volume probably reflects a change of nuclear function. The increase of volume in the blue might be causally related to the increase of protein synthesis under these conditions (Mohr, 1963).

It has been reported more recently (Payer, 1967) that blue light enhanced cytoplasmic protein synthesis as well as plastid protein synthesis and that under blue light sporelings had a higher RNA content. A red to blue transfer also resulted in a rapid RNA increase (as shown by ^{14}C - uridine uptake) and it was suggested that the blue wavelength light led to "blue light specific" RNA synthesis which subsequently controlled the morphogenesis of the sporeling.

Pirson and Kowallik (1964) did not observe the effects found by Bergfeld (size of nuclei, chloroplasts) when applying similar treatments to Chlorella and a range of other algae, and the participation of extra protein in photomorphogenesis could not be proved. However, as they point out photomorphogenesis would require not simply more proteins, but a quantitative change in the proteins directed some way by the genetic apparatus. In this study these authors found no change in DNA production from cells grown under a long pre-culture of either blue or red light. Pre-culture in white light and transfer to red or blue light however presented a different result. In this case blue light inhibited DNA formation to a marked extent and the RNA/DNA ratio in consequence was much higher. This was also related to a reduction in cell division.

(c) Wavelength activation of enzymes

Ogasawara and Miyachi (1969) reported that the blue light effect of enhanced ^{14}C incorporation into aspartic, glutamic and malic acids, was observed in the presence of CMU at concentrations which completely inhibited photosynthesis and that the saturating light intensity for the blue light effect was extremely low, clearly indicating that the ordinary photosynthetic

machinery was not participating in this blue light mechanism. The action spectrum showed a peak at near 420 nm. More recently, Ogasawara and Miyachi (1970) assayed blue and red light treated Chlorella cell suspensions and found that pre-illumination with blue light increased the phosphoenol pyruvate (PEP), carboxylase activity 2 to 3 times compared with the red treated cells. No difference was noted in the activity of ribulose diphosphate (RuDP) carboxylase or of glutamate-aspartate transaminase. This indicated that, at least in Chlorella cells, PEP carboxylase activity was enhanced by blue light. Carbon dioxide fixation by the reductive pentose cycle requires illumination of high intensity light (either red or blue). Blue light specifically increases the activity of PEP carboxylase and the resulting enhancement in production of oxaloacetic acid brings about increases in the amounts of aspartic and malic acids. In photosynthesis under blue light, the transfer of PGA to PEP is accelerated by the increase in activity of PEP carboxylase; consequently the supply of carbon from PGA to sugar phosphates becomes lower than under red light.

Again, Krotkov (1964) had early suggested a hypothesis whereby plants must have some enzyme involved in the early stages of carbon assimilation which is light-activated and which has, therefore, a pigment in its prosthetic group. Depending on the wavelength of incident light this pigment may be present in two different forms, an active and an inactive one. Depending on its form, the flow of the early intermediates in carbon dioxide assimilation may be directed along competing pathways. Tregunna et al (1962) also hold to this hypothesis and use the analogy of phytochrome in their discussions. Krotkov, in support of his hypothesis cited the observation that even small amounts of energy in blue light added to red produce essentially the same effect as blue light alone (see Hauschild et al 1962b). Moreover, Chlorella cells, first pre-illuminated with blue light and then permitted to assimilate $^{14}CO_2$ in red, carry on photosynthesis in the same way as if they were illuminated by blue light. Their total CO_2 absorption is higher than that of comparable red light grown cells and they incorporate larger amounts of ^{14}C into aspartic, glutamic, fumaric and malic acids and smaller amounts into

glycine.

It is apparent then, that the mechanisms involved in the light quality influence are likely to incorporate control steps throughout the plant's metabolism. The first requirement is to get well defined responses from the light/plant system with respect to metabolic product levels, rates of bio-synthesis, turnover and degradation, together with details of parallel responses with different groups of metabolites. The second requirement is to study the biochemistry of the system, with its known limits and flexibilities, to see what explanations can be developed for the occurrence of the responses observed.

In consequence, effects of visible light on plant metabolism not directly due to the primary act of photosynthesis may deserve more attention from all aspects than they have previously attracted.

3.3. The Influence of Light Spectra on Chlorophyll Levels and Chloroplast Structure.

There have been several reports that light quality influences the structure and organisation of chloroplasts and the levels of chlorophyll a and b in the chloroplasts of irradiated cells.

For example, Osipova and Ashur (1965) were able to show that the internal organisation of maize chloroplasts depends both on irradiance level and spectral composition of light during growth. The structural changes observed occurred specifically in the chloroplasts of mesophyll cells. In full daylight, chloroplasts had a high degree of granal organisation whereas at one-third full intensity they were predominantly lamellar in structure. In contrast, chloroplasts from leaves grown in red light had a loose granular structure, which was chiefly evident in the peripheral regions. Chloroplasts from leaves grown under blue light were predominantly cup-shaped with a diffuse granular structure. Those chloroplasts from cells disposed around vascular bundles were uniformly lamellar under all treatments.

Osipova et al (1966) in trials on the absorption of ^{14}C by maize leaves found that under reduced, red or blue light, carbon was incorporated to a considerable extent in proteins and in the pigment-lipoid complex in the chloroplast. It was suggested that the increase in supply of carbon to these compounds was associated with increased chloroplast development in response to a deficiency of light but no spectral dependence was inferred.

Voskresenskaya et al (1968) found a significant effect of spectral quality on the ageing of barley seedling chloroplasts. Ageing (9-12 day old) primary leaves of plants grown in red or blue light were severed and exposed to red or blue light in the presence or absence of kinetin. In leaves of plants grown and exposed in red light a sharp decrease in chlorophyll and protein was observed, whereas introduction of kinetin to the leaves halted the breakdown of these compounds. If leaves had received blue light constantly, the decrease in chlorophyll was insignificant and treatment of such leaves with kinetin did not alter their content of chlorophyll or of protein. Illumination with blue light at the time of exposure of leaves that had first been grown in red light prevented breakdown of the photosynthetic apparatus of these leaves, as did kinetin. An electron microscope control on the condition of the chloroplast structure showed that exposure of leaves to red light leads to a substantial breakdown of the structural organisation of the chloroplasts. This was avoided by the transfer of severed leaves to blue light or by treatment of the leaves with kinetin. The conclusion was drawn that the effect of kinetin and of blue light on the structural protein of chloroplasts was similar, even in a leaf separated from the plant, and that no such similarity existed in the case of red light and kinetin.

In addition to the possibility of a structural change in the chloroplast due to light quality effects there have also been some reports of changes in chloroplast size.

Voskresenskaya and Grishina (1958) found a somewhat larger (almost two-fold) chloroplast size under low nitrogen

conditions in both sand and soil culture with a blue light treatment in comparison to red light. At high nitrogen levels there was a general increase in chloroplast size but the differences between the red and blue light treatments disappeared.

Mohr (1964) also reported that the size of chloroplasts in Dryopteris sporelings was determined by the wavelength of light. When these sporelings were brought into the light the chloroplasts grew until they reached a certain size which was determined by the quality of light. In blue light the chloroplasts were much larger than under red light.

This process of plastid growth was reversible (Berfeld, 1963a, 1963b). If the sporelings were put from darkness into blue and back to darkness, the corresponding changes in plastid size were most marked. If the sporelings were shifted from red light into blue of about the same quantum flux density and back to red after some time, the size of the chloroplast adjusted to the value characteristic of the particular light quality.

Total chlorophyll and chlorophyll a and b levels also appear to be regulated by light quality. Fujita and Hattori (1962), for example, reported that changes in chlorophyll a and b concentrations in Tolypothrix responded to light quality rather than to intensity. Jones and Myers (1965) reached a similar conclusion from work with Anacystis.

Hess and Tolbert (1967) grew Chlamydomonas and Chlorella for 10 days in white light, 95.5 $W\,m^{-2}$ blue light (400-500 nm) or 68.5 $W\,m^{-2}$ red light (above 600 nm). During this adaptation period in blue light, total chlorophyll per volume of algae increased 20% while the chlorophyll a/b ratio decreased. In red light no change was observed in the total amount of chlorophyll or in the chlorophyll a/b ratio.

Voskresenskaya and Grishina (1958) found with sunflower and broad-bean plants which had continuously been in the light of a mercury lamp and of neon tubes, when the light flux was equalized according to the number of incident quanta, no

differences were observed in the chlorophyll accumulation in red and blue light. These workers report earlier Russian work which indicated that not all plants are the same in their response to short-wave and long-wave radiation. For example Ermolaeva (see Voskresenskaya and Grishina, 1958) found perilla and tobacco had a lower chlorophyll content in blue light and fragrant tobacco had a lower chlorophyll content in red light. Kleshnin, Osipova and Timofeeva (see Voskresenskaya and Grishina, 1958) with lettuce found either no effect or lower blue light levels depending on the variety tested.

Pirson and Kowallik (1964) report that blue grown Chlorella cells never contain an increased amount of chlorophyll; based on protein content the chlorophyll content is always markedly lower.

3.4. Summary.

From these preceeding sections there is an apparent consistency of wavelength effects at different stages in the metabolism and organisation of the plant cell. Evidence from higher plants of light quality effects on chloroplast stucture and size, chlorophyll content and composition, and changes evident in carbohydrate and nitrogen metabolism, together with lower plant evidence of changes in nuclei and nuclear material (RNA and DNA), all indicate that there is a chain of cellular events which are each closely related and influenced (directly or indirectly) by one or more specific wavelength regions. Each of these individual sections currently has evidence of a specific wavelength influence in relation to a defined change in either the amount of a particular compound, or in the rate of a reaction step, but the interactions of these changes with other metobolic sequences and the mechanisms of the wavelength action are poorly defined.

4. Light.

4.1. Measurement Systems.

In the past, and too often currently, failure by some biologists to appreciate the purely physical aspects of light and its measurement has sometime led to invalid conclusions

on the influence of light on plant form and behaviour.

It is essential to realize that two systems of evaluation of light flux are possible, one basically objective and the other subjective. In the former the actual radiant flux is measured. However, in the latter radiant energy is expressed in terms of the physiological stimulus to the human eye, and the luminosity of a source is measured by comparison, directly or indirectly, with a standard source producing a certain stimulus. Provided that two sources have the same spectral composition this comparison will give a valid assessment of the radiant flux from the unknown source, but if their compositions differ the spectral sensitivity response of the human eye is involved and the measurement becomes wholly subjective. This system of measurement has been developed in illumination engineering, since the brightness of a light is in essence related to the human eye response. The photosensitive mechanisms of plants, however, have spectral responses wholly unrelated to those of the retina and the only valid assessment of light in relation to plant phenomena is a measurement of radiant energy incident upon the tissue at every wavelength. It is therefore, essential in all such studies that the objective method of measuring the actual radiant flux (i.e. irradiance) should be used. Where photochemical processes are being studied it must of course, be borne in mind that the energy per quantum is inversely proportional to the wavelength and allowance made for this in the examination of molecular reactions.

It is clear therefore that the common practice of exposing plants to light treatments whose intensities are measured in terms of foot-candles, lux, lumens per square foot or similar subjective units leads to invalid comparisons except where the sources are of identical spectral composition. Thus, if two sources of different colour are to be compared in their effect upon plant growth, it must be on the basis of equal irradiance in terms of energy and not of luminous intensity. The correct radiometric (and corresponding photometric) terms, units and definitions to be used in plant physiology studies are presented in Table 1.

Table 1

Radiometric and Photometric Terms

Terms, Units and Concise Definitions.

Modified from: Z. Sestak, J. Catsky and P.G. Jarvis, (1971).

"Plant Photosynthetic Production Manual of Methods" pp. 706-707

Radiometric (Physical)		Photometric (Psychophysical)		
Radiator, Source, Lamp.		Luminator, Source, Lamp.		Device converting a certain form of energy into the radiant one.
Radiation		Lumination		Process of generation of radiant (luminous) energy.
Radiant Energy	J, Ws	Luminous Energy, Light.	lm s	Energy in the form of electromagnetic waves.
Radiant Emittance	$J\ m^{-2}\ s^{-1}$; $W\ m^{-2}$	Luminous Emittance	$lm\ m^{-2}$	Radiant (luminous) flux emitted per unit area of radiation body.
Radiant Flux	$J\ s^{-1}$; W	Luminous Flux	lm	Rate of propagation of radiant energy (light).
Radiant Flux Density	$J\ m^{-2}\ s^{-1}$; $W\ m^{-2}$	Luminous Flux Density	$lm\ m^{-2}$ = lux (lx)	Radiant (luminous) flux passing through a plane of unit area. (N.B. This infers a cosine response consideration).
Radiant Flux Intensity	$J\ sr^{-1}\ s^{-1}$; $W\ sr^{-1}$	Luminous Flux Intensity	$lm\ sr^{-1}$ = cd (candela)	Radiant (luminous) flux emitted by a point-like source into a solid angle.
Radiance	$J\ m^{-2}\ s^{-1}\ sr^{-1}$ $W\ m^{-2}\ sr^{-1}$	Luminance } Brightness } of light sources	$lm\ sr^{-1}\ m^{-2}$ = $cd\ m^{-2}$	Radiant (luminous) flux intensity per unit area in direction of emission.
Irradiance	$J\ m^{-2}\ s^{-1}$; $W\ m^{-2}$	Illuminance	lx	Radiant (luminous) flux intercepted per unit area.
Irradiation		Illumination		Emission of radiant (luminous) flux, which is incident on the surface of some body.
Radiant Exposure	$J\ m^{-2}$; $W\ s\ m^{-2}$	Light Exposure	lx s.	Amount of radiant energy (light) intercepted per unit area during a certain period.

4.1.1. The Measurement of Radiant Flux Density (Irradiance).

The general field of light measurement and instrumentation has been reviewed extensively by Jones and Condit (1948), Anderson (1964), Westlake (1965), McPherson (1969).

It is clear that in considering the reactions of plants to light some means of measuring and expressing levels of irradiation must be derived. Ideally a measure of radiant flux in absolute units should be used and the spectral flux distribution curve for the light in question should either be measured or known. With this information one needs only the spectral sensitivity curve (the "action spectrum") for the physiological response in question to enable a plants reaction to be predicted. Unfortunately there are difficulties in obtaining each of these pieces of information with the precision desired.

In the first place the instrument required to measure radiant flux in absolute units is the thermopile, a sensitive and relatively expensive instrument which is generally not regarded as being portable. A simpler and cheaper alternative frequently adopted is to use a barrier-layer photocell calibrated in flux units for each type of radiation to be measured. The response of these photocells is dependent on temperature and they should also be checked regularly since their sensitivity is liable to change with age.

The measurement of the spectral flux distribution of an unknown radiation source is a more difficult operation which must be carried out using a large and expensive spectrophotometer. Like other sensors this instrument must also be frequently calibrated with a reference standard of some kind. Lamp manufacturers are normally able to supply average curves for their various products but variations from lamp to lamp can be quite large yet still fall within the makers tolerance limits, and further variations can occur with age (Warrington, 1969a).

Finally, the action spectra of very few plant responses

are known in such a way that a precise prediction of the reactions of a particular plant to given spectral flux distributions can be made. An alternative to quoting the full spectral flux distribution was proposed by the Dutch Committee for Plant Irradiation (1953, 1955) and subsequently approved in a slightly amended form by the International Horticultural Congress at Scheveningen in 1955. This called for the radiation characteristics to be specified in terms of the energy radiated in each of eight discrete spectral wavebands, expressed in watts m^{-2} or in any equivalent unit. These wavebands were chosen as follows:

Band 1 : $\lambda > 1000$ nm (heating effect only).
Band 2 : 1000 - 700 nm (elongating effect).
Band 3 : 700 - 610 nm (region of maximum photosynthetic effect, maximum chlorophyll synthesis).
Band 4 : 610 - 510 nm (minimum physiological response).
Band 5 : 510 - 400 nm (absorption by yellow pigments, secondary peak of chlorophyll absorption, secondary peak of photosynthesis, strong formative effects).
Band 6 : 400 - 315 nm (limited formative effect).
Band 7 : 315 - 280 nm (detrimental)
Band 8 : <280 nm (lethal).

In spite of the general acceptance of this proposal in principle, there is little evidence that it has been used very much in practice. This may be due to several limitations. For precise research work it does not give enough detail of the spectral flux distribution for it to be of very great value, and for plant systems, the action spectra do not coincide sufficiently well with the broad bands suggested for their use to be more than approximate. For precise work, the full spectral flux distribution curve should be specified together with the value of total visible flux.

4.2. Illumination Engineering, Lamp Design and Choice, and Lamp Types.

4.2.1. General.

Since the requirements for plant growth, development and response in terms of energy flux density and spectral flux distribution are so varied, it is essential when considering

the use of artificial light sources for plant studies, that the best lamps and lamp combinations are chosen for a particular use. The lamp manufacturer and the lighting engineer, however, are primarily concerned with the problem of improving visibility and are necessarily concerned with luminous flux. Because plants exhibit a variety of responses to light, in no case can the problem be simplified by the use of sensitivity curves analogous to the luminosity function of the human eye. The plant physiologist and horticulturalist must therefore be concerned with the radiant visible flux rather than the luminous flux, using existing knowledge of plant responses and the spectral flux distribution of the artificial light source to help interpret the reactions of plants and to help in the choice and improvement of artificial light sources.

The preoccupation of the lamp and lighting industries with luminous flux does not help to resolve this situation. Not only are lamps specified in respect of photometric units but the lamp designs are, in the main, arranged to match the standard spectral sensitivity of the human eye.

Artificial light sources of a practicable nature for plant irradiation are of two main types, the thermo-emissive or "incandescent" and the vapour discharge. The first type is almost exclusively confined to the tungsten-filament lamp in its various forms and wattages. This provides a continuous spectrum of composition varying with the wattage but having one constant characteristic, that the emission increases toward the longer wavelengths with a peak in the infra-red.

There are two main types of discharge lamps; the direct discharge type exemplified by the high pressure mercury-vapour lamp, the neon lamp, and the sodium lamp, all characterised by line emission spectra, and the fluorescent type in which the discharge is converted to a continuous spectrum emission by the fluorescence of a "phosphor". Choice of appropriate phosphors provides emissions of widely varying composition and it is possible to design a lamp with a peak emission at any point in the visible spectrum. The emission will, however, in all cases have considerable spread, and all lamps so far constructed

will also contain the spectral lines of the mercury discharge.

4.2.2 Lamp Types.

The technical aspects of all the lamp types possible for plant irradiation are considerably involved and do not need to be discussed in total here. Canham (1966) gives a comprehensive description of several lamp types on which the following details are based and several technical reviews are available which give more information of a specific nature. For example, Beijer, Jacobs and Tol (1968) review the high pressure iodide lamp development and report on its performance and technical features, and earlier Elenbaas (1956 - 57) reviewed the high-pressure mercury-vapour lamp development.

4.2.2.1. (a) Incandescent or Filament Lamps.

This is the simplest and by far the cheapest type of lamp and has the advantage of needing no special "control gear". It consists of a coiled filament of tungsten wire, supported in a glass bulb filled with an inert gas such as nitrogen or argon, or both, and connected to appropriate electrical contacts on the metal cap. When a current flows through the filament it gets hot and glows, giving off light of a quality depending on the filament temperature. The efficiency of this lamp is poor, since only about 6 per cent of the input power is emitted as visible radiation. A high proportion of the flux is in the visible region and can be used in photosynthesis but the large amount of far-red has strong photomorphogenetic effects and limits its usefulness for photosynthesis. It has proved to be a suitable and convenient source for low energy requiring photoperiod regulation purposes.

(b) The Quartz Halogen Lamp.

A comparatively recent development in the range of incandescent lamps has been the introduction of a small quantity of iodine vapour into the atmosphere surrounding the tungsten filament. This has effectively reduced the rate of deterioration of the filament and also of the light output. It has

enabled high-powered lamps to be constructed of quite small dimensions and also permits running at a slightly higher filament colour temperature (3000°K compared with 2750°K for a 240 volt 100-watt lamp). This also leads to a higher efficiency : 21-22 lm/W over 2000 hours instead of 17-18 lm/W over 1000 hours. There is little overall difference in the spectral energy distribution curve apart from that resulting from operating at the higher colour temperature and the response of plants is similar to that of the normal tungsten lamp.

Its primary application is for flood-lighting.

4.2.2.2. Electric Discharge Lamps.

(a) General.

When an electric current is passed through an atmosphere of metallic vapour, radiation is emitted which is characteristic of that metal. As electrical energy is transformed directly into radiant energy the process is more efficient than it is when an intermediate thermal process is involved. There is, of course, some loss of efficiency due to the production of heat.

Emission occurs in discrete bands, known as "lines", the number and wavelength of these being characteristic of the vapour used and the strength or intensity of the lines depends on vapour pressure.

Of the wide variety of vapours in which a discharge can be produced there is a limited number which are suitable for practical light sources. These include mercury, sodium, neon and xenon.

The electrical characteristics of a vapour discharge call for a much higher starting voltage than that required for normal running. This necessitates either the provision of a specially high starting voltage, or some means of reducing the voltage after the arc has been struck. To achieve this, various forms of "control gear" are required for the different types of lamps.

(b) High Pressure Mercury-vapour Discharge Lamps.

One of the commonest types of discharge lamp is the mercury-vapour lamp. When a discharge takes place in an atmosphere of mercury vapour the flux emitted is comprised of a number of distinct and narrow lines in the blue-green and ultraviolet portions of the spectrum. If the vapour pressure is low, the amount of visible radiation produced is comparatively small, but about 60 per cent of the input power is emitted in a single band of wavelength 253.7 nm in the UV region.

The amount of visible flux emitted may be increased in two distinct ways. In the first, the vapour pressure is increased, resulting in a higher proportion of the energy being emitted in the lines in the visible portion of the spectrum. Alternatively, or in addition, a coating of fluorescent powder may be used on the inside of the glass. This has the property of absorbing the short wavelength discharge radiation and re-emitting it in the visible range of the spectrum.

The first and simplest type is the high-pressure mercury discharge lamp. Tha basic essentials of the construction consist of (a) a discharge tube made of a suitable type of glass or quartz filled with a small quantity of mercury vapour together with a little argon gas to assist starting, (b) an outer glass bulb, (c) main electrodes at each end of the inner tube, (d) a small starting electrode situated close to one end of the main electrodes and connected to the more distant arc by a high resistance and (e) a suitable cap.

Full mains voltage is required to initiate the discharge but afterwards the arc resistance is very much lower and some form of current-limiting device is essential. On normal A.C. supplies this takes the form of a choke, in series with the lamp. A capacitor is also connected across the input leads to correct the power factor of the circuit. These are normally separate units which must be mounted as near to the lamp as is conveniently possible.

(c) Type HPLR (MBFR) Lamps.

The type HPLR lamp uses the properties of a fluorescent powder operating at suitable temperatures to achieve a high

visible radiation output. In order to distribute the emitted light satisfactorily a reflector of white titanium dioxide powder is used on the internal bulb surface and the shape of the lamp, together with the reflector improve downward light distribution. (Plate 3).

The type HPLR (MBFR/U) lamp is available in sizes of 250, 400, 700 and 1000 watts. The rated life is 5000 hours but the average life obtained is nearer 10,000 hours. (Philips Technical Information).

A further version of this lamp is now made by Philips in the 400 watt size only, especially for horticultural purposes. It is designated as HPLRH and has a coating of fluorescent powder on the base of the bulb as well as on the side walls. For the internal reflector the makers have reverted to a metallic film.

(d) Recent Developments.

The main restriction in the development of a radiation source whose spectral distribution can be chosen within certain limits and which can give a high efficiency has been that, until recently, the only elements that could be used for the excitation of light in gas discharge tubes were sodium, mercury and the inert gases.

It was more recently found that many elements in a lamp system can be evaporated to give a sufficiently high vapour pressure if they are introduced in the form of special volatile compounds. (Beijer et al, 1968). When this is done it is possible to obtain a higher vapour pressure of the element at the centre of the discharge than it would be if the element itself were added. The vapour pressure of the element is not increased in the rest of the tube, but this is not necessary, since the most active part of the gas discharge is found at the centre of the discharge, where most of the radiation is produced. This special method permits the use of elements which are not themselves sufficiently volatile, and it also removes the danger of chemical attack. It was found that iodides produced the most promising results. Indium, thallium and sodium iodides have been used singly and together to add resonance lines at

approximately 411 and 450 nm (indium), 534 nm (thallium) and 588 nm (sodium) together with a small iodine line at 557 nm to the characteristic mercury spectrum. Lithium, gallium and lead iodides have also been used.

These improve the colour of the light considerably and are an improvement over the HPLR type lamps for plant growth in addition to having a much higher (luminous) efficiency. The HPI lamp is typical of this group.

4.2.2.3. Tubular Fluorescent Lamps ("Fluorescent Tubes").

This type of lamp makes use of the low-pressure mercury discharge by employing fluorescent powders to absorb the U.V. radiation and re-emit it as visible radiation, as is done in the type HPL lamp. Tha basic differences are (a) the proportion of the U.V. radiation from the discharge is very much higher, (b) the vapour pressure is low so that the tube is large and the power consumption low, (c) the lamp temperatures are low and (d) different starting arrangements are required.

The lamps consist of a clear glass tube with an internal coating of fluorescent powder and an electrode mounted at each end. The spectral distribution of the light obtained from these lamps depends on the chemical composition of the fluorespowders used, and a wide range of colours can be obtained. A limited number however have been chosen for commercial production in quantity to give either a high efficiency or good colour rendering properties which are maintained throughout the life of the lamp. The majority produce light in varying shades of "white" e.g. "warm white", "white", "daylight", "natural", "colour matching" and "de luxe warm white", although others are available. A range of coloured tubes - red, green, blue, etc. - is also available, and from time to time special lamps have appeared which were claimed to be particularly effective for plant growth purposes, e.g. "phytor" and "gro-lux".

4.2.2.4. Xenon Lamp.

Lamps employing a heavy-current discharge through Xenon gas at a high pressure have been introduced in a range of sizes

up to 10 KW. The spectrum shows an apparent continuum (although it is in fact a series of very closely spaced spectral lines) extending from 200 nm up to 900 nm, with a pronounced peak in the 700-900 nm region, and giving the impression of "white" light. The light appears to be very similar to daylight and therefore gives very good colour rendering. Some versions are water-cooled while others are air-cooled; the control gear is expensive and bulky and the lamp life is short.

4.3. Use of Artificial Light Sources.

4.3.1. General.

A large proportion of growth facilities designed and built to date have used a fluorescent tube or fluorescent tube plus incandescent combinations for plant growth and photoperiod studies (Vince and Stoughton, 1957; Carpenter et al, 1965; Hudson 1957; Montgomery and Riddell, 1959; Morse and Evans, 1962; Ormrod, 1962; Selman and Foster, 1957; Voisey, 1962; Carlson, Motter and Sprague, 1964). The spectral flux distribution characteristics of these lamps suggest that they would be particularly suitable for plant growth purposes, but they do have certain disadvantages. The most important of these is the relatively low output for the physical size of the lamp but installation costs, and ageing characteristics are further undesirable features. However, fluorescent tubes offer several advantages. Apart from a choice of colours if required, they radiate very little heat, reducing substantially the problems of temperature controls in controlled environment units.

In contrast, only a few workers have used high pressure vapour discharge lamps mainly because of spectral output, installation and operational problems compared to fluorescent lamp systems. Their superiority over fluorescent sources, however, is due to higher radiant flux outputs in the visible range, higher luminous efficiencies, and superior ageing characteristics. The HPL colour-corrected mercury vapour lamps have been used in the growth rooms at the Instituut voor Biologisch en Scheikundig Onderzoek van Landbouwgewassen in Wageningen for some years and produce an irradiation level of about 100 $W\,m^{-2}$. Improved types are now available from

comparatively recent technical developments (Canham, 1966; Beijer et al, 1968) and these lend themselves more favourably to controlled environment work.

A large number of reports for day-length supplementation in glasshouses are also available which outline plant response under high-pressure discharge lamps, but these details are of little direct value. (Buntrock 1960, Canham 1965, Gelin 1951, Gelin and Burstrom 1949, Lawrence and Calvert 1951, 1954, Markham 1969, Reinders-Gouwentak and Smeets 1950, Reinders-Gouwentak, Smeets and Andeweg 1951, Roodenburg 1948, 1949, 1952, Swain 1964, Weichold and Heissner 1967, and Withrow and Withrow 1947). In many of these reports, mercury-vapour high pressure discharge tubes are comparative with, or superior to, fluorescent and tungsten combinations for seedling growth under supplementary daylength conditions. Detailed data on growth rates and plant form, however, are not given; earliness of yield being of predominant concern in much of this work. It is concluded, therefore, that results of supplementary day-length experiments are of limited value in controlled environment conditions but that satisfactory results from these lamp types places them under direct consideration for controlled environment work. Theoretically, if these lamps could be used in light rigs as clusters, with adequate cooling facilities together with adequate filtration of infra-red radiation, and perhaps in combination with other lamp types, then very high irradiation levels should be possible. Canham (1966) claims that it can be shown that twenty-five 700 watt (HPLR) lamps, each mounted at the corners of 10 1/2 in squares three feet above a bench and enclosed with perfectly reflecting walls, should theoretically give an illumination level on the bench in excess of 15,000 lm. ft^{-2}. (approx. 500 W m^{-2}). These types of considerations have been, in part, the basis for the studies undertaken in this present work.

4.3.2. Early Studies.

An early report on the use of artificial light sources for plant growth (Arthur and Stewart, 1935) compared relative growth and dry weight production under tungsten, neon, sodium

and mercury vapour lamps (see also Crocker, 1949). Using dry-weight production as the criteria for comparison, the descending order of growth was neon, tungsten, sodium vapour and mercury vapour. Comparisons using a correction for incident visible energy gave the following relationship (in descending order): sodium vapour, neon, tungsten and mercury vapour. The gas discharge lamps all produced greener plants and a lower ratio of stem to leaves than the tungsten lamp. No attempt was made to investigate combined spectra effects.

Mitchell (1937) grew tomato plants under equal intensities of total radiant energy with carbon arc and incandescent lamps. Those illuminated by the arc grew less in height and synthesized more than twice as much solid matter and about four times as much acid hydrolysable materials and sugars during two weeks than the plants under the incandescent lamps.

Parker and Borthwick (1949) determined the growth and composition of Biloxi soybean plants produced in controlled enivronment rooms with a carbon-arc lamp as the principle source of radiation. The arc lamp was used alone with several types of carbons (to vary spectral output), or was supplemented with a small amount of incandescent radiation. The carbohydrate content of leaves and stems of soybeans was greatly increased by supplementing the radiation from "Sunshine" carbons with incandescent-filament radiation. Experimental carbons cored to simulate the spectral distribution of the combined arc and incandescent source failed to produce as much dry weight, protein or carbohydrate as when the arc was supplemented with incandescent radiation.

This, and similar early work carried out, is difficult to interpret because of the inadequacies of intensity and spectral distribution measurements carried out at the time. Combinations of various lamp types would have undoubtedly produced better plant responses, due to a more favourable spectral distribution, than those single lamp types tested.

However, the significance of plant response to specific wavelengths was not fully realised at the time of this earlier

work and it is understandable that the artificial lamp type rather than the spectral output was necessarily the primary consideration in these studies. Interestingly, it was from Parker and Borthwick's (1949) experimental results that led to the subsequent studies into phytochrome, and red-far-red response phenomena, by these two workers.

4.3.3. Fluorescent Tube Development and Use.

The most significant development in light engineering which superceded the use of carbon-arc and incandescent sources was that of the fluorescent lamp. These lamps give off little heat, are more economic and efficient than incandescent filament lamps, and can be grouped together to give variations in spectral quality and intensity as desired. Limitations due to ageing effects and to the maximum light intensities possible do place some limitations on the suitability of this light source.

Naylor and Gerner (1940) report the success of 30-W fluorescent lamps of both white and daylight types as a source of light for growing plants. Plants grown under such lamps, arranged to give an intensity of 600 ft.c. at the leaf surface for 16 hours each day, were superior in rate of growth and sturdy development to the controls grown in ordinary winter daylight and to others grown with ordinary winter daylight supplemented by 9 1/2 hours of approximately 60 ft.c. of light from an incandescent filament lamp.

Withrow and Withrow (1947) compared the radiation from incandescent-filament, fluorescent, and mercury-arc sources on the growth of aster, spinach, soybean, and tomato for varying photoperiods at 15^{o}, 20^{o} and 25^{o}C. On an equal power consumption basis, aster produced more dry weight with incandescent radiation and spinach produced more with fluorescent. Plants grown with the mercury-arc source were very poor. In another series of experiments in which equal radiant energies were maintained, growth of spinach, tomato and soybean were compared when grown with fluorescent lamps and with incandescent and mercury-arc combined in three different proportions. They

report the greatest production of dry matter for all species under the incandescent plus low-mercury combination.

Generally, the high pressure mercury-arc produced the smallest plants because its radiant energy was concentrated at the blue-end of the spectrum. Incandescent lamps produced the greatest fresh and dry weight increments but were undesirably tall and spindly, and the white and daylight fluorescent lamps produced vigorous stocky plants but only at higher temperatures. They concluded that the fluorescent lamps were the best artificial light sources for their experimental work.

More recently, fluorescent-lamp manufacturers have improved the spectral output of their lamps specifically for plant growth experiments (e.g. the "Gro-lux" series from the Sylvania Electric Products Company) and have placed lesser importance on luminous efficiencies and colour rendition properties. Further, experimenters now appreciate more fully the requirements of plant systems for blue-red-far-red balances and have considered these in fluorescent-incandescent combination experiments. Details of results from plants grown under conditions relating to these factors are adequately covered in several papers, (Dunn and Went 1959; Helson, 1965; La Croix et al, 1966; Thomas and Dunn, 1967a, 1967b; McDonough and Brown, 1969; Halpin and Farrar, 1965; Federer and Tanner, 1965).

From the data presented in these papers, for general plant growth purposes one of the "white" fluorescent types is generally most suitable and the lamps with the highest visible flux appear to be the best. Both "3,500^{o}K white" and "warm white" types are widely used and there seems to be little evidence that any other type will give faster or more superior growth. Some of the special blue/red lamps made both in Belgium ("Phytor") and America ("Gro-Lux") have not shown any particular merit in this respect in a number of trials with a wide range of plants (Canham, 1966). It is also widely claimed that when illumination from filament lamps is added to that from fluorescent tubes the rate of growth is increased, but evidence on this seems to be conflicting.

With respect to shoot dry-matter production, Dunn and Went (1959) reported that mixed fluorescent and (5%) incandescent lighting was more effective than fluorescent lighting alone. Of the commercially available fluorescent types, "Warm-white" was the most effective; green and red were both low in effectiveness, and pink and blue were intermediate, but all were surpassed by an experimental red lamp. On the basis of dry matter production per unit of luminosity the red and blue lamps were the most efficient and the yellow and green the least. On a power basis the most efficient lamps were the "Warm-white" and gold types. No energy flux density considerations were made.

La Croix, Canvin and Walker (1966) grew eleven species of plants under illumination from "Cool-white", "Warm-white" and "Gro-lux" fluorescent lamps, with and without incandescent lamps. "Cool-white" lamps appeared to be the best for long term growth, yielding good growth rates and compact plants with good leaf pigmentation. "Warm-white" lamps gave greater dry-weight increases in some species of plants, but internodes were long, growth habit lax, and plants succulent. In most cases, flowering was hastened by the use of "Warm-white" lamps.

Growth, seed yield or flower production of plants under "Gro-lux" light was never superior to that under "Cool-white" or "Warm-white" and in many cases was inferior.

Helson (1965) with tomato, compared "Gro-lux" and "Cool-white" fluorescent lamps with or without the addition of incandescent lamps as light sources. After 5 weeks in terms of the dry weights of stems and leaves the order was gro-lux + incandescent > cool white + incandexcent > gro-lux > cool white.. The addition of incandescent to gro-lux fluorescent lamps resulted in large increases in the dry weight of roots, leaf area, and plant height. There were also corresponding improvements in flower and fruit production. Helson claimed that these improvements were due to the beneficial influence of the additional far-red radiation. Halpin and Farrar (1965) carried out a similar investigation of commercially available fluorescent lamps on the growth of orchid seedlings. Those grown under

light from the "Wide-Spectrum Gro-lux" fluorescent lamp appeared to be superior to those grown under the standard "Gro-lux", "Warm white", or "Cool white" fluorescent lamps. This conclusion was based on the size of seedlings and stand count of the surviving plants after an eight-month test. "Cool-white" was the poorest overall fluorescent light source tested in these studies. No incandescent supplementation studies were undertaken.

Thomas and Dunn (1967a) grew tomato seedlings under seven kinds of fluorescent lamps, including two that are commercially available, and five experimental lamps. Detailed descriptions and spectral emission curves for these lamps are presented in their paper.

The "78/22" lamp, which emitted most of its energy above 500 nm, more than ten per cent above 700 nm, and had a sharp peak output at 660 nm, generally produced superior fresh and dry-weight yields. This effect was considered to be primarily due to the high peak of energy emitted at approximately 660 nm, combined with a considerable emission in the far-red. No leaf epinasty was seen under this treatment and therefore it appears that very little spectral emission below 500 nm is required to prevent this condition.

The "Com I" lamp, which lacked the sharp peak output at 660 nm and emitted more energy on the blue than the "78/22" lamp, was generally second only to the latter in promoting plant growth. A higher moisture content was found in plants under this treatment in some conditions.

The "IR111" lamp had the sharp peak output at 660 nm but greater output in the blue than the "78/22" lamp. The "282" lamp output was similar to the "78/22" but lacked the high peak. Both of these lamps generally gave improved results over those produced by Gro-lux, Warm-white and the experimental "FLAT" lamps. This was attributed to the greater percentage of red and far-red energy emission by the former two lamps. The yields with the "FLAT" lamp were consistently lowest of all and probably were due to the high percentage of emitted energy on the blue

and green portions of the spectrum.

Both length of the experimental period (13 days versus 26 days) and light intensity (55 versus 110 W m^{-2}) were considered to be potentially important factors in deterimining which composition of spectral energy emission produced the greatest (vegetative) yields. Under the low intensity and the short test period the "Com I" light produced the highest fresh and dry-weight yields, but under high intensity and the longer growth period the "78/22" lamp gave greatest yields. This effect was thought possibly to be due to inhibition of leaf expansion by red light in the early stages of growth.

These experiments demonstrated that it is possible to develop a fluorescent lamp for plant growth that combines the desirable characteristics of both incandescent and fluorescent light. This work also showed that the tomato plant in the seedling stage grew best under an artificial light source with a high percentage of energy emission in the red, a considerable amount in the far-red, and a very small amount in the blue part of the spectrum.

More recently McDonough and Brown (1969) have reported that there were no significant differences in stem length and the dry-matter production of four species of grasses (Agastache urticifolia, Agropyron intermedium, Bromus inermis and Coronilla varia) grown under ratios of incandescent to "Cool white" fluorescent wattage of 0.0, 0.16, 0.31 and 0.47 respectively.

Yield results for reproductive plant parts (i.e. pods, flowers) also show marked interactions with fluorescent lamp types.

Thomas and Dunn (1967b) grew bean and marigold plants to maturity under various kinds of fluorescent lamps to evaluate the effects of spectral differences on development and reproduction. Evaluation was by fresh- and dry-yields of immature and mature pods; and of vegetative tops of plants for bean; and by flowering and fresh- and dry-weight yields for marigold.

Bean plants grown under two experimental lamps, "Com I"

and "IR111" produced significantly higher fresh- and dry-weight yields of both mature and total pods than under "warm-white" lamps. This effect could be attributed largely to the considerable energy emitted by the experimental lamps in the red and far-red, as compared to a larger emission in the green and blue for the "Warm-white" lamps. The differences in the yields for immature pods and vegetative portions of the mature tops were not significant.

In a comparison of the effects of three experimental lamps with those of three commercial lamps on the growth response of bean, the yields were in general higher for the experimental lamps, except for immature pods. The yields of vegetative tops were significantly greater for the "78/22" lamp over the yields for all other lamps. The larger proportion of red and far-red light emitted by the experimental lamps is again the probable cause of the higher yields.

The two sets of experiments on growth and flowering of marigold under various experimental and commercial lamps were largely inconclusive although there was some indication of beneficial effects by the experimental lamps.

In a similar study, Kwack (1961) found highest yields (dry weight of pods and number of seeds per plant) of pea with red light, and under conditions of equal intensity, lesser yields with blue, incandescent, pink, "Warm-white", and yellow (in that order) and the least with green light. Tests of light qualities in combination or alone showed that "Warm-white" plus incandescent light or "Warm-white" alone resulted in highest yields. The addition of incandescent to fluorescent light usually resulted in a higher yield than when either of these lights was used alone.

Kwack and Dunn (1961) report a similar study with pea which includes data showing high photosynthetic rates with blue light if the intensity is high, or if it is compared to other coloured lights at equal intensities in foot-candles. However, again no considerations of efficiency are presented in terms of energy flux measurements.

A more complete analysis of vegetative growth responses under various fluorescent and tungsten combinations has been made by Rajan, Betteridge and Blackman (1971).

The interacting effects of the nature of the light source and the temperature of the ambient air on 14 parameters of vegetative growth were examined for Gossypium, Helianthus, Phaseolus and Zea. The comparisons were between fluorescent lighting and mixtures with tungsten lamps (17 and 26 per cent of the total wattage), adjusted to give 32,400 lux and covering six equally spaced and constant air temperatures from 10 to 35°C.

The relationships were highly complex. Species differed in their response to the three light sources and for some parameters (depending on species) there were highly significant interactions between the nature of the light source and the temperature level. Part of this complexity was due to the varying growth potential of species at low and high temperatures but important contributing factors were the differences between the temperatures of the ambient air and the plant parts.

Considering first the total weight per plant, the difference between a high proportion of tungsten as against fluorescent lighting alone was significant for each species but the lower proportion only significantly enhanced the weight of Gossypium and Zea. Only for Phaseolus and Zea did the inclusion of tungsten lamps enhance the leaf weight ratios. Once again only these two species were involved in statistically significant changes in root-weight ratio, but here the inclusion of tungsten lamps in the light source depressed the ratio. For the stem-weight ratio apart from the positive effects of tungsten illumination on Zea the changes in the other species were either not significant or barely significant. In contrast, for stem length all species responded significantly to a low proportion of tungsten lamps, while apart for Phaseolus, the height was further increased by a high proportion of tungsten lighting.

On the basis of total leaf area only for Phaseolus was

the gain induced by a high proportion of tungsten lamps over fluorescent lighting not significant. The differences in the number of leaves per plant between only fluorescent tubes and a high proportion of tungsten were all significant but there were specific differences in the nature of the response : the response to tungsten illumination was negative for Phaseolus but positive for the remainder.

With respect to growth analysis functions, in three out of the four species that received a high tungsten proportion, the net assimilation rate (NAR) statistically exceeded that of plants illuminated solely with fluorescent lamps, but the differences between "low tungsten" and fluorescent light was only significant for Gossypium. The nature of the light source had little influence on the leaf area ratio (LAR) where only for Phaseolus was there a significant change (higher tungsten = smaller ratio). In each species except for Phaseolus, where there were compensatory effects on LAR and NAR, increasing the tungsten content increased the relative growth rate (RGR).

4.3.4. High-Prssure Discharge Lamp Use.

Reports on the effects of new high-pressure discharge lamps on plant growth are not entirely adequate for evaluating their usefulness for plant growth. Leiser, Leopold and Shelley (1960) compared tungsten, fluorescent, mercury vapour and their combined effects on the growth of Knox wheat and red-kidney bean. Knox wheat grew more favourably under the fluorescent/mercury vapour combination than under fluorescent or tungsten separately or under the other combinations used. Red kidney bean grew best with the fluorescent/tungsten combination. Confusion as to the reliability of these results arises because of injury to bean leaves at the higher irradiances used. The effects of radiant heat from light sources probably due to the inefficiencies of the water filter used between lamps and plants was considered to be a major cause of this response.

Schmidtchen (1967), reporting preliminary results of experiments on the raising of cucumber seedlings with light

supplied by high pressure mercury vapour lamps, found no essential difference between these plants and those grown under low pressure fluorescent lamps. Similarly, Austin (1965) reported that a given amount of radiation from a high-pressure mercury-vapour (HPLR) lamp produced larger plants than a similar amount from a mercury tungsten (ML) lamp and for all three species tested (Chenopodium amaranticolor, Daucus carota and Brassica oleracea) the mean relative growth rates were about 40% greater under the HPLR than under the ML lamp at any given irradiance.

These preliminary results give some lead as to the suitability of high-pressure discharge lamps but further information does not appear to be present in the literature.

5. Current Studies.

These present studies were undertaken with three main objectives under consideration. The first was to investigate closely the response of several plant species to light spectra from three main high-pressure vapour-discharge lamp types together with similar degrees of red and blue light supplementation. This was considered essential since there were a number of recently developed lamps on which there was little information currently available with respect to plant response and which offered the advantages of high visible radiant flux and much higher operating efficiencies than many of the other older lamp types. They also had considerably improved visible spectra compared with earlier high pressure lamp types.

The second objective was to examine, under a similar system, the variation of plant response due to a marked imbalance of radiation distribution in the visible spectral region. This was intended to be a quantitative redistribution of energy flux between specific wavebands rather than an undefinable, haphazard series of various visible light spectra. By varying the proportions of visible wavebands it was hoped that generalized predictions of responses, due to treatment trends, may have been possible for other artificial light spectra and from each of these studies some parameters may be established for a

standardized artificial radiation source.

The examination of responses due to interactions of artificial light quality with light irradiance ("light intensity") was the third main objective and was considered in conjunction with each of the other two.

Each of these objectives was the basis for two major studies; one examining the Spectral Balance and the other the Spectral Bias situation and both incorporating a study of light irradiance.

The Spectral Balance study consisted of three treatments at a similar irradiance based on high-pressure discharge lamps supplemented with blue-fluorescent and tungsten lamp types, and three subsequent treatments based on one high-pressure discharge lamp type with varying supplementation and different irradiance levels. Although this particular experimental design did not allow extrapolation of data between irradiance treatments it did allow insight to spectral and irradiance effects on a general basis.

The Spectral Bias study consisted of blue-biased, balanced and red-biased spectral treatments obtained by varying the proportions of different artificial lamp types. Each spectral treatment was studied at two irradiance levels.

III MATERIALS AND METHODS

1. Controlled Environment Facilities.

1.1. Spectral Bias Experiment.

1.1.1. Climate Rooms.

The experiment was carried out in Rooms 11, 12 and 13 of the Climate Laboratory, Plant Physiology Division, D.S.I.R., Palmerston North. Each growth room measures approximately 2.7 x 2.7 x 2.7 m, with an effective growing area of 2 x 2 m.

A diagrammatic side view of a typical Climate Room is shown in Diag. 1 which indicates the main features in the overall design. Conditioned air from ducting along the top of each side wall is passed over the plant trolleys and is recycled, via the false floor to the machinery chamber at the rear of each room. The artificial light is supplied from each source in the light rig located in the loft region above each room. Radiation from the rig is passed through a temperature controlled one-inch water screen heat barrier supported on a sheet of plate glass. Plates 1 and 2 show general photographs of light rigs in servicing and operating positions. The development of this type of lighting system allows the adoption of light types beyond those generally used in many controlled environment units in the past. The overall concept of a small number of specific lamp types means that there can be more complexity in the types of lamp combinations possible and that there is greater flexibility in changing between the various units in use. Equally, the heat barrier (water screen) renders the use of high output lamps (high temperature or long-wave infra-red radiation) possible as compared to the low temperature (lower visible output) fluorescent tube systems which frequently operate without a heat barrier.

1.2. Spectral Balance Experiment.

1.2.1. Growth Cabinets.

The Spectral Balance experiment was carried out in Cabinet "X" at the Plant Physiology Division, D.S.I.R., Palmerston North. The plant growing area measures 1.5 x 1.3 m

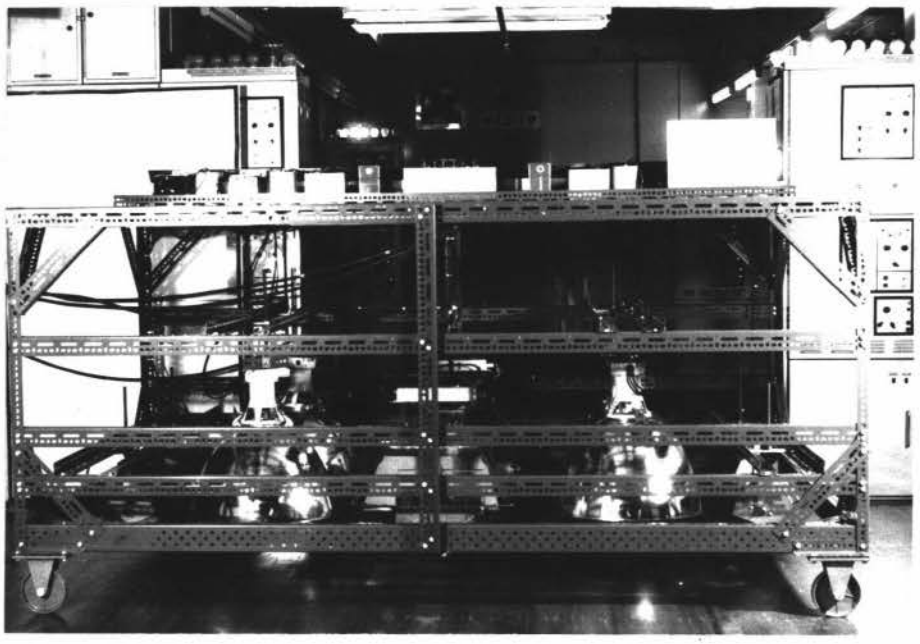


PLATE 1. Light rig from Balanced treatment in servicing position in control gallery.

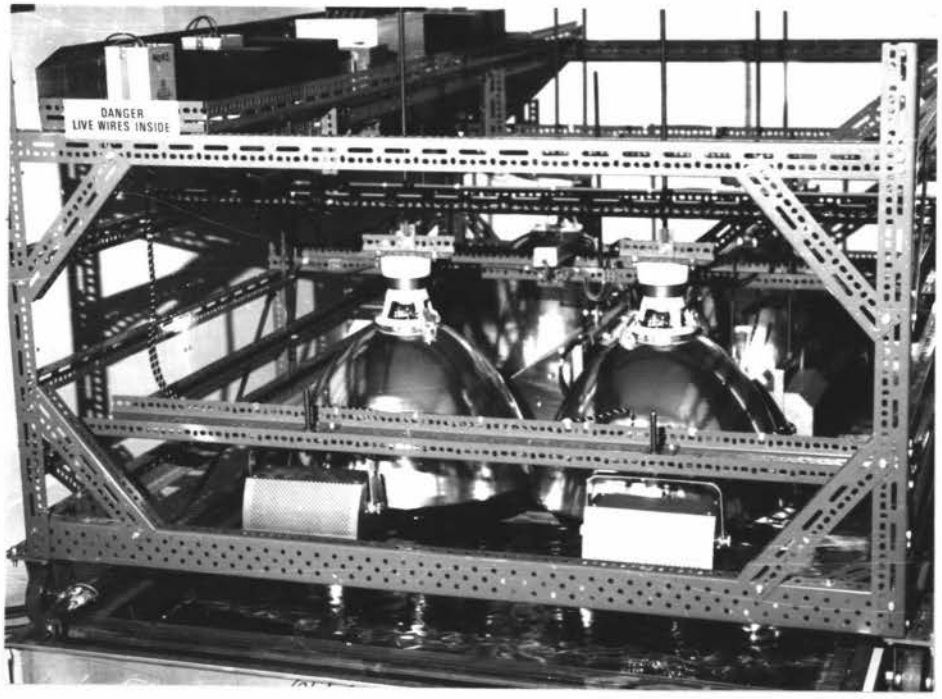


PLATE 2. Light rig as in Plate 1 shown in operating position above the water-screen heat barrier.

Lamp types, control gear, fuses, construction and general layout are shown in these photographs.

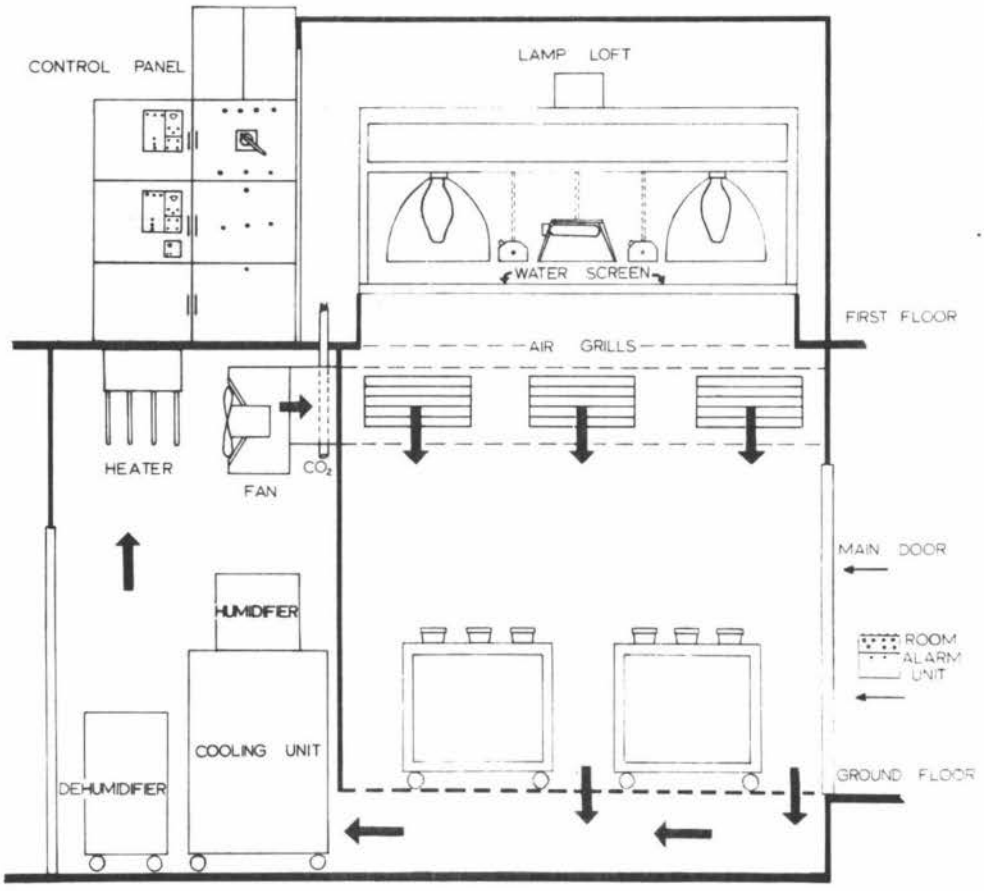


Diagram 1. Climate Room, Side View.

and the average plant height - water screen distance is 1 m. A diagrammatic front view of this cabinet, the prototype of a commercially available unit (Temperature Control Ltd, 1971), is shown in Diag. 2. Overall, the features are similar to those of a Climate Room with the main exceptions of a reversed (upward) airflow and a smaller scale of unit.

2. Lighting Systems.

2.1. Spectral Bias Experiment.

The lamp combinations chosen for this experiment have been on the basis of producing the required biased spectral treatments with particular reference to the blue and red regions of the visible spectrum. This bias was achieved simply by concurrently reducing, on a wattage basis, one lamp type while increasing the content of another. Each of the spectral treatments were examined at two irradiance levels.

The resultant lamp combinations used for each of the two biased and the balanced spectral treatments were as outlined in Table 2.

TABLE 2

Spectral Bias Experiment

Spectral Treatments

	Wattage
Room 11 (Balanced treatment)	
4 x 1000W "Metal-arc"	4000
1 x 2000W Blue HPI	2000
6 x 1000W Quartz Halogen	6000
	12000
Room 12 (Red-biased treatment)	
4 x 1000W "Metal-arc"	4000
12 x 1000W Quartz Halogen	12000
	16000
Room 13 (Blue-biased treatment)	
4 x 1000W "Metal-arc"	4000
2 x 2000W Blue HPI	4000
	8000

CABINET "X"

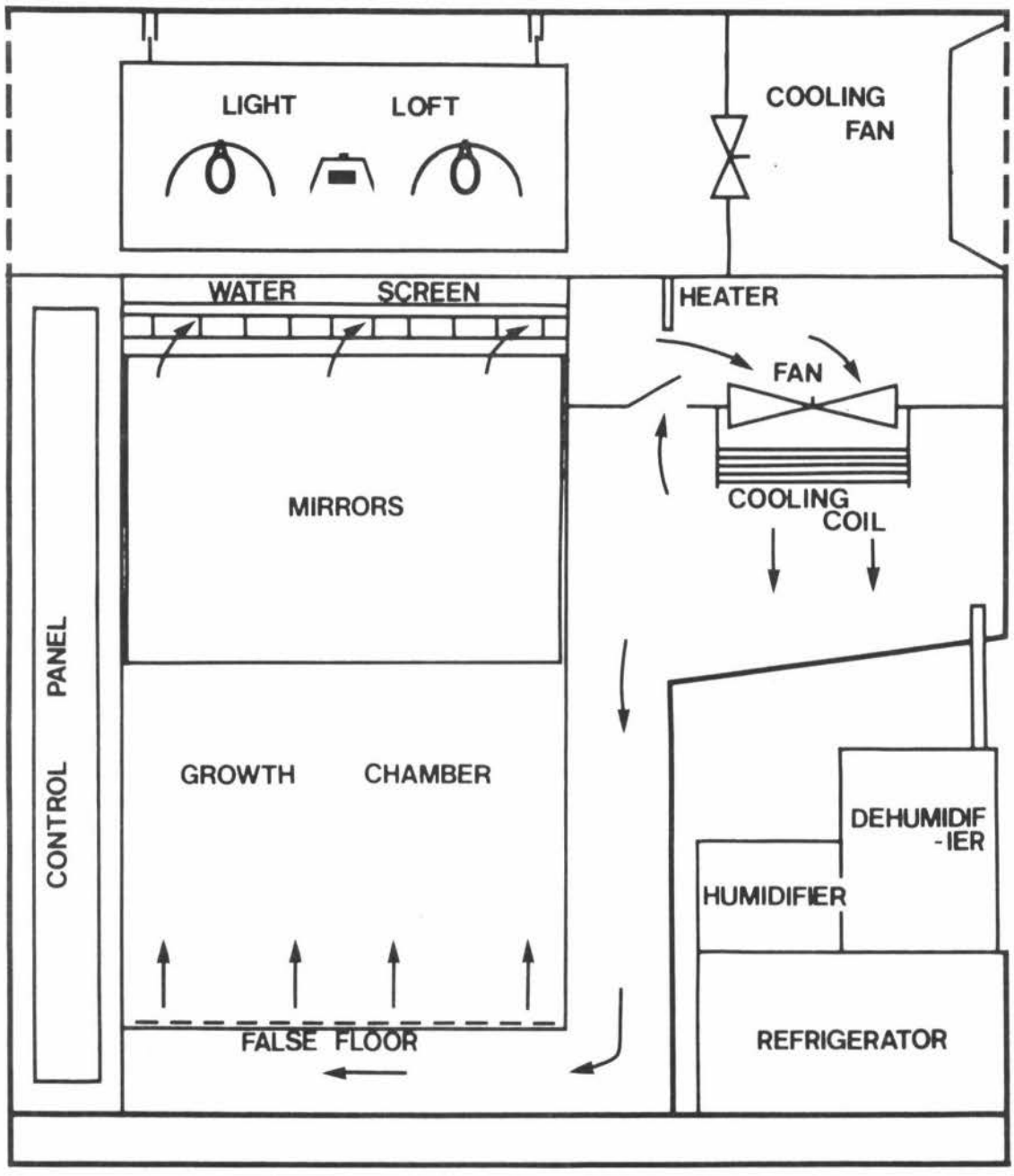


Diagram 2. Growth Cabinet, Front View.

These lamp types and reflector systems used were:

"Metal-arc": 1000W Sylvania 1000 BU Metal-arc lamp (Manufactured by Sylvania Division, G.T. and E. Danviers, U.S.A.) with modified Electrolier Corporation lamp holders (Electrolier Corporation, Montreal, Canada) and Sylvania 400W Vanguard reflectors (see Warrington, 1969).

Blue HPI: 2000W Philips Blue High Pressure Iodide lamp type No. 8222 205 06703 with modified reflector panels from a Philips HNF 002 floodlight fitting (Warrington, 1971, unpublished data) (manufactured by Philips Electrical Pty. Ltd., Eindhoven, Holland)

Quartz Halogen: 1000W Philips 240V. Halogen lamp type 12012R with Philips reflector housing NK17/00.

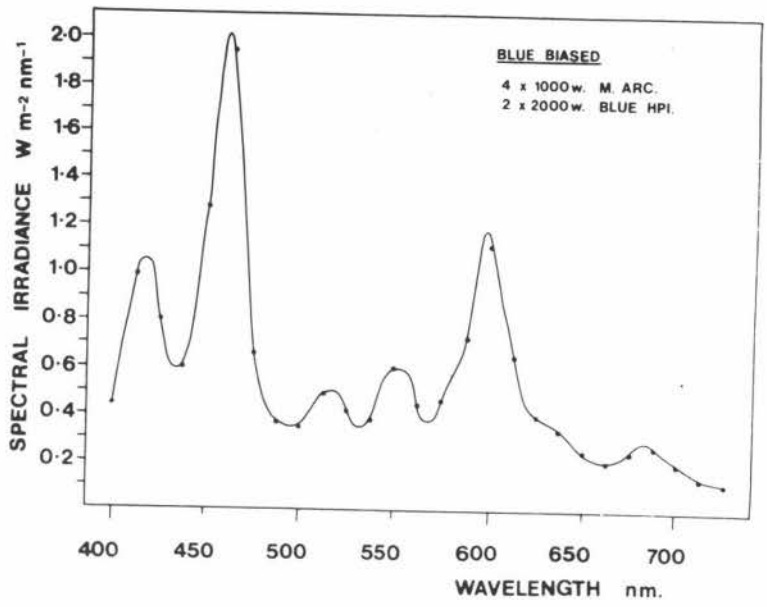
The spectral data and a summary of the irradiance values in each treatment are presented in the form suggested by the Dutch Committee on Plant Irradiation (1953, 1955; see also Norris, 1968). The relative spectral distribution of the energy flux density (irradiance) of each light treatment in the 400-725 nm region was determined using an ISCO SR Spectro-radiometer and an SRR Spectro-radiometer Recorder Scanner.

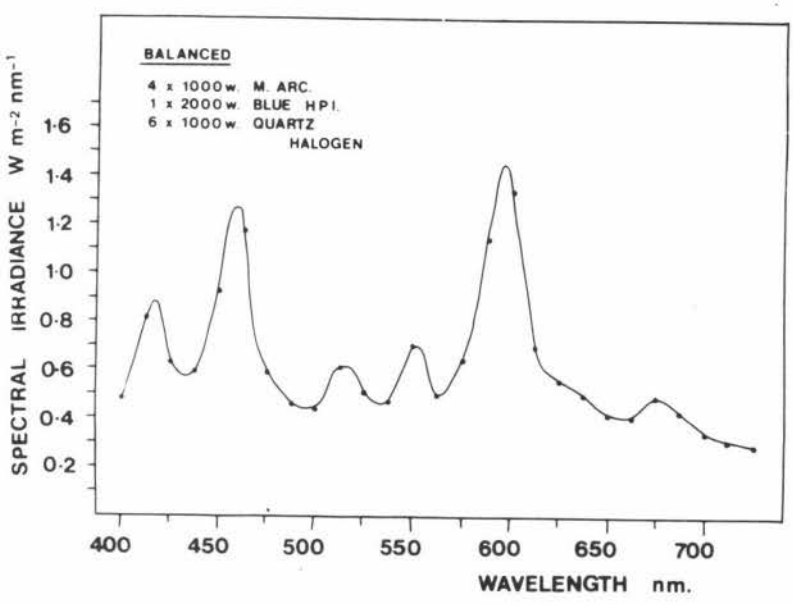
Fig. 1 shows the corrected curves for the three Spectral-Bias experiment treatments at the high irradiance level. Neutral screens of standard wire gauge mesh were used for shading for the low irradiance treatment such that the spectral outputs were identical at each irradiance level.

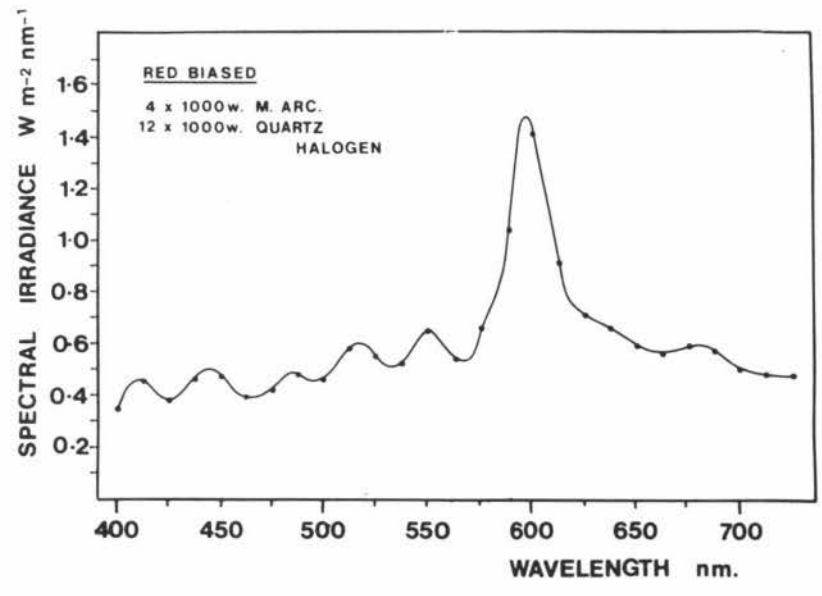
The contribution of each of these three lamp types to the resultant spectra used in these studies, is represented in Diag. 3. This is typical of the additive use of more than one artificial light spectrum in order to achieve a total visible output close to that desired. In this respect, a solar radiation curve (see section V.1.6. below, and Appendix 6) is presented as a generalized spectrum to give a ready comparison of the actual spectrum derived in this diagrammatic example.

Fig. 1. Spectral Bias Experiment. Spectral Irradiance Distribution Curves for the High Irradiance treatment.

A. Blue Biased Treatment.
B. Balanced Treatment.
C. Red Biased Treatment.


BLUE BIASED
4 x 1000w. M. ARC.
2 x 2000w. BLUE HPI.
SPECTRAL IRRADIANCE W m⁻² nm⁻¹
2·0
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
400
450
500
550
600
650
700
WAVELENGTH nm.


BALANCED
4 x 1000w. M. ARC.
1 x 2000w. BLUE HPI.
6 x 1000w. QUARTZ
HALOGEN
SPECTRAL IRRADIANCE W m⁻² nm⁻¹
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
400
450
500
550
600
650
700
WAVELENGTH nm.


RED BIASED
4 x 1000w. M. ARC.
12 x 1000w. QUARTZ
HALOGEN
SPECTRAL IRRADIANCE W m⁻² nm⁻¹
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
400
450
500
550
600
650
700
WAVELENGTH nm.

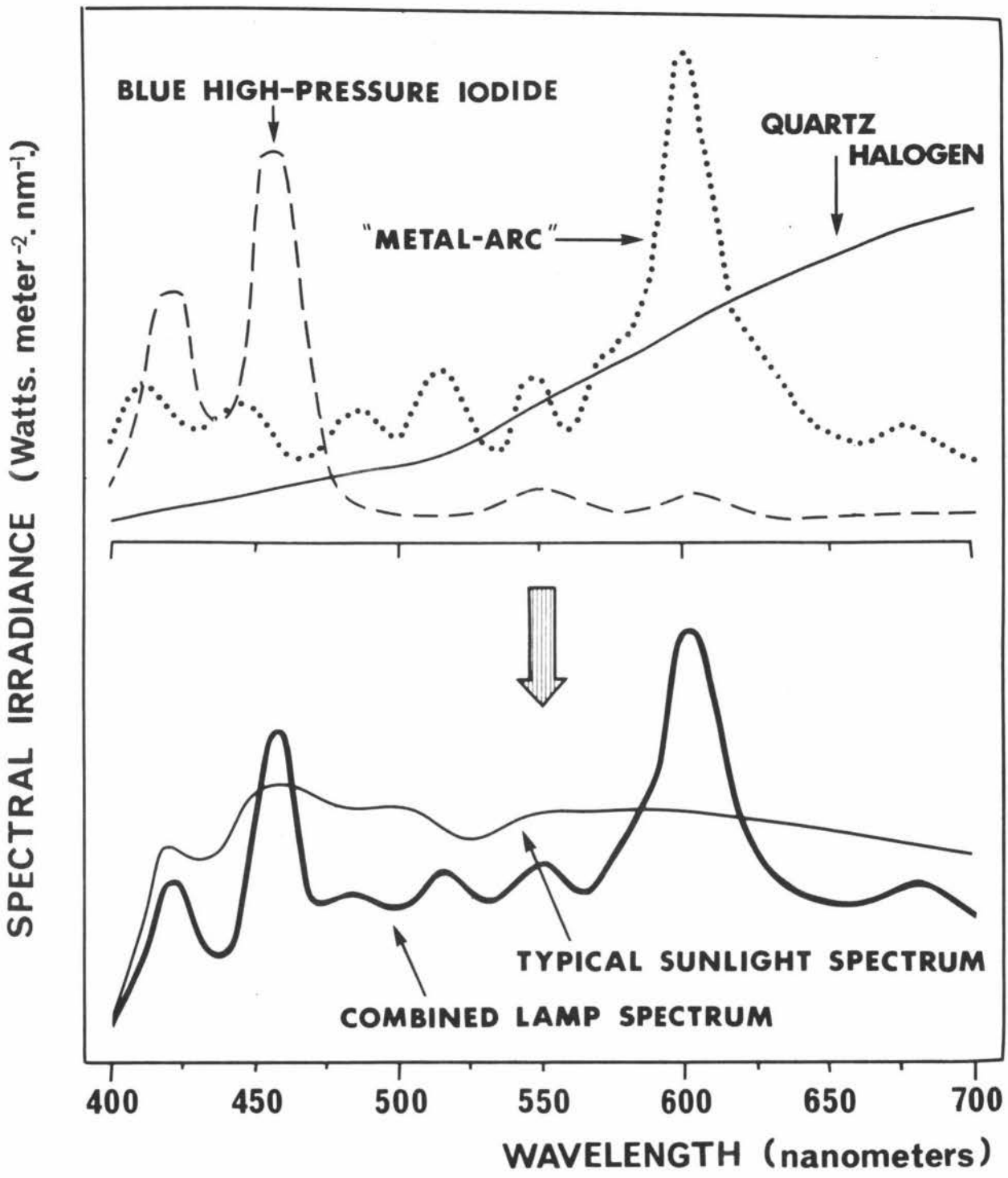


Diagram 3. Contribution of Individual Lamp Types to a Combined Spectral Irradiance Distribution.

The mean visible (400-725 nm) irradiance for each treatment at plant canopy level, and the percentage of the total visible radiation from the light source emitted in each 25 nm bandwidth as measured by the ISCO spectro-radiometer, are given in Tables 3 and 5 respectively.

The irradiance values at the beginning and end of each treatment were also measured with an Eppley pyranometer and a Schott RG8 filter system (see Appendix 1). The values with this system and their means for 380-700, 700-1400 and 380-1400 nm bandwidths are presented for each treatment in Tables 6A, B and C. Each value is the mean of 5 readings taken over the growing area.

The proportion of total irradiance (380-1400 nm) contributed by each lamp type as a percentage of the total is given in Table 4.

Finally, the light data is presented in a form which takes consideration of the energy per quantum in each treatment. Table 7 presents data converted to Einsteins m^{-2} sec^{-1} from the ISCO spectro-radiometer values. The relationship used for conversion is that presented by McPherson (1969).

Each lamp type in a light rig is independently adjusted to give uniform light distribution at the plant growing level within the room. A grid of 41 points at 20 cm centres was recorded for each lamp type and for all lamps in each treatment using an EEL light-meter (Evans Electro-selenium Ltd., England, Meter No. LM 1458).

Records of the distributions achieved are presented in Appendix 2.

2.2. Spectral Balance Experiment.

The base lamp types used in this study were selected as being potentially suitable for both plant growth and technical operation under controlled environment conditions. This study consisted of three treatments, at a similar light

Table 3

Spectral Bias Experiment

Mean Visible Irradiance Values ($W\ m^{-2}$)

And Spectral Distribution (%)

ISCO Spectroradiometer
(400-725 nm)

Spectral Treatment	Total 400-725	%		
		400-500	500-600	600-725
High Irradiance				
Blue Biased	194.9	48.77	28.34	22.88
Balanced	213.7	35.76	33.05	31.17
Red Biased	202.7	22.13	35.44	42.45
Low Irradiance				
Blue Biased	128.1	50.14	27.67	22.17
Balanced	135.8	36.17	32.08	31.73
Red Biased	131.3	22.32	33.76	43.93

Table 4

Spectral Bias Experiment

Proportion of Total Irradiance Contributed

By Each Lamp Type

(%)

Eppley Pyranometer

(380-1400 nm)

Spectral Treatment	Lamp Type		
	"Metal-arc"	Blue HPI	Quartz Halogen
Balanced	42.7	16.9	40.3
Red Biased	40.8	-	59.2
Blue Biased	58.6	41.4	-

Table 5

Spectral Bias Experiment

Energy Distribution Per 25 nm Band-width
(%)

ISCO Spectroradiometer
(400-725 nm)

Wave-Band (nm)	High Irradiance			Low Irradiance		
	Blue Biased	Balanced	Red Biased	Blue Biased	Balanced	Red Biased
400-425	11.82	8.91	5.35	12.56	8.81	5.34
425-450	9.81	7.87	5.61	10.89	7.96	5.33
450-475	21.75	13.05	5.22	21.27	13.62	5.44
475-500	5.39	5.93	5.95	5.42	5.78	6.21
500-525	5.97	6.80	7.03	5.66	6.27	6.96
525-550	5.85	6.50	7.24	5.71	6.42	7.17
550-575	6.45	7.12	7.53	6.04	6.89	7.12
575-600	10.07	12.63	13.64	10.26	12.50	12.51
600-625	10.29	10.68	13.26	9.34	10.41	12.42
625-650	4.46	6.01	8.43	4.36	6.47	8.72
650-675	2.94	5.21	7.39	3.23	5.34	8.08
675-700	3.32	5.42	7.27	3.26	5.43	7.86
700-725	1.87	3.85	6.10	1.98	4.08	6.85

Table 6

Spectral Bias Experiment

Beginning, End and Mean Irradiance Values for each Treatment

($W\ m^{-2}$)

Spectral Treatment	Start	End	Mean
A. Eppley Pyranometer with RG8 Filter (380-700 nm)			
High Irradiance			
Blue Biased	215.0	210.5	212.8
Balanced	216.1	222.7	219.4
Red Biased	226.1	225.8	225.9
Low Irradiance			
Blue Biased	151.3	133.8	142.6
Balanced	157.2	133.5	145.4
Red Biased	150.1	139.2	144.7
B. Eppley Pyranometer with RG8 Filter (700-1400 nm)			
High Irradiance			
Blue Biased	35.9	37.1	36.5
Balanced	106.4	103.1	104.8
Red Biased	170.6	177.4	174.0
Low Irradiance			
Blue Biased	24.6	24.2	24.2
Balanced	77.4	68.5	73.0
Red Biased	122.8	118.2	120.5
C. Eppley Pyranometer (380-1400 nm)			
High Irradiance			
Blue Biased	250.9	247.6	249.3
Balanced	322.5	325.8	324.2
Red Biased	396.7	403.2	400.0
Low Irradiance			
Blue Biased	175.9	158.0	167.0
Balanced	234.6	202.0	218.3
Red Biased	272.9	257.4	265.2

Table 7

Spectral Bias Experiment

Visible Photon Flux Density Per 25 nm Band-width
(Einsteins $m^{-2}s^{-1} \times 10^{-9}$)

ISCO Spectroradiometer
(400-725 nm)

Wave-Band (nm)	High Irradiance			Low Irradiance		
	Blue Biased	Balanced	Red Biased	Blue Biased	Balanced	Red Biased
400-425	7.54	6.26	3.56	5.55	4.12	2.42
425-450	6.64	5.87	3.95	5.10	3.95	2.56
450-475	15.55	10.29	3.89	10.54	7.15	2.76
475-500	4.06	4.92	4.68	2.83	3.20	3.32
500-525	4.73	5.94	5.81	3.11	3.65	3.92
525-550	4.86	5.95	6.27	3.29	3.92	4.23
550-575	5.61	6.82	6.82	3.64	4.40	4.40
575-600	9.15	12.64	12.91	6.45	8.34	8.07
600-625	9.74	11.14	13.09	6.12	7.24	8.35
625-650	4.40	6.53	8.66	2.98	4.69	6.10
650-675	3.01	5.88	7.88	2.29	4.02	5.88
675-700	3.53	6.35	8.05	2.40	4.24	5.93
700-725	2.06	4.67	7.01	1.51	3.30	5.36
Total 400-725	80.86	93.25	92.55	55.82	62.20	63.29

irradiance, based on different high-pressure discharge lamps with supplementation from blue fluorescent and tungsten lamp types, and three subsequent treatments based on one high-pressure discharge lamp type with varying levels of supplementation and different irradiance levels.

The lamp combinations used are presented in Table 8 where abbreviations represent the following lamp types:

HPLR: 1000W Philips HPLR High-pressure mercury-vapour lamp type No. 572416/93.

HPI: 2000W Philips HPI Mercury-iodide lamp type No. 126399 (with Philips HNF 002 Floodlight fitting).

M.ARC: 1000W Sylvania 1000BU Metal-arc lamp (with Benzamin High Bay reflector).

BL. FL: 80W Philips 65W Fluorescent (blue) type 126221.

TUNG(300W): 300W Philips Comptalux 220-230 V Tungsten type 13320 E/44.

TUNG(100W): 100W Mazda 240 V Floodlight Tungsten.

C. FLOOD TUNG: 150W Philips Comptalux Flood 240 V Tungsten type 13012 E/99.

Each of these lamp types and reflector systems, together with those used in the Spectral Bias experiment, are illustrated in Plate 3.

Fig. 2 shows the corrected spectral irradiance curves for the three spectral treatments used. The mean visible (400-725 nm) irradiance values for each treatment at plant canopy level, and the percentage energy distribution per 25 nm waveband are presented in tables 9 and 11 respectively. Table 10 presents mean total (380-1400 nm) irradiance values for each experiment and the percentage contribution to the total by each lamp type.

Table 12 presents the data from Table 11 converted to photon flux density values (E m^{-2} sec^{-1}).

In each treatment the total irradiance from the lamp combination was adjusted by means of a standard wire gauge mesh

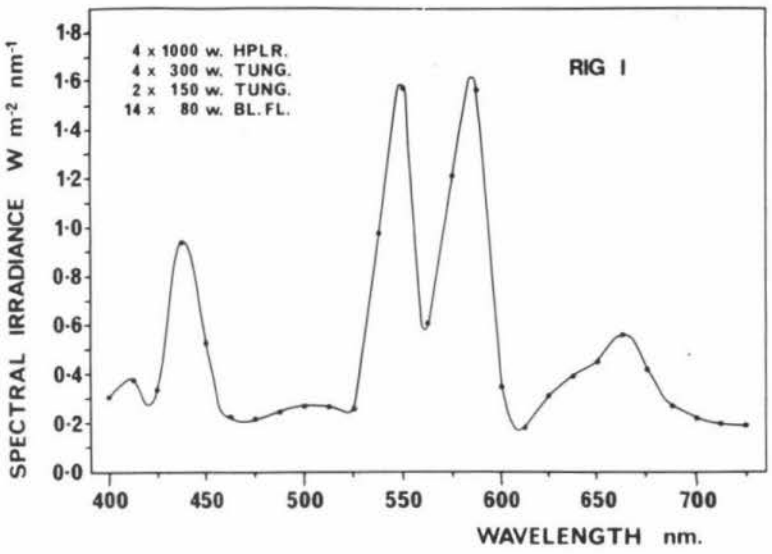
PLATE 3. The major lamp types used in the Spectral Bias and Spectral Balance experiments are shown here. The lamp types are as supplied by manufacturers but reflector systems have been substantially altered by the author.

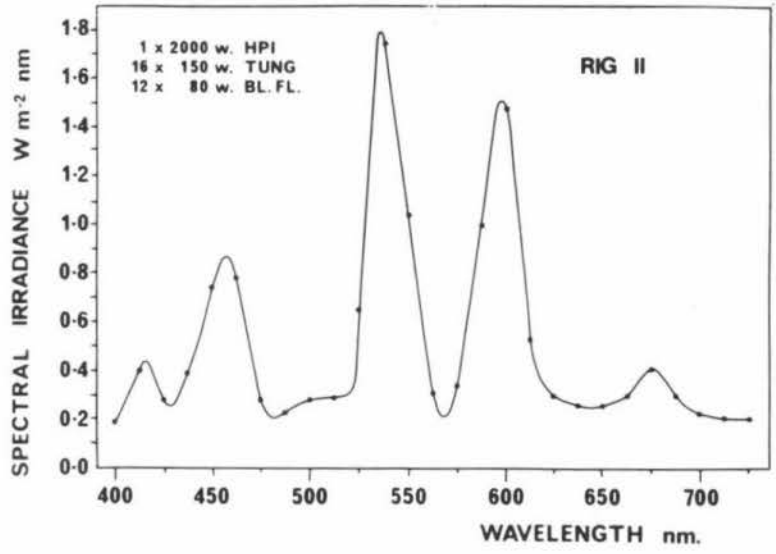
Fig. 2. Spectral Balance Experiment. Spectral Irradiance Distribution Curves.

A. Rig I.

B. Rig II.

C. Rig III.


4 x 1000 w. HPLR.
4 x 300 w. TUNG.
2 x 150 w. TUNG.
14 x 80 w. BL. FL.
RIG I
SPECTRAL IRRADIANCE W m-2 nm-1
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
0·0
400
450
500
550
600
650
700
WAVELENGTH nm.


1 x 2000 w. HPI
16 x 150 w. TUNG
12 x 80 w. BL. FL.
RIG II
SPECTRAL IRRADIANCE W m-2 nm
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
0·0
400
450
500
550
600
650
700
WAVELENGTH nm.

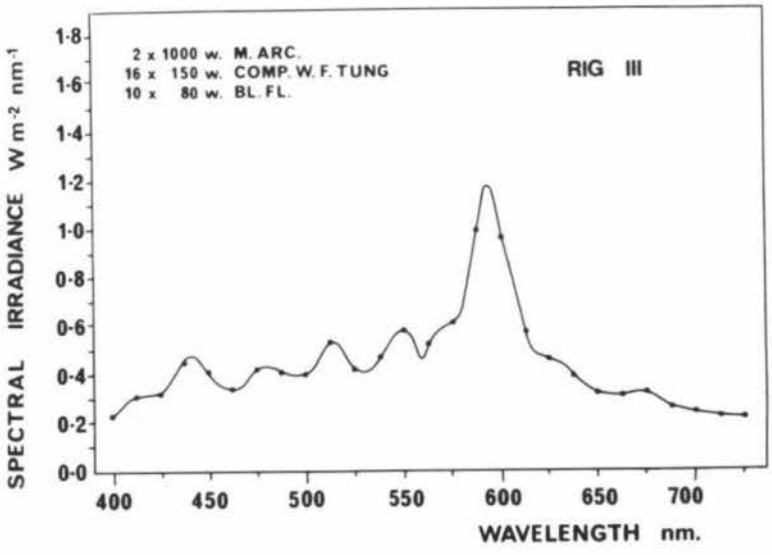

2 x 1000 w. M. ARC.
16 x 150 w. COMP. W. F. TUNG
10 x 80 w. BL. FL.
RIG III
SPECTRAL IRRADIANCE W m-2 nm-1
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
0·0
400
450
500
550
600
650
700
WAVELENGTH nm.

Table 8

Spectral Balance Experiment

Spectral Treatments
(Light Rig)

Light Rig	Lamp Component	Wattage
I	4 x 1000 W. HPLR.	4000
	4 x 300 W. TUNG.	1200
	2 x 150 W. TUNG.	300
	14 x 80 W. BL. FL.	1120
		6620
II	1 x 2000 W. HPI.	2000
	16 x 150 W. TUNG.	2400
	12 x 80 W. BL. FL.	960
		5360
III	2 x 1000 W. M.ARC.	2000
	16 x 150 W. COMP. FLOOD. TUNG.	2400
	10 x 80 W. BL. FL.	800
		5200
IV	2 x 1000 W. M.ARC.	2000
	4 x 300 W. TUNG.	1200
	12 x 150 W. COMP. FLOOD. TUNG.	1800
	10 x 80 W. BL. FL.	800
		5800
V	2 x 1000 W. M.ARC.	2000
	4 x 150 W. COMP. FLOOD. TUNG.	600
	12 x 100 W. TUNG.	1200
	10 x 80 W. BL. FL.	800
		4600
VI	2 x 1000 W. M.ARC.	2000
		2000

Table 9

Spectral Balance Experiment

Mean Visible Irradiance Values (W m^{-2}) and

Spectral Distribution (%)

ISCO Spectroradiometer

(400-725 nm)

Light Rig	Total 400-725	%		
		400-500	500-600	600-725
I	157.0	26.0	46.6	26.8
II	168.1	26.5	43.0	30.5
III	151.0	26.2	43.2	30.6
IV	250.1	27.7	39.5	32.8
V	106.6	28.7	42.6	28.7
VI	199.9	28.6	42.4	29.0

Table 10

Spectral Balance Experiment

Mean Total Irradiance Values (W m^{-2}) and Contribution of Lamp Types (%)

Eppley Pyranometer

(380-1400 nm)

Light Rig	Total	% Contribution from Lamp Type		
		High Pressure Discharge	Tungsten	BL. FL.
I	230	62.0	11.0	27.0
II	230	46.1	9.9	43.0
III	219	62.5	5.5	32.0
IV	430	69.0	4.2	27.8
V	154	75.0	6.8	18.2
VI	253	100.0	0.0	0.0

Table 11

Spectral Balance Experiment

Spectral Flux Distribution Per 25 nm Bandwidth
(%)
ISCO Spectroradiometer
(400-725 nm)

Wave-band (nm)	Spectral Treatment (Light Rig)					
	I	II	III	IV	V	VI
400-425	6.18	4.96	5.41	7.19	7.96	7.82
425-450	11.91	6.63	7.23	7.25	7.50	7.31
450-475	4.41	10.69	6.49	6.20	5.95	6.15
475-500	4.11	3.82	7.09	6.90	7.35	7.08
500-525	4.29	4.98	8.28	7.85	8.77	8.17
525-550	14.26	16.56	8.42	7.25	7.50	7.31
550-575	13.18	6.32	10.00	8.98	9.18	8.36
575-600	14.91	13.18	16.25	15.50	17.31	16.38
600-625	3.70	14.29	10.50	12.43	11.87	14.92
625-650	6.52	4.21	6.61	6.88	6.40	6.91
650-675	8.44	5.07	5.35	5.28	4.17	4.13
675-700	4.64	4.78	4.55	4.66	3.55	3.53
700-725	3.45	3.50	3.82	3.64	2.48	1.95
	100	100	100	100	100	100

Table 12

Spectral Balance Experiment

Visible Photon Flux Density Per 25 nm Band-width
(Einsteins $m^{-2} s^{-1} \times 10^{-9}$)

ISCO Spectroradiometer
(400-725 nm)

Wave-band (nm)	Spectral Treatments					
	I	II	III	IV	V	VI
400-425	3.13	2.70	2.70	6.55	2.80	5.69
425-450	6.40	3.83	3.83	6.77	2.98	5.36
450-475	2.51	6.53	3.64	6.52	2.67	4.76
475-500	2.46	2.46	4.19	7.37	3.12	5.67
500-525	2.70	3.38	5.14	8.59	3.65	7.16
525-550	9.41	11.76	5.49	8.78	3.55	6.90
550-575	9.11	4.70	6.82	10.32	4.44	9.41
575-600	10.76	11.01	11.57	20.19	9.85	18.03
600-625	2.79	11.57	7.79	16.17	6.22	12.55
625-650	5.11	3.55	5.11	9.66	3.59	6.53
650-675	6.87	4.44	4.30	7.59	2.81	4.02
675-700	3.92	4.35	3.79	6.87	2.33	3.36
700-725	3.02	3.30	3.30	5.50	1.83	1.92
Total 400-725	68.18	73.59	67.66	120.85	49.85	91.34

screen (neutral spectral sensitivity) to achieve the required experimental value. The output from each combination, therefore, is not a direct indication of the efficiency of light conversion by the lamp types being examined.

2.3. Spectro-radiometer Calibration.

The ISCO Spectro-radiometer and recorder were calibrated in the visible andnear infra-red ranges using techniques outlined by Norris (1968). The spectral emission of a tungsten standard lamp (P.P.D. Standard, R.103 3.62) was recorded and relative spectral flux densities at 25 nm wavelength intervals estimated from the known standard lamp emission. Absolute flux density values, and hence appropriate calibration factors for these wavelengths were determined from sunlight data recorded simultaneously with an Eppley pyranometer (Serial No. 8143), a Linke and Feussner actinometer (CM 1 Serial No. 660158) and the test instrument, using Moon's (1940) curves as reference data. Several specific wavelength locations were checked against the known line emissions from high-pressure discharge lamps as an assessment of the reliability of the reference wavelength scale.

3. Environmental Conditions.

3.1. Spectral Bias Experiment.

The environmental conditions used in the Spectral Bias experiment were as follows:

3.1.1. Temperature and Humidity.

The air temperature was $22.5^{o} \pm 0.5^{o}C$ day and $17.5^{o} \pm 0.5^{o}C$ night and the relative humidity was $60 \pm 5\%$ (V.P.D. -10 mb) day and $90 \pm 5\%$ (V.P.D. -2 mb) night. The alarm monitor was set at $\pm 3^{o}C$ and $\pm 10\%$ R.H. but no breakdowns in control occurred. The programmed time for change from day to night for these parameters was 60 minutes.

The temperature control and alarm calibration settings were checked weekly during the course of the experiment with

a reference calibrated platinum thermometer. Similarly, the humidity sensor (type PCRC 11 Humidity Transducer, Phys. - Chemical Research Corp., U.S.A.) was checked using either an Assman hygrometer or a Honeywell Humidity and Temperature meter (Model W809A, Honeywell Inc., U.S.A.) every two days throughout the experiment.

3.1.2. Carbon Dioxide.

Carbon dioxide was monitored but not controlled in each room and found to be 350 $\pm$ 10 ppm for day and night conditions.

3.1.3. Air Speed.

The air flow down through the plants was 20 $\pm$ 10 m. min^{-1} at the top of the plant canopy as measured by an Alnor thermo-anemometer (Alnor Instruments Co., Chicago, U.S.A., Model No. 2242).

3.1.4. Daylength.

All treatments were run with a constant 12 hour photo period (600h lights on, 1800h lights off).

3.2. Spectral Balance Experiment.

The operating conditions for temperature, humidity and daylength were the same in the Spectral Balance experiment as those in the Spectral Bias experiment. The basic controller design, calibration and operation in the growth cabinet were similar to those in the Climate Rooms.

4. Plant Materials.

4.1. Propagation.

4.1.1. Spectral Bias Experiment.

Seed of White Clover (Trifolium repens L., N.Z. Government stock cv "Huia"), Perennial Ryegrass (Lolium perenne L. N.Z. Government stock cv. "Ruanui"), Sorghum (Sorghum

bicolor L. Moench, Hybrid NK 145) and Soybean (Glycine max L., cv. Amsoy) were sown in a 4:1 pumice:peat potting media (pumice, a 1:1:1 mixture of 3 grades 1/4" x 1/16" : 1/16" x 20 mesh: 40mesh x 20 mesh) and germinated in a propagation pit. They were then transferred to a temperature controlled glasshouse (25°C max / 15°C min, 16 hour photoperiod) for growing on.

Seedlings were pricked out, at the cotyledonary expansion growth stage or equivalent, into 15 cm diameter 1.2 litre plastic pots (one plant per pot) containing a 14:3:3 washed gravel (1/4 - 1/8") : vermiculite (grade 3) : peat potting mix. One 100 ml North Carolina State University nutrient solution application (see Appendix 3), and one 100 ml water application were applied to each pot daily.

4.1.2. Spectral Balance Experiment.

Seed of white clover, perennial ryegrass, sorghum and soybean (cv. Merit replaced cv. Amsoy) were propagated as outlined in section III. 4.1.1.

Seedlings were pricked out into 15 cm diameter plastic pots (two plants per pot) containing a 4:1 pumice:peat potting mix and supplied with one application of Hoaglands A nutrient solution (see Appendix 3) and one application of water to each pot daily.

4.2. Experimental Conditions.

Plants were transferred to the experimental conditions (growth cabinets or Climate Rooms) at a 1 - 2 tiller (ryegrass and sorghum) or 1 - 3 trifoliate - leaf growth stage (white clover and soybean), after a 7 - 10 day establishment period in the glasshouse. In both experiments, the plants were grown for 7 - 10 days under experimental conditions before the first harvest.

4.2.1. Spectral Bias Experiment (Climate Rooms).

24 plants (pots) of each species were arranged on trolleys in each of the treatments. 4 plants of each species per treatment were carried as replacement material if required.

All plants received 3 applications of 100 ml N.C.S.U. nutrient solution daily (700, 1200, 1900 hrs) through an automated micro-tube system until the second harvest when this rate was increased to 200 ml per application for the remainder of the treatment period.

Each plant was randomised on each trolley and all trolleys were relocated in the rooms every two days. Plants were respaced and randomized at each harvest. Where practical there was one species per trolley or two species of similar size (ryegrass:clover, soybean:sorghum) per trolley. Plant growing height was adjusted throughout the experiment by removing sections of the trolleys such that the top one-third of the leaves on the main shoot remained at approximately the same mean distance from the glass-water light-screen as at the end of the conditioning period.

4.2.2. Spectral Balance Experiment (Growth Cabinet).

16 pots (32 plants) per species were grown under each treatment and were randomised twice weekly on the growing platform. All plants received manually two 100 ml applications of Hoaglands A solution daily. Plant height was adjusted as in section III 4.2.1. throughout the duration of the experiment.

5. Experimental Layout.

5.1. Spectral Bias Experiment.

32 plants per species were grown in each treatment, 8 of which were harvested at 7 day intervals following an initial 7-10 day establishment period.

At the preliminary harvest, stem length, tiller number,

stem number, leaf number, shoot fresh-weight and shoot dry-weight were recorded. For subsequent harvests stem length, sheath length, leaf number (on main stem), length and breadth of the last mature leaf on the main stem, tiller number, stem number, main-stem angle, shoot fresh weight, and the dry weights of leaves, stems, petioles, sheaths and recovered roots (after washing) were, depending on species, recorded. For the preliminary, second and third harvests all material was dried in a hot-air oven set at 95°C for 24 hours. Leaf and petiole material from the final harvest was frozen and subsequently freeze-dried; other material was dried in the same way as in the first three harvests.

The procedure adopted at each harvest was to measure all the shoot parameters (stem length, leaf number etc) on the intact plants after the removal of each plant from a treatment. Shoot fresh-weight was assessed immediately after cutting the shoot from the roots in order to avoid any loss of water due to the shoot wilting after abscission. The roots from each plant were recovered from the potting-mix by careful washing after the shoot harvest was completed.

All material was weighed in a constant temperature and humidity controlled room (22°C, 50% RH) after drying.

A separate drying experiment indicated that the difference in final dry-weights with the different drying methods were of no significance and no corrections to the data obtained were made.

The freeze-dried material was ground in a Culatti micro-hammer mill (Model C580) and stored in sealed glass vials for subsequent chemical analyses.

5.2. Spectral Balance Experiment.

16 pots (32 plants) per species were grown in each treatment. One plant per pot was harvested following an initial 7-10 day establishment period and two following harvests of 8 pots each at 7-10 day intervals completed each treatment.

At the preliminary harvest stem length, leaf number (on the main stem), stem number, tiller number and shoot fresh- and oven dry-weights were recorded. In addition at the second and third harvests, the length and breadth of the last mature leaf on the main stem, sheath length, and the dry weights of leaves, stems, petioles, sheaths and roots were, depending on species, recorded.

The general harvesting and experimental procedures were the same as those for the Spectral Bias Experiment.

6. Plant Measurements.

6.1. Methods of Measurement.

The following methods were used to measure the growth parameters recorded in the Spectral Bias and Spectral Balance experiments.

Leaf number - the number of mature and developing leaves on the main stem or shoot; soybean: trifoliate leaves, ryegrass and sorghum: main shoot leaf lamina, white clover: the number of trifoliate leaves on the longest stem.

The mature leaves were gauged consistently on a subjective basis and the next developing leaf was scored by a decimal system (see for example, Maurer et al., 1966).

Stem (shoot) length - ryegrass and sorghum: from the tip of the last mature leaf blade to the sheath base, soybean: main stem length from the base of the developing stem apex to the stem base, white clover: length of the longest stem from the base of the developing stem apex to the stem base.

Sheath length (sorghum) - length of the sheath from the last mature leaf base (ligule) to the base of the shoot.

Stem angle (sorghum):the tillers and the main shoot in sorghum are co-planar; the angle of the main stem from the horizontal was measured at right angles to that plane using

a protractor (with the pot surface as the horizontal reference).

Stem number, tiller number - this represents the number of tillers or stems greater than 1 cm in length but does not include the main tiller or stem.

Sample leaf length and breadth-from 8 plants per species in each treatment, the length and breadth (at the mid-point) of the last mature leaf (centre leaflet on soybean, two centre leaflets from white clover) were recorded, bulked, oven-dried and weighed.

Mean length and breadth values were used to determine the sample leaf area by the relationship: L x B x conversion coefficient = area. The specific conversion coefficients for each species are:

Soybean	0.725
Sorghum	0.719
White clover	0.709
Perennial ryegrass	0.826

These coefficients were derived at Plant Physiology Division (Forde, pers, comm., 1969) and appear to agree approximately with previously publised coefficients. (Sestak et al., 1971). From the mean sample (last mature) leaf areas and the mean dry weights for the sample leaves, dry-weight per unit area of the sample leaves and total leaf area (from total leaf dry-weight) may be determined.

7. Data Analysis.

7.1. Spectral Bias Experiment.

The data for each parameter measured were analysed as a two-way analysis of variance using the eight plants as replicates and the three spectral treatments at two light irradiance levels as six treatments. Lowest significant difference values for 5 and 1% confidence limits were derived as part of each analysis of variance .

From the raw data, leaf area per plant, and the leaf, stem, petiole, sheath and root: shoot weight ratios per plant were derived and analysed as above. Using the dry-weights and leaf areas, the data was further analysed by traditional growth analysis techniques. Net assimilation rate (NAR), leaf-area ratio (LAR), relative growth-rate (RGR) and the relative rate of leaf-area expansion (RLAGR) of all species were calculated from shoot data using regression techniques (see Vernon and Allison, 1963; Radford, 1967). The dry-matter percentage was also calculated from arithmetic means of shoot fresh and dry weights.

The growth analysis functions used were as follows:

Relative Growth Rate (RGR) -

$$RGR = \frac{1}{W} \cdot \frac{dW}{dt} = \frac{d}{dt} (\log_e W).$$

i.e. the increase of plant material per unit of material present per unit of time.

$$\overline{RGR} = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \frac{1}{W} \cdot \frac{dW}{dt}$$

$$= \frac{\log_e W_2 - \log_e W_1}{(t_2 - t_1)}$$

Net assimilation rate (NAR) -

$$NAR = \frac{1}{A} \cdot \frac{dW}{dt}$$

i.e. the rate of increase of dry weight per unit leaf area.

$$\overline{NAR} = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \frac{1}{A} \cdot \frac{dW}{dt} \cdot dt$$

$$= \frac{W_2 - W_1}{A_2 - A_1} \cdot \frac{(\log_e A_2 - \log_e A_1)}{(t_2 - t_1)}$$

Assuming that:

(i) once the period t_1-t_2, A and W are linearly related, and

(ii) A and W are not discontinuous with time.

Leaf area ratio (LAR) -

$$LAR = \frac{A}{W}$$

i.e. the ratio of total leaf area to total (shoot) dry weight.

Relative rate of leaf area expansion (RLAGR) -

$$RLAGR = \frac{1}{A} \cdot \frac{dA}{dt} = \frac{d}{dt} \cdot (\log_e A)$$

i.e. the increase of leaf area per unit of leaf area present per unit of time.

$$\overline{RLAGR} = \frac{\log_e A_2 - \log_e A_1}{t_2 - t_1}$$

7.2. Spectral Balance Experiment.

The design of this experiment, which compelled the use of successional treatment runs in the same growth cabinet, introduced problems of comparative plant size and development at the start of each treatment. In this respect, the index of treatment time was not consistent between treatments and could not be used as a basis for statistical analysis. To partially overcome this problem the growth measures presented in the results have been expressed as a function of plant dry weight and the variability at each harvest period is expressed as a standard error (S.E.) value. No analysis of variance tests were undertaken.

Functions derived from raw data and presented in the results section were calculated as outlined in Section III 7.1.

8. Biochemical Analyses.

8.1. Carbohydrate Determinations.

8.1.1. Spectral Bias and Spectral Balance Experiments.

Freeze-dried powdered plant material (0.1 gm) was suspended twice with 10 ml 20% ethanol to extract soluble carbohydrates ("sugars"). Duplicate 0.5 ml samples from the supernatant were taken for Anthrone determinations.

The residue was resuspended in 2.5 ml distilled water and boiled in a water bath for 15 minutes to gelatinise the starch. This was followed by solubilization in 3.3 ml 52% perchloric acid at 25°C for 20 minutes (Pucher et al, 1948) before being centrifuged.

The residue was discarded and the supernatant made up to 100 ml. A 3 ml aliquot from this volume was hydrolysed in 3 ml 3N H_2SO_4 for 2 hours at 100°C. Duplicate 0.5 ml aliquots of the starch hydrolysate were taken for Anthrone determinations. (Viles and Silverman, 1949).

Anthrone test.

50 mg Anthrone was dissolved in 100 ml 70% H_2SO_4. All Anthrone solutions were discarded after 72 hours and were stored at 0°C when not in use.

A 0.5 ml: aliquot of the prepared sample for each determination was pipetted into 5 ml Anthrone solution in large boiling tubes. The tubes were placed in a boiling water bath for 7 minutes and then cooled before reading the optical densities at 625 nm on a Bausch and Lomb Spectronic 20 colorimeter/spectrophotometer with standard cuvettes. A water blank was included in each batch of analyses and standard curves for each anthrone solution were constructed using serial dilutions of a 100 mgm/l D-glucose standard solution.

8.2. Protein Nitrogen Determination.

8.2.1. Spectral Bias and Spectral Balance Experiment.

Protein nitrogen determinations using the Kjeldahl digestion technique, incorporating selenium as a catalyst,

were carried out on individual leaf samples and bulked petiole material for each species from all treatments.

A 280 mgm freeze-dried sample was digested in a 5 ml digestion mixture in a 100 ml Kjeldahl flask for 2 hours until the mixture was clear. The digestate was made up to a 100 ml standard volume in a volumetric flask.

Nitrogen was determined on a 5 ml (duplicate) sample of the digestate by steam distillation in a Markham still, after release with NaOH, and collection in a boric acid-indicator mixture solution.

The corrected sample titre expressed in ml 0.01N HCl was equivalent to the percentage of nitrogen in the sample.

Digestion mixture: 100g K_2SO_4 + 1g Se granules in 1l 36N H_2SO_4.

Boric acid-indicator mixture: 2% $^{W}/_{V}$ aqueous solution of boric acid, containing 2% $^{V}/_{V}$ indicator mixture (5 vol 0.1% ethanolic solution of bromocresol green + 1 vol 0.1% ethanolic solution of methyl red).

Protein content was calculated from the relationship:

$$\%N \times 6.25 = \% \text{ Protein}$$

8.3. Chlorophyll Determinations.

8.3.1. Spectral Bias Experiment.

Total chlorophyll concentration and chlorophyll a: chlorophyll b ratios were determined for all species and treatments immediately prior to the final harvest.

Two sample leaf discs per plant were taken from the youngest mature leaves on the 8 plants in each treatment for sorghum and soybean (approximately 300-500 mgm fresh weight) and two entire youngest mature leaves were taken per plant for ryegrass and white clover (approximately 1-2 gms fresh weight). No allowance for this small tissue loss was made

to the total or plant-part weights.

Sample tissue was immediately cut into thin sections and ground in 10 ml 80% acetone in a Ten-Broek hand ground-glass tissue grinder. The extract was centrifuged to remove the residue and the supernatant was made up to 30 ml with 80% acetone. Duplicate samples at two dilutions were transferred to cuvettes and absorbance values at 645 and 663 nm were read in a Perken-Elmer Model 450 Spectrophotometer.

Total chlorophyll, chlorophyll a and chlorophyll b concentrations were determined using the following relationships (Arnon, 1949).

Chlorophyll a = $(12.7\ A_{663} - 2.69\ A_{645})$ µgms/ml.
Chlorophyll b = $(22.9\ A_{645} - 4.68\ A_{663})$ µgms/ml.
Total chlorophyll = $(20.2\ A_{645} + 8.02\ A_{663})$ µgms/ml.

8.4. Amino Acid Analysis.

8.4.1. Spectral Bias Experiment.

At the final harvest in the low irradiance treatment, small (400-450 mgm) samples of fresh tissue were taken randomly from the youngest mature leaf lamina (lateral leaflet) of eight soybean plants in each treatment.

The sample was extracted in 5 ml 1:2 chloroform:methanol in a Ten-Broek hand ground-glass tissue grinder. The residue was then centrifuged down and re-extracted with 1.5 ml water and centrifuged again. The two supernatants were recombined and the methanol:chloroform:water ratio adjusted for phasic separation (12:11:10).

The aqueous phase containing the amino acids was retained, reduced to 50% in a rotary evaporator and freeze dried.

Each sample was re-suspended in 1.5 ml of 0.2 M Na Citrate pH 2.2 buffer and 100 µl aliquots were taken for analysis in a Beckman/Spinco model 120 amino acid analyser.

All samples were run as duplicates and the data is presented as means of these results.

9. Electron Microscopy.

9.1. Spectral Bias Experiment.

At the final harvest of each treatment a sample piece of leaf tissue approximately 5 x 5 mm was taken from the youngest mature leaf (lateral leaflet) for an electron microscope study. All the samples were taken at the end of the 12 hour night period to allow easier cutting of material and for grana and thylakoid structures to be unobscured and undistorted by starch-grain formation.

Only two species were used in this study: soybean because of earlier reports of environmental effects on chloroplast changes (Ballantine and Forde, 1970) and white clover because of its suitability for electron microscope studies. Sorghum and ryegrass, although of interest because of different leaf structures were not used because of difficult sectioning properties (see Ballantine, 1969).

Leaf sections 1 x 5 mm were cut from each sample under cold 3% gluteraldehyde/2% formaldehyde one-half strength Karnovsky fixative (Karnovsky, 1965)., in 0.1 M phosphate buffer, vacuum infiltrated for 10 min. and fixed in fresh fixative at $4^{o}C$ for 3-4 hours.

Specimens were subsequently washed twice in 0.1 M phosphate buffer (pH 7.2, $4^{o}C$ for 30 min.), post-fixed in 1% OsO_4 (0.1 M phosphate buffer, pH 7.2; 3 hr. at $4^{o}C$), buffer washed twice and dehydrated at room temperature in a graded ethanol series: 25%, 10-15 min., 50% 30 min., 75% overnight, 95% 30 min., 100% 10 min., 100% 60 min. They were then washed twice with propylene oxide for 15 min. at room temperature, infiltrated via a propylene oxide/epoxy resin series (Luft, 1961): 75:25%, 1-2 hours, 50:50% 1-2 hours, 25:75% overnight, 0:100% 6-8 hours embedded in complete epoxy resin mixture (Durcupan ACM, Fluka, Buchs, Switzerland) and polymerized at $60^{o}C$ for 48 hours.

Prepared sections were cut using an L.K.B. "Ultrotome" and a glass knife, were picked up on carbon-coated Formvar support-films on 200 mesh copper grids, post-stained for 5 min in aqueous uranyl nitrate and for 5 min. in lead citrate (Reynolds, 1963).

All samples were examined using a Philips EM-200 electron microscope.

IV RESULTS

1. Spectral Balance Experiment.

1.1. General.

The choice of lamp combinations made in the Spectral Balance experiment resulted in a close similarity between each of the spectral treatments with respect to their intrinsic visible wavelength balance. Table 9 shows that on a broad waveband (100 nm) consideration the differences between light treatments in the visible range were only small; more specifically the blue (425-475 nm) : red (625-675 nm) ratio for each rig was calculated as being similar as is shown by the following arbitrary ratios based on the percentage values for spectral distribution : rig I 1.2, III and IV 1.35, II and V 1.7, VI 1.8. Similar calculations for the red:infra-red (700-1400 nm) ratio showed the following ascending order of ratios for each rig : IV, V, III, VI, II, I where the relative differences between rigs were greater than for the other narrow visible waveband ratios.

Hence, although the base lamp, and therefore the base spectral emission, varied between rigs I, II and III there were no sharp contrasts between each of the spectral outputs of these rigs expecially within the photosynthetically active wavelength region and marked plant response differences between these spectral treatments on this account were not expected.

Likewise with rigs IV - VI, where small spectral balance differences existed, the major response was considered most likely to arise from the differences in the irradiance levels.

These six treatments are discussed therefore on the basis of spectral (rigs I - III) and irradiance (rigs IV - VI) treatment differences.

1.2. Plant Weight.

1.2.1. Shoot Weight.

The data for mean shoot dry-weight (g) at each harvest are presented as plots of dry weight (log. scale) against time in Fig 3 for each of the four species studied. Mean leaf number at the preliminary harvest is presented on each graph.

Examination of the dry weight and leaf number at the first harvest for each treatment, and for each species, clearly demonstrates the problem encountered with variable plant size and stage of development, in an experiment of this nature, where successional treatments were necessary.

The main feature of these results is that for each of the species studied, the responses shown have been predominantly influenced by irradiance rather than by spectral quality. This irradiance response is apparent from the varying slopes (i.e. interval RGR's) of each weight increase under light rigs IV to VI.

1.2.2. Relative Growth Rate.

RGR (g g^{-1} day^{-1}) data for each harvest interval and for total treatment time are presented in Table 13. In most instances the RGR either decreased or remained constant with time under treatment. Mean RGR for sorghum showed a close relationship to irradiance. Increased irradiance (rig IV) markedly increased $\overline{RGR}$, whereas decreased irradiance (rig V) had the reverse effect compared to the other treatments. Ryegrass and white clover showed a similar response to sorghum, but soybean $\overline{RGR}$ did not respond except that the rate of decrease in each interval RGR was not as great at the high irradiance as at the lower irradiance.

Generally, no obvious effect of varying spectral quality was noted in the results as expected from the shoot dry-weight data. In each of the different light treatments there were no unusually high or low $\overline{RGR}$ values for each of the species tested, although it is accepted that exclusion

KEY:

SPECTRAL BALANCE EXPERIMENT

▲——▲	RIG	I	HPLR	BASED		
●——●	"	II	HPI	"		
■——■	"	III	METAL-ARC		BASED	
▲——▲	"	IV	"	"	"	(HIGH)
●——●	"	V	"	"	"	(LOW)
■——■	"	VI	"	"	ONLY	

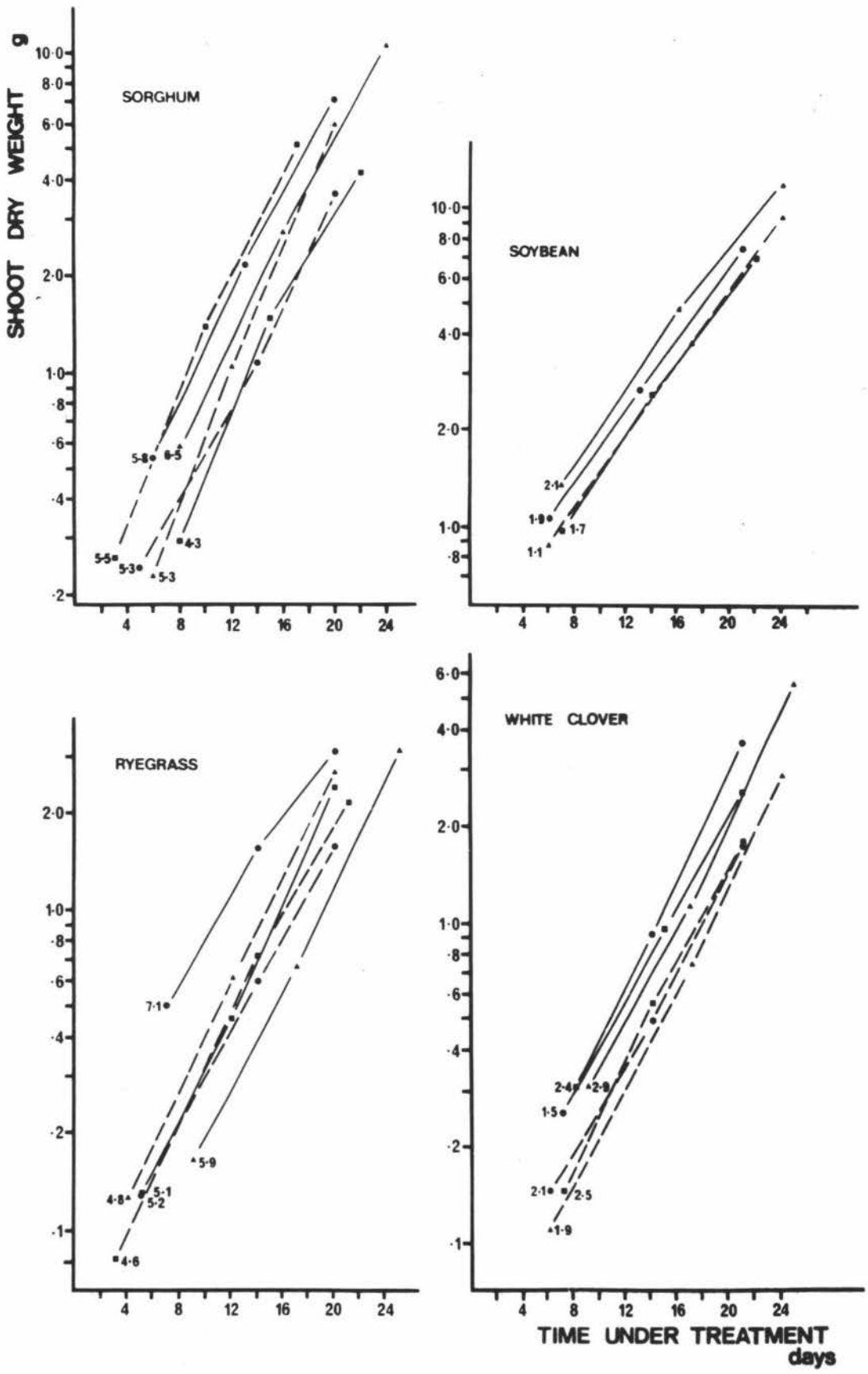


Fig. 3. Spectral Balance Experiment.
Shoot Dry-Weight increase with time under each treatment (all species).

Table 13

Spectral Balance Experiment

Relative Growth Rate (RGR)

All Harvest Intervals and Total Experimental Period RGR's

($g\ g^{-1}\ day^{-1}$)

(S.E. in Brackets)

Species / Treatment	Harvest Interval			Species / Treatment	Harvest Interval		
	1 - 2	2 - 3	1 - 3		1 - 2	2 - 3	1 - 3
SORGHUM				SOYBEAN			
I	0.191 (0.009)	0.164 (0.009)	0.180 (0.004)	I	0.143 (0.006)	0.110 (0.005)	0.130 (0.003)
II	0.204 (0.017)	0.162 (0.009)	0.187 (0.007)	II	0.132 (0.009)	0.127 (0.008)	0.131 (0.004)
III	0.224 (0.015)	0.148 (0.017)	0.192 (0.007)	III	0.139 (0.009)	0.121 (0.007)	0.132 (0.004)
IV	0.255 (0.017)	0.210 (0.013)	0.233 (0.007)	IV	0.133 (0.005)	0.130 (0.007)	0.131 (0.003)
V	0.167 (0.008)	0.197 (0.019)	0.176 (0.005)	V			
VI	0.234 (0.015)	0.179 (0.019)	0.210 (0.008)	VI			

Table 13 contd.

Species / Treatment	Harvest Interval			Species / Treatment	Harvest Interval		
	1 - 2	2 - 3	1 - 3		1 - 2	2 - 3	1 - 3
PERENNIAL RYEGRASS				WHITE CLOVER			
I	0.170 (0.009)	0.195 (0.009)	0.184 (0.005)	I	0.167 (0.017)	0.196 (0.017)	0.180 (0.008)
II	0.161 (0.016)	0.112 (0.021)	0.144 (0.008)	II	0.182 (0.016	0.182 (0.024)	0.185 (0.008)
III	0.174 (0.013)	0.208 (0.014)	0.195 (0.006)	III	0.167 (0.018)	0.143 (0.032)	0.164 (0.009)
IV	0.204 (0.009)	0.185 (0.012)	0.192 (0.005)	IV	0.174 (0.010)	0.192 (0.018)	0.180 (0.006)
V	0.173 (0.009)	0.146 (0.025)	0.166 (0.007)	V	0.160 (0.014)	0.175 (0.018)	0.164 (0.007)
VI	0.200 (0.009)	0.149 (0.023)	0.184 (0.007)	VI	0.197 (0.018)	0.167 (0.025)	0.181 (0.009)

of root weights may have biased the results in relation to total plant weight - based $\overline{RGR}$ values.

1.2.3. Dry Matter Percentage.

Dry-matter percentage values for each harvest are shown in Fig 4.

The relationship between treatments varied with time under treatment (increase in dry-weight), however, there were two obvious groups of results for each species. The HPLR-, HPI, and low intensity "Metal-arc"-based rigs gave consistently lower values than the "Metal-arc"-based medium and high-irradiance and "Metal-arc"-only treatments.

There were also some species - specific trends of dry-matter percentage with increasing plant weight. Sorghum showed comparatively steady, white clover showed downward and soybean and perennial ryegrass upward trends with increasing plant weight for a majority of the treatments studied.

1.3. Stem Length.

Stem (shoot) length (cm) results are plotted for each species in Fig 5.

The most significant response of stem length was to the different irradiance levels rather than to the different spectral treatments. High irradiance resulted in shorter stems in sorghum and ryegrass but had little effect on soybean and white clover. Low irradiance increased stem length in sorghum and ryegrass but, like the high irradiance treatment, had no effect on white clover.

In relation to the spectral treatments, in sorghum an effect on stem length was apparent in the "Metal-arc" based rig (Rig III) where lower values were obtained compared with the HPLR and HPI based rigs (I and II). In soybean this effect was reversed (especially at earlier harvests) but no response was noted in the other species.

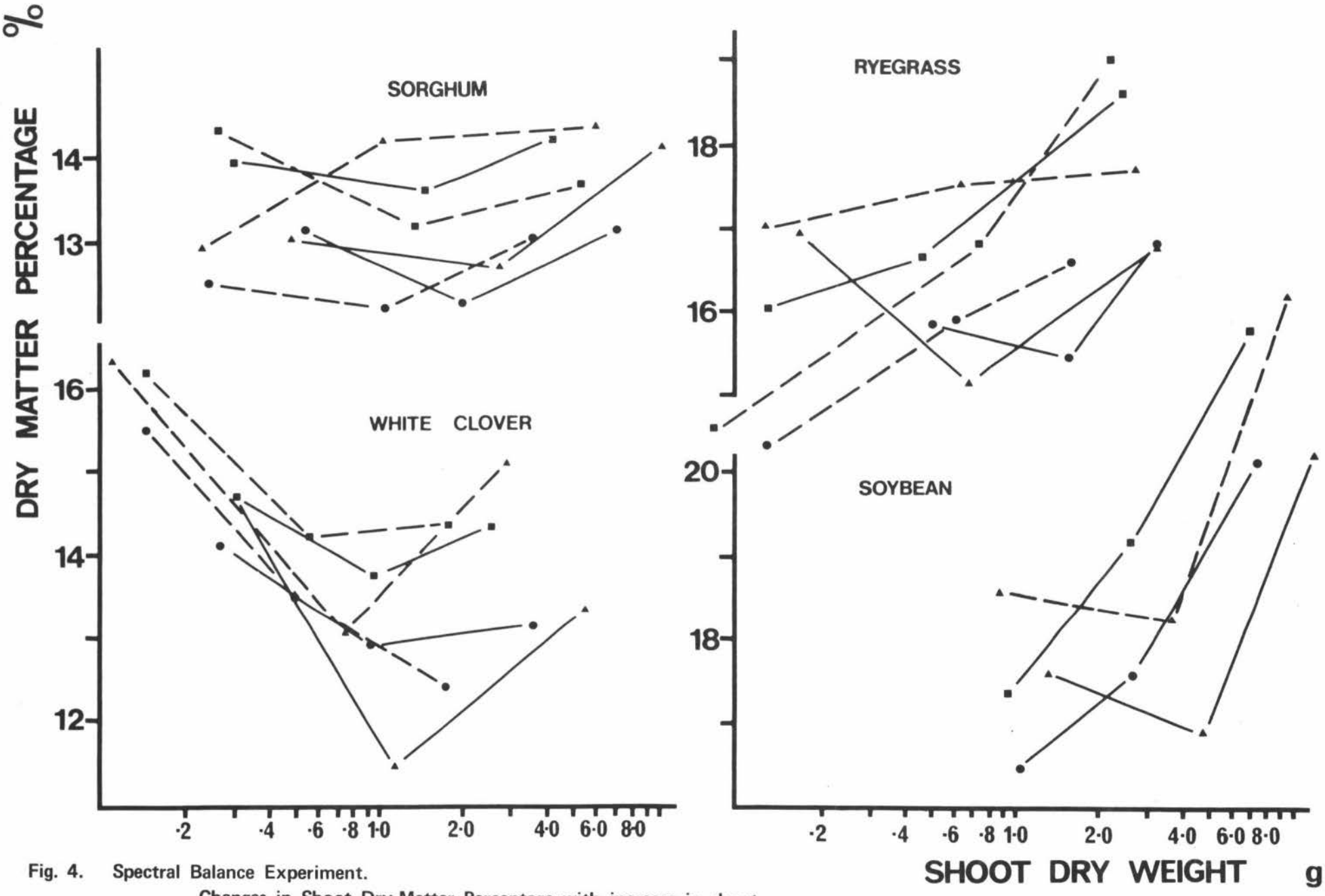


Fig. 4. Spectral Balance Experiment.

Changes in Shoot Dry-Matter Percentage with increase in shoot dry-weight for all treatments.

The "Metal-arc" only rig (VI) produced intermediate stem length values compared to the high and low irradiance treatments. There appeared to be no spectral effect in this treatment.

1.4. Leaf Area Per Plant.

Results for mean leaf area per plant (cm^{-2}) are presented in Fig. 6.

Generally, there was little difference noted between either the spectral quality or light irradiance treatments. High irradiance (Rig IV) significantly depressed leaf area in soybean, but showed no obvious effect in the other species studied. In each species, however, there did appear to be a trend towards higher leaf areas under the HPLR- and HPI-based treatments.

1.4.1. Dry Weight Per Unit Area (Last Mature Leaf Blade).

The results for dry-weight/unit area (g cm^{-2}) show a positive influence of light irradiance but no significant response to spectral quality (Fig 7).

High irradiance (Rigs IV and VI) markedly increased dry-weight per unit area in soybean, white clover and ryegrass but only marginally in sorghum. Low irradiance (Rig V) produced lower values for each species but these were little different from the intermediate irradiance treatments.

An unusual response for both soybean and ryegrass was the decrease in dry-weight/unit area with time under the HPI-based treatment compared with the obvious increase in values under the other treatments tested. The final harvest value in soybean is comparable to the other spectral treatments but the second harvest value is markedly higher. No obvious explanation can be given to account for this difference.

1.4.2. Leaf Shape (Last Mature Leaf Blade).

The leaf length, and leaf length:width ratio for each

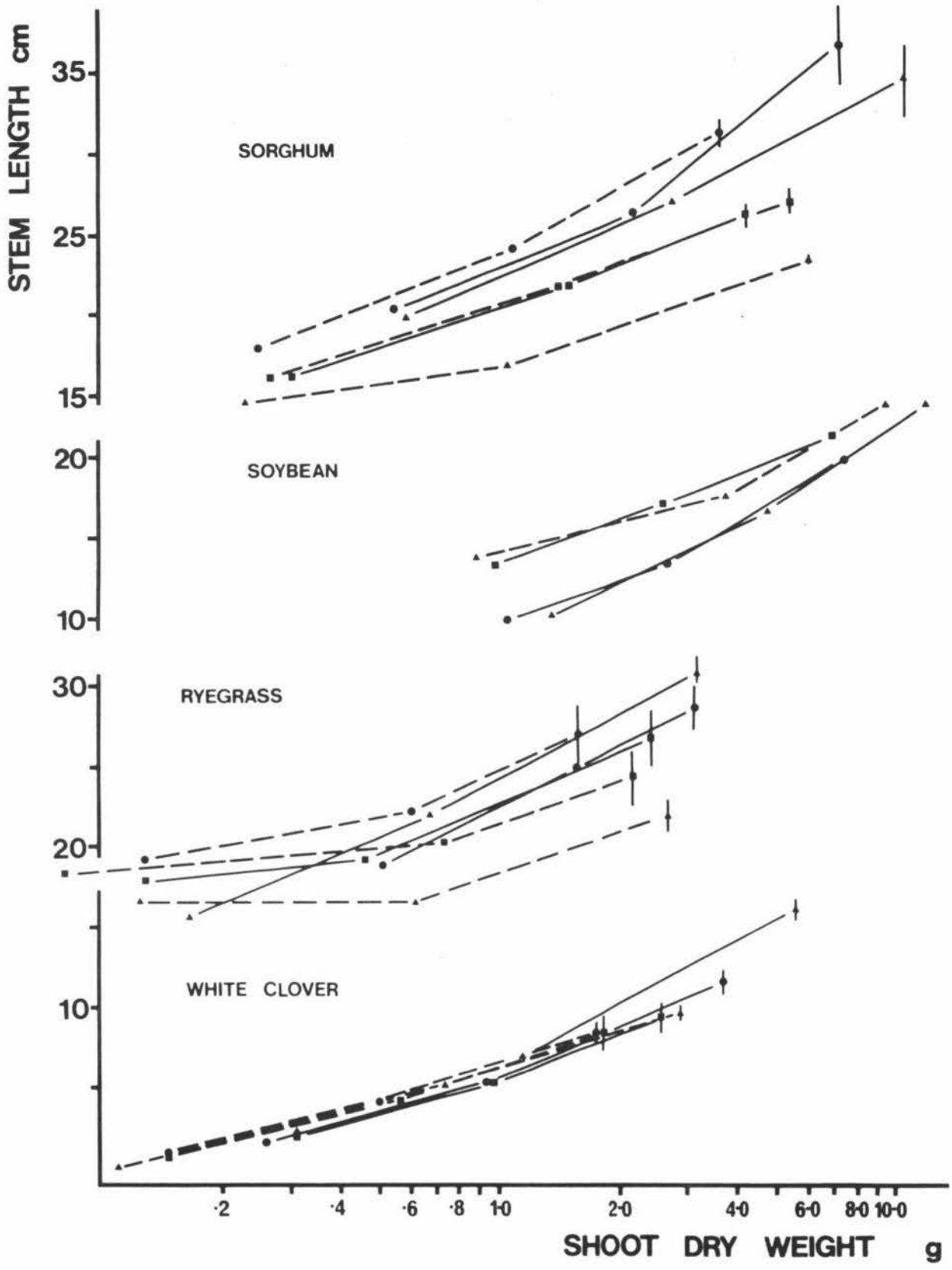


Fig. 5. Spectral Balance Experiment.

Increase in Stem (Shoot) Length with increase in shoot dry-weight for all treatments.

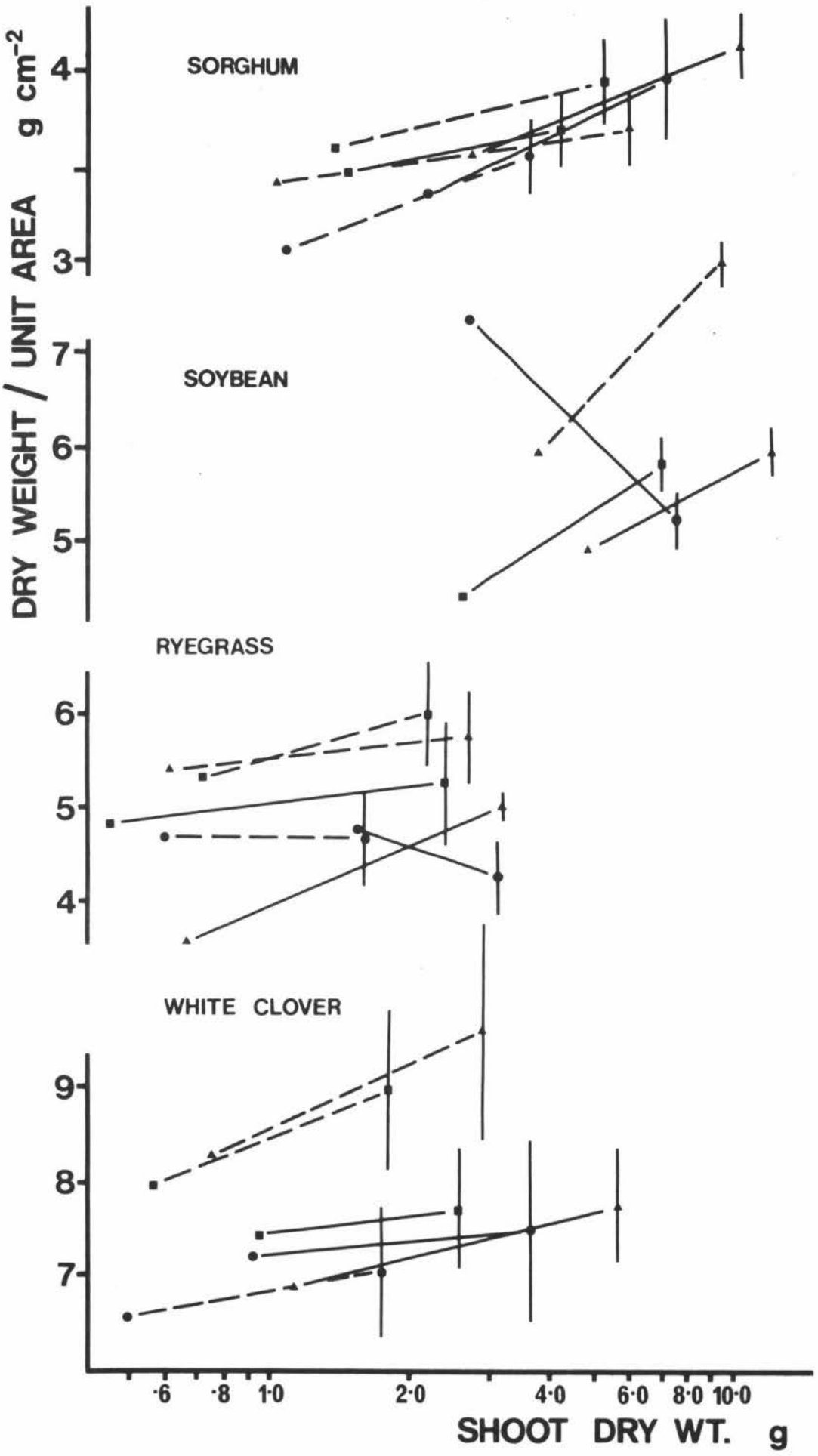
(S.E. shown for final harvest values).

Fig. 6. Spectral Balance Experiment.
Mean Leaf Area per plant plotted against shoot dry-weight for final two harvests. (S.E. shown for final harvest value).

Fig. 7. Spectral Balance Experiment.

Mean Dry-Weight per Unit Area of Leaf plotted against shoot dry-weight for the final two harvests.

(S.E. shown for final harvest values).


DRY WEIGHT / UNIT AREA g cm^{-2}
SORGHUM
4
3
SOYBEAN
7
6
5
RYEGRASS
6
5
4
WHITE CLOVER
9
8
7
·6
·8
1·0
2·0
4·0
6·0
8·0
10·0
SHOOT DRY WT. g

species are shown in Fig 8 and Table 14 respectively.

Generally, as with the dry-weight per unit area the predominant influence on each parameter was light irradiance rather than spectral quality. High irradiance tended to decrease leaf length and in some cases leaf width (data not presented) and therefore decrease the length:width ratio. The low irradiance level produced similar leaf length and leaf width values as the intermediate treatments, but increased the length:width ratio in some cases.

With respect to the HPLR, HPI and "Metal-arc" based intermediate irradiance treatments, longest leaves resulted under the HPLR based and shortest leaves under the "Metal-arc" based treatment. These differences were not large but were consistent for each species studied. Also noted was a higher rate of leaf length increase under the HPI based treatment compared to other treatments. Leaf width results were similar to those for leaf length but treatment differences were smaller. Soybean showed decreasing leaf width with increasing shoot dry-weight (narrower new leaves) under the HPLR based treatment.

1.5. Tiller Number (Sorghum).

Sorghum tiller number showed little response to varying spectral or intensity treatments with a short period under treatment (Fig 9). However with increasing time under treatment, high irradiance (Rig IV and Rig VI) markedly increased tiller number whereas other treatments produced no obvious effects.

1.6. Proportions of Plant Parts.

1.6.1. Shoot Components.

The proportions of plant parts (leaves, petioles, stems and sheaths, to total shoot dry-weight) are shown for each species in Table 15a.

At the final harvest particularly, differences between treatments were clear but no consistent trends were noted.

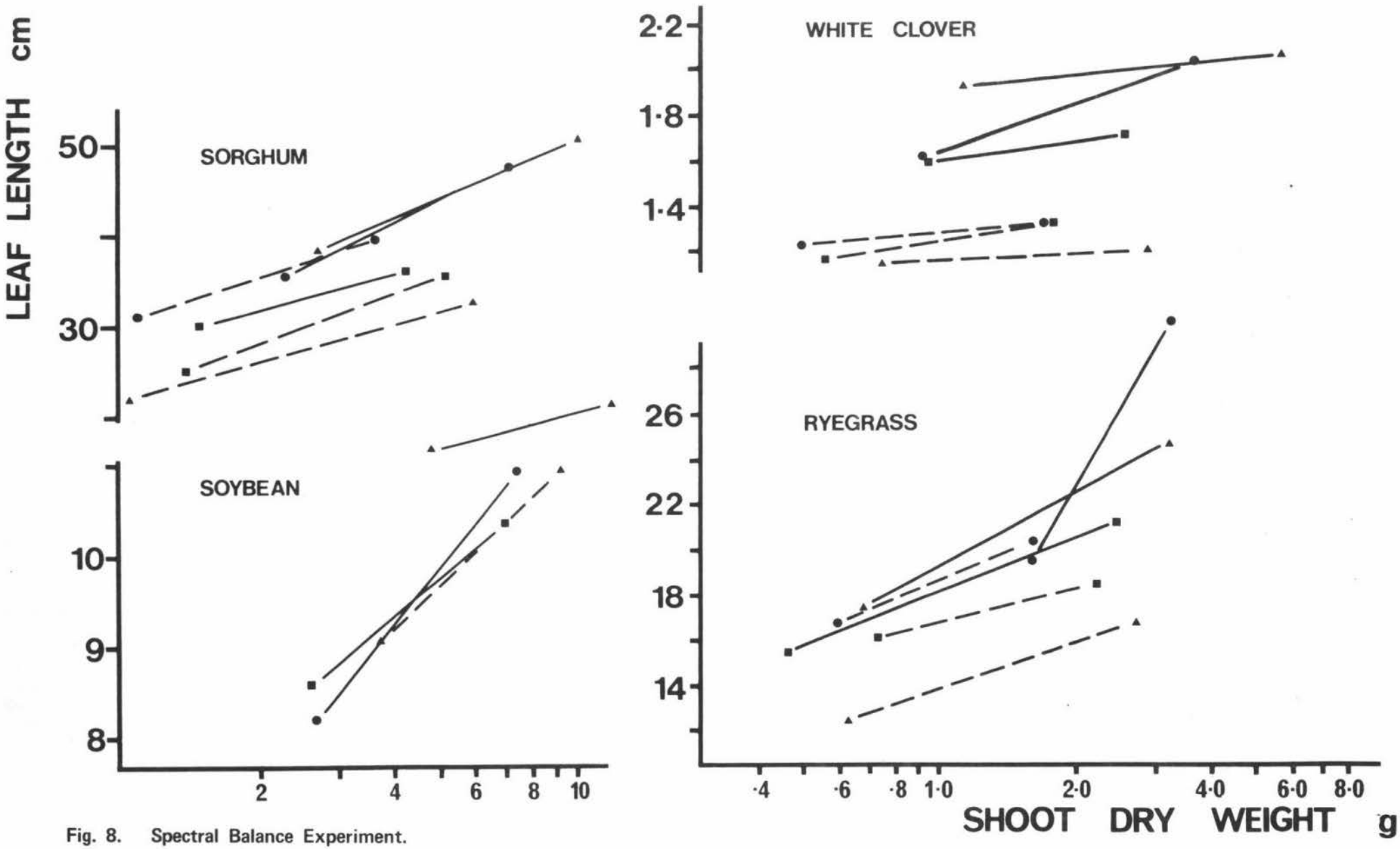


Fig. 8. Spectral Balance Experiment.
Last Mature Leaf Length plotted against shoot dry-weight at the final two harvests.

TABLE 14

Spectral Balance Experiment

Leaf Length : Breadth Ratio

Harvest 2 and 3

Species / Harvest		Spectral Treatment (Light Rig)					
		I	II	III	IV	V	VI
Sorghum	2	11.24	12.83	11.51	10.11	14.71	9.53
	3	11.53	12.70	10.92	9.10	14.34	10.50
Soybean	2	1.53	1.51	1.53	1.60		
	3	1.87	1.84	1.73	1.80		
Perennial Ryegrass	2	40.93	42.67	41.33	32.83	44.07	40.28
	3	55.91	63.82	44.80	35.54	49.47	42.18
White Clover	2	1.15	1.07	1.08	1.08	0.95	1.01
	3	1.10	1.07	1.10	1.04	1.06	1.22

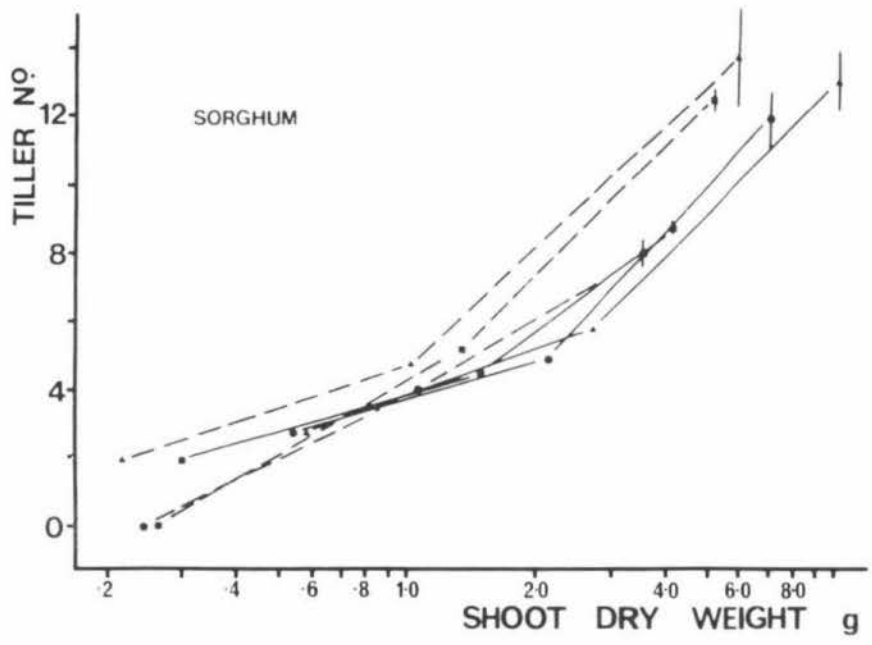


Fig. 9. Spectral Balance Experiment.

Sorghum Tiller Number increase plotted against shoot dry-weight for all harvests and treatments.

(S.E. shown for final harvest values).

Table 15a

Spectral Balance Experiment

Ratios of Plant Parts

(Dry Weight)

Final Harvest Data Only

Shoot = 100

(S.E. in Brackets)

Species / Plant Part	Spectral Treatment (Light Rig)					
	I	II	III	IV	V	VI
SORGHUM						
Blades	68.24 (2.01)	65.74 (1.09)	66.84 (0.26)	65.50 (0.94)	64.50 (0.31)	66.95 (0.53)
Sheaths	31.91 (2.01)	34.26 (1.09)	33.16 (0.26)	34.50 (0.94)	35.50 (0.31)	33.05 (0.53)
SOYBEAN						
Blades	72.41 (0.25)	74.79 (0.36)	74.84 (0.27)	74.60 (0.21)		
Petioles	8.19 (0.31)	6.99 (0.11)	6.02 (0.20)	5.62 (0.12)		
Stems	19.39 (0.19)	18.24 (0.27)	19.14 (0.32)	19.80 (0.18)		

Table 15a contd

Species / Plant Part	Spectral Treatment (Light Rig)					
	I	II	III	IV	V	VI
PERENNIAL RYEGRASS						
Blades	66.63 (0.50)	66.06 (0.98)	67.48 (0.95)	68.94 (0.98)	67.75 (0.59)	66.06 (0.90)
Sheaths	33.38 (0.50)	33.94 (0.98)	32.53 (0.95)	31.16 (0.98)	32.26 (0.60)	33.94 (0.90)
WHITE CLOVER						
Blades	46.01 (1.60)	49.38 (0.96)	48.95 (0.88)	49.64 (1.59)	48.04 (1.19)	48.89 (1.97)
Petioles	20.23 (0.76)	21.14 (0.85)	19.55 (0.74)	15.03 (1.11)	19.01 (1.14)	16.38 (1.52)
Stems	33.74 (1.98)	29.50 (1.14)	31.53 (0.76)	35.34 (2.18)	32.96 (1.77)	34.75 (1.50)

Table 15b

Spectral Balance Experiment

Root:Shoot Ratio

(Dry Weight)

Final Harvest Data Only

(S.E. in Brackets)

Species	Light Rig Treatment					
	I	II	III	IV	V	VI
SOYBEAN	38.99 (4.06)	32.69 (1.76)	29.83 (1.00)	34.61 (0.97)		
SORGHUM	87.05 (8.59)	43.36 (0.39)	43.69 (1.37)	41.68 (1.60)	49.45 (1.87)	56.83 (1.92)
PERENNIAL RYEGRASS	44.31 (3.59)	42.65 (0.93)	39.63 (2.46)	39.86 (1.47)	52.34 (10.87)	41.41 (2.15)
WHITE CLOVER	33.20 (2.69)	29.38 (2.42)	27.91 (1.82)	27.88 (1.20)	34.83 (1.42)	39.10 (2.97)

White clover and soybean had a lower proportion of leaf and a higher proportion of petiole under the HPLR based treatment but this effect was opposite in sorghum where the leaf proportion was highest.

In the high irradiance treatments (Rigs IV and VI) white clover showed higher proprtions of stems and lower petiole:shoot ratios. The high irradiance treatments produced shorter and thicker stems and shorter petioles.

1.6.2. Root:Shoot Ratio.

The root:shoot ratios are presented in Table 15b.

The HPLR-based treatment markedly increased the root:shoot ratio in sorghum, soybean, white clover and to a lesser degree in ryegrass. Similarly, the "Metal-arc" based (Rig III) treatment ratios were smaller than the HPI based (Rig II) treatment values. The high and low irradiance treatments had no obvious effects on root:shoot ratio but the "Metal-arc" only rig (VI) produced high root:shoot ratio values in sorghum and white clover compared with treatments other than Rig I.

1.7. Biochemical Results.

1.7.1. Carbohydrate Content.

Leaf soluble sugar, starch and total carbohydrate results (%) are presented in Figs 10,11, and 12.

At similar irradiance levels the soluble sugar and starch (and hence total carbohydrate) levels showed no consistent differences between spectral treatments (Rigs I-III) for each species.

Soluble sugar content levels in soybean and ryegrass were similar under the three spectral treatments, whereas in sorghum and white clover, higher content levels were found under the HPI-based treatment.

With the exception of white clover, starch content levels were lowest under the HPI-based treatment (Rig II)

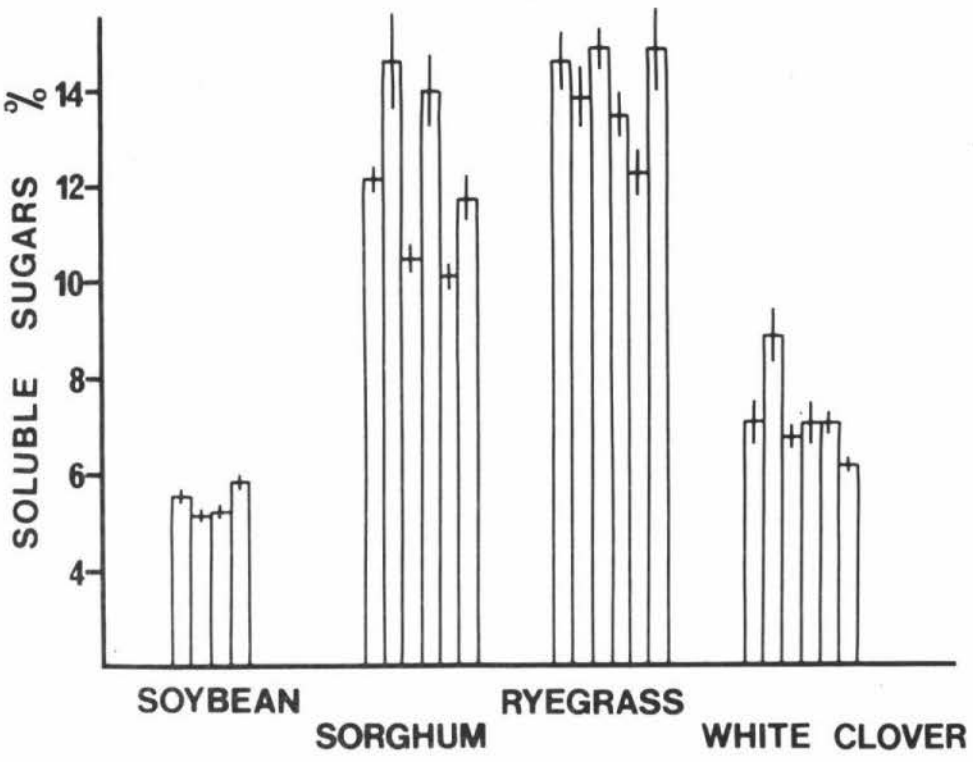


Fig. 10. Spectral Balance Experiment.
Final harvest Leaf Soluble Sugar Content (%) for all treatments.
(Treatments I–VI shown left to right; S.E. shown for each value).

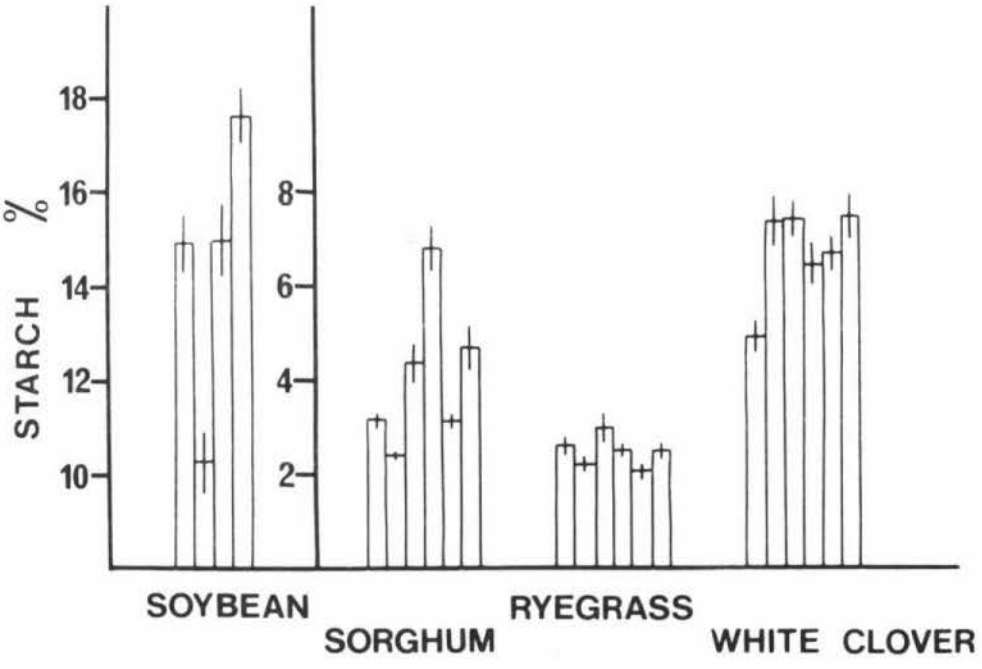


Fig. 11. Spectral Balance Experiment.
Final harvest Leaf Starch Content (%) for all treatments.
(Key as for Fig. 10).

and highest under the "Metal-arc"-based (Rig III) treatment. In white clover, the HPLR-based treatment (Rig I) produced the lowest starch content.

High irradiance (Rig IV) markedly increased starch and soluble sugars in soybean and sorghum wereas low irradiance decreased content levels in comparison with the intermediate irradiance treatments. The response was similar, but less pronounced, in ryegrass, while no significant trend was noted in white clover.

In general, sorghum was the most responsive species to both irradiance and quality treatments whereas, in comparison, white clover was the least responsive.

Results for petiole starch and soluble sugar levels were similar to the lamina results.

1.7.2. Protein Content.

The protein content (%) under each spectral and irradiance treatment are shown in Fig 13 for each species.

Lower protein content levels were noted in white clover and ryegrass under the HPI-based treatment but this effect was reversed in soybean. The HPLR-based treatment produced lowest protein levels in sorghum. It is clear then that whereas these differences existed between treatments within each species, they were neither large nor consistent.

In parallel with the spectral results, the irradiance treatments produced only small changes in the protein content. In ryegrass and white clover there were small increases with a decrease in irradiance (Rig V content > Rig IV) but the "Metal-arc" only treatment (Rig VI) produced the lowest content levels in contrast to these other treatments.

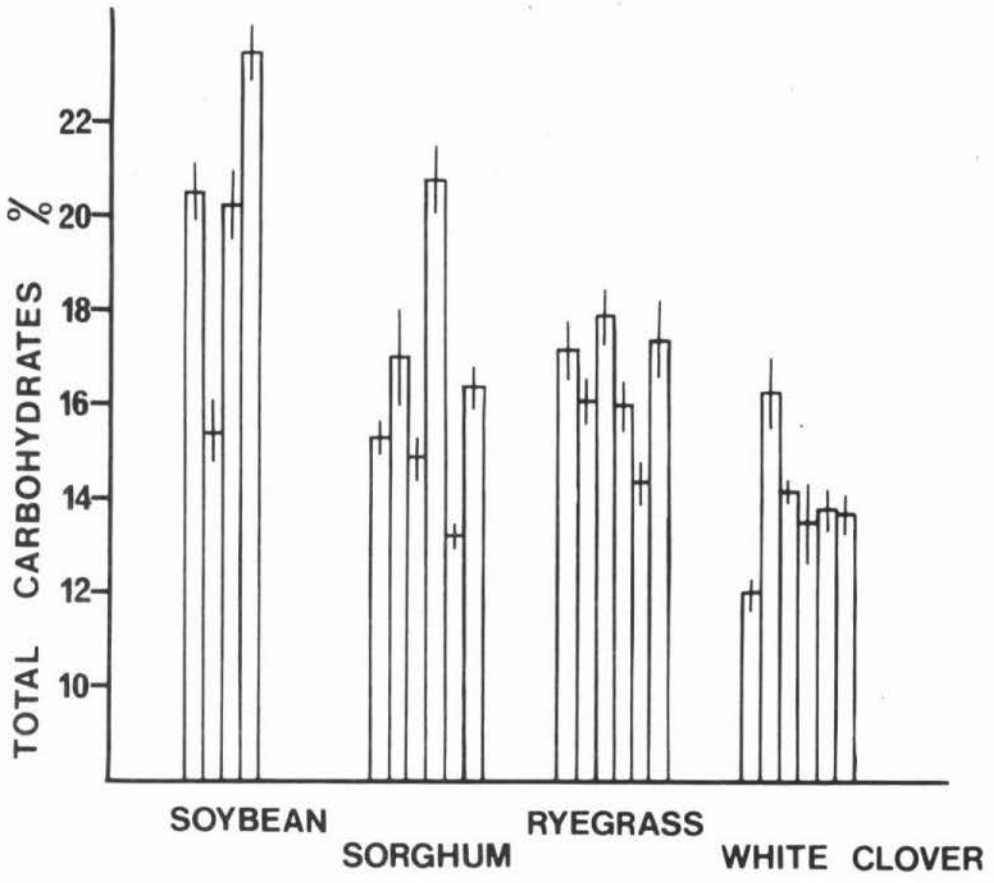


Fig. 12. Spectral Balance Experiment.
Final harvest Leaf Total Carbohydrate Content (%) for all treatments.
(Key as for Fig. 10).

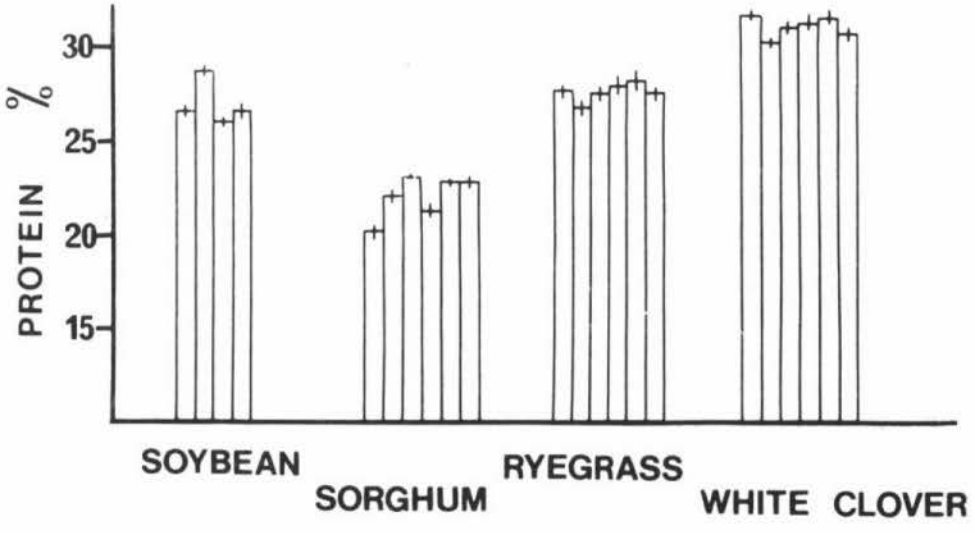


Fig. 13. Spectral Balance Experiment.
Final harvest Leaf Protein Content (%) for all treatments.
(Key as for Fig. 10).

2. Spectral Bias Experiment.

2.1. General.

The Spectral Balance experiment results demonstrated that within the range of spectral emissions tested there was a marked consistency in the response of each plant species with respect to growth, development and biochemistry. However, within that experiment, there were no major differences in the spectral treatments and therefore no indication of plant responses to substantially imbalanced spectra. To this end the Spectral Bias experiment was conceived and designed.

Spectroradiometer plots (Fig 1A, B and C) and narrow bandwidth values (Table 5) for each treatment show the major bias of each spectral treatment investigated, particularly with respect to the blue and red wavelength regions. Arbitrary blue:red ratios (on the same basis as the Spectral Balance experiment) were: red-biased 0.8, balanced 2.0 and blue-biased 5.0 which incorporate the treatment range in the Spectral Balance experiment and at the same time examine more extreme ratio values.

2.2. Plant Appearance.

Photographs of typical plants from each spectral treatment under the low irradiance treatment are shown in Plates 4, 5, 6 and 7. It is obvious from these examples that the form and development of all species varied in response to each particular spectral treatment. For each irradiance treatment the appearance of these plants was similar but each characteristic was shown most strongly at the low irradiance level.

Sorghum. Red-biased treatment plants were upright in stature with a dominant main shoot and several well developed tillers. These plants were in strong contrast to the blue-biased treatment plants which showed a more prostrate form, a poorly developed main shoot and a strong multi-tillate habit. The balanced treatment plants were intermediate in appearance in each of these features to the biased treatment plants.

PLATE 4. Sorghum plants from the three spectral treatments under low irradiance conditions prior to the final harvest.

Plant size, tiller number and development, and main stem dominance and angle are shown under each treatment. (See also Plate 8).

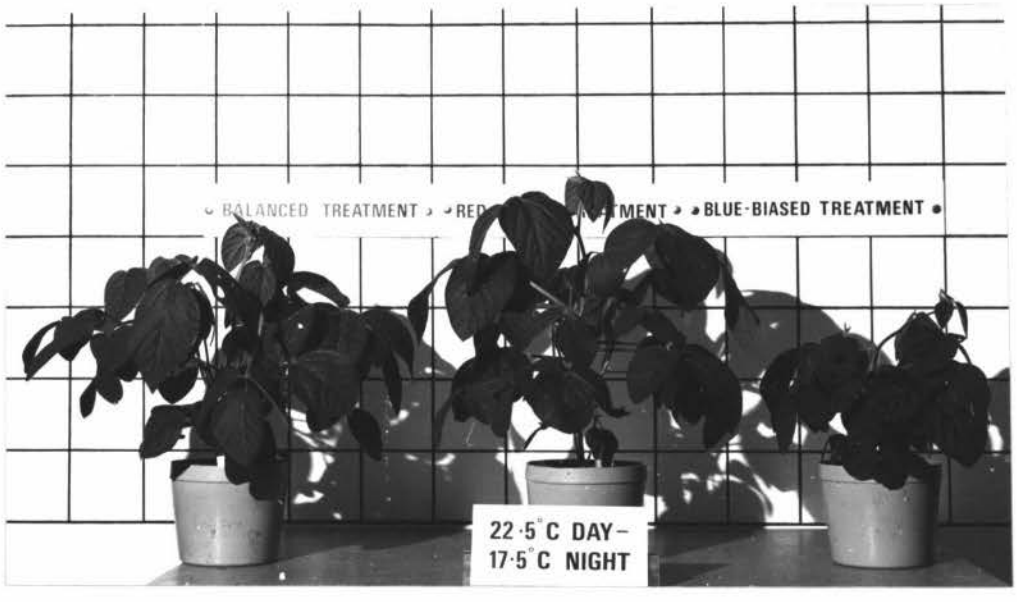


PLATE 5. Soybean plants (as for plate 4).

Leaf area, petiole and stem development, and plant form are clearly shown in each treatment.

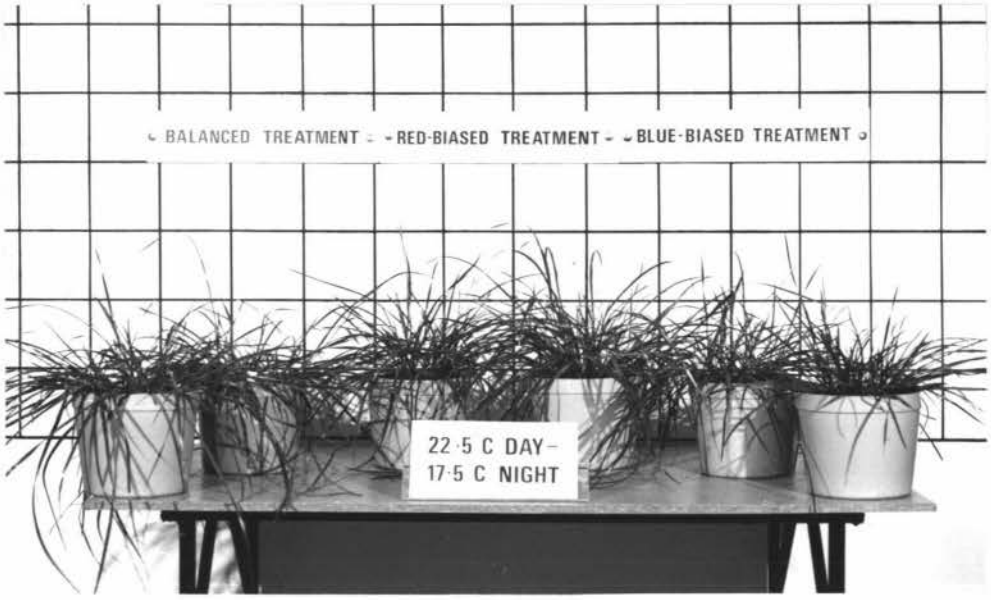


PLATE 6. Ryegrass (as for plate 4).
Leaf size (and leaf area) and general growth form obviously differ between treatments.

PLATE 7. White Clover (as for plate 4).
Clearly the red and blue-biased treatments influence the development, and form of growth, of the plants.

Soybean. The largest and most leafy plants grew under the red-biased treatment where there was strong petiole and main stem development. Blue-biased treatment plants were, in comparison, more squat in appearance with smaller, thicker leaves and shorter petioles. The balanced treatment plants were more "normal" with strong stem and petiole development and large but well formed leaves.

Ryegrass. The variation between plants within each treatment population was more noticeable in this species than in either sorghum or soybean. However, red-biased treatment plants were more upright in stature and had much longer leaves than the more flat, short-leaved blue-biased treatment plants. The balanced treatment plants were of a more "normal" type and were intermediate to the biased treatment plants in appearance.

White Clover. The plant variability within each treatment population was higher in white clover than any of the other species. As with soybean, sorghum and ryegrass, however, treatment differences were clearly apparent. Red-biased treatment plants produced long fleshy stems and petioles, and large, thin leaves. These features resulted in a large, prostrate, fleshy plant. Blue-biased treatment plants had short, thick stems, short petioles, and small, thick leaves. Balanced treatment plants were intermediate in appearance to the biased treatments and were the most "normal" type.

In each of these four species there were no undesirable treatment responses such as malformed leaves, unusual pigmentation or necrotic leaf areas, but responses of growth and development to each of the treatments were obvious.

2.3. Plant Weight.

2.3.1. Shoot Dry-Weight.

Log. - transformed shoot dry-weight (g) results for each harvest are shown as plots against time in Fig 14. Results for soybean and sorghum show that the highest dry weights were found under the red-biased and the lowest under the blue-biased treatment. The balanced treatment produced dry weights intermediate to the biased treatments, but depending on harvest number (i.e. time under treatment), these

KEY:

SPECTRAL BIAS EXPERIMENT

●——●	BLUE BIASED	HIGH IRRADIANCE
■——■	BALANCE	
▲——▲	RED BIASED	
●— —●	BLUE BIASED	LOW IRRADIANCE
■— —■	BALANCED	
▲— —▲	RED BIASED	

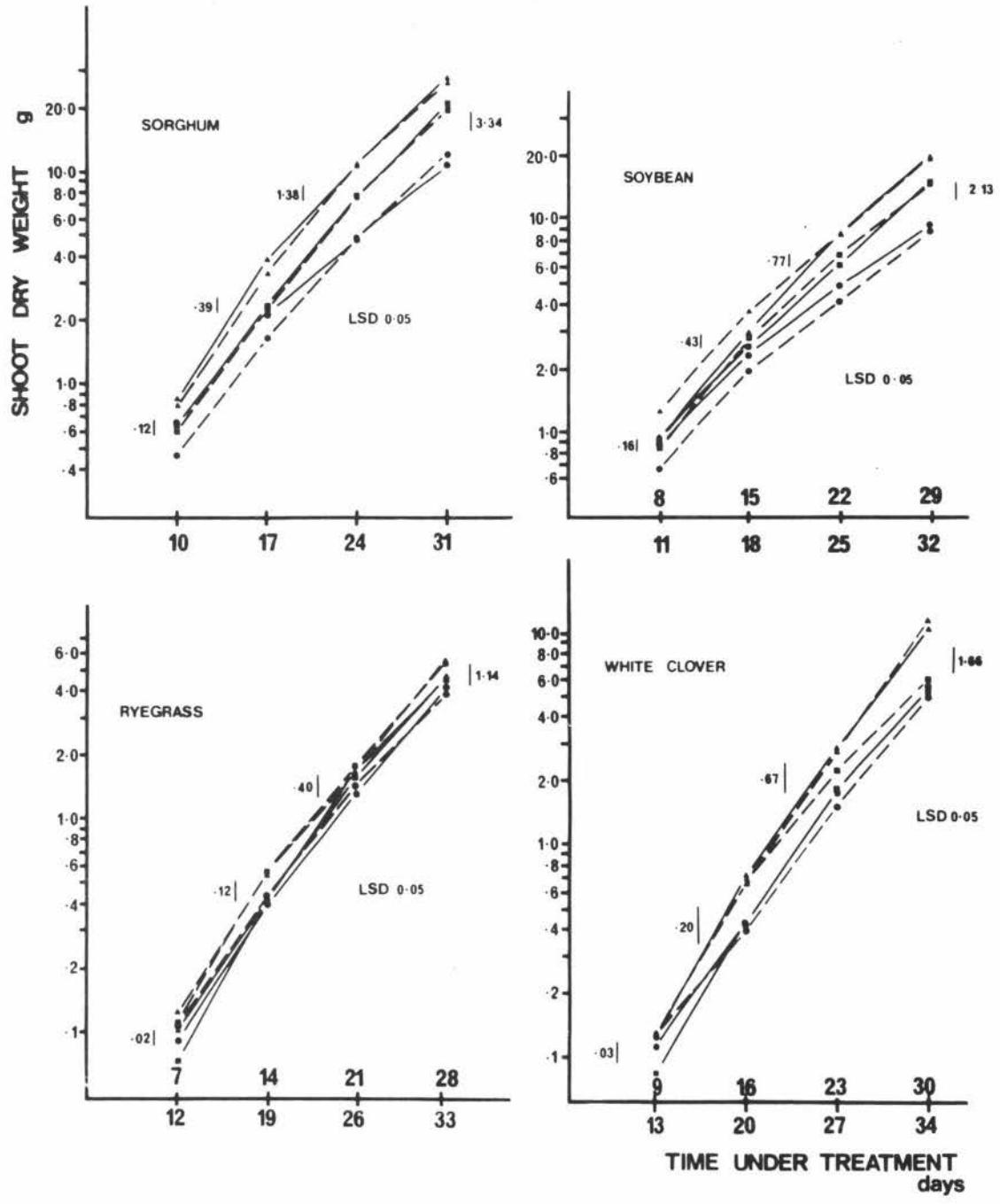


Fig. 14. Spectral Bias Experiment.

Shoot Dry-Weight increase with time under treatment. (LSD = 0.05 values presented for each harvest).

Key for Figs. 14–25 presented opposite.

were sometimes closer to the blue-biased and in others closer to the red-biased treatment.

The differences between treatments with ryegrass and white clover were not as marked as those shown for soybean and sorghum. The red-biased treatment results showed the highest dry weight values as with the other two species, and the blue-biased results were often the lowest (although these were often not significantly different e.g. ryegrass, high irradiance). However, the balanced treatment results showed no consistent relationship to the biased treatments, and was often closely similar to the red-biased values in some instances (e.g. ryegrass, low irradiance) whereas in others it was closer to the blue-biased values (e.g. white clover, high irradiance).

From these data one of the more obvious results has been the effect of the initial establishment period under each spectral treatment on the dry-weight increase up to the first harvest. All material prior to placing in the rooms was randomly allocated to each spectral treatment so all plants from each treatment prior to this time can be assumed to have had the same mean dry-weight. The establishment period effect, however, was not consistent in all cases. In some instances the difference between the mean dry-weight under each spectral treatment was significant ($P = 0.05$), (e.g. Soybean and Sorghum, low irradiance) whereas in others there were no significant differences (e.g. White Clover, low irradiance; Soybean, high irradiance).

This initial response complicates the results when the irradiance treatments are evaluated. Based on final harvest values only, the differences between each irradiance treatment were either small or negligible.

2.3.2. Dry-Matter Percentage of Shoot.

The results for the shoot dry-matter percentage for each species (Fig 15) show complex trends which are dependent on both the spectral and irradiance treatments. Final harvest

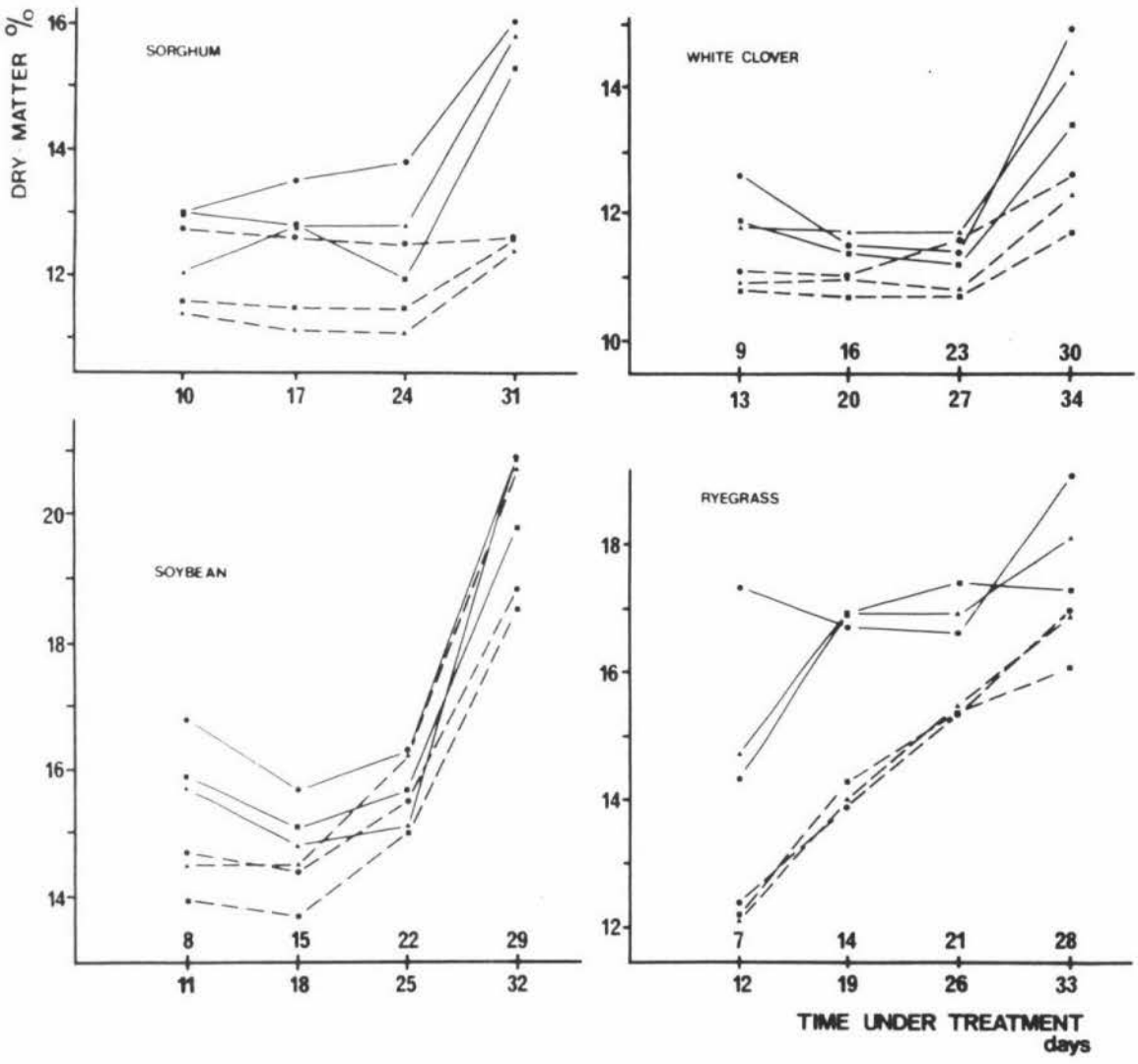


Fig. 15. Spectral Bias Experiment.
Change in Shoot Dry-Matter Percentage with time under each treatment.

values were normally highest and increased in the order balanced, red-, blue-biased treatment for each species and irradiance. However, this relative order was strongly dependent on the time under treatment and was seldom consistent.

The dry-matter percentage was highest under the high, compared to the low, irradiance treatment for all spectral treatments and for all species.

2.4. Leaf Area Per Plant.

Graphs of leaf area (log. scale) vs. time under each treatment are shown in Fig. 16.

The species response differences characterised in the shoot dry-weight results were seen to be similar in the leaf area per plant responses. The results in soybean and sorghum showed consistently smaller areas in the balanced and blue-biased treatments respectively, compared to the red-biased treatment.

This progression of the red-, balanced, blue-biased order was not as obvious in the ryegrass and white clover leaf area responses. Ryegrass under the high irradiance had no leaf area response to the spectral treatments whereas white clover under low irradiance had a similar spectral treatment response to sorghum and soybean. However, ryegrass under low irradiance had a lower leaf area under the blue-biased treatment than either the balanced and red-biased treatments which were similar. Likewise, white clover at the high irradiance had a higher leaf area under the red-biased treatment than either the balanced or blue-biased treatments which were similar.

For all species and spectral treatments the leaf area under the high irradiance treatment was similar to, or less than, the area under the low irradiance treatment.

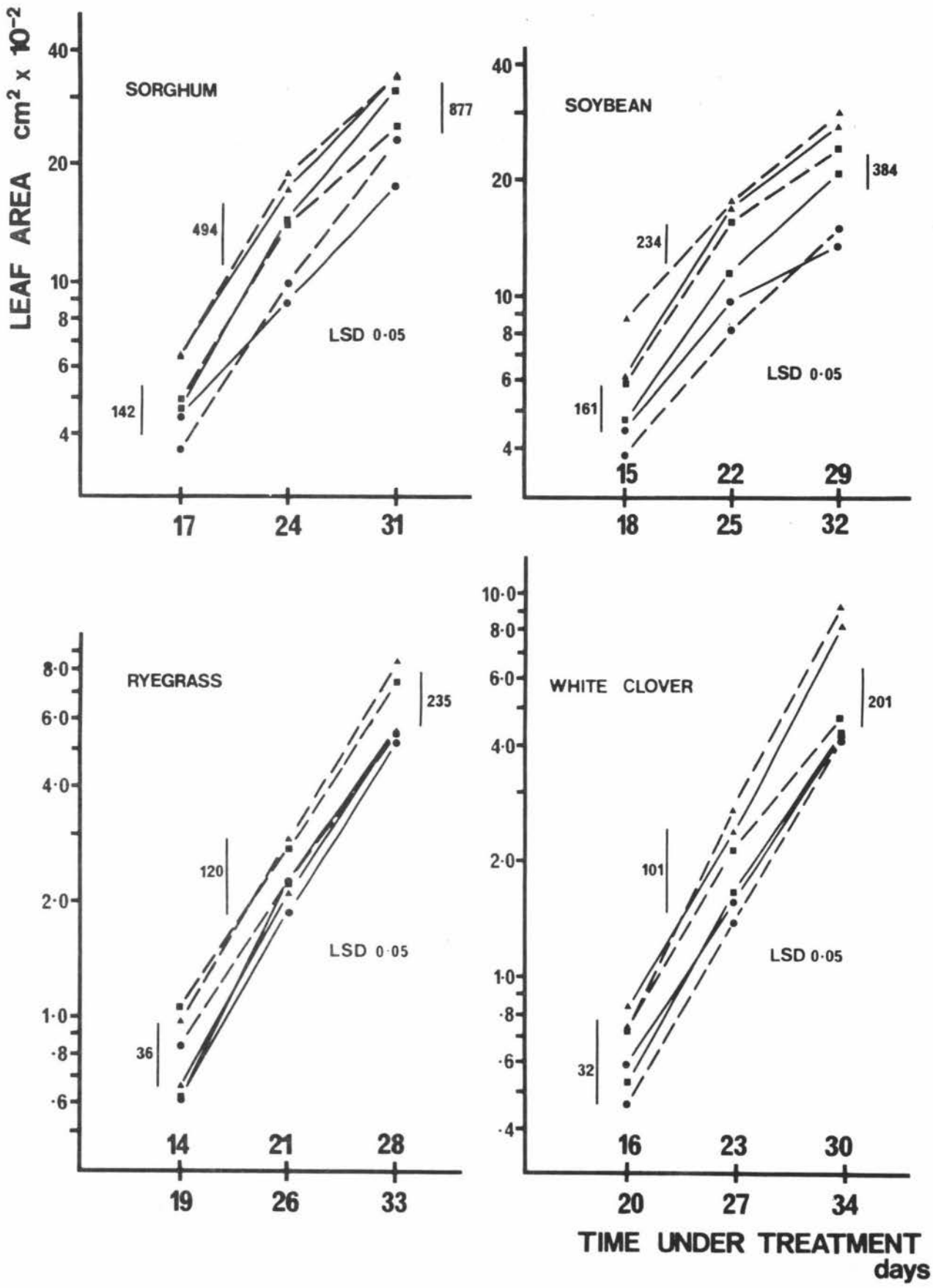


Fig. 16. Spectral Bias Experiment.
Mean Leaf Area per plant for final three harvests.
(LSD = 0.05 values presented for each harvest).

2.5. Growth Analysis Components.

2.5.1. Relative Growth Rates.

Relative growth rate results for each harvest interval and for the total treatment time (between harvests 1 and 4) are presented for each species in Table 16.

This data shows that RGR values declined for each successive harvest interval, for all species and for most treatments. The information obtained from harvest interval relative growth rates was transformed into graph form where RGR was related to plant size (Fig 17).

It is apparent in sorghum and soybean that there were generally higher RGR values under the red-biased treatments at the earlier growth stages. Similarly, the rates under the blue-biased treatments were initially low at these early stages and progressively declined with increasing plant size. The balanced treatment, however, had intermediate rates compared with the biased treatments initially, but the decline in rate was usually much less than the biased treatments and final relative growth rates were therefore often highest.

In white clover and perennial ryegrass the responses were considerably more complex. The blue-biased treatment rates for white clover, for example, showed a lag in RGR for the initial harvest interval, followed by an increase to higher rates at the intermediate growth interval, and a subsequent decline in rate over the final harvests. Under low irradiance conditions with both of these species, a marked decline was observed in the red-biased treatment RGR's at the intermediate interval which was followed by a recovery to comparatively higher values. This effect was atypical of other species and treatments.

With respect to the influence of irradiance level on $\overline{RGR}$ there is again a species dependent response. Sorghum results showed significantly higher $\overline{RGR}$ values at the low irradiance level in both the blue- and red-biased treatments. The balanced treatment showed no irradiance treatment influence.

Table 16

Spectral Bias Experiment

Relative Growth Rate (RGR)
($g\ g^{-1}\ day^{-1}$)

All Harvest Interval and Total Experimental Period RGR's
(S.E. in Brackets)

Species / Treatment	Harvest Interval			
	1 - 2	2 - 3	3 - 4	1 - 4
Sorghum				
High Irradiance				
Blue Biased	0.167	0.118	0.117	0.132 (0.004)
Balanced	0.180	0.173	0.142	0.166 (0.004)
Red Biased	0.215	0.149	0.135	0.164 (0.005)
Low Irradiance				
Blue Biased	0.183	0.152	0.134	0.156 (0.005)
Balanced	0.192	0.173	0.134	0.167 (0.005)
Red Biased	0.207	0.171	0.125	0.168 (0.005
Soybean				
High Irradiance				
Blue Biased	0.144	0.108	0.094	0.115 (0.004)
Balanced	0.146	0.129	0.127	0.133 (0.003)
Red Biased	0.167	0.153	0.118	0.147 (0.004)
Low Irradiance				
Blue Biased	0.153	0.110	0.107	0.122 (0.003
Balanced	0.172	0.131	0.106	0.136 (0.005)
Red Biased	0.157	0.121	0.119	0.131 (0.004)

Table 16 contd

Species / Treatment	Harvest Interval			
	1 - 2	2 - 3	3 - 4	1 - 4
Ryegrass				
High Irradiance				
Blue Biased	0.214	0.168	0.167	0.182 (0.005)
Balanced	0.247	0.191	0.157	0.198 (0.006)
Red Biased	0.209	0.191	0.144	0.182 (0.005)
Low Irradiance				
Blue Biased	0.202	0.169	0.143	0.171 (0.006)
Balanced	0.236	0.162	0.154	0.182 (0.007)
Red Biased	0.217	0.157	0.177	0.181 (0.006)
White Clover				
High Irradiance				
Blue Biased	0.183	0.210	0.163	0.188 (0.005)
Balanced	0.226	0.209	0.160	0.199 (0.009)
Red Biased	0.243	0.209	0.182	0.211 (0.007)
Low Irradiance				
Blue Biased	0.160	0.182	0.176	0.174 (0.007)
Balanced	0.232	0.177	0.140	0.182 (0.007)
Red Biased	0.241	0.120	0.207	0.215 (0.007)

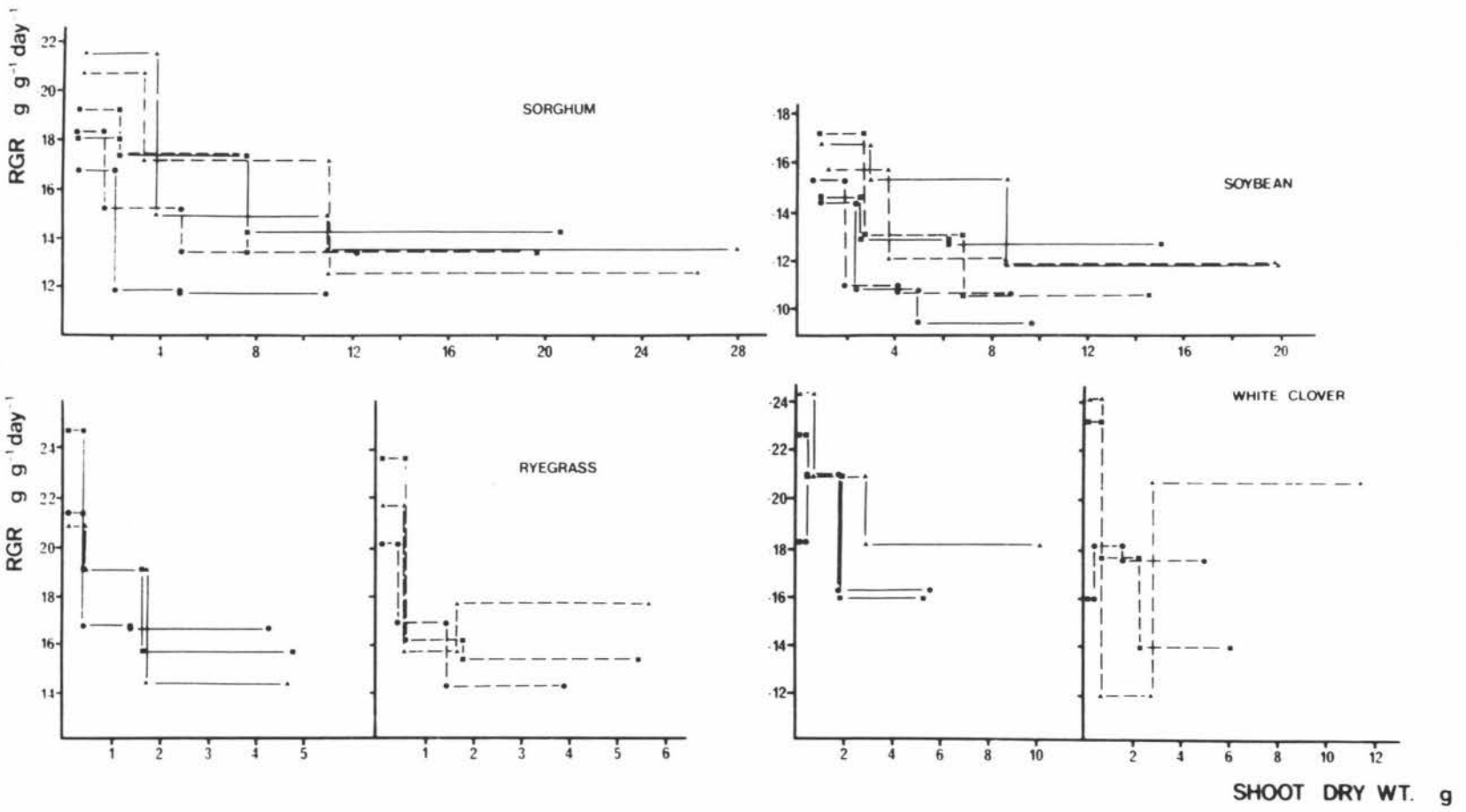


Fig. 17. Spectral Bias Experiment.
Relative Growth Rate change with increasing shoot dry-weight.

Soybean $\overline{RGR}$ value trends for the blue-biased and balanced treatments were similar to sorghum but the red-biased irradiance effect was reversed with higher mean values at the high irradiance.

Ryegrass and white clover, however showed significantly higher $\overline{RGR}$ values at the high irradiance under both the blue-biased and balanced treatments but no obvious difference at either irradiance in the red-biased treatment.

The resultant $\overline{RGR}$ was, therefore, dependent on each of the species, light irradiance levels and spectral treatments examined.

2.5.2. Leaf Area Ratio.

Leaf area ratio values at each harvest, determined from mean total leaf area and mean total shoot dry-weight values, are presented in Table 17 and show obvious responses to both spectral and irradiance treatments.

Highest LAR values were found under the low irradiance for each spectral treatment with white clover and ryegrass. With soybean, the balanced and blue-biased treatment irradiance differences were similar to ryegrass and white clover but the red-biased treatment irradiance differences, although of a similar trend, were much smaller. Sorghum responses to irradiance were considerably more complex; at the low irradiance the blue-biased LAR values were lowest, balanced highest and red-biased treatment similar to the high irradiance LAR values.

The relative influence of each spectral treatment on LAR was closely dependent on both the irradiance treatment and on the species being studied. Under the high irradiance, for all species the highest LAR values were found under the blue-biased and the lowest under the red-biased treatment. Balanced LAR values were either intermediate to both biased treatments (sorghum and ryegrass) or similar to the red-biased treatment (soybean and white clover). At the low irradiance treatment, the responses were considerably more complicated. White clover

Table 17

Spectral Bias Experiment

Leaf Area Ratio, LAR ($cm^2\ g^{-1}$); Net Assimilation Rate, NAR ($mg\ dm^{-2}\ wk^{-1}$); and Mean Relative Growth Rate, RGR ($g\ g^{-1}\ day^{-1}$).

Data for Final Three Harvests.

Treatment	Blue Biased			Balanced			Red Biased		
Time (days)	LAR	NAR	$\overline{RGR}$	LAR	NAR	$\overline{RGR}$	LAR	NAR	$\overline{RGR}$
Sorghum									
High Irradiance									
17	210.5	.388		211.1	.518		174.1	.572	
24	185.9	.440	.117	182.8	.598	.156	149.6	.665	.142
31	164.2	.498		158.3	.691		128.6	.774	
Low Irradiance									
17	227.2	.475		227.5	.442		199.7	.520	
24	175.0	.616	.154	210.7	.477	.144	163.3	.636	.148
31	134.8	.800		195.0	.515		133.5	.778	
Soybean									
High Irradiance									
15	206.4	.341		199.2	.449		223.1	.425	
22	174.7	.403	.101	169.9	.527	.128	180.1	.526	.135
29	147.9	.476		144.9	.618		145.4	.652	
Low Irradiance									
18	207.5	.366		232.4	.361		245.1	.341	
25	191.0	.398	.109	202.3	.414	.120	195.0	.429	.120
32	175.8	.432		176.1	.476		155.2	.539	

Table 17 contd.

Treatment	Blue Biased			Balanced			Red Biased		
Time (days)	LAR	NAR	$\overline{RGR}$	LAR	NAR	$\overline{RGR}$	LAR	NAR	$\overline{RGR}$
Ryegrass									
High Irradiance									
14	159.6	.741		158.2	.766		144.4	.816	
21	141.8	.834	.169	136.9	.886	.173	129.7	.908	.168
28	126.0	.939		118.6	1.023		116.5	1.011	
Low Irradiance									
19	194.7	.564		192.6	.585		187.8	.619	
26	166.4	.659	.157	165.0	.682	.161	172.5	.674	.166
33	142.2	.772		141.4	.796		158.5	.733	
White Clover									
High Irradiance									
16	133.4	.967		133.3	.949		119.0	1.124	
23	100.2	1.287	.184	102.6	1.233	.181	97.4	1.373	.191
30	75.3	1.714		79.0	1.602		79.7	1.678	
Low Irradiance									
20	121.0	1.047		117.1	.953		117.1	1.208	
27	101.5	1.248	.181	96.5	1.156	.159	98.4	1.438	.202
34	85.2	1.487		79.5	1.403		82.6	1.713	

and ryegrass had the highest LAR's under the red-biased treatment and similar values under the blue-biased and balanced treatments. Sorghum and soybean had highest values under the balanced and lowest under the red-biased, with the blue-biased values either being similar to the red-biased (sorghum), or similar to the blue-biased (soybean), treatments.

LAR values decreased with time under all spectral and irradiance treatments.

2.5.3. Net Assimilation Rate.

As with the other growth analysis components RGR and LAR, NAR showed variability of response between species, spectral treatments and irradiance levels. NAR responded positively to irradiance in all cases except for sorghum under the blue-biased and soybean under the balanced treatments where a negative response was shown (Table 17). The spectral response trends under the high irradiance conditions were consistent for sorghum, soybean and ryegrass where highest NAR values were found under the red-biased, intermediate under the balanced and lowest under the blue-biased conditions. The order of response for white clover was reversed for the blue-biased and balanced treatments. However, under low irradiance conditions there was little consistency in the response between each of the species. Red-biased treatment values were highest in sorghum, soybean and white clover, but lowest in ryegrass. Balanced treatment values were lowest in sorghum and white clover, intermediate in soybean and highest in ryegrass, and blue-biased treatment values were lowest in soybean, intermediate in ryegrass and clover and highest (with red-biased) in sorghum.

NAR values increased with time for all spectral and irradiance treatments.

2.6. Proportions of Plant Parts.

The root:shoot, leaf:shoot (LW/SW), petiole:shoot (PW/SW), stem:shoot (StW/SW) and sheath:shoot (ShW/SW) ratios at the final harvest only are presented in graph form in Fig 18 and 19.

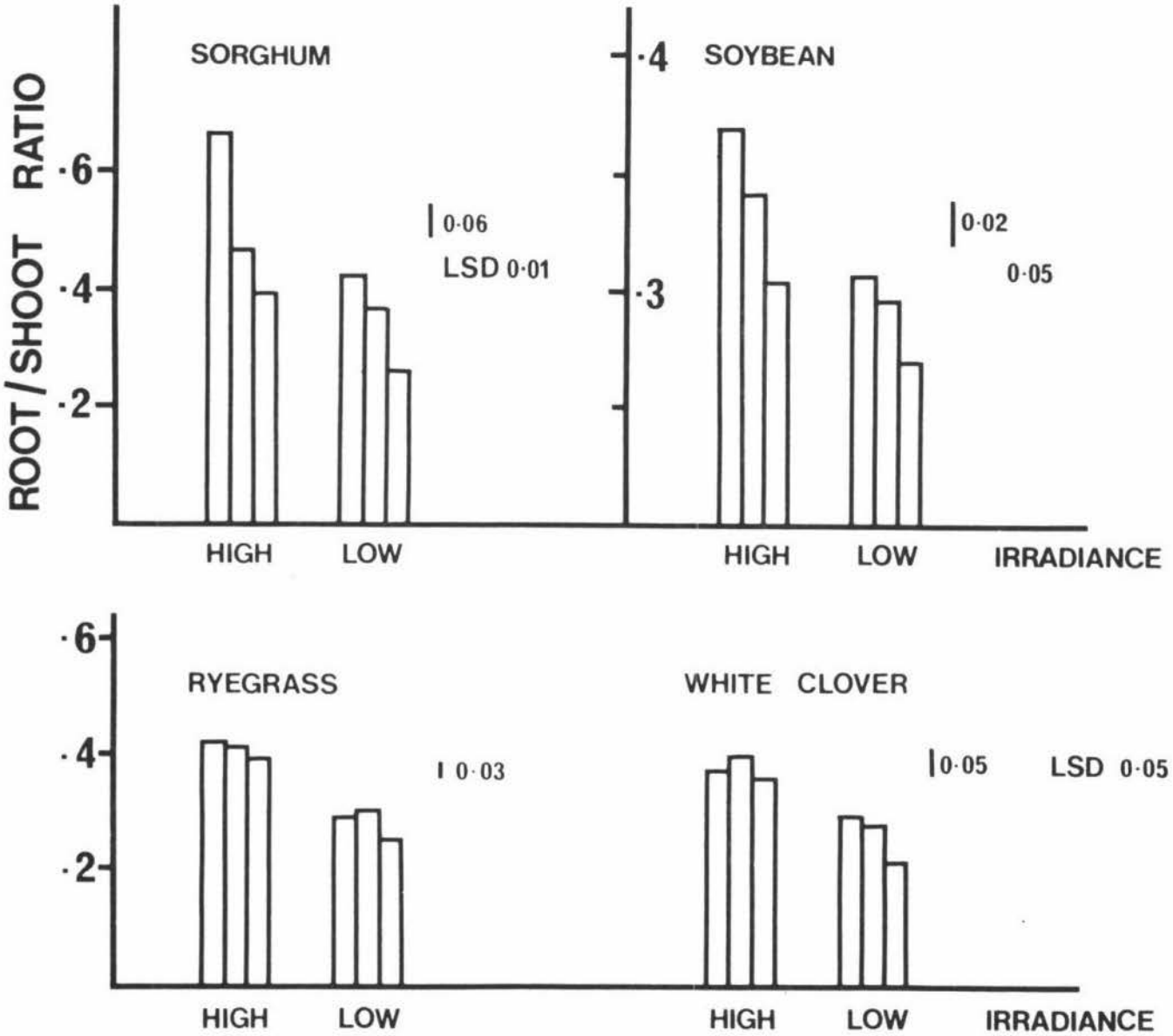


Fig. 18. Spectral Bias Experiment.

Root : Shoot Ratio values at the final harvest for all treatments.
(Left to Right: Blue Biased, Balanced, Red Biased treatment).

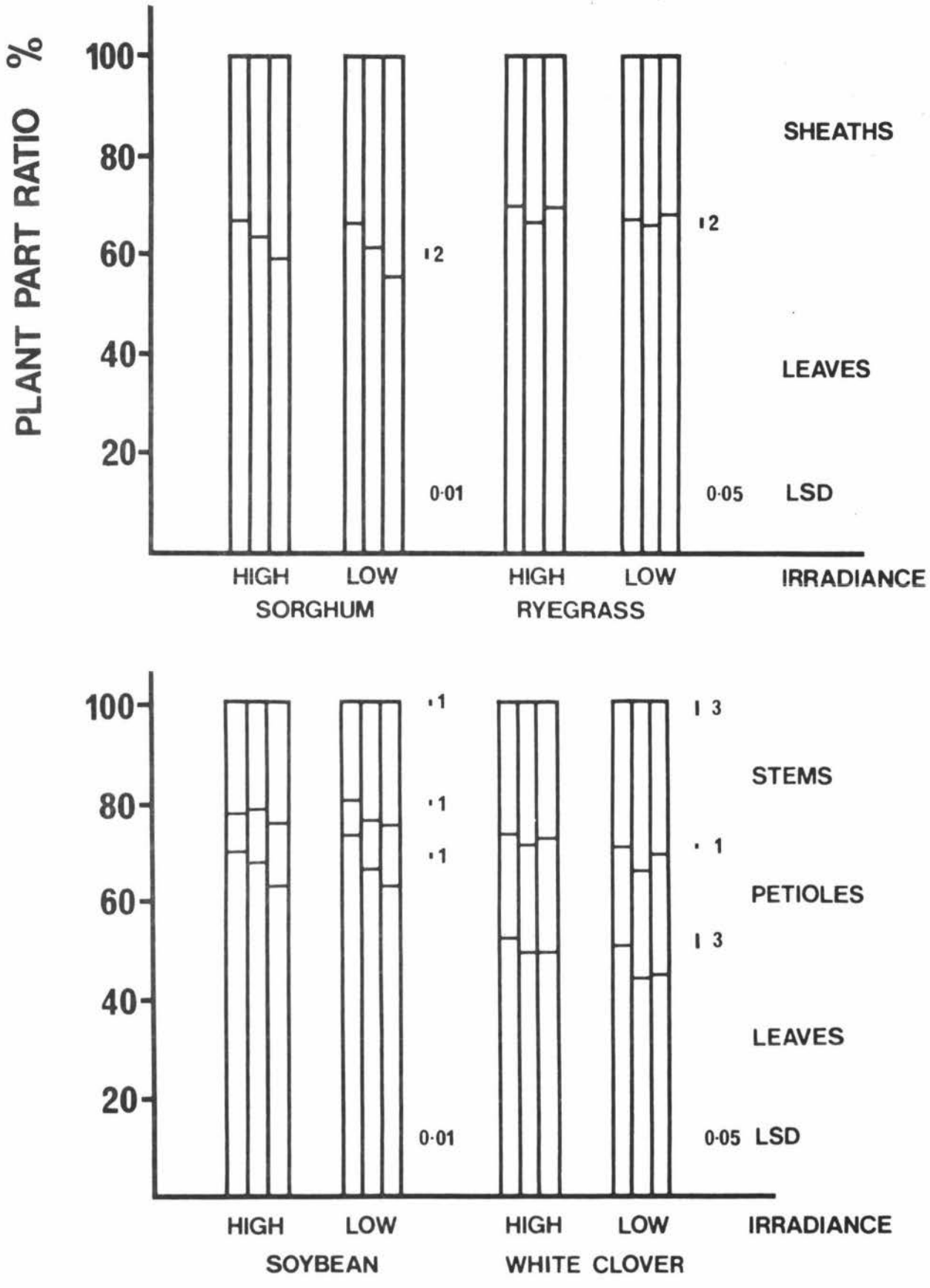


Fig. 19. Spectral Bias Experiment.
Plant Part Ratios at the final harvest for all treatments.
(Total shoot = 100; LSD values for each Ratio presented with significance level shown.)

2.6.1. Root:Shoot Ratio.

The root:shoot ratio for all species showed an interaction with both spectral and irradiance treatments (Fig 18). In all species the ratios for each spectral treatment were significantly higher at the high irradiance compared with the low irradiance treatment. Generally for all spectral treatments the ratio decreased with increasing treatment time (plant age, data not presented in text).

For sorghum and soybean there was a decreasing root: shoot ratio through the blue-biased, balanced and red-biased ratios respectively. This response was marked and differences between spectral treatments became greater with increasing time under treatment.

In ryegrass and white clover the responses between the spectral treatments were much less pronounced. However, there were similar red- and blue-biased responses (i.e. high blue-biased compared to red-biased values) but the balanced treatment results were quite different. Ryegrass (low irradiance) and white clover (high irradiance) balanced treatment ratios were higher than either of the biased treatment values.

2.6.2. Leaf:Shoot Ratio.

The proportion of leaf in the shoot of sorghum and soybean was consistently affected by the spectral treatments at each irradiance. There were significantly higher proportions of leaf to shoot on a dry-weight basis under the blue-biased, intermediate values under the balanced, and significantly lower proportions under the red-biased treatment. With the exception of the soybean blue-biased result, there was an increase in the leaf proportion for both soybean and sorghum under all spectral treatments at the high, compared with the low, irradiance level.

The ryegrass and white clover leaf proportions were not influenced by the spectral treatments in the same way as recorded for soybean and sorghum. In both of these species the balanced treatment proportion was smaller, or similar to, each of the biased treatment results. In ryegrass the blue-

and red-biased treatment proportions were equal to each other, but in white clover the blue-biased proportions were significantly higher than those under the red-bias. The irradiance effect in soybean and sorghum was repeated in ryegrass and white clover where higher proportions were found under the higher irradiance.

The sheath:shoot ratio in sorghum and ryegrass, by derivation, showed an inverse response to each treatment compared to the leaf:shoot ratio.

2.6.3. Petiole:Shoot Ratio.

The proportion of petiole in the shoot (petiole:shoot ratio), for both white clover and soybean was highest under the red-biased, intermediate under the balanced, and smallest under the blue-biased treatment. These trends became more significant with increasing time under treatment but showed no response to the different irradiance levels.

2.6.4. Stem:Shoot Ratio.

The soybean stem:shoot ratio was similar to the petiole: shoot ratio with increased values for the red-biased treatment and smaller (highly significant) values for both the balanced and blue-biased treatments. The responses were more pronounced under the low irradiance than under the high irradiance treatment and the ratio was significantly greater at the low irradiance than at high irradiance for all spectral conditions.

In white clover the stem:shoot ratio was highest under the balanced and lowest under the blue-biased treatment but the differences in this ratio between all spectral and irradiance treatments were barely significant.

2.7. Plant Leaf Characteristics.

2.7.1. Dry Weight/Unit Area of the Last Mature Leaf Blade.

The dry weight per unit area of the last mature leaf for each species and each treatment is presented in Fig 20. With one exception (sorghum, balanced treatment) in all

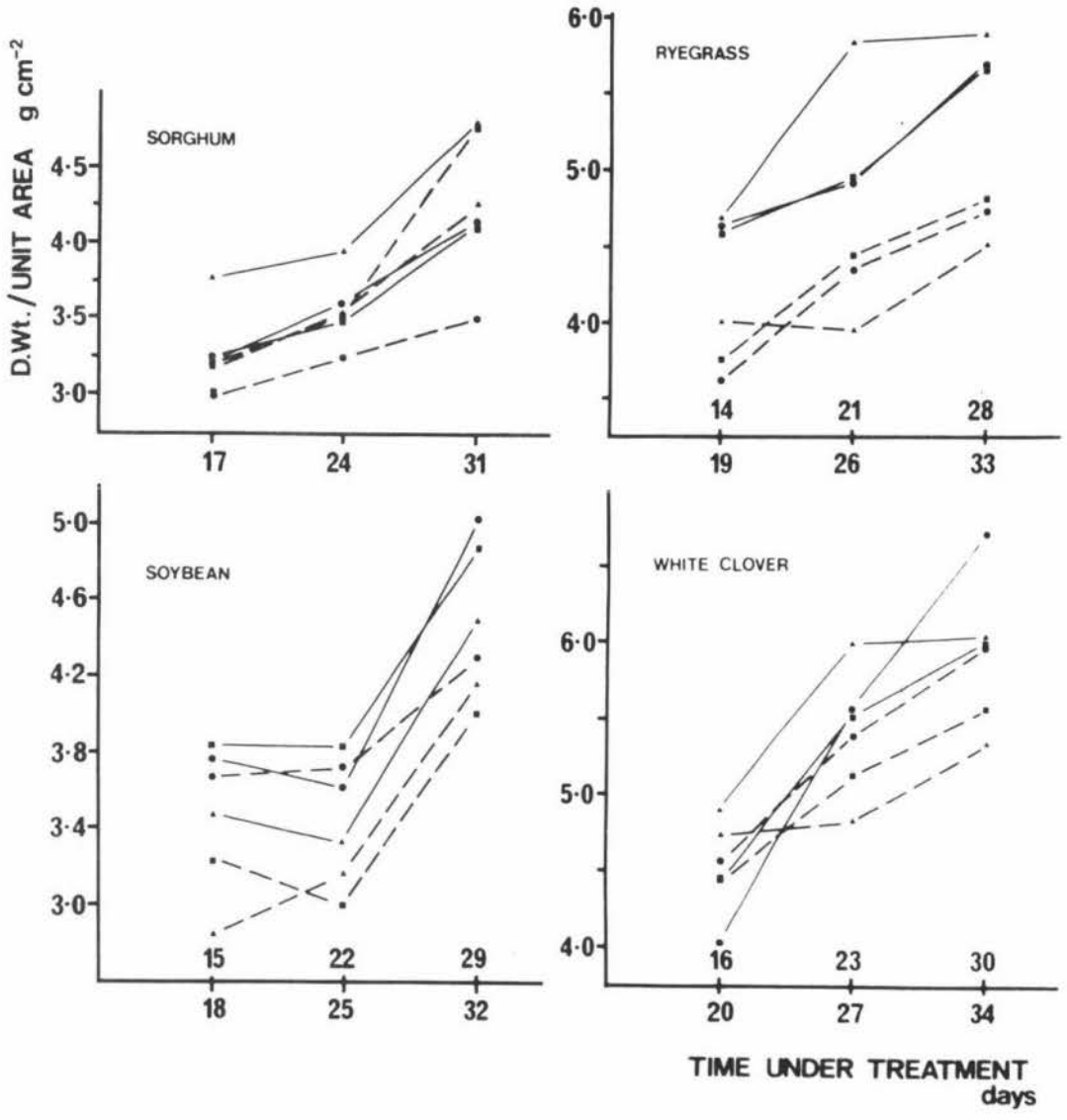


Fig. 20. Spectral Bias Experiment.
Mean Dry-Weight per Unit Leaf Area for final three harvests.

species and spectral treatments the values under the high irradiance treatment were considerably higher than those under the low irradiance treatment.

With respect to the spectral treatments, differences in values were not consistent either between species or between irradiance levels and varied with time under treatment. In sorghum, under high irradiance, the highest dry weight per unit area values were under the red-biased treatment and the lowest under the blue-biased and balanced treatments which were themselves similar. This red- and blue-biased relationship at the low irradiance was consistent but here final harvest balanced treatment values were highest.

Soybean showed the reverse response (i.e. higher blue-biased than red-biased values) to sorghum and again the balanced treatment response was unusual. At the high irradiance it was similar to the blue-biased response (high values) but under the low irradiance it was similar to the red-biased response (low values). This relative response to irradiance of the balanced treatment compared with the biased treatments was the reverse of that shown for sorghum.

Ryegrass showed a close similarity between the blue-biased and balanced treatments at both irradiances but the red-biased values were variable, showing higher values than the other treatments at the high irradiance but lower values at low irradiance.

White clover response under low irradiance was similar to the ryegrass response but with white clover the balanced treatment gave intermediate values. At high irradiance the red-biased values were higher than those from the balanced treatment (cf. ryegrass, high irradiance) but the blue-biased treatment values were initially lowest, and finally highest, of the three spectral treatments.

2.7.2. Leaf Shape (Last Mature Leaf Blade).

The sample leaf blade length and width (at midpoint) values are presented in Figs 21 and 22.

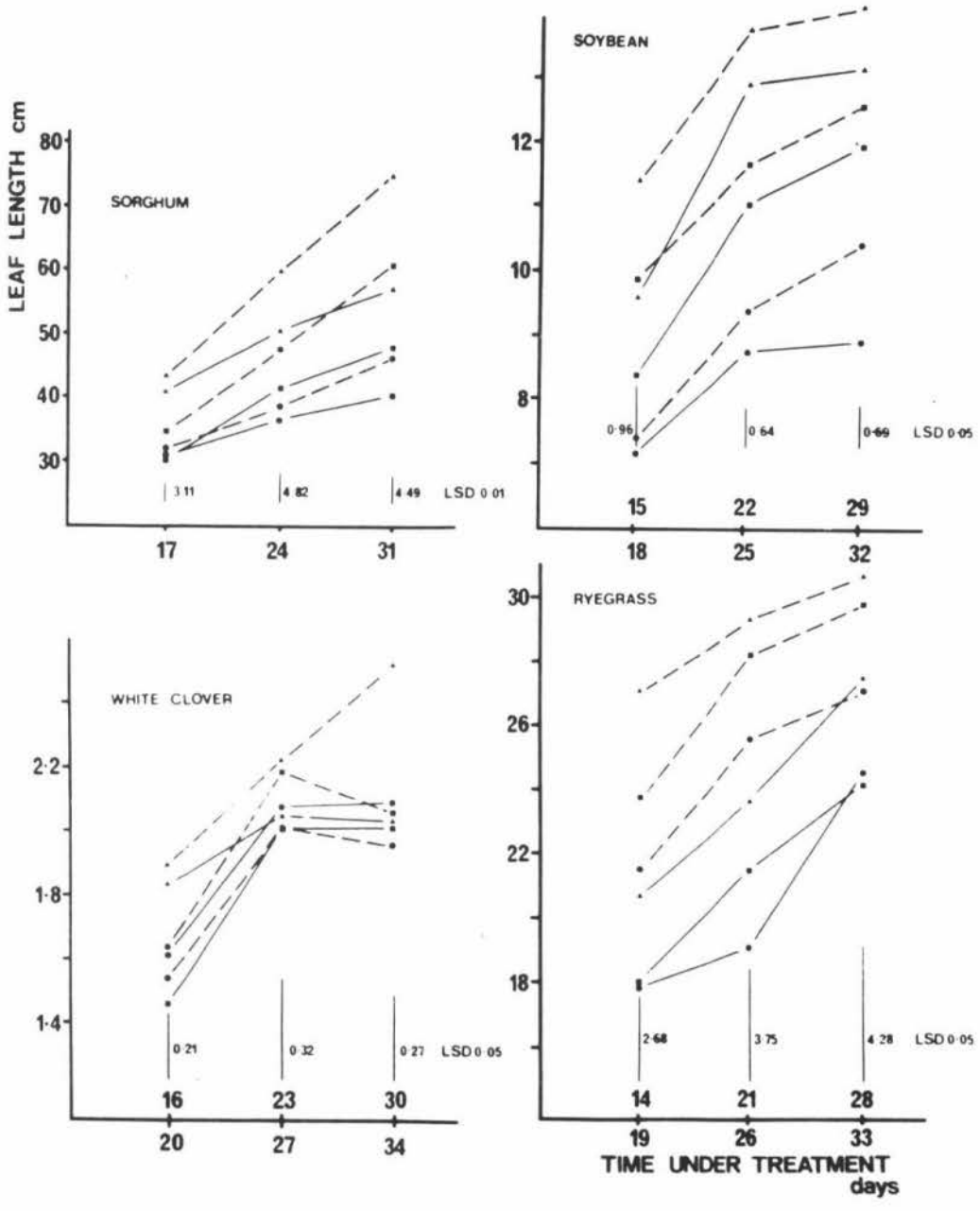


Fig. 21. Spectral Bias Experiment.
Last Mature Leaf Length at the final three harvests.
(LSD values presented for each harvest).

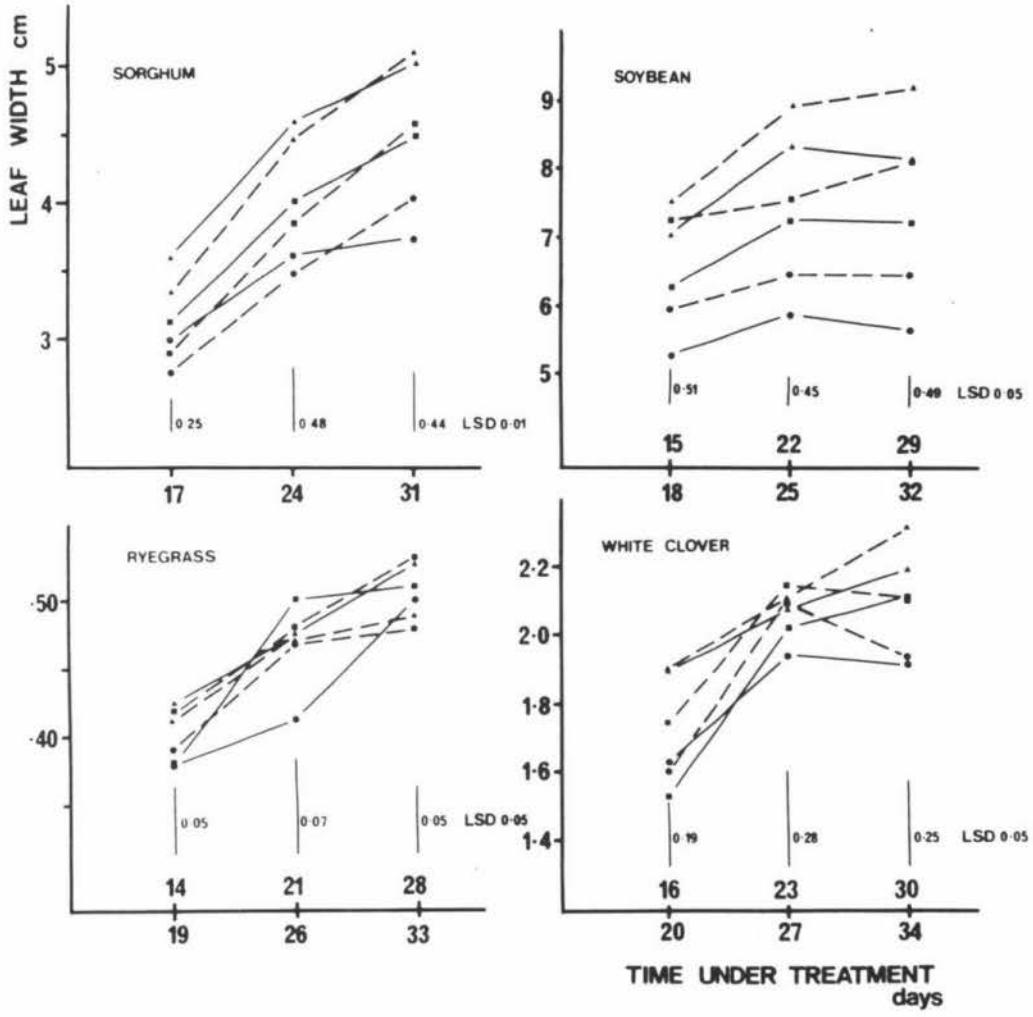


Fig. 22. Spectral Bias Experiment.
Last Mature Leaf Width at the final three harvests.
(LSD values presented for each harvest).

The most noticeable response was the marked increase in leaf length under low, compared to high, irradiance conditions. Leaf width showed no response to irradiance level.

With respect to spectral quality, sorghum, soybean and ryegrass leaf length, at both irradiance levels, was greatest under the red-biased, intermediate under the balanced, and least under the blue-biased treatment. White clover showed a similar response under low irradiance conditions, but under high irradiance conditions the longest leaves were from the blue-biased treatment and the shortest from the balanced treatment.

All species showed widest leaves under the red-biased and narrowest under the blue-biased treatment under both high and low irradiance conditions.

Derived data for the length:width ratios (data not presented) showed that the highest ratios were, for most species and irradiance levels, from the red-biased treatment. The balanced and blue-biased treatment ratios were similar in most cases. The most obvious exception was the response of white clover under the high irradiance where the blue-biased treatment ratio was highest and the red-biased and balanced treatment ratios were similar.

2.7.3. Leaf Number.

It is apparent from the leaf dimension (length and breadth) and leaf area results, that the number of leaves on the main stem or shoot would be similar under each of the spectral and irradiance treatments. This is borne out in results presented in Table 18 for final harvest values.

Generally leaf number was highest under the red-biased treatment and lowest under the blue-biased treatment at each irradiance level. The balanced treatment showed no consistent relationship to the red- or blue-biased treatments for each species and irradiance level.

There was a small increase in final leaf number under

Table 18

Spectral Bias Experiment

Leaf Number (Final Harvest)

	Sorghum	Soybean	Ryegrass	White Clover
High Irradiance				
Blue Biased	11.22	6.81	9.30	7.36
Balanced	12.07	6.50	9.43	7.05
Red Biased	12.16	7.01	9.60	8.35
Low Irradiance				
Blue Biased	11.08	6.38	8.82	7.52
Balanced	11.85	6.51	9.53	8.01
Red Biased	11.96	7.01	8.88	8.78
LSD 0.05	0.33	0.33	0.43	0.94

the higher irradiance for each species.

2.7.4. Relative Rate of Leaf Area Expansion.

The results for the relative rate of leaf area expansion (RLAGR) for harvest intervals 2-3 and 3-4, and for the total period (2-4) along with the standard errors (in parentheses) are presented in Table 19.

Under high irradiance conditions with all species tested and under low irradiance conditions with ryegrass and white clover, the highest RLAGR was found under thr red-biased treatment, and the lowest RLAGR under the blue-biased treatment. This effect was reversed with sorghum and soybean under low irradiance conditions where the highest RLAGR occurred under the blue-biased treatment.

In most instances, the RLAGR declined with time under treatment. There appeared to be no consistent effect on RLAGR attributable to irradiance levels within each spectral treatment.

2.8. Plant Height.

2.8.1. Stem and Shoot Length.

The stem (shoot) length response of each species to the spectral and irradiance treatments are shown in Fig 23. There are clear spectral, irradiance and species determined stem length responses presented in these results.

Sorghum showed a consistant decrease in shoot length in the order of red-biased, balanced, and blue-biased treatments, where the differences between each biased treatment and the balanced treatment were similar. The rate of increase in shoot length increased with time under the red-biased and balanced treatments but remained constant with time under the blue-biased treatment.

Soybean produced a comparable result to sorghum under the low irradiance treatment, but under higher irradiance conditions the stem length under all spectral conditions was

Table 19

Spectral Bias Experiment

Relative Rate of Leaf Area Expansion (RLAGR)

($cm\ cm^{-2}\ day^{-1}$)

(S.E. in Brackets)

Species / Treatment	Harvest Interval		
	2 - 3	3 - 4	2 - 4
Sorghum			
High Irradiance			
Blue Biased	0.099	0.098	0.098 (0.007)
Balanced	0.162	0.114	0.138 (0.009)
Red Biased	0.138	0.102	0.120 (0.009)
Low Irradiance			
Blue Biased	0.141	0.123	0.132 (0.010)
Balanced	0.149	0.084	0.116 (0.010)
Red Biased	0.153	0.085	0.119 (0.007)
Ryegrass			
High Irradiance			
Blue Biased	0.155	0.148	0.152 (0.013)
Balanced	0.183	0.133	0.158 (0.013)
Red Biased	0.160	0.139	0.150 (0.011)
Low Irradiance			
Blue Biased	0.142	0.128	0.135 (0.012)
Balanced	0.135	0.140	0.138 (0.016)
Red Biased	0.152	0.161	0.157 (0.016)

Table 19 contd

Species / Treatment	Harvest Interval		
	2 - 3	3 - 4	2 - 4
Soybean			
High Irradiance			
Blue Biased	0.112	0.046	0.079 (0.009)
Balanced	0.125	0.088	0.107 (0.009)
Red Biased	0.148	0.069	0.108 (0.010)
Low Irradiance			
Blue Biased	0.108	0.086	0.097 (0.008)
Balanced	0.138	0.061	0.100 (0.010)
Red Biased	0.099	0.076	0.088 (0.008)
White Clover			
High Irradiance			
Blue Biased	0.155	0.142	0.149 (0.014)
Balanced	0.156	0.149	0.153 (0.020)
Red Biased	0.154	0.178	0.166 (0.016)
Low Irradiance			
Blue Biased	0.144	0.164	0.154 (0.017)
Balanced	0.152	0.118	0.135 (0.013)
Red Biased	0.184	0.181	0.183 (0.013)

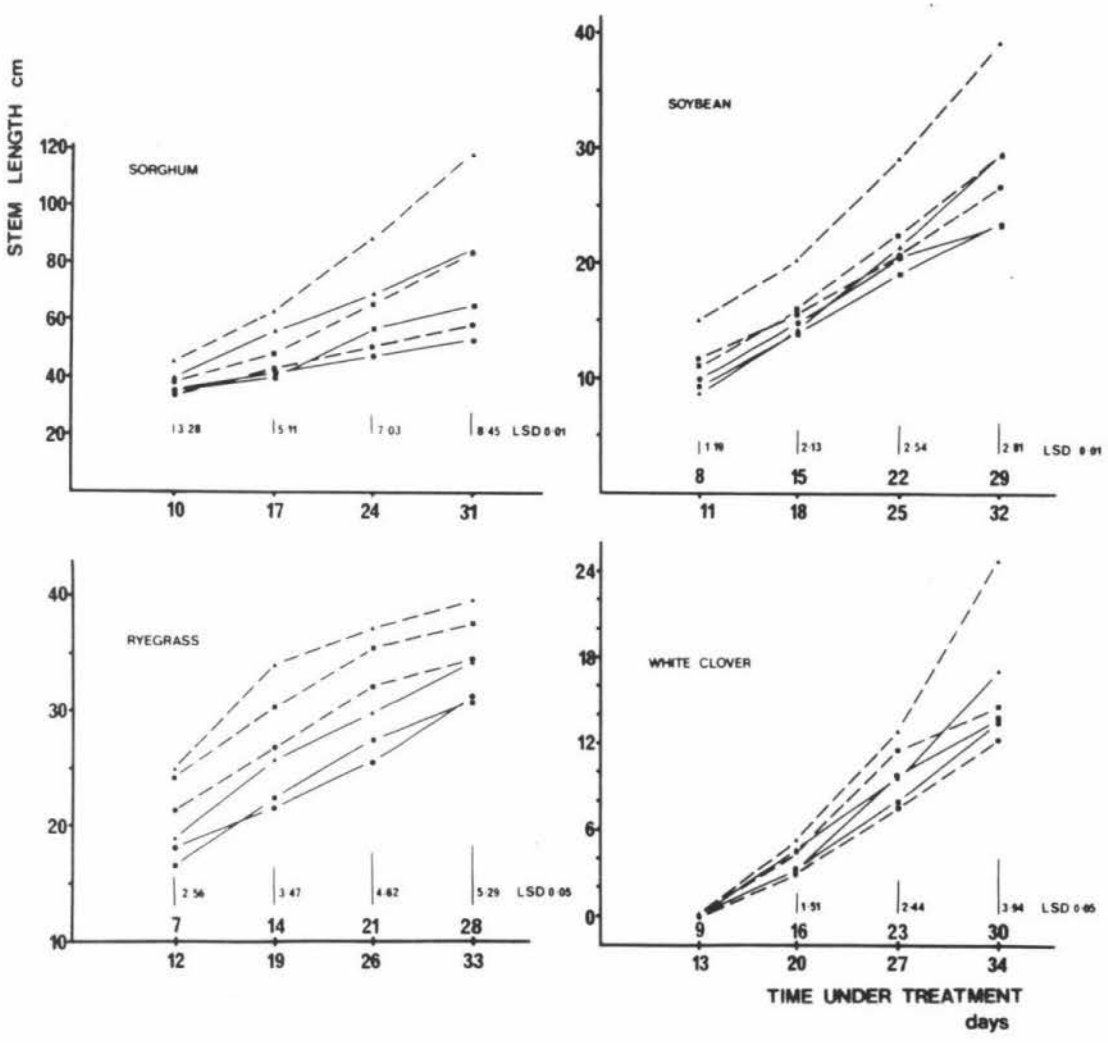


Fig. 23. Spectral Bias Experiment.
Stem (Shoot) Length increase with time under each treatment.
(LSD values presented for each harvest).

closely similar except after a considerable treatment time (harvest 4) when the red-biased treatment values were highest.

Ryegrass and white clover each showed similar results, depending on the irradiance, to the spectral treatments. Under high irradiance conditions, the values were similar under the balanced and blue-biased conditions but less than the red-biased treatment values. This can be compared to the low irradiance conditions where the balanced treatment values were intermediate to the biased treatments (c f. sorghum, low irradiance).

For all species, the influence of different spectra was enhanced by a low irradiance and was increased with time under treatment in many cases.

Low irradiance stem length values were in all species and spectral treatments higher, (often significantly at the 5% level), than the high irradiance values.

2.8.2. Sheath Extension (Sorghum).

Sheath extension data for sorghum (data not presented) shows results which closely follow those for shoot length.

In both the high and low irradiance treatments the sheath length was significantly greater under the red-biased treatment than under either the balanced or blue-biased treatments respectively. All treatments showed an increasing rate of sheath extension with time.

2.9. Main Stem Angle (Sorghum).

The influence of the spectral treatment on the form of these plants was most noticeable and was markedly shown in the main stem angle response. Plate 8 shows the visual effect of each treatment and actual values for the main stem angle are shown in Fig 25.

The most upright plants (high stem angle) were those from the red-biased and the most prostrate (low stem angle)

PLATE 8. This photograph of sorghum under each spectral treatment (see Plate 4 for reference) shows clearly the main stem angle, stem height and tiller development.

from the blue-biased treatment, with those under the balanced treatment producing an intermediate stature. At the low light irradiance, the difference between spectral treatments was highly significant ($P = 0.01$) and became greater with time under treatment. Increasing the light irradiance markedly increased the initial spectral effect and accelerated the rate of decrease of the main stem angle. Final stem angles were similar at both irradiance levels for the blue-biased treatment but significantly different ($P = 0.05$) for balanced and red-biased treatments where there were higher values under the low irradiance treatment.

2.10. Tiller Number (Sorghum).

The trends for tiller number in sorghum under the different irradiance and spectral bias treatments (Fig 24) show inverse relationships under these treatments compared with the main stem angle and stem length data previously presented.

Under the low irradiance, final tiller number was highest under the blue-, intermediate under the balanced and lowest under the red-biased treatments. Under the high irradiance, final tiller number was similar under the blue-biased and balanced treatments but higher than the red-biased treatments.

The differences between the spectrally-biased treatments and the balanced treatment were highly significant ($P = 0.01$) under the low irradiance at the final two harvests. They were only significant ($P = 0.05$) between the spectrally-biased treatments at the final harvest under high irradiance conditions and between the balanced treatment and the biased treatments at the second and third harvests.

In both the red-biased and balanced treatments tiller number was highest at the high irradiance but this effect was reversed under the blue-biased treatment.

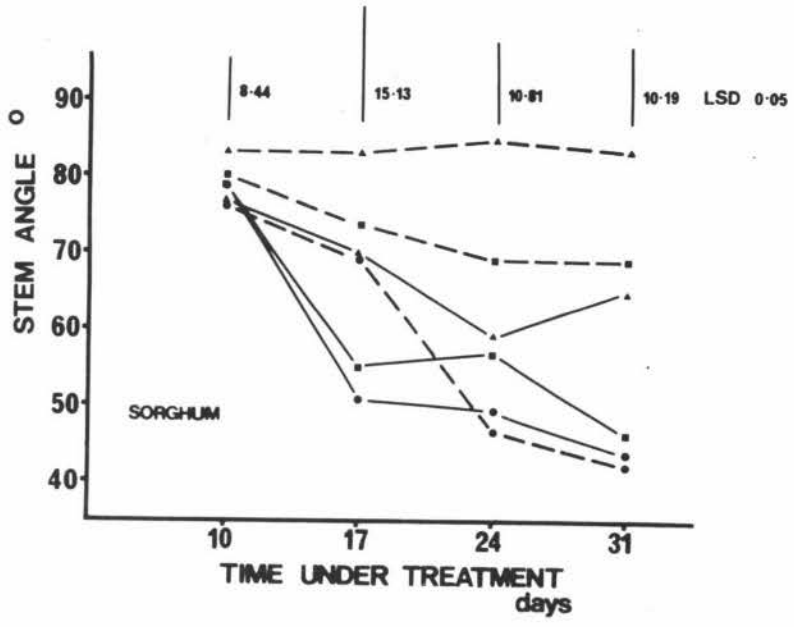


Fig. 25. Spectral Bias Experiment.
Sorghum Main Stem Angle at each harvest for all spectral treatments. (LSD = 0.05 presented for each harvest).

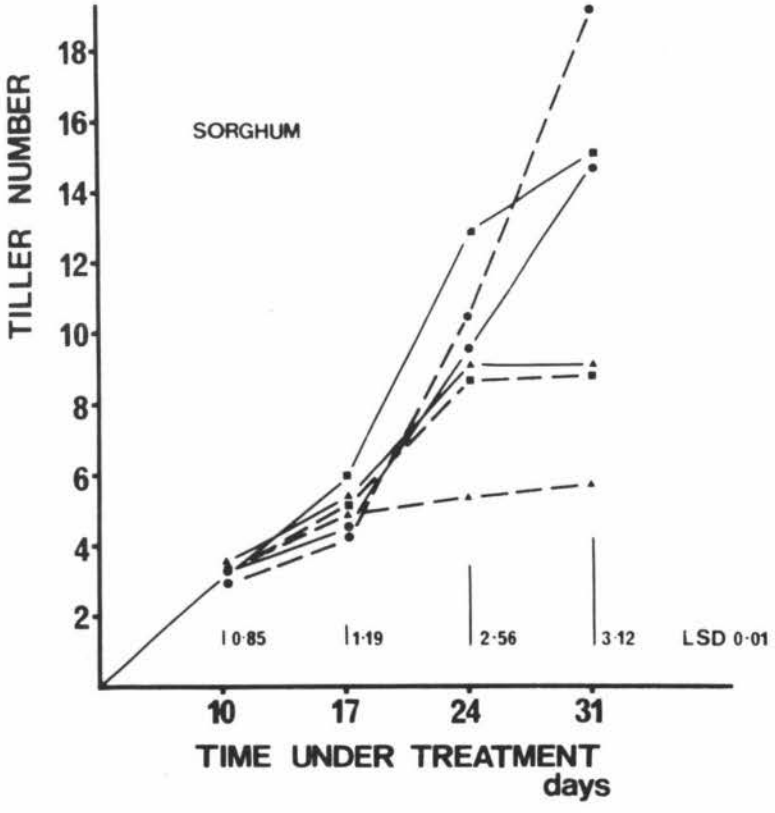


Fig. 24. Spectral Bias Experiment.
Sorghum Tiller Number increase with time under treatment. (LSD = 0.01 presented for each harvest).

2.11. Biochemical Results.

2.11.1. Total Chlorophyll, Chlorophyll a and Chlorophyll b Levels.

The results for total chlorophyll, chlorophyll a and chlorophyll b content, and chlorophyll a:b ratios are shown in Figs 26 and 27.

Chlorophyll content, on a fresh-weight basis, was generally higher under each spectral treatment for all species at the high irradiance level.

Total chlorophyll levels were similar at all spectral treatments for sorghum and, except for a lower blue-biased treatment level at the high irradiance, also for white clover. Soybean and ryegrass had highest levels under the blue-biased, and lowest levels under the red-biased treatments.

The results for the chlorophyll a:b ratio fell broadly into three categories. Soybean and white clover at the high irradiance, and soybean at the low irradiance, had a high ratio under the red-biased, intermediate under balanced, and a low ratio under the blue-biased treatment. Ryegrass at the high irradiance, and white clover at the low irradiance, showed an inverse response to this previous group. Sorghum at the high and low irradiance, and the low irradiance ryegrass treatments, formed the third category with less differences shown between the biased treatments but with higher balanced treatment values.

2.11.2. Carbohydrate Content.

Soluble sugar, starch and total carbohydrate contents for leaf tissue only are presented in Figs 28, 29 and 30.

2.11.2.1. Leaf Carbohydrate Content.

(a) Soluble Sugar.

For each species the soluble sugar content was higher at the high irradiance compared with the low irradiance treatment

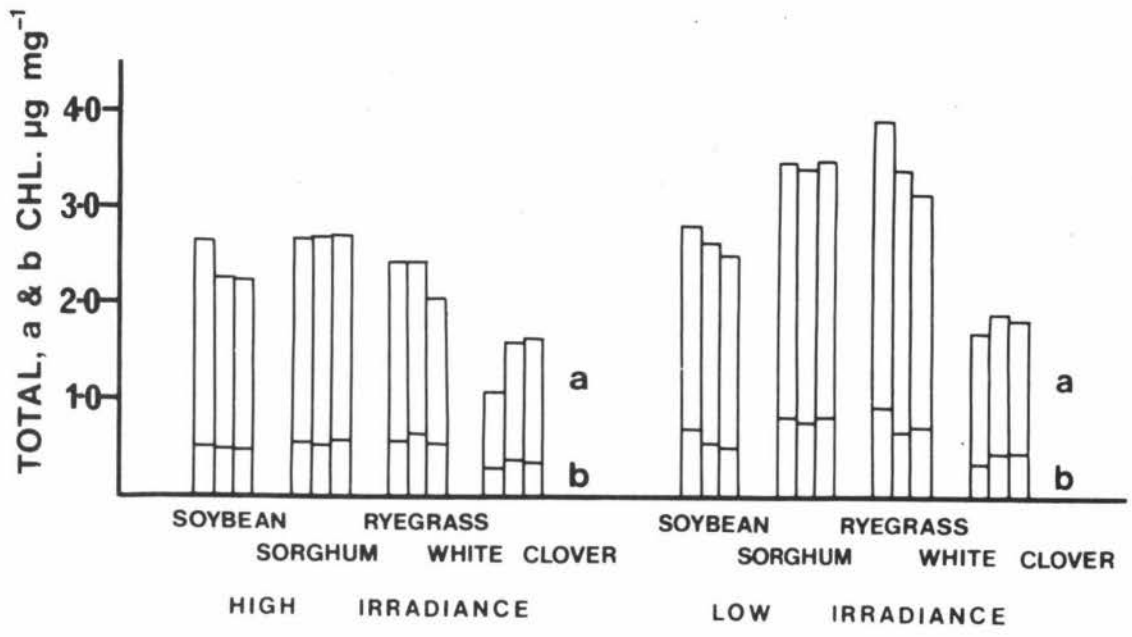


Fig. 26. Spectral Bias Experiment.
Total Leaf Chlorophyll, Chlorophyll a and b Content.
Final harvest values.
(Left to Right : Blue Biased, Balanced, Red Biased treatments).

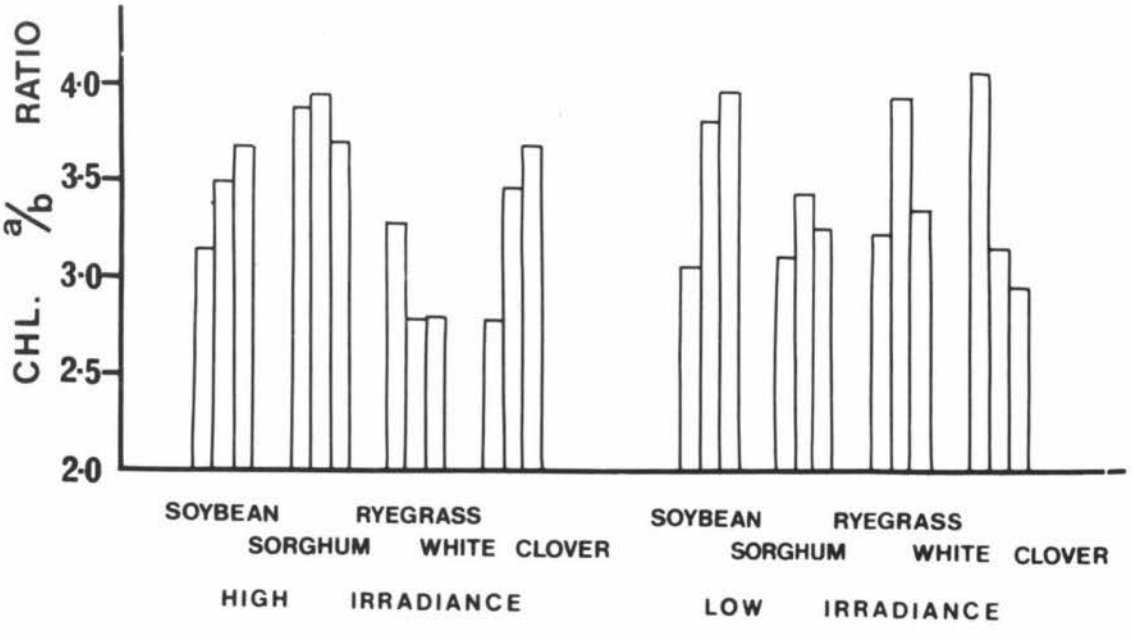


Fig. 27. Spectral Bias Experiment.
Leaf Chlorophyll a : b Ratio.
(Data derived from results presented in Fig. 26).

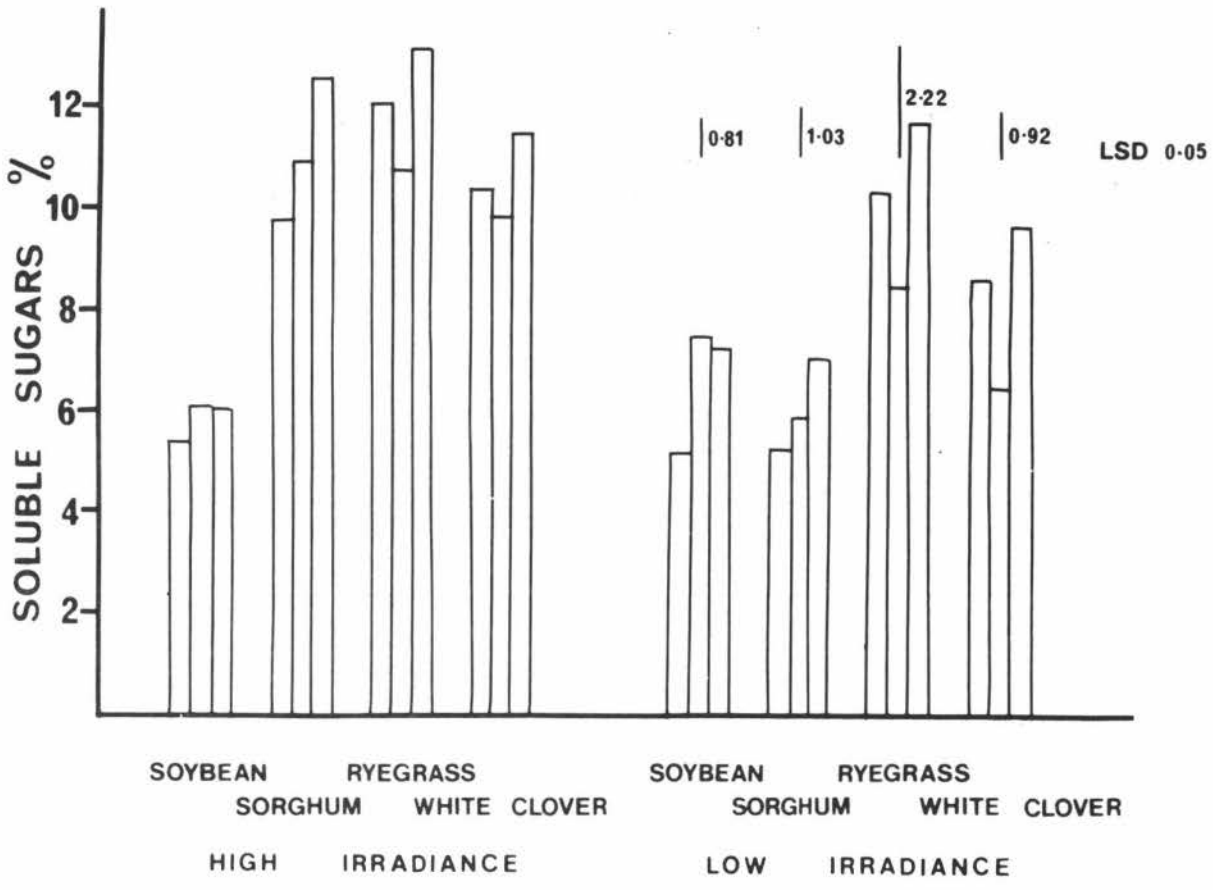


Fig. 28. Spectral Bias Experiment.
Leaf Soluble Sugar Content. Final harvest values.
(LSD = 0.05 values presented for each species).

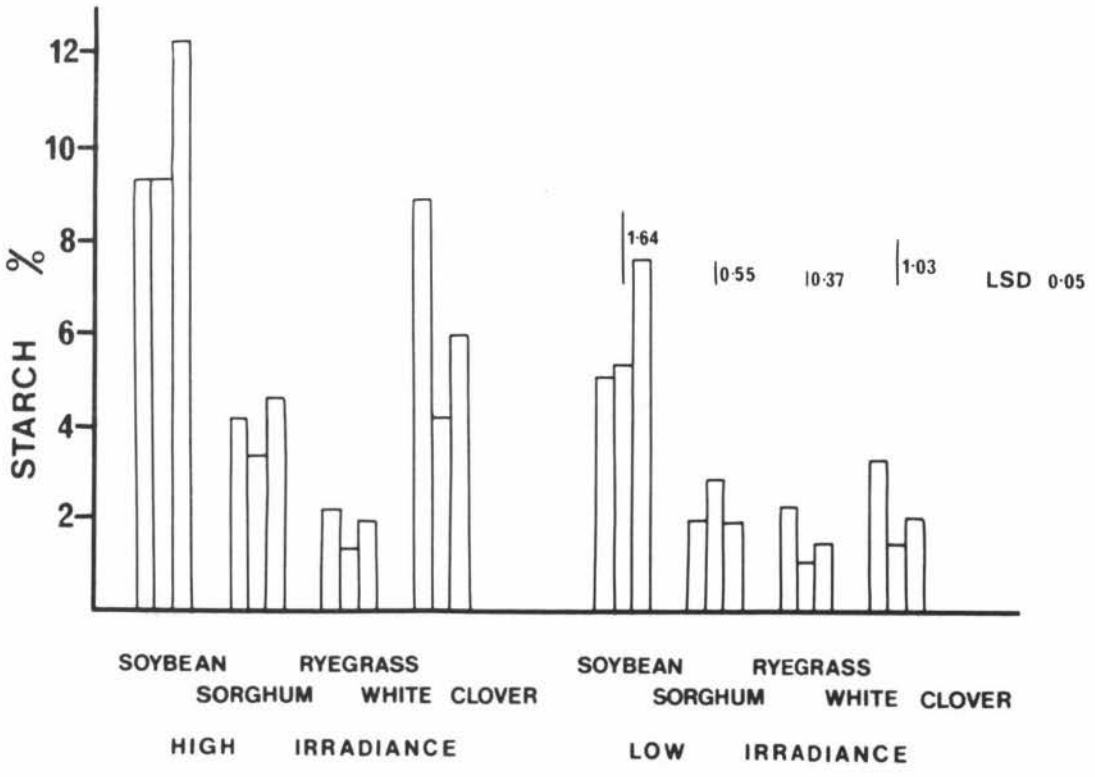


Fig. 29. Spectral Bias Experiment.
Leaf Starch Content. Final harvest values.
(LSD = 0.05 values presented for each species).

except with soybean where results were similar.

Sorghum soluble sugar content was highest under the red-biased, intermediate under the balanced and lowest under the blue-biased treatment. Soybean results closely matched those for sorghum except that the balanced and red-biased treatment results were similar.

Ryegrass and white clover, however, had similar red- and blue-biased trends to these other species but here the balanced treatment results were significantly lower than the biased treatment contents.

(b) Starch.

Starch content, like soluble sugar content, was higher at the high irradiance compared to the low irradiance treatment.

Soybean and sorghum each showed similar responses to the biased treatments where higher contents were found under red-bias conditions. In these two species, however, the balanced treatment starch content varied in relation to the biased treatments; it was similar to the blue-biased content at both irradiances in soybean, lower than both biased treatment contents in sorghum at the high irradiance but higher at the low irradiance.

In comparison, white clover and ryegrass had the highest starch content under the blue-biased treatment at both irradiance levels, and lowest levels under the balanced treatment.

(c) Total Carbohydrate.

Total carbohydrate (soluble sugar and starch) content was highest for all species and spectral treatments under the high irradiance level.

Soybean and sorghum showed significantly increased levels under the red-biased compared to the balanced and blue-biased treatments respectively.

In ryegrass, the same biased treatment relationship held, but the content under the balanced treatment was

significantly lower than under the biased treatments. This balanced treatment response in white clover, in relation to the contents under the biased treatments, was reversed where the balanced treatment resulted in the highest total carbohydrate content levels.

2.11.2.2. Petiole Carbohydrate Content.

(a) Soluble Sugar.

Petiole soluble sugar content results (data not presented) showed no differences between spectral treatments at the high irradiance but similar results to the leaf lamina at the low irradiance. The content for each spectral treatment was highest under the high irradiance for soybean but similar for white clover.

(b) Starch.

Petiole starch content (data not presented) showed similar trends to the leaf starch content under each spectral and irradiance treatment.

(c) Total Carbohydrate.

Soybean petiole total carbohydrate content (data not presented) was similar to the leaf content results for each spectral and irradiance treatment. This response held also for the white clover petiole content at the high irradiance, but at the low irradiance the red-biased content was highest and the balanced and blue-biased treatment contents were similar.

2.11.3. Protein Content.

The results from the leaf protein N analyses are presented on a dry-weight basis in Fig 31 for each treatment.

The response of leaf protein content to light irradiance was small with higher values being found under the low-irradiance treatment.

Soybean and sorghum at both irradiance levels had higher

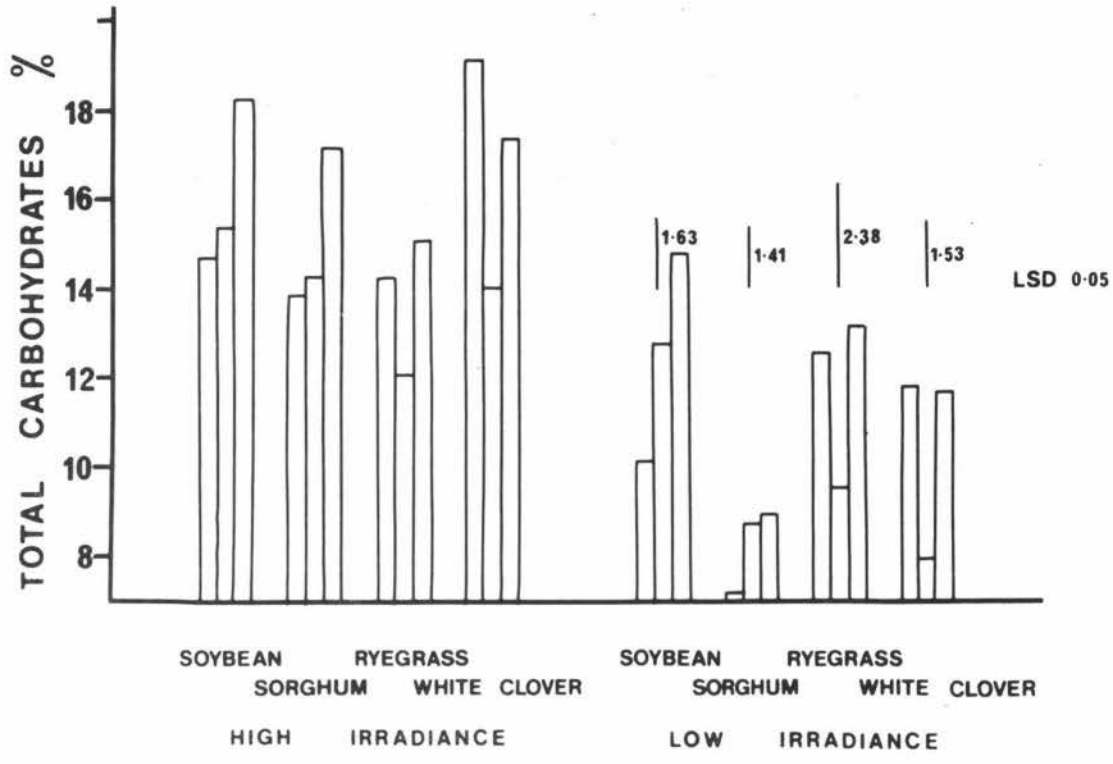


Fig. 30. Spectral Bias Experiment.
Leaf Total Carbohydrate Content. Final harvest values.
(LSD = 0.05 values presented for each species).

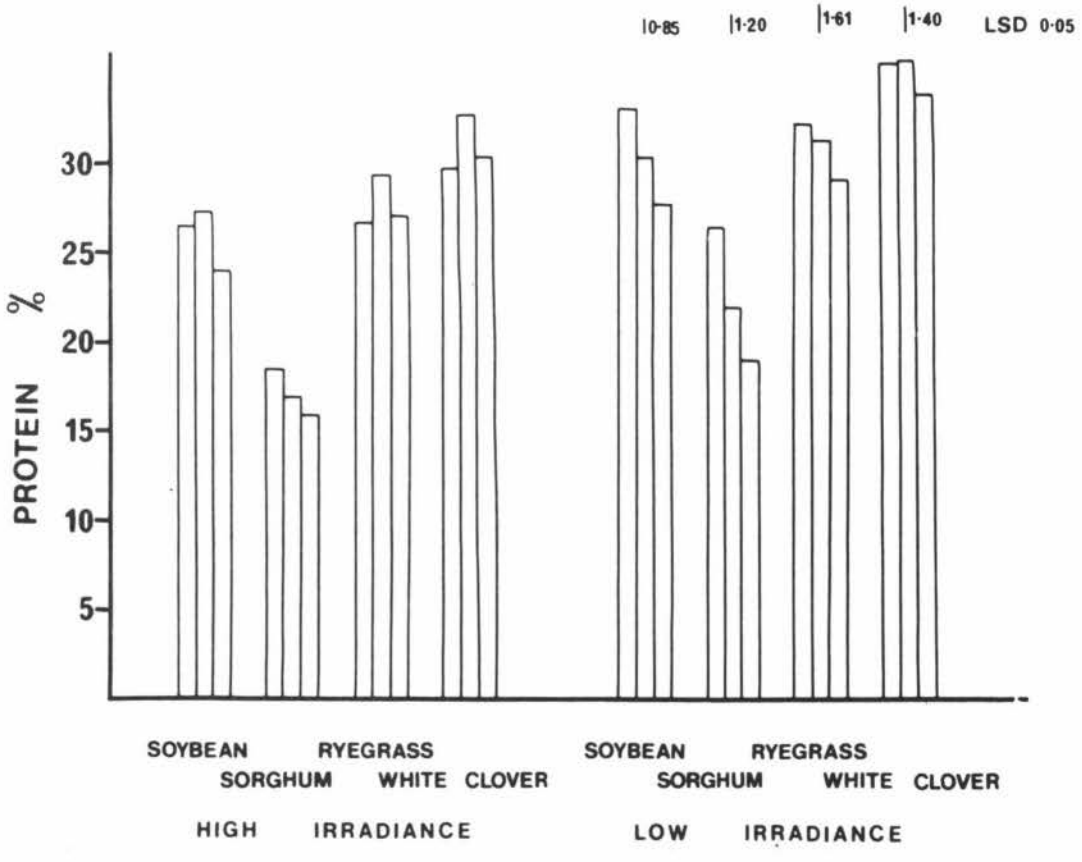


Fig. 31. Spectral Bias Experiment.
Leaf Protein Content. Final harvest values.
(LSD = 0.05 values presented for each species).

leaf protein contents under the blue-biased, intermediate under the balanced, and lowest under the red-biased treatments.

Ryegrass under the low irradiance had a similar spectral treatment response to soybean and sorghum, but ryegrass under the high irradiance treatment, and white clover under both irradiance treatments, had similar biased spectral treatment protein contents and higher balanced treatment contents.

Petiole protein content results (data not presented) for both soybean and white clover at the low irradiance decreased in the order blue-biased, balanced, red-biased treatment. At the high irradiance the blue-biased and balanced treatment contents were similar and higher than the red-biased treatment contents.

Decreasing the light irradiance increased the petiole protein content.

2.11.4. C:N Ratio.

The C:N ratio results, calculated from total leaf carbohydrate and leaf protein content results, for each species and treatment are presented in Fig 32.

The general trends shown in the total carbohydrate and protein results are evident in the C:N ratio data. Soybean and sorghum showed an increasing C:N ratio from the blue-biased to the balanced through to the red-biased treatment at both irradiance levels. Ryegrass and white clover showed a much less marked blue-biased to red-biased treatment response and the balanced treatment ratios were consistently lower than the biased treatment ratios for each of these species at both irradiance levels.

The ratio for each species and spectral treatment was highest at the high irradiance level.

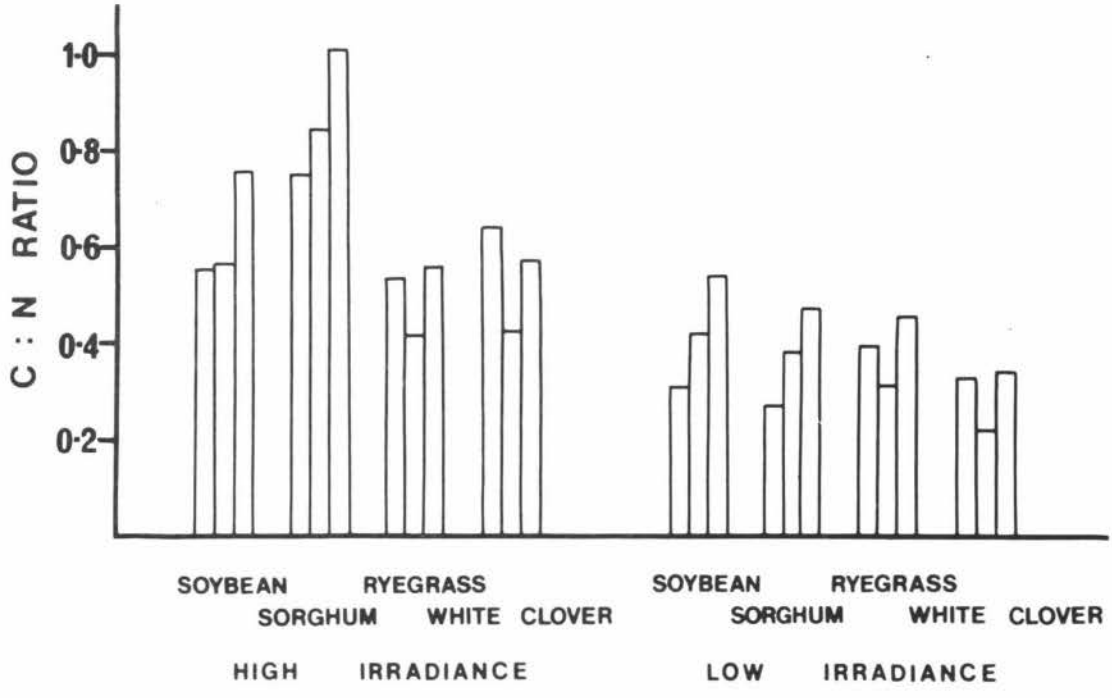


Fig. 32. Spectral Bias Experiment.
Leaf C : N (Carbohydrate : Protein) Ratio. Final harvest values.

2.11.5. Amino Acid Content.

The results from the soybean, low irradiance treatment amino acid analysis are presented in Table 20.

The blue-biased treatment caused a higher, and the red-biased treatment a lower, total amino acid content than the balanced spectral treatment.

Levels of aspartic acid, serine, alanine and phenyl alanine were all increased under the blue-biased treatment and the levels of arginine, glycine, valine and of the free ammonium ion were increased under the red-biased relative to the balanced treatment. Glutamic acid levels were highest under the balanced and lowest under the red-biased treatments.

2.12. Investigation of Treatment Effects on Chloroplast Structure.

The results from the electron-microscope study of soybean and white clover chloroplast ultrastructure are presented in Appendix 5.

2.12.1. Chloroplast Types, General.

(a) Soybean

The chloroplast types examined in soybean could be separated into three main types in relation to the cell-type in which they were located. These were the upper and lower palisade mesophyll (Plate EM 1a) and spongy mesophyll (Plate EM 1b) chloroplasts.

Chloroplasts of the upper palisade mesophyll cells were typically elongate under all conditions (Plate EM 3). The granal organisation in these chloroplasts was very poorly developed and consisted normally of two or three thylakoids appressed along portions of their length. (Plate EM 2a).

In the lower palisade mesophyll cells (Plate EM 4), the chloroplasts exhibited increased grana formation (Plate EM 2b)

Table 20

Spectral Bias Experiment

Amino Acid Content

(µg/g)

Soybean, Low Irradiance Treatment

	Blue-Biased	Balanced	Red-Biased
NH_4	17.63	25.01	32.88
Arginine	15.96	44.09	58.94
Aspartic Acid	116.75	77.71	70.65
Serine	887.73	738.42	647.93
Glutamic Acid	26.95	30.04	21.43
Glycine	25.89	30.02	42.03
Alanine	209.06	169.28	173.20
Valine	22.53	22.54	31.91
Phenyl Alanine	113.74	104.53	86.53
Total	1436.24	1241.64	1165.50

and were broader and less elongate than the upper palisade chloroplasts. The lower palisade chloroplasts were also more lens-shaped compared to the upper palisade chloroplasts which were normally closely appressed and parallel to the cell wall.

The spongy mesophyll chloroplasts were typically lens-shaped and had an extremely well developed granal system (Plates EM 5, 8.).

In each chloroplast type the thylakoid system always appeared to be organised parallel to the long axis of the chloroplast.

(b) White Clover.

The cells in white clover were differentiated into an upper columnar palisade mesophyll and a lower spongy mesophyll.

In both palisade and spongy mesophyll cell chloroplasts the granal system was well developed (Plate EM 9a, 9b). This granal system ran more or less parallel to the long axis of the chloroplast but was in a cup-shaped form. The tract of grana was curved away form the cell wall and towards the cell vacuole leaving a large region of structure-free stroma towards the cell wall.

All intra-organelle structures such as starch-grains and osmiophilic globules were found within the tract of grana.

Plates EM 10 - EM 13 show the typical chloroplasts from the palisade and spongy mesophyll cells. No obvious treatment effects are shown.

2.12.2. Chloroplast Types : Treatment Effects.

Examination of over 150 different chloroplasts from the 30 different types studied, examples of which are presented, showed no obvious differences in ultrastructure resulting from the spectral or irradiance treatments.

Although chloroplast size and shape were not specifically measured, from the material examined there appeared to be no obvious differences in these factors.

V DISCUSSION

1. Plant Response to Various Spectra and Irradiance Levels.

1.1. General.

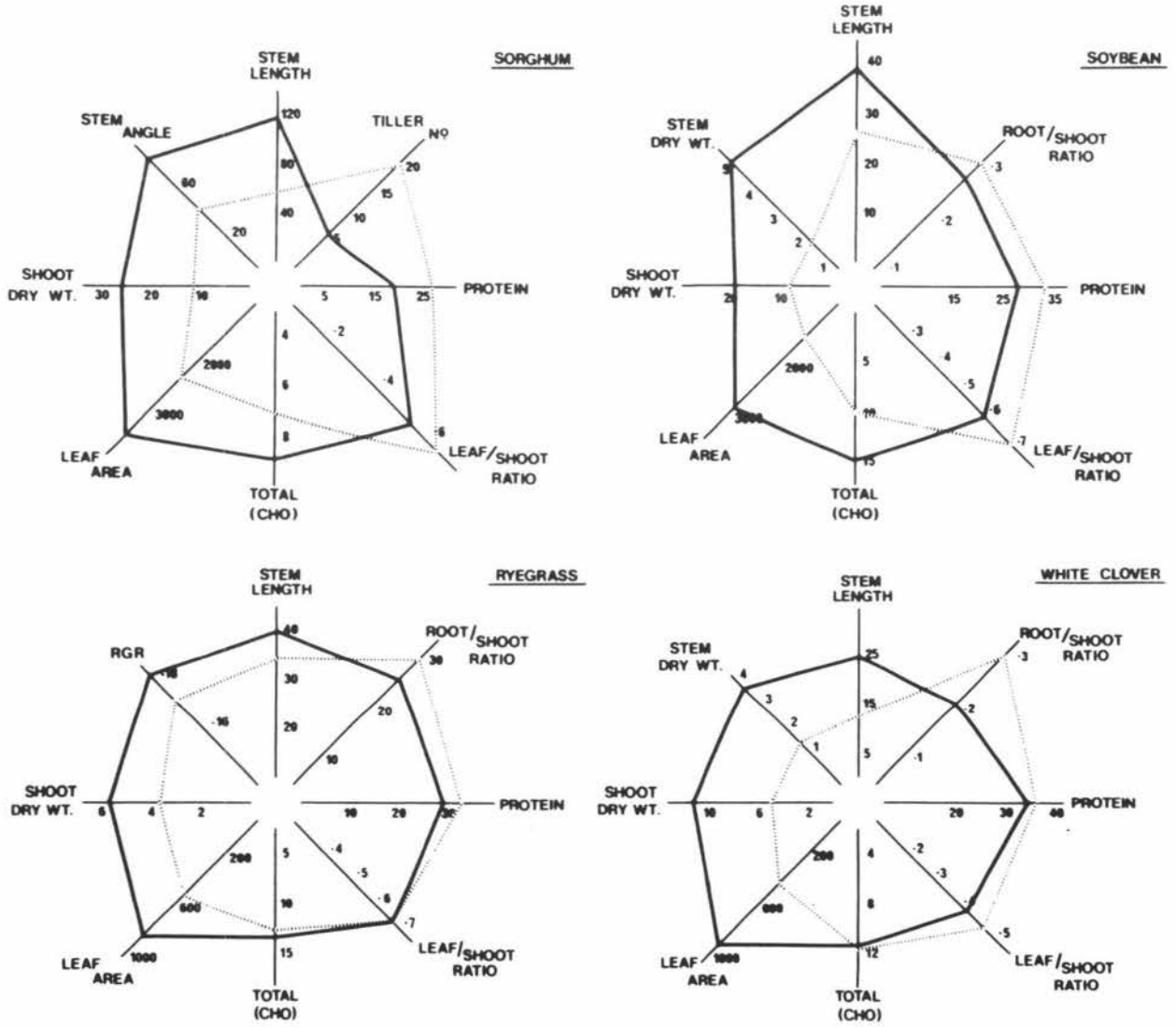
It is obvious from the results presented, that considerable differences were detected in a majority of the growth parameters measured, particularly under variable spectral bias and irradiance conditions. Such is the degree of variability between treatments that a complete assessment of the effects shown is difficult to comprehend when examining individual parameter responses in isolation. In relation to this problem, the data collected in the Spectral Bias experiment has been reduced to show the main treatment effects for the low irradiance treatment at the final plant harvest.

The data for each of the species are presented in Fig 33. Of necessity the parameters presented and the scale ranges used vary between species and to avoid unnecessary complication, data for the balanced spectral treatment in each case are omitted.

Clearly, two main effects are apparent. In the first case, the differences due to each spectral treatment showed similar relationships in each of the species studied (e.g. stem length, leaf protein N content, leaf area). However although this similarity is evident, the species responses differed in their magnitude to each spectral treatment. This difference, in turn, could generally be resolved into two species groups : sorghum and soybean, and ryegrass and white clover. In a significant number of the parameters measured sorghum and soybean showed similar large differences between each of the spectral treatments studied whereas ryegrass and white clover differences were often small and not as well defined as the sorghum and soybean responses. In the second case, spectral difference effects were greatest in each species at the low irradiance level examined. From this assessment it is reasonable to assume that a similar mechanisn is operating for each growth parameter for each of these groups of species and that the response is more evident under the

Fig. 33. Spectral Bias Experiment.

Final harvest values for 8 plant factors under the Red Biased (solid line) and Blue Biased (dashed line) High Irradiance treatment conditions for each of the four species studied. Factors presented and scale ranges vary for each species.


SORGHUM
STEM LENGTH
TILLER Nº
PROTEIN
LEAF/SHOOT RATIO
TOTAL (CHO)
LEAF AREA
SHOOT DRY WT.
STEM ANGLE
SOYBEAN
STEM LENGTH
ROOT/SHOOT RATIO
PROTEIN
LEAF/SHOOT RATIO
TOTAL (CHO)
LEAF AREA
SHOOT DRY WT.
STEM DRY WT.
RYEGRASS
STEM LENGTH
ROOT/SHOOT RATIO
PROTEIN
LEAF/SHOOT RATIO
TOTAL (CHO)
LEAF AREA
SHOOT DRY WT.
RGR
WHITE CLOVER
STEM LENGTH
ROOT/SHOOT RATIO
PROTEIN
LEAF/SHOOT RATIO
TOTAL (CHO)
LEAF AREA
SHOOT DRY WT.
STEM DRY WT.

more limiting growth conditions. (i.e. the low light irradiance).

It is interesting to speculate that the more pronounced effects of the spectral treatments are shown with sorghum and soybean because they were grown under more limiting temperature conditions, as compared to ryegrass and white clover which were grown under conditions close to their optima. In respect of this issue, Rajan et al (1971), in a study similar to that presented here showed a marked temperature x light source interaction with Gossypium, Helianthus, Phaseolus and Zea which depended partly on the parameter recorded and partly on the species studied. Part of this complexity was discussed as being due to the varying growth potential of species at low and high temperatures but it was also shown that important contributing factors can be the temperature differences between the ambient air and the plant parts.

Pallas and Michel (1971) also examined the infra-red component of artificial light sources but found that in Zea, Phaseolus, Gossypium, and Glycine, although higher leaf temperatures were observed under high infra-red treatments, growth was not significantly increased. With Sorghum vulgare, high infra-red did not increase the leaf temperature but did produce better growth than the low infra-red treatment. In the temperate species tested, although leaf temperatures were generally below ambient and were not affected by the proportion of infra-red, Pisum and Vicia grew less, Avena grew equally, and Brassica grew better at high infra-red indicating the complexity of the environment and plant responses being examined.

In the present study, no measurements were taken of leaf and root temperatures in relation to the ambient temperature, but it is conceivable that these may have varied between the blue-biased (8 kw of lighting) and the red-biased (16kw) treatment. This could arise through either an increased radiant heat loading on the water screen, and therefore an increased loading on the plants in the room, or simply through the higher near infra-red (700-1400 nm) content of the spectral output recorded under each treatment.

Table 68 shows that the near infra-red content in the red-biased treatment was 5-fold greater than that in the blue-biased treatment. This could account for such differences as shown in the initial dry-weight data recorded in each of the spectral treatments. However, the relationships were not altogether simple as is shown by differences between species, spectral treatments and light irradiance levels and in this respect the spectral treatment responses are considered the primary influence in each of the parameter responses studied. Consistent leaf ventilation, leaf orientation and whole plant effects would also tend to minimize this possible temperature effect.

2. Morphological

2.1. Division of Assimilates.

The results for the ratios of plant parts in both the Spectral Bias and Spectral Balance studies show a noticeable influence of light spectra on the division of assimilates between the various plant components. It is apparent that the blue-biased treatment increased both the leaf:shoot and root:shoot ratios whereas the red-biased treatment, in comparison, increased the petiole:shoot, stem:shoot and associated sheath:shoot ratios to a greater or lesser extent depending on each of the species studied. Equally decreasing the irradiance level also affected these ratios, generally by increasing the spectral influence.

Helson (1965) showed low root:shoot ratios with high incandescent supplementation treatments agreeing with the red-biased treatment results presented above. Rajan et al (1971) examined root-weight ratios (RW/PW) and found that the inclusion of incandescent lamps in the light source (fluorescent tubes) depressed the ratio significantly in Phaseolus and Zea but had no effect on Helianthus and Gossypium where the ratio was similar under all treatments. There was also a significant interaction, in the two species showing a response, between the light source and treatment temperature. Considering first the root:weight ratio for Zea, between 10 and 20°C the ratio was depressed as the proportion of incandescent lamps increased: this negative response was less marked between 25 and 30°C

while at 35°C it became positive. For Phaseolus over the whole range of temperature there were only small differences in the effects induced by fluorescent lighting and a low proportion of tungsten lamps, whereas for a high proportion the ratio depressed at some temperatures but not at others.

Mitchell (1955) with paspalum, cocksfoot and perennial ryegrass found a reduction in root:shoot ratio with an increase in temperature or a decrease in light irradiance and Luxmoore and Millington (1971) with perennial ryegrass showed an increase in root:shoot weight ratio with an increase in irradiance. Silsbury (1971), however, found that the proportion of the total dry matter occurring as root in perennial ryegrass seedlings was not influenced by the environment in that there were no significant differences in root proportion between irradiance and temperature treatments at any time. Within each treatment no trend with time was evident but the average over all environments showed a fairly steady decrease with time.

With shoot components, Rajan et al (1971) found that all species did not react to the spectral treatments in a similar manner with respect to leaf-weight ratio (LW/PW) and stem-weight ratio (SW/PW). Only for Phaseolus and Zea did the inclusion of tungsten lamps enhance the leaf-weight ratio. For the stem-weight ratio, apart from the positive effects of tungsten illumination on Zea, the changes in the other species were either not significant or barely significant. This latter response was partly dependent on temperature as shown in Zea where the partial substitution of tungsten lamps favoured the stem:weight ratio at all temperatures apart from 35°C, whereas in Phaseolus, the ratio was enhanced by fluorescent lighting at 10 and 15°C but was diminished at 35°C.

2.2. Leaf Area, Leaf Shape and Leaf Number.

In the Spectral Bias experiment it is clear that the red-biased treatment markedly increased the leaf area in all species compared to the blue-biased treatment. The increase in area under the red-biased treatment was coincident with an increase in mean leaf weight per plant which under some conditions

corresponded to a decrease in dry weight per unit area of the leaf. Similarly the relative rate of leaf area expansion was highest under red-biased treatment conditions in most cases. The increase in leaf area is largely dependent on the increase in individual leaf size since leaf number was only slightly affected by spectral quality. Data for last mature leaf length and width indicate that both of these parameters are increased under red-biased conditions thus resulting in the increase in area.

Although the leaf area of plants of each of the species studied showed marked changes under the Spectral Bias experiment conditions there were only small affects on leaf area under the Spectral Balance experiment conditions. Similarly, dry weight per unit area, relative rate of leaf area expansion and leaf shape (i.e. length and width) were little affected by the Spectral Balance treatments.

Whereas in both these experiments the quality of light influenced leaf morphology and development it is clear that the light quantity (i.e. irradiance) had only a small influence on these parameters. In most instances increasing the irradiance did not increase leaf area and actually decreased it in some cases within the ranges studied. For example, in the Spectral Balance experiment, the high irradiance treatment ($250\ W\ m^{-2}$) markedly depressed leaf area in soybean. The absence of a response of leaf area to increasing irradiance reflects on the RLAGR values which, by derivation, also showed no differences. However, it was clear that the higher irradiances did increase leaf weight and consequently the dry weight per unit area in each species.

In relation the overall plant growth form, it is noted that although the leaf area per plant for each species was highest under the red-biased treatment, the leaf:shoot ratio was in each case highest under the blue-biased treatment. On a weight basis, therefore, the blue-biased treatment enhanced leaf tissue formation relative to other tissue formation but this ratio can not be used as an indication of relative leaf areas under each of the spectral treatments.

The results in relation to light irradiance levels, agree well with previously reported data. Mitchell and Soper (1958) found that an increase in light irradiance shortens and widens leaves of both Lolium and Paspalum and Freind, Helson and Fisher (1962) found an increase in temperature to decrease, and an increase in light irradiance to increase, the breadth of Marquis wheat leaves.

The results for leaf number indicated that there was little influence of light irradiance on the rate of leaf appearance, and thus final leaf number, in these experiments. High irradiance marginally increased leaf number and thus the rate of leaf emergence which agrees well with the results of Mitchell (1953) who found for ryegrass that the rate of leaf appearance was influenced more by a temperature increase from 10°C to 20°C than by a substantial increase in irradiance. Silsbury (1971) with ryegrass also found that the leaf appearance interval decreased markedly with increase in temperature from 10° to 20°C but was not affected by a further increase to 30°C. The interval decreased with increase in irradiance at each temperature particularly at the lower irradiance level but to a lesser extent at higher irradiances; there was an apparent interaction between temperature and light.

In general, therefore, the main spectral influence on the leaves of plants under each treatment has been on the leaf dimensions of length and width, and therefore on area, and on thickness. Since there was only a small difference in leaf number under each treatment there appears to have been no major spectral influence on leaf initiation.

Borrill (1961) reported for Lolium temulentum that differences in blade width mainly reflected differences in cell number whereas changes in blade and sheath length resulted mainly from differences in cell length. Since changes in both width and length (in parallel) occurred in response to each spectral treatment it is possible that both number and size of cells have been affected. However there is also the relative effects of each treatment on the vascular and mesophyll growth of the leaves which will also regulate their ultimate shape.

2.3. Stem Length.

It is clear from the Spectral Bias experiment that the type of responses noted were the same for each species and irradiance level; that is, the red-biased treatment increased stem length compared to the balanced and blue-biased treatments respectively. Relative spectral effects were the same at both irradiance levels although the differences were smaller at the higher irradiance where stem length under each treatment was decreased. Similarly, in the Spectral Balance experiment, the spectral treatments had only a small effect on stem length wereas the irradiance treatments produced more significant responses; in species where a response was noted, stems were significantly shorter under the high irradiance compared to the low irradiance conditions examined.

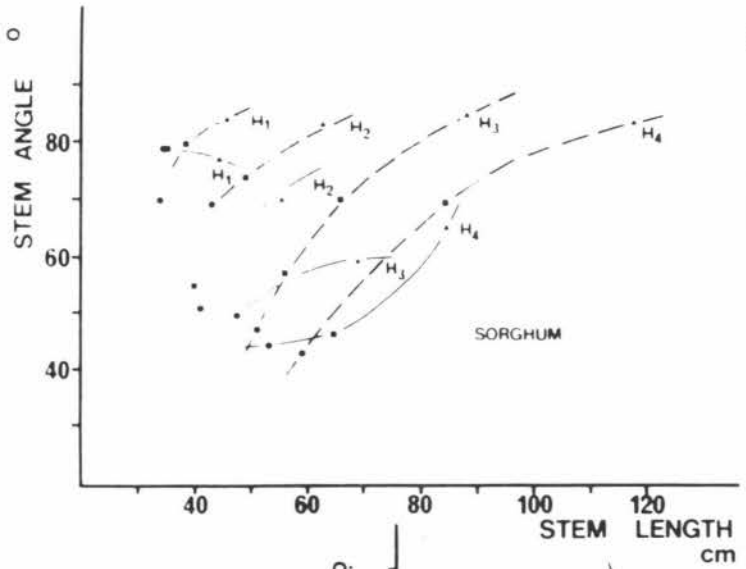
The increase of plant stem length under a red-bias or red light treatment has been well established by other investigators. Rajan et al (1971) for example, found that stem length significantly responded to a low proportion of tungsten supplementation in Gossypium, Helianthus, Phaseolus and Zea while, apart from the latter two, the height was further increased by a high proportion of tungsten lighting compared to fluorescent lighting alone.

Clearly then, there is obviously an underlying series of control mechanisms within the plants metabolism which are influencing the partitioning of the photosynthetic assimilates to the various plant components. The changes in leaf, root, stem and petiole:shoot ratios all indicate that there is a change being made by the plant in response to each spectral treatment which will influence the subsequent plant form and its potential to photosynthesize. This response will be cumulative in nature and the differential between treatments will increase as the plant grows, i.e. with time under treatment, unless the plant system adapts in some way to the spectral influence and a reversion to a "white" light or balanced spectrum plant-type occurs. Obviously, from the results, there was no clear adaptation of the plants under these treatments and the relative differences between spectral treatments,

Fig. 34. Stem Angle vs Stem Length.

Fig. 35. Stem Angle vs Tiller Number.

Fig. 36. Tiller Number vs Stem Length.
Spectral Bias Experiment. Data presented for high and low irradiance treatments, all harvests and spectral treatments.
Coding as used in Figs. 14–32.
H_1–H_4 represents Harvest 1 – Harvest 4.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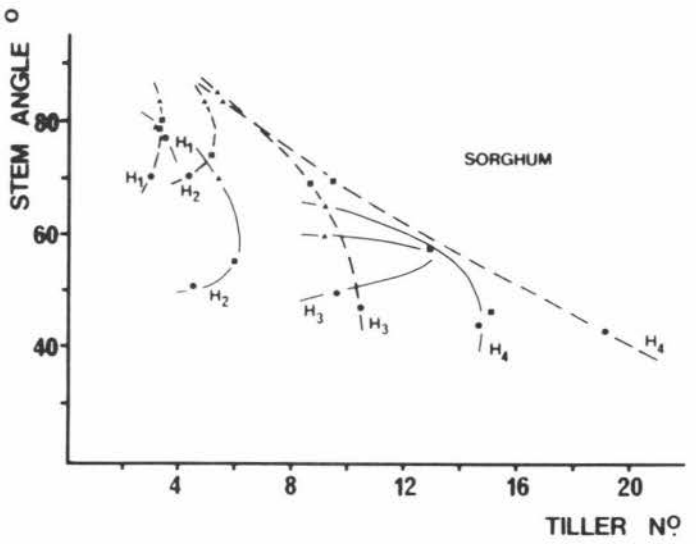
60
40
40
60
80
100
120
STEM LENGTH
cm
SORGHUM
H1
H2
H3
H4


STEM ANGLE °
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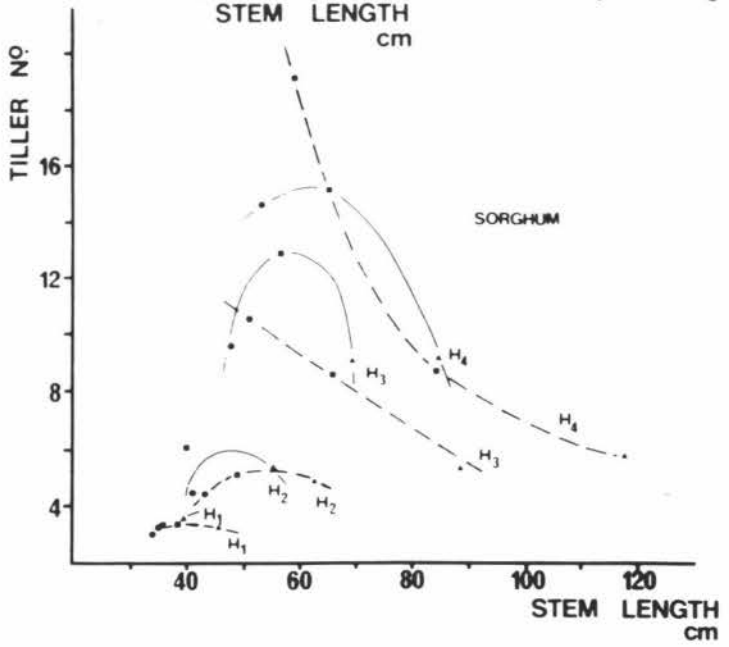
60
40
4
8
12
16
20
TILLER Nº
SORGHUM
H1
H2
H3
H4


TILLER Nº
16
12
8
4
40
60
80
100
120
STEM LENGTH
cm
SORGHUM
H1
H2
H3
H4

as measured, for example, by the plant part ratios, became greater with time under treatment.

2.4. Sorghum Stem Length, Stem Angle and Tiller Number Interactions.

There appeared to be, from the data presented in Fig 23, 24 and 25 an interaction between stem angle, stem length and tiller number. These relationships are presented in Fig 34, 35 and 36. Fig 34 shows the relationship between stem length and stem angle at each harvest time for each spectral treatment at both irradiance levels. Generally, increasing stem angle was highly correlated with increasing stem length under all conditions tested. The results from the low irradiance treatments showed more consistent trends than those for the high irradiance treatments but basically the results for each irradiance were the same.

The relationships between stem angle and tiller number, and tiller number and stem length were considerably more complex (Figs 35 and 36). Under the low irradiance conditions high tiller number corresponded to low stem angles and short main stem lengths, particularly after long periods of time under each spectral treatment. Under high irradiance conditions, the relationships were much less clear and interactions between the spectral and irradiance treatments were shown. In general, the red- and blue-biased results show the same reponses relative to each other, but in these treatments the balanced treatment results were displaced from the typical responses shown under the low irradiance treatment. Reference to the individual results for each of these three parameters indicate that the variability in tiller development was, in the main, responsible for the differences shown in these relationships.

This interrelationship of a reciprocal influence of light quality on the growth and development of various parts of the plant appears to be an apical dominance correlation. Philips (1969) lists three ways in which apical dominance is

manifest in plants:-

(a) by complete or almost complete inhibition of growth in the axillary, or lateral buds by the presence of an apical bud.

(b) by inhibition of the growth of one shoot by the presence of another dominant shoot, and

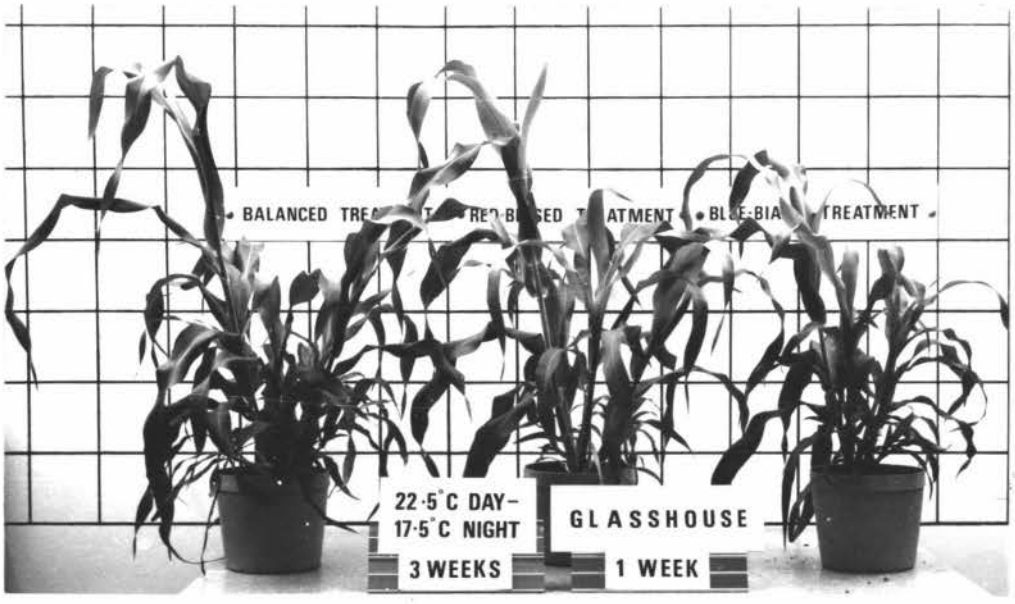
(c) in effects of the apical part of the shoot upon orientation and development of lateral organs such as branches, leaves, rhizomes and tillers. The degree of apical dominance in a shoot is determined by genetic and environmental factors and is also greatly influenced by the physiological age of the plant.

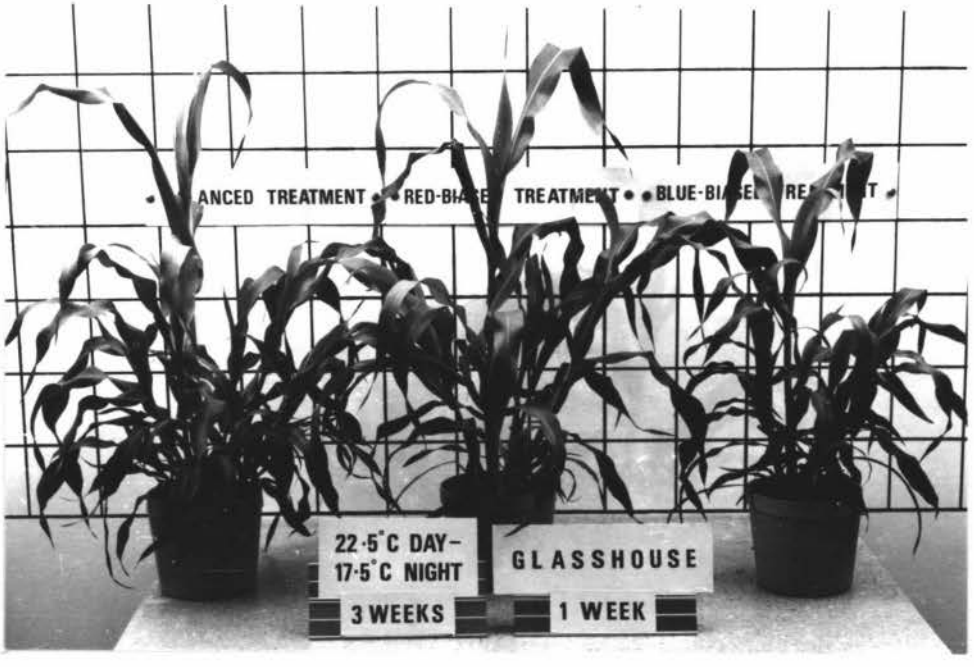
The responses shown then were of the apical dominance type where the degree of axillary bud development (i.e. tillers) was inhibited by the relative dominance of the apical bud. This held when either the main shoot was either longest or more upright.

The main stem angle - stem length - tiller number interaction was further examined in a transfer study. Plants were grown under each of the biased spectral treatments for three weeks and were subsequently grown for 8 days under summer glasshouse conditions in order to examine whether or not the effects demonstrated were reversible under daylight conditions.

Plates 9 and 10 show face and side views of these plants and, although pre-treatment differences between the three treatment plant types are still manifest, the form of growth of each is more similar than under the spectral treatments.

Examination of the main stem showed clearly that the reversion to a more upright form was brought about by a process occurring at the stem base rather than a bending in the main-shoot itself. Dissection studies revealed that the apical meristem was still in the vegetative form at this growth stage and that consequently no elongation of the true vegetative stem had occurred. It is apparent then that the effect on stem angle is due to a process occurring in the true stem region of these plants.





Plates 9 and 10.

These plants have developed from seedlings under the three spectral treatments (low irradiance) for three weeks - see plates 4 and 8 and were subsequently grown for 8 days under summer glasshouse conditions.

Although pre-treatment differences between the three plants are still manifest, the form of growth is more similar than that under each of the spectral treatments.

Hence, this is a further obvious influence of light quality on the division of assimilates within the plant where, like the change in plant-part ratios, the change in one growth factor results in a change (often reciprocal in nature) in others. With respect to a wavelength influence on leaf area this reflects in a change in photosynthetic potential and a subsequent change in growth rates; here with the influence on stem length, and presumably on stem angle, the change is reflected in a shift in the degree of apical dominance and hence a parallel change in the amount of tiller development.

2.5. Morphogenesis Response Control Mechanisms.

It is not clear from the present study what the nature of the various control mechanisms for the partitioning of assimilates might be. It was seen in Section IV 2.11. that considerable changes in carbohydrate and protein levels, for example, occurred under these same treatments and these compounds must inevitably reflect concurrent changes in other plant assimilates, their rates of turnover, accumulation and transport to various parts of the plant. The implications of these changes in plant part ratios in relation to the photosynthetic capacity of the plant are discussed later in Section V 3.

The largest amount of evidence centreing around wavelength effects on plant development is established on the functioning of phytochrome and predominantly red far-red response systems (see Section II 1.3.). No doubt in these current studies where the red, far-red and blue regions of the spectrum were dominant, the role of phytochrome played a major part in the control of plant growth and development. In examining previously reported literature the conclusion that an optimum action of phytochrome requires a favourable, relatively low ratio $[P_{730}]/[P]$ (where $[P_{730}] + [P_{660}] = [P]$) is supported by the results of yield experiments where different types of fluorescent lamps were compared. The greatest yield of tomato plants in the vegetative stage were produced by a lamp combining a small amount of blue light with a large amount of red light. The yield could be enhanced by the addition of some emission in the photosynthetically ineffective

far-red region, above 700 nm (Thomas and Dunn, 1967a - see section III 5.3.3.). It is interesting to note that natural light to which the plant is adapted is characterized by similar amounts of red and far-red light.

The effect of the spectral composition of the fluorescent light on growth and reproduction of mature plants was evaluated with bean by these same authors. In general the results with bean agree with those for tomato in that best growth (i.e. best yield) was obtained with a lamp high in red light emission, a moderate amount in the far-red, and very little in the blue part of the spectrum (Thomas and Dunn, 1967b).

However, it is not clear in these papers as to why the increase in dry-weight occurred - presumably because of a greater leaf area and hence greater light interception and utilization - nor is there evidence relating to the form of the plants under study, These results could infer unsatisfactory plant growth under the red predominant conditions even where the increase in plant weight was greatest. Rajan, Betteridge and Blackman (1971) found a similar result to Thomas and Dunn (1967) with tungsten supplementation of fluorescent lamp systems, i.e. increasing the dominance of red and far-red light increased the dry-weight yield, but in this case changes in plant form (stem length, leaf area) and dry-matter distribution (plant part ratios) present similar results to the Spectral Balance and, more particularly, the Spectral Bias study. Interestingly, in none of these studies have the authors attempted to relate their observed responses back to actual physiological process such as, for example, to processes relating to phytochrome control. It would be naive to expect that these data interpretations would be straight forward, but since phytochrome is known to mediate formative processes such as leaf enlargement and stem growth (internode elongation) it is reasonable to expect that each of these broad spectral treatments are conditioning the phytochrome system and establishing different steady-state equilibria between the various phototransformations possible.

This steady-state equilibrium under each particular type of irradiation is reached within a short time, depending on the irradiance level of the radiation applied. The steady-state equilibrium itself is determined by the absorption spectra of the two forms, by the quantum efficiency of the interconversion in both directions, and by the energy distribution in the spectrum applied. Since this latter aspect (i.e. the energy distribution of the spectrum) varied markedly in each spectral treatment in the Spectral Bias experiment, then the steady-state equilibrium can also be expected to have varied. This is in contrast to the Spectral Balance experiment where the similar spectral distributions resulted in similar plant responses.

The wide variety of types of phytochrome responses in plants do not immediately provide any useful clues as to the mechanisms of action. Two main different mechanisms have been suggested. Hendricks and Borthwick (1965) speculate that control over a diversity of expressions can be achieved by regulation of a basic metabolic reaction or of cell permeability. Mohr (1966) proposes control by gene repression or activation. In neither case is it clear how phytochrome interacts with the control system proposed.

This discussion, like many on photomorphogenesis, has centred around the role of phytochrome in the plant system, but this does not preclude the possibility that other photoreceptors and other wavelength regions are active and are controlling aspects of plant development.

2.6. Relationships to Other Environmental Studies.

Since the treatments other than light quality in these experiments were selected as a compromise between the four species studied, it was considered essential to relate these particularly to the previously determined optima for temperature and irradiance as found by other investigators.

(a) Effects of Temperature.

All festucoid grasses examined to date grow relatively

well at low temperatures (e.g. 10°C), have an optimum temperature for growth below 27°C (usually 20-25°C), and grow poorly at temperatures around 30-35°C. Mitchell (1956) for example found the highest percent increase in shoot weight per day for Lolium perenne at a mean day temperature of 20-22°C which was similar to other festucoid grasses studied. Similarly Silsbury (1971) found RGR to be maximal at 20°C at each light irradiance investigated and increased toward a maximum with increased irradiance at each temperature. Maximum RGR for seedling plants of L. perenne was about 25% per day.

The non-festucoid grasses, on the other hand, have a high temperature optima, grow vigorously at 35°C, and extremely slowly at temperatures below 15°C, as shown previously with Paspalum dilatatum (Mitchell, 1956), Sorghum sudanense (Sullivan, 1961) and S. halepense (Ingle and Rogers, 1961). Unfortunately results for Sorghum bicolor do not appear to be present in the literature.

Similar marked differences between the two groups also occur in response to fluctuating day and night temperatures. Sprague (1943) found considerable growth at 12°/4°C, optimal growth at 21°/12°C, and none at 38°/30°C for a range of festucoid grasses, whereas there was no growth at 12°/4°C and optimum growth between 30°/21°C and 38°/30°C in the non-festucoid Sorghum sudanense. Similar results tend to indicate that decreased night temperatures increase top and root growth in the festucoids but reduce growth in the non-festucoid grasses (Hiesey, 1953; Ingle and Roberts, 1961).

In contrast to the festucoid grasses, white clover has been shown to have a higher temperature optima of 24-25°C (Mitchell, 1956), but similar maxima and minima responses. Similarly, it is expected that soybean has an optima in the 25-30°C range because of its sub-tropical nature, but evidence of its response under various environmental conditions do not appear to exist in the literature.

From this brief survey it appears that the choice of

temperature in these studies has been close to the optimum for perennial ryegrass and white clover, near to the optima for soybean, and sub-optimal for sorghum. The situation of limiting or near-limiting conditions, however, does not appear to have been approached for the tropical species as adequate growth was obtained.

Similarly, it is considered that the humidity (V.P.D.) and daylength conditions used are sufficiently "normal" to pose no major limitations on the growth of these various species.

(b) Effects of Light Irradiance.

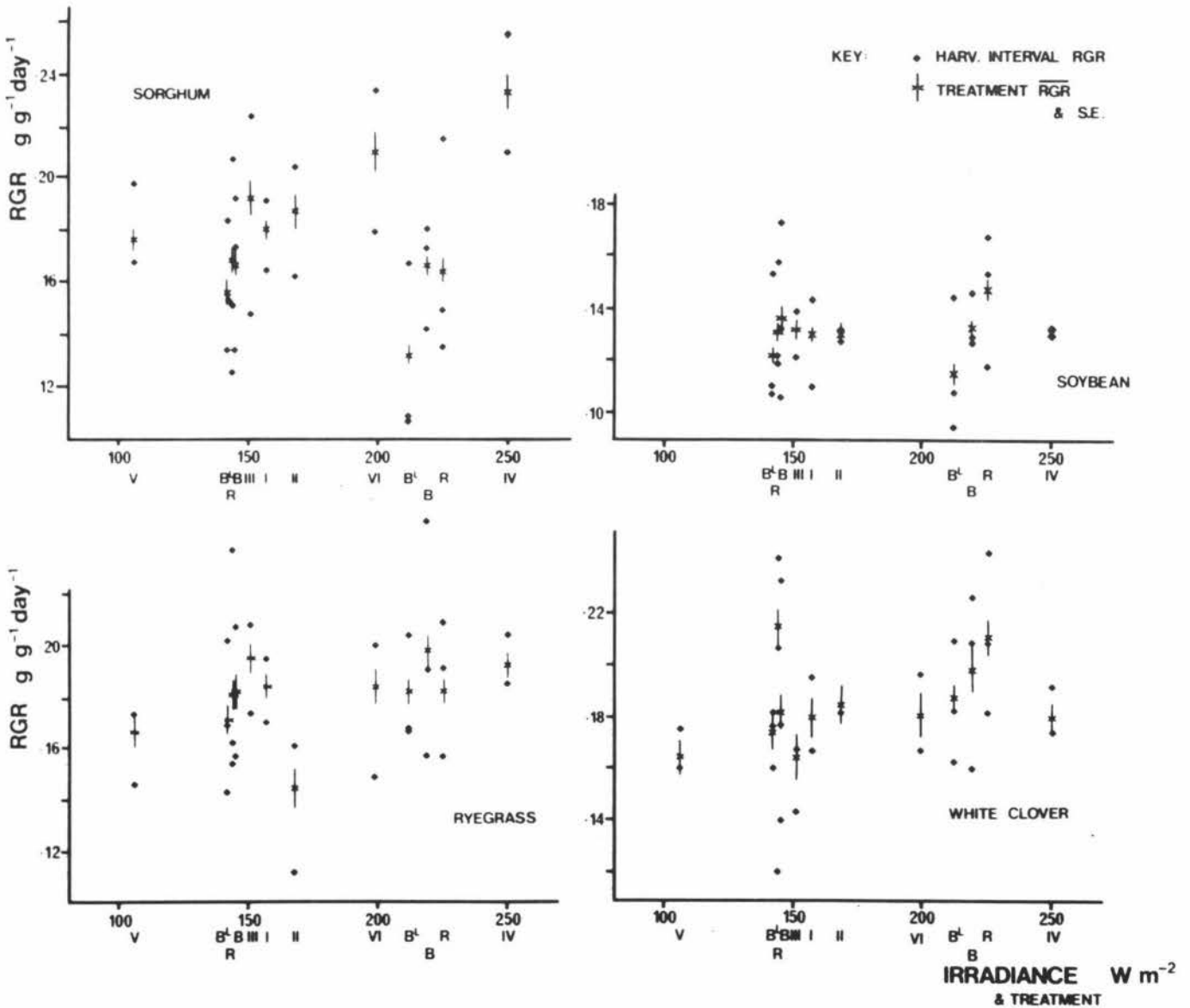
The influence of light irradiance on growth rate has often been examined by using natural daylight modified by shading (Mitchell, 1953; Blackman and Black, 1959). It is only recently that sufficiently high irradiances have been available in controlled environments to enable the effects of a wide range of levels on plant growth to be studied.

Blackman and Black (1959) showed maximum growth rates at 80-100% of full summer daylight in most temperate grasses such as L. perenne, reduction below this level reducing the growth rate. Later work in controlled environments (Cooper, 1968) has shown that in L. perenne grown in a 17hr day at 20°C, RGR increases up to 0.20-0.25 g g^{-1} day^{-1} at about 15,000 lux and then remains steady, even up to 43,000 lux. These figures corresponded to the RGR's obtained outdoors in mid-summer.

Silsbury (1971) for Lolium seedlings found rates of 0.20 g g^{-1} day^{-1} at 50 W m^{-2} and 0.24 g g^{-1} day^{-1} at 117 W m^{-2} agreeing closely with Cooper's results. However, Silsbury did demonstrate an increase in RGR with increasing irradiance but failed to show an optima within the irradiance range studied. This absence of optima held for 10°, 20° and 30°C temperatures.

Fig 37 shows the RGR and SE's for each treatment in the

Fig. 37. Spectral Balance and Spectral Bias Experiments.
Figs of harvest interval and mean Relative Growth Rates (with S.E's.) plotted against visible irradiance for all treatments and species studied.


KEY
HARV. INTERVAL RGR
TREATMENT $\overline{RGR}$ & S.E.
SORGHUM
SOYBEAN
RYEGRASS
WHITE CLOVER
RGR g g^{-1} day^{-1}
IRRADIANCE W m^{-2}
& TREATMENT

Spectral Balance and Spectral Bias experiments. Harvest interval RGR values are also plotted to give an indication of the changes possible in RGR over the growth period due to ontogenetic drift. In general the values obtained in these experiments have shown an increase with an increase in irradiance from 100 to 250 W m^{-2} and are lower than the values quoted by Silsbury and by Cooper. The most obvious explanation is that the increased plant size in these experiments will account for the lower $\overline{RGR}$ value since in several cases harvest-interval RGR values exceed 0.20 g g^{-1} day^{-1}. Cooper (1968) and Silsbury (1971) also used longer photoperiods (17 hr and 16 hr respectively) than the present study (12 hr) which would also account for these higher values.

Forde (Pers. comm., 1971) found RGR values for soybean (cv Merit) to be unaffected by irradiance at low temperatures ($20^{o}/12.5^{o}C$) but to increase with increasing irradiance at higher temperatures ($27.5^{o}/20^{o}C$). A similar result was determined for sorghum (NK 145) and for white clover (N.Z. Huia). The results are shown in the following table and are for mature plants in the vegetative growth stage prior to flowering.

Table 21

RGR (g g^{-1} day^{-1})

Day/Night Temperature	$20.0/12.5^{o}C$			$27.5/20.0^{o}C$		
Irradiance W m^{-2}	100	150	200	100	150	200
Soybean	0.09	0.09	0.08	0.13	0.14	0.15
Sorghum	0.11	0.12	0.12	0.17	0.26	0.25
White clover	0.14	0.14	0.13	0.11	0.14	0.15
Perennial Ryegrass	0.13	0.15	0.16	0.11	0.14	0.13

The ryegrass values are included as a comparison with previously published results and show lower values compared with studies on seedling material (e.g. Silsbury, 1971).

These are in general agreement with the Spectral Balance and Bias experiments and show increasing values with increasing irradiance levels.

The soybean and sorghum results are typical of the tropical plant type and show highest $\overline{RGR}$ values with high temperature/high irradiance treatments. Soybean, in the Spectral Balance experiments, shows no obvious increase in $\overline{RGR}$ with increasing irradiance in agreement with Forde's data; the actual $\overline{RGR}$ results are similar to Forde's high temperature figures. Similarly, the results for sorghum agree well with markedly increased values for the high irradiance treatments, however, one anomally does appear evident. In comparing the Spectral Bias experiment results the differences between $\overline{RGR}$'s are very small between the high and low irradiance treatments as compared with the results from the Spectral Balance experiments where large differences were recorded. No obvious explanation for these results is available and this effect was not noted for the other species studied.

White clover also showed a considerable response to increasing irradiance with $\overline{RGR}$ values for spectrally non-biased treatments ranging from 0.16-0.20 g g^{-1} day^{-1}.

3. Photosynthesis and Dry-Matter Yield.

3.1. General.

It is important from the present study that an attempt is made to account for the observed responses in relation to current understanding of the various physiological phenomena involved. If such predictions are plausible then it should ideally be possible to extrapolate the data collected in this and other studies, to predict plant growth, and morphological and biochemical responses which are likely to occur under any known artificial light spectra in controlled environment conditions.

For example, it should be possible from published data on quantum yield, leaf absorptance and leaf orientation for each of the species studied, to make some predictions on the relative

rates of dry-matter accumulation under each of the spectral treatments, particularly the contrasting biased treatments, examined in these studies.

The results presented for mean dry-matter accumulation (Section IV 2.3.1.) show that in all the four species studied, the mean dry matter accumulation decreased from the red, through balanced, to the blue-biased treatment. It is possible that these effects could have arisen from the photochemical efficiency varying among spectral treatments.

However, it was also possible that the effects were brought about through differences in the quantity of photochemical energy actually received by the photosynthetic system. independently of photochemical considerations.

This alternative was examined as follows:
Using data to be published shortly (McCree, 1972) for quantum yield and leaf absorptance for sorghum, soybean and white clover, together with photon flux density values for each treatment (Table 7) the following relative results were obtained which indicate that, with certain assumptions, accurate predictions can be made given the appropriate information on the light environment under study. (Table 22).

3.2. Interception of Photons.

It is apparent from the results obtained in the Spectral Bias experiment that the plant altered its partitioning of assimilates to the various plant parts in response to each spectral treatment. There was, for example, generally an increase in root:shoot ratio under blue-biased conditions indicating that a smaller proportion of photosynthates were being utilized to produce further assimilating tissue (leaf area) under this treatment. (see Section V. 2.1.).

An assessment of the relative "interception" area (i.e. total leaf area) per plant under the blue-biased and balanced treatments, in relation to the red-biased treatment, was made by assessing the area ratios at each harvest (2-4), and by

Table 22

Spectral Bias Experiment

Relative Relationships of Leaf Area, Photon Flux Absorption and Dry-matter Accumulation

All Species, Spectral and Irradiance Treatments
(Full Description and Derivation in Text)

SPECIES / TREATMENT	Mean Leaf Area Ratio	Photon Flux Density	Photon Flux Ratio	Rel. Photon Flux Interceptn.	Photon Flux Absorptn.	Photon Flux Absorptn. Ratio	Relative Absorptn. Ratio	Relative Mean D.M. Accumulatn.
SORGHUM								
High Irradiance								
Blue Biased	0.57	78.8	0.92	0.53	67.6	0.94	0.54	0.58
Balanced	0.83	88.6	1.04	0.86	75.1	1.04	0.87	0.70
Red Biased	1.00	85.5	1.00	1.00	71.9	1.00	1.00	1.00
Low Irradiance								
Blue Biased	0.60	54.3	0.94	0.56	46.71	0.96	0.57	0.53
Balanced	0.76	58.9	1.02	0.77	50.09	1.03	0.78	0.75
Red Biased	1.00	57.9	1.00	1.00	48.81	1.00	1.00	1.00
SOYBEAN								
High Irradiance								
Blue Biased	0.59	78.8	0.92	0.54	71.54	0.93	0.55	0.71
Balanced	0.73	88.6	1.04	0.76	80.00	1.04	0.76	0.80
Red Biased	1.00	85.5	1.00	1.00	76.93	1.00	1.00	1.00
Low Irradiance								
Blue Biased	0.47	54.3	0.94	0.44	49.45	0.95	0.44	0.52
Balanced	0.79	58.9	1.02	0.80	54.82	1.05	0.83	0.78
Red Biased	1.00	57.9	1.00	1.00	52.30	1.00	1.00	1.00

Table 22 contd

SPECIES / TREATMENT	Mean Leaf Area Ratio	Photon Flux Density	Photon Flux Ratio	Rel. Photon Flux Interceptn.	Photon Flux Absorptn.	Photon Flux Absorptn. Ratio	Relative Absorptn. Ratio	Relative Mean D.M. Accumulatn.
RYEGRASS								
High Irradiance								
Blue Biased	0.94	78.8	0.92	0.87				0.88
Balanced	1.03	88.6	1.04	1.07				0.97
Red Biased	1.00	85.5	1.00	1.00				1.00
Low Irradiance								
Blue Biased	0.75	54.3	0.94	0.70				0.82
Balanced	0.98	58.9	1.02	1.00				1.08
Red Biased	1.00	57.9	1.00	1.00				1.00
WHITE CLOVER								
High Irradiance								
Blue Biased	0.60	78.8	0.92	0.55	68.81	0.94	0.57	0.62
Balanced	0.62	88.6	1.04	0.64	76.44	1.05	0.65	0.65
Red Biased	1.00	85.5	1.00	1.00	73.10	1.00	1.00	1.00
Low Irradiance								
Blue Biased	0.54	54.3	0.94	0.51	47.50	0.96	0.52	0.60
Balanced	0.76	58.9	1.02	0.77	50.92	1.03	0.78	0.92
Red Biased	1.00	57.9	1.00	1.00	49.64	1.00	1.00	1.00

taking a mean value as an approximation for this parameter. This will necessarily influence the results slightly, as the leaf area increase was not similar for each treatment but, increased at different rates for the separate harvest intervals under each treatment (see Section IV. 2.4.). These values calculated for the mean area ratio are presented in column (col) 1, Table 22.

The photon flux density for each of the spectral treatments was calculated previously (Table 7) and values for the visible flux are shown in col 2 with their ratios in col 3. Assuming that all the incident photon flux is absorbed uniformly per unit leaf area, then the product of the mean area ratio and the photon flux ratio will give an estimation of relative photon flux interception (col 4). This calculation assumes that there is an equal opportunity for absorption of the incident flux in each of the spectral treatments, that differences in leaf and shoot orientation are negligible, and mutual shading effects are either absent or small. Clearly each of these factors also varied to some degree under each treatment. Plant and leaf orientation obviously varied as shown in the measurements taken for sorghum (section V. 2.4.) and more subtly for the other species as shown in Plates 4-8. Intraplant mutual shading of leaves would have occurred to a degree, particularly in the older plants, and interplant shading certainly occurred immediately prior to each harvest to a small degree, although attempts were made to minimize this effect by carefully positioning the plants on the trolleys.

3.3. Absorption of Intercepted Photons.

Although the data is presented here for relative photon flux interception an allowance must be made in these values for absorptance of the incident energy particularly at specific wavelengths. Using McCree's (1972) results for leaf absorption, the photon flux absorption was determined by integrating 25 nm bandwidths over the visible range (400-700 nm) of the corrected photon flux density values (see Appendix 4). The photon flux absorption values and ratios are shown in col 5 and 6 respectively. Although it is clear that the correction made for absorption has altered the number of quanta available to the plant for photosynthesis, the ratio between the treatments has been altered only slightly. It is conceivable that

there may be a further error in accepting McCree's absorption figures for the plants grown under the current experimental conditions. It is known, for example, that the chl a : b ratio and the leaf thickness both changed in response to the spectral treatments and this may have influenced the absorptance by leaves of incident quanta from each treatment. However, as seen above, and for other environmental parameters discussed in McCree's paper, these are unlikely to greatly influence absorptance and would probably not, therefore, affect the absorption ratio.

The relative absorption ratio is therefore the product of the mean area ratio and the photon flux absorption ratio. A further assumption in the extrapolation of the relative absorption ratio to relative dry-matter accumulation is that absorbed quanta at any wavelength over the 400-700 nm visible bandwidth contribute equally to photosynthesis. This assumption is generally accepted (McPherson, 1969) and is supported by evidence from Bjorkman (1968), and McCree (1972) who indicates from his data that the use of the flux of absorbed quanta as a perfect measure of "photosynthetically active radiation" will systematically overestimate the effectiveness of blue light relative to red, but that for the practical purpose of defining "PAR" the differences are probably insignificant.

Finally the relative mean dry-matter accumulation was determined in a similar manner to the mean area ratio where values were derived using total plant dry-matter results (i.e. including root dry-matter) from harvests 2 and 3. These results are shown in col 8 from which it is clear that in a majority of cases the predicted ratios are closely similar to the actual ratios obtained under the experimental conditions. Where the actual results do not agree with the derived ratios in all cases (except one) this was due to high actual ratios under the blue-biased treatment. This is most likely due to low red-biased treatment ratios resulting from mutual shading effects under experimental conditions (increasing actual red values will decrease the blue ratios); that this is the most likely explanation is enhanced by the fact that the higher ratios were mostly found under low irradiance conditions where leaf areas were found to be greater.

It is apparent from these results that the initial (photomorphogenetic) response "advantage" of increased actual and relative leaf area under the red-biased treatment is retained by the plant subsequently and is reflected directly in the ratio of accumulated assimilates (total plant dry matter). This relationship was found to be consistent for all treatment conditions (spectral and irradiance) and for each of the species tested.

This means therefore that comparable flux densities of quanta above the plants gave production which varied with spectral quality and was directly dependent on the leaf area development. From the above discussion it is clear that regardless of the wavelength distribution of each radiation treatment, similar absorbed flux densities of quanta gave similar plant dry-matter production in terms of total root and shoot components.

Conversely, since the end dry-matter produced per unit of quantum number absorbed was the same this confirms that the quantum efficiency was the same for all wavelengths i.e. for all spectral combinations such as those used in these studies. If the quantum efficiency was not the same for each of the spectral treatments then the conversion differentials between each treatment leaf area and total dry weight would not have been the same and therefore would not have been equal to unity.

These results make it clear that the important (direct) influence of light spectra, whether artificial or natural, in relation to plant growth, is the influence of that spectra on leaf area development and, therefore, the indirect influence on the potential energy interception capacity of that plant system. Photosynthesis will be independent of the light quality and will depend solely on the number of absorpted quanta in the visible wavelength range.

4. Biochemical Analyses.

4.1. General.

The results from chlorophyll, starch, soluble sugar, protein and amino acid analyses indicate clearly that the spectral treatments studied have a marked influence on plant matabolism.

A general scheme for the results shown under these treatments, incorporating the results reported in the literature, is presented in Scheme 1.

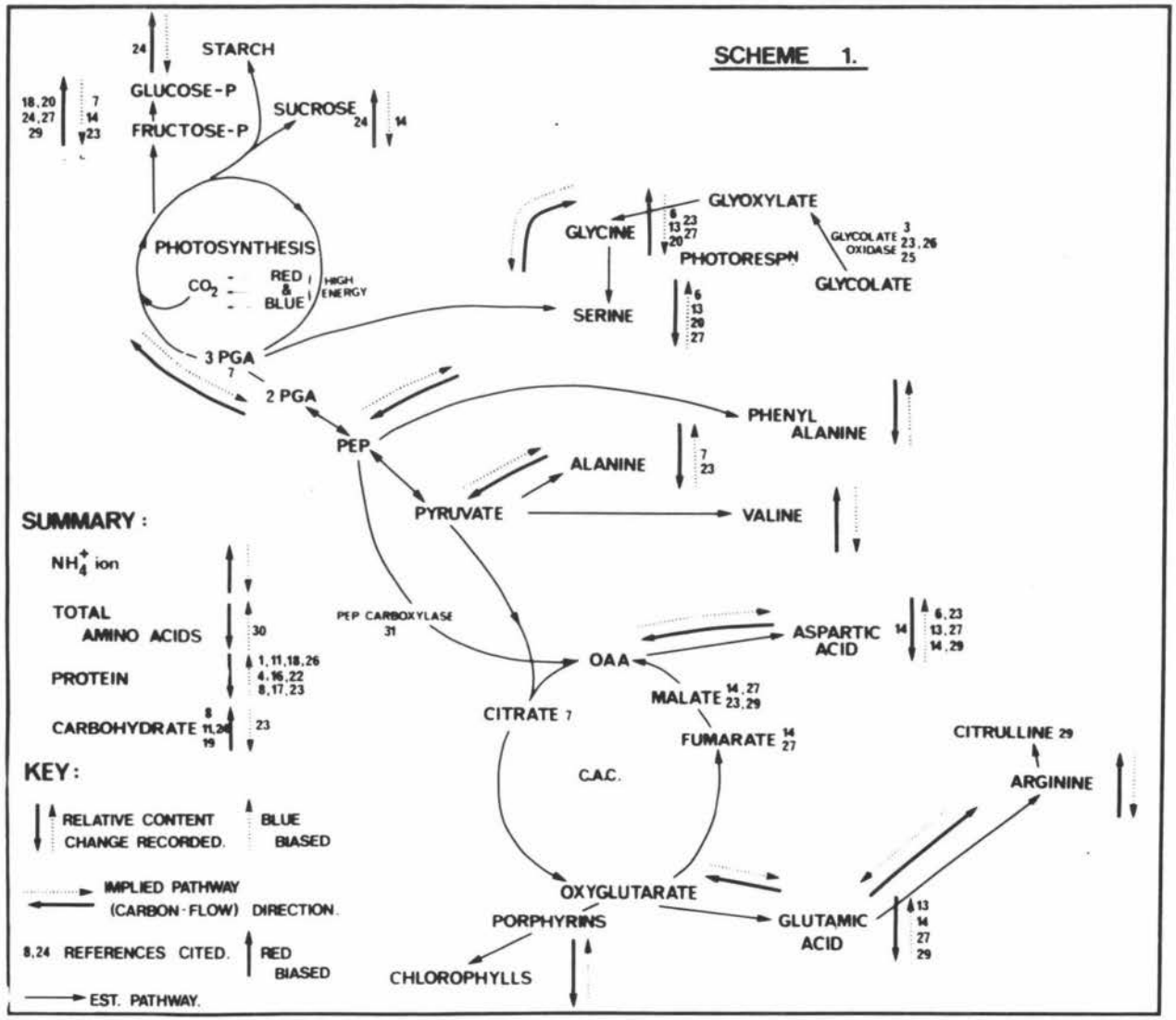
The vertical arrows indicate the relative direction the levels of each compound took under each treatment and the arrows along each pathway indicate the logical pathway direction (either as an actual direction or as a change in reaction rate) which must occur if the compound levels are changing. Numbers indicate the references repeating similar results for each response.

Two main aspects regarding the experimental results in relation to previously reported data are apparent. Firstly, the general effects shown for each spectral treatment agree well with published results in a majority of cases (the only marked exception is serine which showed results contrary to published information), and secondly the opposite spectral treatments have produced opposing metabolic responses indicating alternative sinks for the carbon dioxide synthesized under each particular spectral treatment.

The scheme presented indicates that red light enhances those metabolites which are not directly related to the citric acid cycle whereas blue light has a reverse effect. The general "switch point" in the scheme centres around phosphoenol pyruvate carboxylase which agrees well with the proposal of Mijachi and Hogetsu (1970) of a blue light stimulation of this enzyme.

4.2. Glutamic and Aspartic Acids.

Increase in aspartic acid levels under the blue-biased


SCHEME 1.
STARCH
GLUCOSE-P
FRUCTOSE-P
SUCROSE
PHOTOSYNTHESIS
CO_2
RED & BLUE
HIGH ENERGY
3 PGA
2 PGA
PEP
PYRUVATE
GLYOXYLATE
GLYCINE
PHOTORESPN
GLYCOLATE OXIDASE
GLYCOLATE
SERINE
PHENYL ALANINE
ALANINE
VALINE
PEP CARBOXYLASE
OAA
ASPARTIC ACID
MALATE
FUMARATE
CITRATE
C.A.C.
OXYGLUTARATE
GLUTAMIC ACID
CITRULLINE
ARGININE
PORPHYRINS
CHLOROPHYLLS
SUMMARY :
NH_4^+ ion
TOTAL AMINO ACIDS
PROTEIN
CARBOHYDRATE
KEY:
RELATIVE CONTENT CHANGE RECORDED.
BLUE BIASED
IMPLIED PATHWAY (CARBON-FLOW) DIRECTION.
8,24 REFERENCES CITED.
RED BIASED
EST. PATHWAY.

treatment agrees well with Krotkov (1964), Hauschild et al (1962a, 1962b) and Ogasawara and Miyachi (1970) who showed similar results from ^{14}C incorporation and turnover studies. Andreeva and Korozheva (1964), Miyachi and Hogetsu (1970) and Voskresenskaya (1967) produced similar results for aspartic acid and Ogasawara and Miyachi (1970) showed low glutamic acid levels under red light. Red-biased light decreased (compared with the balanced treatment) both glutamic and aspartic acid contents in contrast to the blue-biased results.

Interestingly, the blue-biased treatment not only enhanced glutamate formation from citric acid cycle stimulation but presumably also from arginine since arginine levels were lower under these conditions. The normal synthesis of arginine is via the ornithine cycle from glutamic acid. It would normally be expected then that if the glutamate level increased, as under the blue-biased treatment, then arginine would increase also. However, as noted above, the reverse effect was shown. Red-biased light enhanced arginine content.

4.3. Carbohydrates.

At the opposing end of the scheme the red-biased light enhanced glucose, fructose and starch levels whereas the blue-biased treatment depressed these carbohydrate contents. The red enhancement of glucose and fructose agrees well with results from Ogasawara and Miyachi (1969, 1970), Szasz and Barsi (1971), Krotkov (1964) and Salcheva et al (1964) who present evidence for stimulation of sugar synthesis, increase in sugar accumulation and an increase in ^{14}C uptake into free sugars under red light conditions. Tregunna et al (1962) with tobacco, however, could find no evidence for this response. Increase in starch levels under red light have been shown in Vicia by Szasz and Barsi (1971).

The decrease of glucose and fructose levels shown under the blue-biased treatment is similar to that reported by Voskresenskaya (1967), Hauschild et al (1962a, 1962b), Das and Raju (1965) and Szasz and Barsi (1971). Low starch levels under blue-biased light have also been reported by Szasz and Barsi (1971).

4.4. Photorespiration Intermediates.

The spectral treatments have also influenced the levels of the photorespiration intermediates, glycine and serine. The glycine level decreased under blue-biased conditions in agreement with results from several workers (Hauschild et al, 1962; Tregunna et al, 1962) and increased under red-biased light similar to reports from Krotkov (1964) and Tregunna et al (1962). However, both Andreeva and Korozheva (1964) and Voskresenskaya (1967) found blue enhancement of glycine synthesis in contrast to the results presented here.

In contrast to glycine, the serine results do not agree well with published information. Hauschild et al (1962), Krotkov (1964) and Tregunna et al (1962) all demonstrated a decrease in serine accumulation under blue light conditions, and Krotkov (1964) showed an increase under red light conditions whereas Tregunna et al (1962) could trace no red light effect at all. However, Andreeva and Korozheva (1964) found a similar response under blue light conditions as that presented here.

The explanation for these results appears to lie in the association of these amino acids with the glycolate pathway. Any shift in glycolic acid metabolism or in photosynthesis will independently alter the rates of formation and turnover of glycine and serine. Furthermore, these amino acids are also in equilibrium with each other and with other glycolic acid metabolism intermediates and so will change depending on the reaction sequence. Blue light activation of glycolate oxidase has been shown by Voskresenskaya et al (1970) and by Voskresenskaya (1967) and glycolate levels have been shown to decrease under blue light conditions by Hauschild et al (1962) in agreement with the enzyme data.

Related to glycolate oxidase enhancement by blue light is evidence that oxygen absorption is increased also by short-wave radiation (Voskresenskaya and Grishina, 1960). The oxidase taking part in the absorption of oxygen by leaves in the light in this process, differs in its susceptibility to

sodium azide from the oxidases in the respiratory cycle, indicating that photorespiration is involved. Lee et al (1971) present evidence that the blue light stimulated oxygen uptake is mediated by the coenzyme FMN which may function directly as the primary light receptor.

4.5. Other Amino Acids.

Enhancement of alanine levels under the blue-biased treatment agreed well with ^{14}C uptake reports (Das and Raju, 1965) and with rates of synthesis (Voskresenskaya, 1967) previously examined under blue light conditions. Andreeva and Korozheva (1964) however, found that blue light suppressed alanine synthesis which contrasts with other results. The red-biased treatment results show depressed alanine synthesis.

Results for phenylalanine were similar to those for alanine and agreed generally with the concept of blue enhancement of amino acid synthesis. Valine, however, showed an enhancement under red-biased conditions and a small suppression under blue-biased conditions in comparison with the other amino acids studied.

In addition to the results and reports detailed above, an interesting contrast is reported by Hess and Tolbert (1967). With Chlorella, they found that after growth in blue light, $^{14}CO_2$ fixation in white light produced the same ^{14}C distribution among products as in blue light. Algae grown in red light incorporated more ^{14}C into malate, aspartate, glutamate and alanine which is in contrast to all the other reports detailed here.

4.6. Summary.

The results for increased protein formation under blue-biased light conditions coincide with many published reports (e.g. Raghavan and De Maggio, 1971; Voskresenskaya et al, 1970; Kowallik, 1965; Pavlov, 1965; Pirson and Kowallik, 1964) and is contrary to the red-biased light response. Carbohydrate synthesis, on the other hand, was markedly increased under

red-biased conditions and suppressed under the blue-biased conditions. Szasz and Barsi (1971), Thomas (1967), Pirson and Kowallik (1964) and Bergfeld (1965) showed similar red light effects whereas Voskresenskaya (1967) reported a similar blue light suppression of carbohydrate formation.

In summary, therefore, the blue-biased treatment was shown to increase the level of many amino acids (so decrease the free NH_4^+ ion content of the cell), and to stimulate the formation of proteins as measured by protein nitrogen. At the same time, the total carbohydrate level of the plants under this treatment decreased presumably because incorporated carbon in the cell was directed into amino-acid synthesis. In contrast, the red-biased treatment showed the opposite response in each case.

It should, however, be noted that these results were not obtained under equal photosynthesis conditions as shown either by weight increase results or by quantum considerations.

However, the results were consistent both between species, and more importantly, at each of the irradiance levels studied. Hence the trends are undoubtedly effective trends directly related to the spectral treatments studied. This aside, there is also the previously published data which agrees well with the present study.

5. Chloroplast Form and Size and Chlorophyll Contents.

It seemed possible, particularly from the changes in protein levels within each treatment, that there may have been a reorganisation within the chloroplasts of the cell to balance the shifts in metabolism occurring under each of the spectral treatments. This would be possible through either a change in the structure of each chloroplast within a particular cell type in the leaf, or through a change in chloroplast size or number.

The influence of the environment on chloroplast ultrastructure of developing and mature leaves of normal plants has not been studied very intensively. Recently, Ballantine and

Forde (1970) showed that both light irradiance and temperature could markedly affect chloroplast ultrastructure in soybean. Leaves grown under low light irradiance (90 W m^{-2}) at both their temperature regimes (27.5-22.5°C, 20.0-12.5°C) had palisade mesophyll chloroplasts containing well-formed grana. The corresponding leaves developed under a higher irradiance (220 W m^{-2}) had very rudimentary grana. Chloroplasts from high temperature and high light had grana consisting of two or three appressed thylakoids, while grana from the low temperature were confined to occasional thylakoid overlap. Spongy mesophyll chloroplasts, in comparison, were less sensitive to these growth conditions. Transfer experiments showed that the ultrastructure of chloroplasts from mature leaves could be modified by changing the conditions, though the effect was less marked than when the leaf was growing.

It is clear from these results that the chloroplasts in the cell are in a dynamic state and can modify their ultrastructure depending on the current environmental (light irradiance and temperature) conditions.

Lyttleton, Ballantine and Forde (1971) in a similar study on Amaranthus lividus, found that compared with low light conditions, high light markedly reduced the granal content in chloroplasts of both mesophyll and bundle sheath cell types. This, together with changes in the degree of development of the peripheral reticulum, is in general agreement with the concept of environmental modification of the chloroplast ultrastructure.

In section II. 3.3. it was clearly indicated from the literature that a similar response to different light quality regimes may be expected in chloroplasts of higher plants (Osipova and Ashur, 1965; Osipova et al, 1966). However, the conclusions to be drawn from such existing data are not altogether clear. Pirson and Kowallik (1964) argued that since, on a protein basis, the chlorophyll content was markedly lower in blue light grown cells, the surplus protein of these cells is not used to increase the chloroplast, at least not in its normal composition. They state that:

"this protein would reflect nothing else than a disturbance in the intracellular equilibrance of the photoautotrophic cell, whether it may be deposited in the cytoplasm or perhaps

added to the non-photosynthetic material of the chloroplast".

The results from the Spectral Bias study appear to substantiate these predictions as there were no obvious ultrastructure changes from each of the spectral treatments.

6. Artificial Light Sources.

6.1. Lamp Selection.

The present study brings out many of the problems which are currently faced in the use and selection of artificial light sources for plant growth under controlled environment conditions. It is apparent from the data presented, that within a range of artificial light sources currently available, combinations are possible which give satisfactory plant growth and "normal" plants for a range of experimental uses. However, it is also evident from these studies that any degree of deviation of an artificial spectra from a balanced output will be reflected in changes in plant growth, form and metabolism.

These reactions of plants to broad-band spectra are necessarily complicated and it is often difficult in such studies to see which is the predominant effect and to which wavelength region the effect is attributable. These responsse however, are important in controlled environment studies and, moreover, their analysis can often lead to important physiological implications.

However, the problem still arises as to what should be used as a reference for such artificial spectra studies. Clearly, some standardization of a light source would be desirable but it is difficult to foresee the form that this should take. Hudson (1957) stated the problem very aptly:

"In assessing results of work it must be borne in mind that there is no such thing as a "neutral" environment, to which plants do not react at all, and which can therefore be used as a convenient reference point; nor are there "normal plants", produced in response to a "neutral background". The condition of a plant, at any moment in time, is a summation of all its reactions to all the levels of all the environmental factors which it has experienced up to that

time, and one of the difficulties of this type of work is to decide what should be used as a yardstick in assessing the effects of any particular factor. We can certainly not use a "perfect plant" as the criterion, since we do not yet know how to produce one and would not be able to recognize its unique status if we did!"

Hence it would appear to be impossible to define a "normal" plant and therefore to grow it under test (light) environmental conditions in order to screen these for suitability.

Similarly, there is the problem of a "neutral" environment in which to grow a plant species and thus use this as a reference in studying specific variables. Light quality, quantity and duration are all continuously variable in natural environments and the use of sunlight poses as many different problems as those faced in controlled environment situations. Of the main difficulties, the variation of energy flux density with time both diurnally and especially instantaneously (i.e. cloudiness) are of greatest significance. Strictly speaking the diurnal variability of light in natural environments is not the problem of that environment, of course, but rather the problem of simulation in controlled environments.

Rapid variations in irradiance, however are a real problem together with temperature control in either natural or glasshouse environments. Although daylength is also an important variable the problems of controlling this are much smaller than those involved in the other main light properties. Along with the diurnal variablilty in light irradiance there is also the important spectral shift associated with sun angle and air mass which each change with both time of day and with season. Each of these factors are important in natural environments both as physical parameters, and as factors in controlling plant growth, and require consideration in controlled environments.

It is apparent in the previous work reported that no attempt has been made to define a standard spectral output in physical terms for controlled environment work. Canham

(1966) suggests the use of:

"a spectral distribution very similar to that of daylight.....(with).....the spectral composition of the light to be within 10 per cent of the accepted daylight values in four specified bands.....and within 15 per cent in two others.....Wavelengths below 3,800 Å were to be ignored and those above 14,000 Å removed with a water filter."

The light-quality specification was presented as:-

BAND	1	2	3	4	5	6
WAVELENGTH RANGE, nm	380-460	460-510	510-560	560-610	610-700	700-850
% ENERGY SPECIFIED	16 (12.1)	13 (12.6)	12 (12.7)	11 (12.5)	18 (21.9)	27 (28.1)
TOLERANCE ± %	10	10	15	15	10	10

The reference to the origin of these values is not given by Canham except that this is a "daylight" spectrum. However this approach is the only logical one to take and a standardisation on either this set of data or one based on say Moon's curves appears to be the best solution to this problem. There may be some contention on the choice of air mass when considering this possibility and it is proposed here that a standard solar curve based on an air mass = 2 in agreement with engineering standards be regarded as the reference value. The percentage energy in the wavebands specified by Canham on this assumption would be as given in parentheses in the above table. These figures are derived from Moon (1940). It is clear that there is little defference between these two sets of figures and in actual fact any close approach to this general distribution should suffice for all practical purposes.

The remaining problems relating to the light environment are more easily resolved. In all controlled environment work every attempt must be made by the investigator to

(a) achieve an even spatial distribution of energy flux over the plant growing area which includes an even spectral regime where two or more lamp types are being used to provide the artificial light,

(b) measure the energy flux density of the light source before and after each treatment and where possible measure the energy flux from each lamp type as well as total output as a cross check with (c) in relation to spectral changes,
(c) measure the energy flux density of specific spectral bandwidths before and after each treatment, in order both to define the light regime used, and to examine the possibility of a spectral change during the treatment.

It is important that aspects of sections (b) and (c) are presented in publications relating to controlled environment work, or in cases where this is not possible, that energy flux density values and the types, and numbers of artificial lamps used, should be quoted. It is possible to extrapolate this information to give an approximation of spectral conditions in the experiment reported.

These suggestions are in agreement with those of the Dutch Committee on Plant Irradiation (1953, 1955) and of the more recent ASHS Working Group on Controlled Environments (Krizek, 1970). The retention of illuminance units (lux) by this latter group, however, is to be deplored.

The ASHS group's suggestions for reporting the light regime used in controlled environment studies are:-

(a) Minimum requirements

(i) Lamp types and percent input wattage for each type.

(ii) Light meter readings at beginning and end of each experiment, indicating type, manufacturer, and model of meter used (preferably cosine corrected).

(iii) Location of reading in relation to plant height.

(iv) Photoperiod. Indicate if lights are turned on gradually or abruptly; if gradual, indicate programme.

(v) Indicate whether a barrier is used between lamps and growing area, and type of material.

(b) Desired additional information

(i) Manufacturer and designation of lamp (a) for incandescent lamps, indicate lamp voltage and line voltage (b) for fluorescent lamps, indicate loading

(ii) Fluctuations in light readings during the

experiment.

(iii) Gradient in light intensity over the growing area.

(iv) Frequency of light measurements.

(v) Spectral energy distribution; total radiant energy per given wavelength band (μ watts cm^{-2} nm^{-1}): or ratio of visible to infra-red radiation, indicating instrument used.

6.2. Lamp Performance.

In the Spectral Balance experiment, the plants grown under the spectral and irradiance treatments tested did not vary substantially in their growth or biochemical response. No consistent trend favouring one lamp type over another in the responses was apparent between the species tested.

In considering closely the percentage distribution of the various wavebands, these results are not surprising, at least with respect to rigs I-IV. With these conditions, the proportions of short-wave and long-wave radiation remain approximately consistent; the green-yellow region of the spectrum showing the most variation between treatments. A survey of the literature indicates that this central wavelength region in comparison with other regions is of least significance in plant growth and development.

With respect to rigs V (low intensity) and VI (Metal-arc only) the ratio of short (blue) to long (red) wave radiation increased considerably, but plant response appeared to be mediated by the irradiance level rather than the spectral treatment in each of these rigs.

Similarly, the proportions of near infra-red in each treatment varied widely but did not appear to influence plant response. It is assumed in this case that red far-red mediated reactions would be saturated (i.e. under the same steady state condition) at each of the irradiances used. This is most apparent in comparing rigs I and III (1.5 and 2.5 Kw of tungsten) with the equivalent irradiance of rig VI (no tungsten)

where plant response was similar over all treatments.

However, although plant response was consistent under each lamp combination tested, the Sylvania "Metal-arc" high pressure discharge lamp had obvious advantages. On the one hand, its spectral distribution was superior to the other lamps of the same type tested, particularly with respect to providing a more uniform distribution of energy over the photosynthetically-active range. Deficiencies in the 400-450 nm range are satisfactorily overcome by supplementary illumination with specific lamps which emit in this range. The Philips blue fluorescent lamp as used in these studies is satisfactory for this purpose, but the more recently developed Philips blue HPI experimental lamp is considered to be a superior alternative. Similar deficiencies in the 540-700 nm range and in the near infra-red range can be overcome using either the quartz-halogen lamp or the more conventional tungsten lamps as used in each of these experiments.

On the other hand, the efficiency (watts m^{-2} output/watt power input) of the "Metal-arc" lamp is far superior to the HPLR and HPI lamps.

Details of light rig components and irradiance outputs have been presented in Section III. 2. but because of selective screening, this data does not give a true representation of the actual irradiance output of each of the lamp combinations used in rigs I to VI.

Performance in relation to irradiance output per watt input decreased in the order "Metal-arc", HPI, HPLR. Further, unpresented results from tests (Warrington, 1969) on lamp holders and reflectors indicated that the Electrolier Corporation lamp holders, in combination with the Sylvania Vanguard reflectors, would increase the intensity output three-fold in comparison with the G.E.C. lamp holder - Benzamin High Bay reflector combination as used in the Spectral Balance experiment.

Based on these results, the best "Metal-arc" lamp-reflector combination is 4-6 times more efficient than the HPLR

lamp (internal reflector) system on a watt input basis.

The efficiency of these lighting systems is of considerable importance in installations with large numbers of growth cabinets and climate rooms in relation to power consumption and cost of operation. It is true, from a practical consideration, that this factor can often be of greater significance in the choice of lamps for this purpose than considerations of spectral quality.

VI CONCLUSION

1. General.

There is currently available to the physiologist a number of commercial lamp types which offer a wide range of variability in spectral emission and technical characteristics which can be used to provide the artificial light required in controlled environment installations. There is not, however, one lamp which will meet all the operating requirements which are often specified for these environments; that is, good spectral emission (comparable to sunlight), high irradiance potential, low heat output, high operating efficiency, good ageing characteristics, uniform distribution patterns, ad infinitum which in total are difficult to meet accepting the present stage of development in lighting technology. This accepted, it is also doubtful whether some of these requirements are restrictive to the use of several systems currently available providing other limitations are overcome satisfactorily.

2. Controlled Environment Requirements.

Controlled environment conditions in growth rooms or cabinets should primarily fulfil the following requirements:-

(a) precisely reproducible (and hence definable) environments,

(b) uniform controlled climatic conditions over the plant growing area, and

(c) conditions which are similar to those in natural environments and which will produce "normal" growth and development of plants.

The artificial light systems used in controlled environments must therefore, meet these three requirements. In many growth rooms and cabinets, lighting is usually provided by low-pressure fluorescent tubes that can give irradiances up to a maximum of 40,000 lux or about 175 W m^{-2} of visible radiation (Thorne, 1971). For many studies, plants will grow satisfactorily at levels below this value but these limits may be restricting in physiological studies where irradiance can be the most critical climatic factor under investigation. In addition,

the spectral quality of light provided by existing fluorescent lamps differs considerably from sunlight and although it may be satisfactory for photosynthesis in many species, it has some adverse effects on others by influencing plant morphology and vegetative and reproductive development. (Gaastra, 1970). This probably occurs because the ratio of near infra-red to red light is much less in the artificial sources than in daylight even when tungsten supplementation is used. This latter aspect is often technically limiting because these lamps should normally be separated from the growing space by a transparent ceiling, when they require their own cooling system, or be suspended in the growing space where there is a greater heat load on the air-conditioning system of the growing space, and a greater infra-red loading on the plants.

The systems defined in these studies offer satisfactory ways of overcoming each of these particular limitations. From the results of both the Spectral Bias and Spectral Balance experiments, it has been established that satisfactory plant growth and development can be obtained from recently developed high-pressure discharge lamps together with varying degrees of red and blue wavelength supplementation. With these high-pressure lamps, particularly of the "Metal-arc" type, it is possible to obtain a continuous visible spectrum with considerable output at each wavelength in the visible region, and to avoid the narrow line-emission characteristics of the older mercury-vapour lamp types. The basic nature of this continuous spectral output is similar to many of the fluorescent lamp spectra, but it offers more to controlled environment use than the fluorescent lamp types because of the higher visible (400-700 nm) energy output. It appears from rig VI in the Spectral Balance experiment, that these lamps without additional supplementation can give satisfactory plant growth, but the use of blue and red wavelength supplementation allows operating flexibility within these regions and a greater opportunity to achieve the spectral distributions desired. These characteristics, therefore, offer higher maximum irradiance levels than fluorescent tube systems and the added supplementary light for specific wavelength regions gives increased operating flexibility.

The uniformity of light over the growing area (item "b" above) was achieved, as outlined previously (section III. 2.) by considerably modifying reflector systems and by individually adjusting each lamp in a light-rig until a satisfactory distribution was achieved. The modification of reflector systems for use under controlled environment situations is critical if the point source (i.e. the lamp arc) is to give an acceptable diffuse output. This irradiance variation across the plant growing area is also improved with the use of the mirrored walls in the rooms and cabinets and by focussing the individual lamps, but a more effective and less time-consuming arrangement would be to use a diffusing screen under the light-rig in order to scatter the incoming radiation. Providing this reduced the total irradiance (i.e. the operating or conversion effiency) only slightly then the advantages of this lighting system over others will still hold.

The third aspect (item "c") is the issue which affects the plant physiologists most directly and which has been the central issue in these studies; this is, that the lighting system employed must relate closely to natural conditions and provide an environment for the normal growth and development of plants. This problem of definition, or at least of recognition, has been discussed previously and places this issue in its true perspective (section V. 6. and Hudson, 1957). However, if the philisophy of "normal plants" and "neutral environments" was to be accepted, then the progress of physiology would be very restricted indeed. What is essential in this work is that there is a definition of plant responses under a series of controlled conditions which span over the range of the variable under study such that the variability rather than the normality of the response is definable. This is typified by the Spectral Bias experiment treatments where the variance in the visible spectra has been adjusted to span the climatic factor under study.

3. Plant Systems' Responses.

The results obtained from these contrasting biased treatments give a clear indication of the plant's response for a

large and diverse number of parameters. This is in contrast to the Spectral Balance experiment treatments where there was a marked consistency in the responses recorded and where small differences gave no clear indication of the changes that were occurring. Hence, although similar artificial light spectra (i.e., for example, those with a similar red:blue ratio) gave similar plant responses, there were more obvious changes which occurred under markedly biased conditions in response to the changes in particular wavelength relationships. From this present study it is clear that a number of morphological and biochemical changes occurred in response to the spectral treatments. However, in relation to present understanding in basic plant physiology, there remains the deficiency of being able to predict both the magnitude and the relativity of the changes that occurred. From this difficulty it follows that there is the problem of defining in terms of general plant response, and therefore ultimately in terms of an acceptable standard spectrum, the specification for a "normal" operating environmental condition.

There is, from these studies, a series of results which make clear several facets of environmentally induced changes which occur under these controlled environment conditions. Primarily, the affects of the spectral and irradiace environments are far more than those expressed simply in the visual appearance of the plant. In order that the events determined by these environments are described fully, it follows that the biochemistry of the plant, along with a complete growth description of the induced responses, is required. Subsequent to this, some means of integrating this information into whole plant systems in the form of (mathematical?) models is required for comprehension of the bulk of response information inevitably compiled.

If this end result is to be achieved then more intensive studies, of a similar nature to those undertaken in these investigations, must be entertained.

One most obvious area of previous neglect which is apparent

from the present study is that centreing on the wavelength control of biochemical metabolism. This holds with respect to both the small amount of work carried out in this field and the task of integration of that work by many authors with respect to their own studies. This latter aspect is in turn aggrevated by examples of conflict between results from one set of workers with another (e.g. Hess and Tolbert, 1967). The scheme presented in section V. 4. is an attempt to overcome part of this lack of integration and to possibly account for the differences which appear to exist in reported responses. However, the shortcomings of such an attempt are clear and for this reason the following points require further examination:

(i) Individual compound levels.

The response to specific wavelength regions is well established for several major compounds; i.e. short-wave enhancement of aspartic and glutamic acids, fumarate and malate; long-wave enhancement of glucose, fructose, starch, sucrose. However, the evidence for changes in other intermediary metabolites, particularly of other amino acids, is not available in the literature. Particular confusion with respect to serine appears to exist but this may be resolved as more information regarding photorespiration becomes available.

(ii) Relationships of various pathways.

There is adequate evidence for short-wave enhancement of total amino acid and protein levels and for long-wave enhancement of total carbohydrates in plant systems. However the interrelationships of the various pathways in respect to these wavelength affects is not established, with the exception that the photosynthetic carbon-fixing systems are not directly involved. Intermediary product turnover rates, pool values and end-product accumulation can all influence the interpretations possible for the relationships that might exist between groups of compounds. This is in turn related to:

(iii) Mechanisms of wavelength action.

Evidence is available for specific wavelength activation of PEP carboxylase (Ogasawara and Miyachi, 1970) and of glycolate oxidase (Voskresenskaya et al, 1970) by short-wave radiation. However, evidence for other enzyme responses, changes in pigment systems (and related reducing power and photophosphorylation changes) and effects on the genetic status of the

cell are not clear with respect to currently available information. Similarly, there is no clear indication of the location of these changes within the cell system and whether these changes influence structural alterations of various organelles (e.g. chloroplasts) or merely occur under normal cellular conditions.

The influence of specific wavelength regions on morphological changes such as leaf growth, stem elongation and, in general, the division of assimilates to various plant parts, has been broadly established but not in sufficient detail to be able to predict plant form from known artificial spectra. In some instances the spectral sensitivity curve (i.e. the "action spectrum") for the physiological response in question has been broadly defined (e.g. stem elongation in tomato, Stolwijk, 1954), but this is species-specific and dependent on other growth conditions (daylength, temperature and irradiance). This is not helped by the absence of explanations for control mechanisms even where detailed evidence is available from some wavelength receptors (e.g. phytochrome), or where responses cannot be accounted for in terms of currently known receptor systems (e.g. the uncertainty of the association of phytochrome with Mohr's High Energy Reaction system).

With respect to photosynthetic responses at various wavelengths, recent work (McCree, 1972) has established the reliance of the flux of absorbed quanta as a practical absolute measure of the amount of photosynthetically active radiation available to the plant. The assessment of photosynthesis is, therefore on this assumption, a matter of determining wavelength influence on interception and absorptance (i.e. on leaf area, dry weight per unit area, leaf display, pigmentation) as illustrated in Section V. 3. McCree (1972) showed some obvious differences in relative quantum yield, absorptance and relative action spectra between field and growth-chamber grown plants which was probably due to variable absorption by non-chloroplastic material. These differences under normal operating conditions, however, are likely to be small but, nevertheless, require explaining.

4. Concluding Remarks.

In conclusion, it has been shown that the complexity of interactions between environments, development and metabolism can not be resolved simply by identifying a single operative environmental variable, or a single parameter by which its action may be traced. Interactions between variables (i.e. the spectral quality of the light treatment and the irradiance level) are of major importance; their consequences reflect in changes in metabolism within the plant and are expressed differently in different organs of the plant and at different stages of the life cycle (see Steward, 1971 for a treatment of *Mentha*).

".....Genetics prescribes the range of chemical and morphological events that are feasible; the responses of plants to nutrition and environment select from the feasible and convert it into the practicable. This is indeed a feat of "biological engineering," because it takes the attributes of life and the properties of matter and the laws of energy to produce a mechanism that works. It is a major physiological task to describe, to document, to explain, how all this is done and, having done so, to see the potential applications as plants are exploited for the benefit of man and his environment....." (Steward, 1971).

VII. APPENDICES.

Appendix 1. Procedure for Measuring Irradiance (Energy Flux Density)

Determination with Eppley Pyranometer

(a) Unshielded Eppley = horizontal flux density of short-wave (SW).

$$SW = mV \times K_{Eppley}$$
$$= \ldots\ldots\ldots\ldots\ldots W\ m^{-2}$$

(b) Shielded Eppley = restricted horizontal flux density of short-wave (SW_R).

$$SW_R = mV \times K_{Eppley}$$
$$= \ldots\ldots\ldots\ldots\ldots\ldots W\ m^{-2}$$

(c) Shielded Eppley + Schott RG8 filter = restricted horizontal flux density of near infra-red radiation (NIR_R).

$$NIR_R = mV \times K_{Eppley} \times \text{Filter Transmission Factor}$$
$$= mV \times K_{Eppley} \times 1.09\ W\ m^{-2}$$
$$= \ldots\ldots\ldots\ldots\ldots\ldots\ldots W\ m^{-2}$$

(d) Photosynthetically active radiation restricted

$$PAR_R = SW_R - NIR_R$$
$$= \ldots\ldots\ldots\ldots\ldots\ldots W\ m^{-2}$$

(e) Horizontal flux density of PAR

$$PAR = SW \times \frac{PAR_R}{SW_R}$$
$$= \ldots\ldots\ldots\ldots\ldots\ldots W\ m^{-2}$$

Appendix 2.

Table 23

Spectral Bias Experiment

Distribution Values of Light Irradiance Over the Plant Area for Individual Light Types and Each Total Lamp Combination

EEL Light-Meter (Values Approximately in lm ft^{-2} x 10)

Readings Taken at 20 cm Centres

A. Balanced Treatment (Room 11)

High Irradiance Treatment

4 x 1000 W. "Metalarc"

	290	290	290	280	
300	300	300	300	290	270
	320	320	310		
300	300	310	320	300	290
	300	310	300		
300	300	310	300	290	280
	310	300	300		
300	300	320	320	300	300
	300	330	320	290	

12 x 1000 W. Quartz Halogen

	73	78	76	72	
70	82	84	84	80	63
	84	89	82		
63	79	80	79	76	62
	78	84	75		
66	81	83	84	78	65
	83	91	85		
65	81	84	84	78	66
	69	70	71	67	

1 x 2000 W. Blue HPI

	78	69	79	65	
54	80	73	81	74	56
	93	70	85		
59	85	83	82	74	58
	93	68	90		
56	75	83	86	83	61
	94	67	91		
54	73	71	74	75	59
	71	70	66	73	

Total Lamp Combination

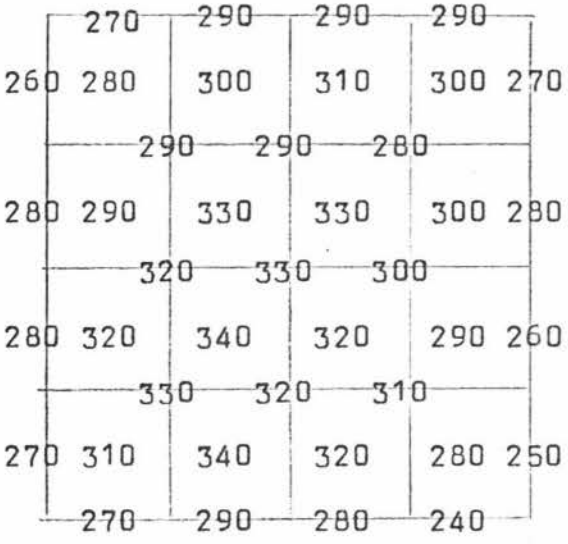
	450	450	450	420	
430	470	470	470	450	400
	500	480	490		
430	470	480	470	460	400
	480	460	460		
430	460	470	470	450	400
	490	460	470		
420	450	480	460	440	410
	430	470	430	420	

Table 23 contd.

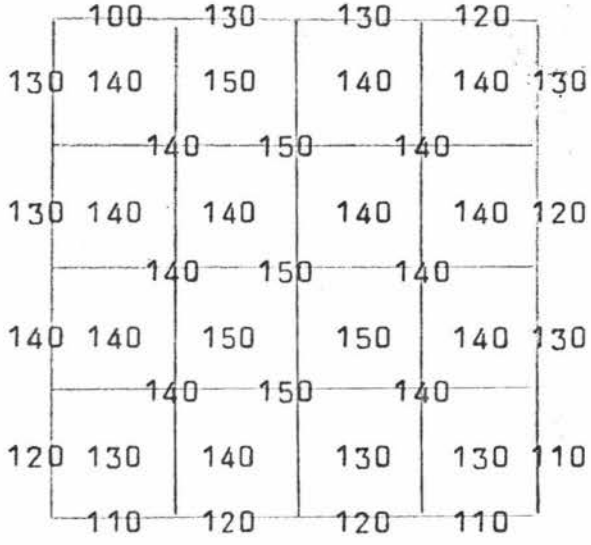
B. Red-Biased Treatment (Room 12)

High Irradiance Treatment

4 x 1000 W. "Metalarc"



12 x 1000 W. Quartz Halogen



Total Lamp Combination

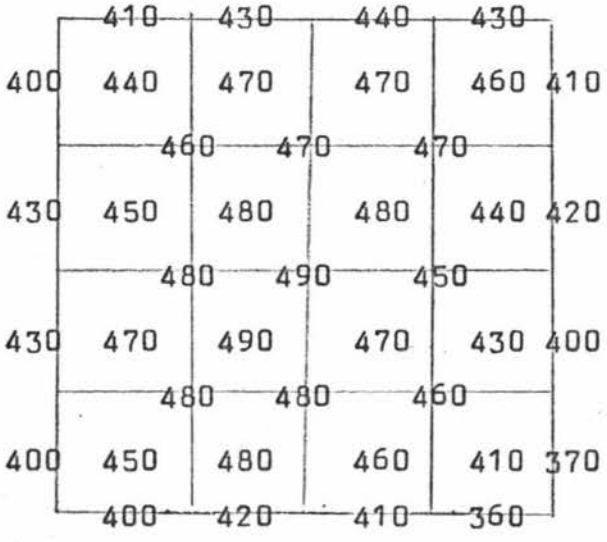


Table 23 contd.

C. Blue-Biased Treatment (Room 13)

High Irradiance Treatment

4 x 1000 W. "Metalarc"

	290	310	310	300	
300	290	290	310	300	300
	290	310	320		
300	290	280	300	290	300
	250	270	280		
300	290	270	280	270	290
	260	290	280		
310	310	290	280	270	280
	280	270	260	250	

2 x 2000 W. Blue H.P.I.

	120	110	110	120	
130	130	130	130	130	130
	140	130	140		
120	130	130	140	140	130
	140	130	140		
130	140	140	140	140	130
	140	130	130		
110	130	120	120	130	110
	110	100	100	110	

Total Lamp Combination

	410	430	430	420	
430	430	430	450	440	430
	440	450	460		
420	430	420	430	430	430
	420	410	410		
440	420	420	410	400	420
	430	420	410		
430	420	410	400	400	390
	390	390	360	360	

Table 23 contd.

D. All Spectral Treatments

Low Irradiance Treatment

Total Lamp Combination Only

Balanced Treatment

	280	280	270	260	
270	290	290	280	270	250
	310	300	290		
270	290	290	290	280	250
	290	270	280		
260	290	290	280	270	250
	300	280	290		
260	280	290	280	270	250
	270	280	260	250	

Red-Biased Treatment

	250	270	280	270	
260	270	290	300	290	260
	290	290	300		
260	270	290	290	270	250
	290	290	290		
270	290	290	280	270	250
	290	290	290		
250	270	280	270	260	230
	240	250	250	230	

Blue-Biased Treatment

	260	250	260	260	
270	270	260	270	270	270
	280	270	280		
270	270	260	260	270	260
	270	250	260		
280	280	260	260	260	260
	270	260	260		
270	280	250	250	250	250
	250	230	230	230	

Appendix 3. Nutrient Solutions

A. Hoagland's 1

The nutrient solutions used in the experiments are those adopted by Plant Physiology Division, D.S.I.R.

In the cabinet experiments the nutrient used was one-half strength Hoagland's 1 with some modifications (i.e. the use of chelated iron and the addition of chloride ions). This choice was based on Hoagland and Arnon (1938), and recommendations of

Dr. Albert Ulrich, University of California, Berkeley;
Phytotron, Californian Institute of Technology;
Plant Research Institute, Canadian Department of Agriculture, Ottowa.

The solution was used at a rate of 2 c.c. of each stock solution per litre (1:500) and the pH was adjusted to 6.5.

Stock Solution A.	gm./litre	ppm in final solution	
Calcium nitrate			
$Ca(NO_3)_2 \cdot 4H_2O$	295.19	Ca	100.20
		N	70.03
Sequestrene			
NaFe chelate *	10.4	Fe	2.50
Stock Solution B.			
Potassium phosphate	34.02	K	19.55
KH_2PO_4		P	15.49
Potassium nitrate	126.39	K	97.76
KNO_3		N	35.02
Magnesium sulphate	123.24	Mg	24.31
$MgSO_4 \cdot 7H_2O$		S	32.06

Boric acid H_3BO_3	0.715	B	0.2500
Manganous chloride $MnCl_2 \cdot 4H_2O$	0.4525	Mn	0.2512
		Cl	0.3243
Zinc sulphate $ZnSO_4 \cdot 7H_2O$	0.055	Zn	0.0250
		S	0.0123
Copper sulphate $CuSO_4 \cdot 5H_2O$	0.020	Cu	0.0102
		S	0.0051
Molybdic acid $Na_2MoO_4 \cdot 2H_2O$	0.005	Mo	0.0053
Potassium chloride KCl	1.575	K	1.6522
		Cl	1.4980.

* The Sequestrene used was Geigy 138 Fe chelate; Na/Fe^{3+} ethylene diamine di(O-hydroxy-phenylacetate).

B. N.C.S.U. Nutrient Solution.

The nutrient solution used in the climate-room experiments is identical with that in use at the North Carolina State University Phytotron at Raleigh, U.S.A.

Its components, which are similar to the Hoagland's solution components, are:-

Stock Solution A.	gm./litre	ppm in final solution	
Ammonium nitrate NH_4NO_3	80.05	NH_4-N	28.0
		NO_3-N	28.0
Calcium nitrate $Ca(NO_3)_2 \cdot 4H_2O$	159.25	Ca	54.8
		N	37.6
Sequestrene NaFe chelate**	29.8	Fe	3.0

Stock Solution B.

Potassium phosphate KH_2PO_4	12.5	K P	7.2 5.6
Potassium phosphate K_2PO_4	5.5	K P	5.0 2.0
Potassium nitrate KNO_3	63.9	K N	48.8 17.8
Magnesium sulphate $MgSO_4 \cdot 7H_2O$	30.81	Mg S	6.2 8.2
Sodium sulphate Na_2SO_4	35.50	Na S	13.8 19.2
Zinc sulphate $ZnSO_4 \cdot 7H_2O$	0.025	Zn S	0.012 0.070
Manganous chloride $MnCl_2$	0.26	Mn Cl	0.113 0.146
Copper sulphate $CuSO_4 \cdot 5H_2O$	0.01	Cu S	0.005 0.003
Boric acid H_3BO_3	0.35	B	0.127
Molybdic acid $Na_2 MoO_4 \cdot 2H_2O$	0.002	Mo	0.002

The stock solutions were used at a rate of 1 to 500 or 200 ml stock per 50 litres of water. The pH of the nutrient solution was adjusted to 6.5.

** The Sequestrene used was Geigy 330 Fe chelate; Na/Fe^{3+} di ethylene triamine pentaacetate.

A comparison of component concentrations (ppm) in the

nutrient solution as applied is given in the following table.

Element		Hoagland's Solution	NCSU Solution	
N	NO_3	105.05	83.4	111.4
	NH_4	-	28	
P		15.50	7.6	
K		118.96	61.0	
Ca		100.2	58.4	
Mg		24.3	6.2	
S		32.08	24.3	
Na		-	23.0	
Fe		2.5	3.0	
Zn		0.025	0.012	
Mn		0.25	0.145	
Mo		0.005	0.0016	
B		0.25	0.127	
Cu		0.01	0.005	
Cl		1.82	0.187	

It is noted that although the two nutrient solutions vary greatly in their composition, the potting media : nutrient solution combination used in each experiment gave very satisfactory plant growth.

Appendix 4

Table 28

Spectral Bias Experiment

Absorbed Photon Flux Density For 25 nm Wavebands

Data Derived Using Absorptance Data From McCree (1972) and Photon Flux Density Values from Table 7

Values for Sorghum, Soybean and White Clover Under all Spectral and Irradiance Treatments

Waveband (nm)	Absorptance	High Irradiance			Low Irradiance		
		Blue Biased	Balanced	Red Biased	Blue Biased	Balanced	Red Biased
Sorghum							
400-425	0.92	6.94	5.76	3.28	5.10	3.79	2.23
425-450	0.92	6.11	5.40	3.63	4.69	3.63	2.36
450-475	0.92	14.23	0.42	3.56	9.70	6.58	2.54
475-500	0.90	3.65	4.43	4.21	2.55	2.88	2.99
500-525	0.83	3.93	4.93	4.82	2.58	3.03	3.25
525-550	0.74	3.60	4.40	4.64	2.43	2.90	3.13
550-575	0.74	4.15	5.05	5.05	2.69	3.26	3.26
575-600	0.80	7.32	10.11	10.33	5.16	6.67	6.46
600-625	0.84	8.18	9.36	11.00	5.14	6.08	7.01
625-650	0.88	3.85	5.71	7.58	2.62	4.13	5.37
650-675	0.90	2.71	5.29	7.09	2.06	3.62	5.29
675-700	0.83	2.93	5.27	6.68	1.99	3.52	4.92
400-700		67.60	75.13	71.87	46.71	50.09	48.81

Table 28 contd

Waveband (nm)	Absorptance	High Irradiance			Low Irradiance		
		Blue Biased	Balanced	Red Biased	Blue Biased	Balanced	Red Biased
Soybean							
400-425	0.94	7.09	5.88	3.35	5.22	3.87	2.28
425-450	0.94	6.24	5.52	3.71	4.79	3.71	2.41
450-475	0.94	14.54	9.62	3.64	9.91	6.72	2.59
475-500	0.93	3.78	4.58	4.35	2.63	2.98	3.09
500-525	0.90	4.26	5.35	5.23	2.80	3.29	3.53
525-550	0.85	4.11	5.03	5.30	2.80	4.77	3.60
550-575	0.84	4.71	5.73	5.73	3.06	3.70	3.70
575-600	0.88	8.01	11.06	11.30	5.68	7.34	7.10
600-625	0.90	8.77	10.03	11.78	5.51	6.52	7.52
625-650	0.92	4.03	5.98	7.92	2.74	4.32	5.61
650-675	0.93	2.80	5.47	7.33	2.13	3.74	5.47
675-700	0.91	3.20	5.75	7.29	2.18	3.86	5.40
400-700		71.54	80.00	76.93	49.45	54.82	52.30
White Clover							
400-425	0.93	7.01	5.82	3.31	5.16	3.83	2.25
425-450	0.94	6.20	5.49	3.69	4.79	3.71	2.41
450-475	0.94	14.62	9.67	3.66	9.91	6.72	2.59
475-500	0.93	3.78	4.58	4.35	2.63	1.98	3.09
500-525	0.86	4.07	5.11	5.00	2.67	3.14	3.37
525-550	0.75	3.65	4.46	4.70	2.47	2.94	3.17
550-575	0.74	4.15	5.05	5.05	2.69	3.26	3.26
575-600	0.80	7.32	10.11	10.33	5.16	6.67	6.46
600-625	0.85	8.28	9.47	11.13	5.20	6.15	7.10
625-650	0.89	3.92	5.81	7.71	2.65	4.17	5.43
650-675	0.92	2.77	5.41	7.25	2.11	3.70	5.41
675-700	0.86	3.04	5.46	6.92	2.06	3.65	5.10
400-700		68.81	76.44	73.10	47.50	50.92	49.64

Appendix 5. Chloroplast Ultrastructure.

Abbreviations Used:-

CI cytoplasmic invagination, CM chloroplast membrane, CW cell wall, CY cytoplasm, G grana, IS intercellular space, M mitochondria, N nucleus, OG osmiophilic globule, S starch, ST stroma, T thylakoid(s), To tonoplast, V vacuole.

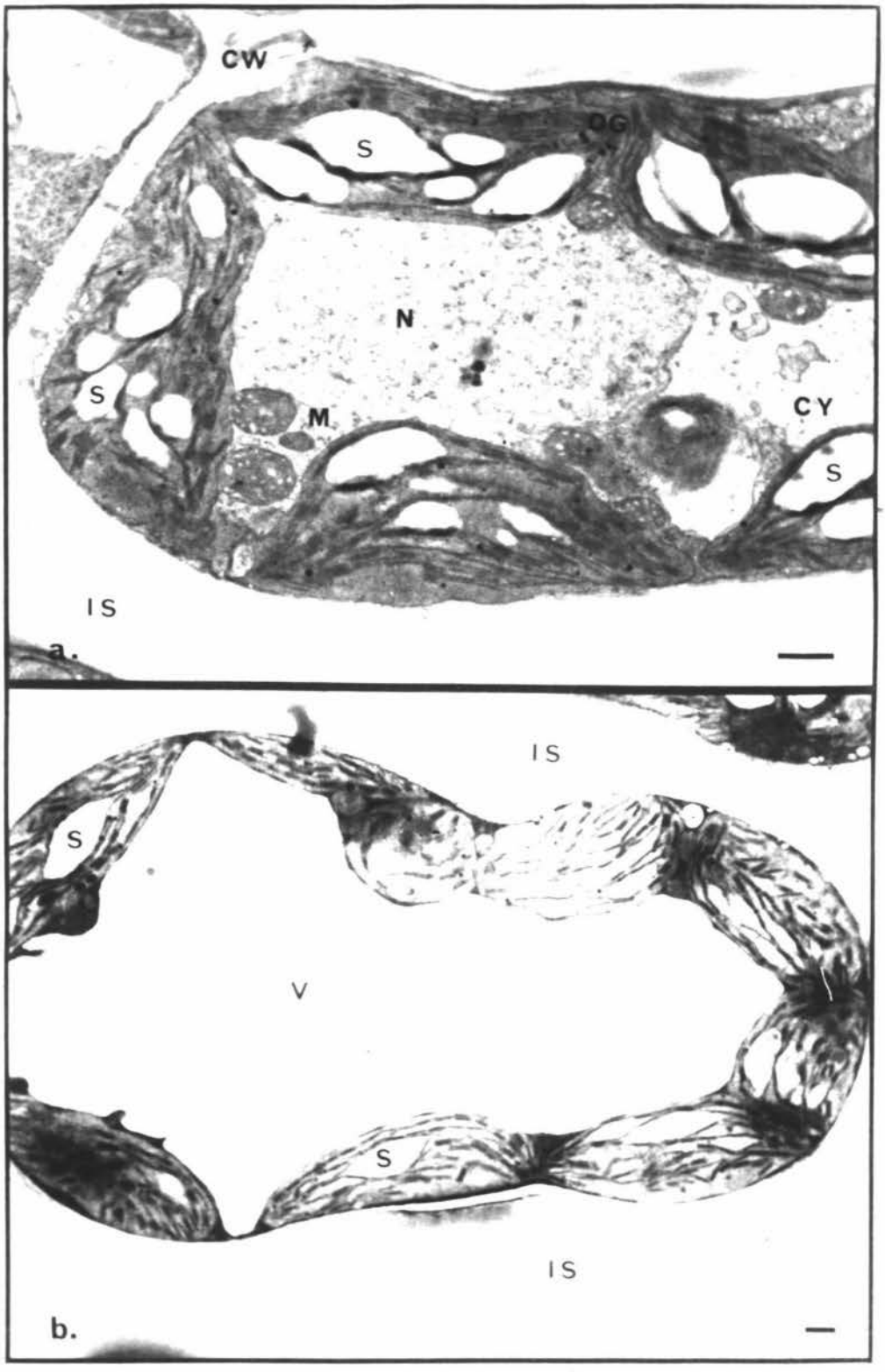


Fig. EM 1. (a. 705·27, b. 705·19)

SOYBEAN. a. Lower palisade mesophyll.
b. Spongy mesophyll.
(a. Red biased, low light. b. Balanced, high light).

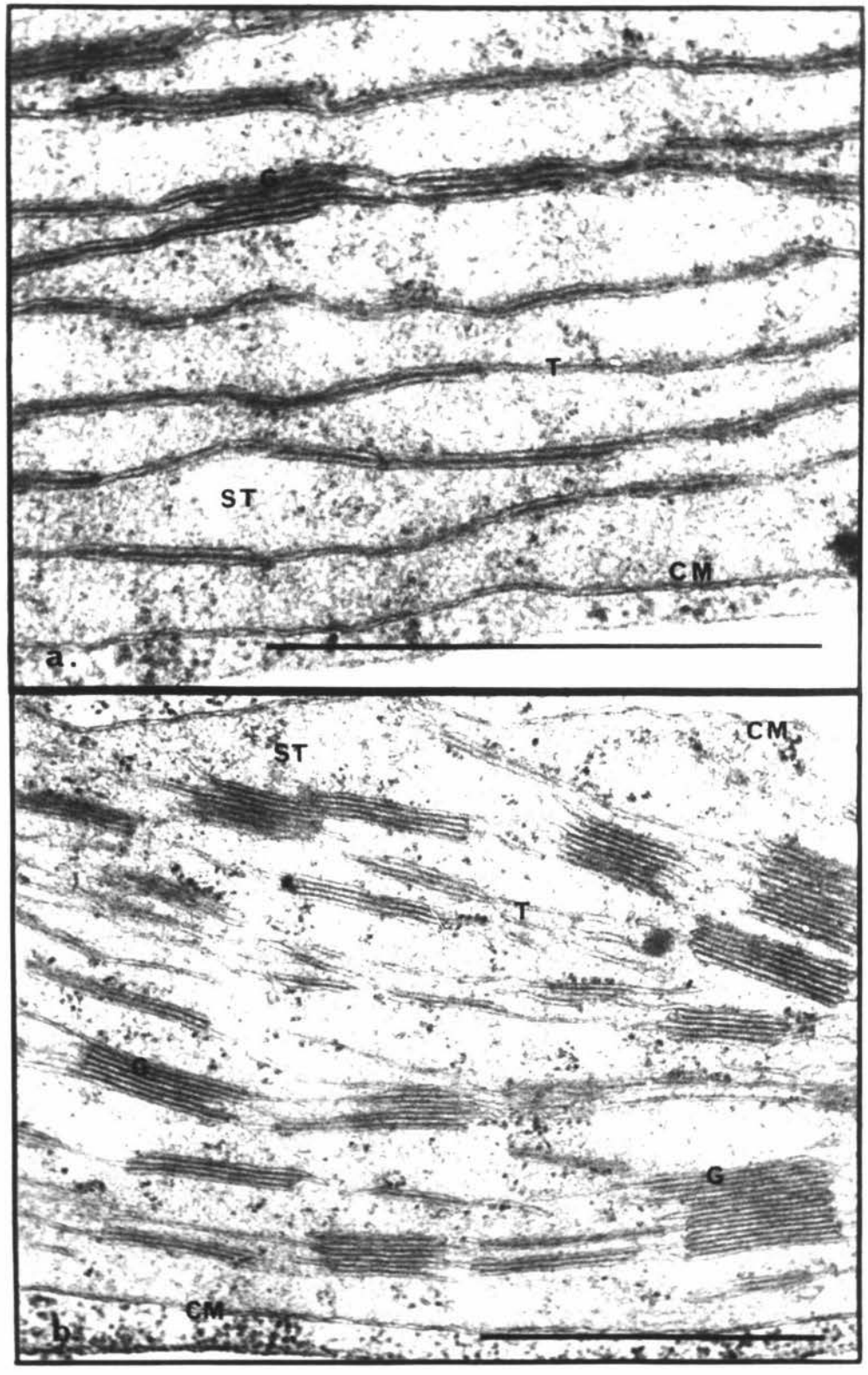


Fig. EM 2. (a. 705·31, b. 694·30)

SOYBEAN. a. Upper palisade mesophyll.
b. Spongy mesophyll.
(Blue biased, high light).

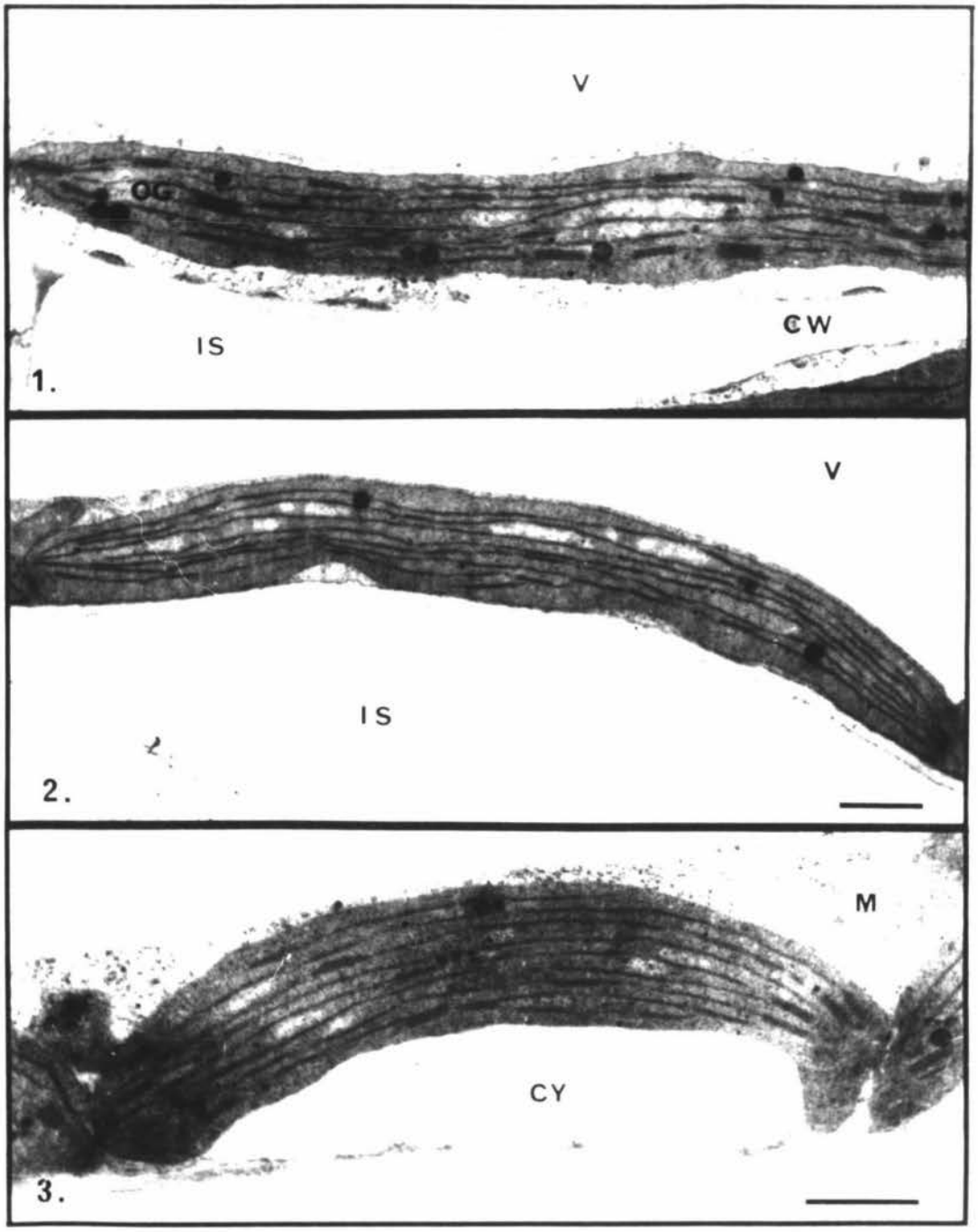


Fig. EM 3. (1. 706·4, 2. 705·18, 3. 692·14)

SOYBEAN. High light.

Upper palisade mesophyll.

1. Blue biased.
2. Balanced.
3. Red biased.

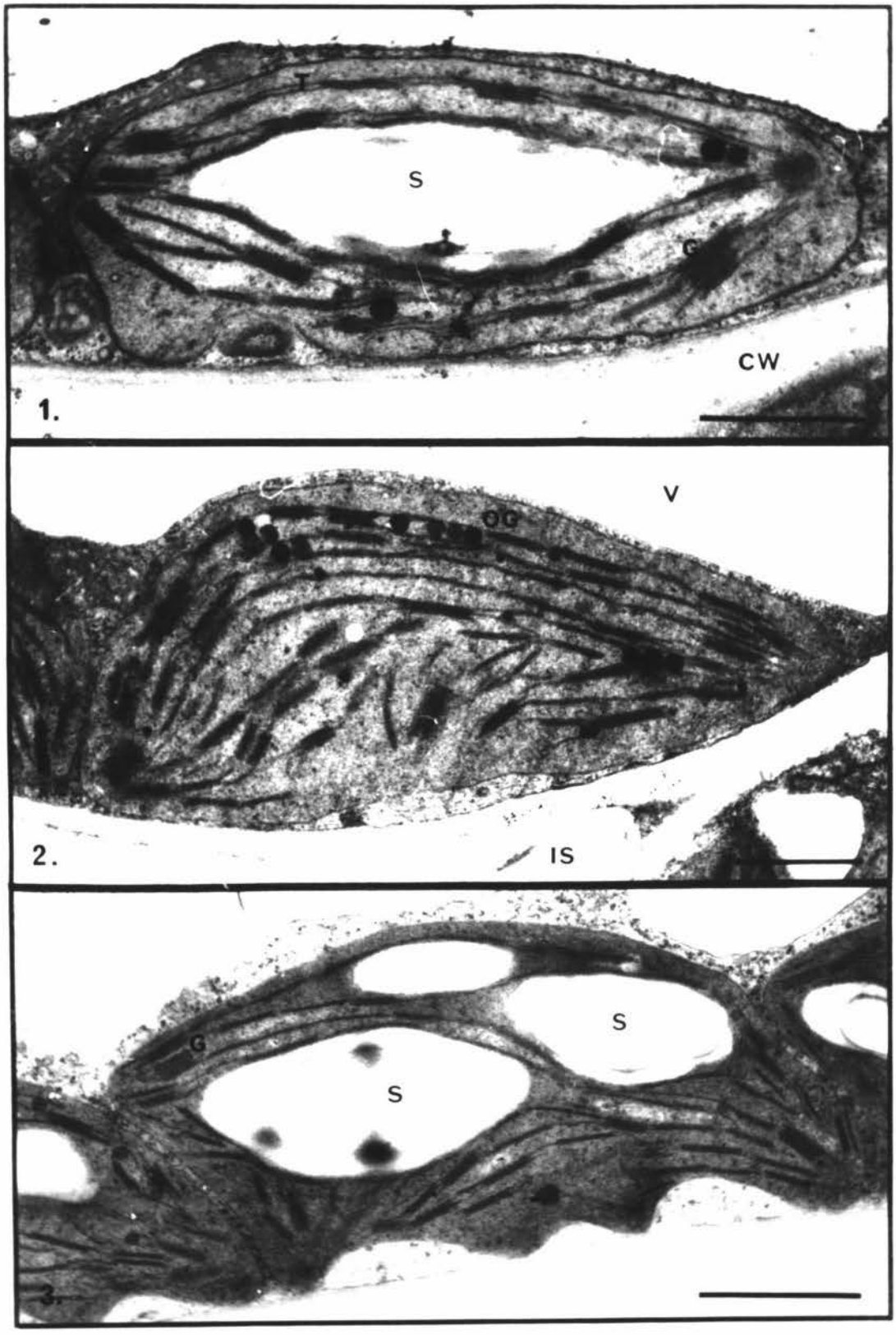
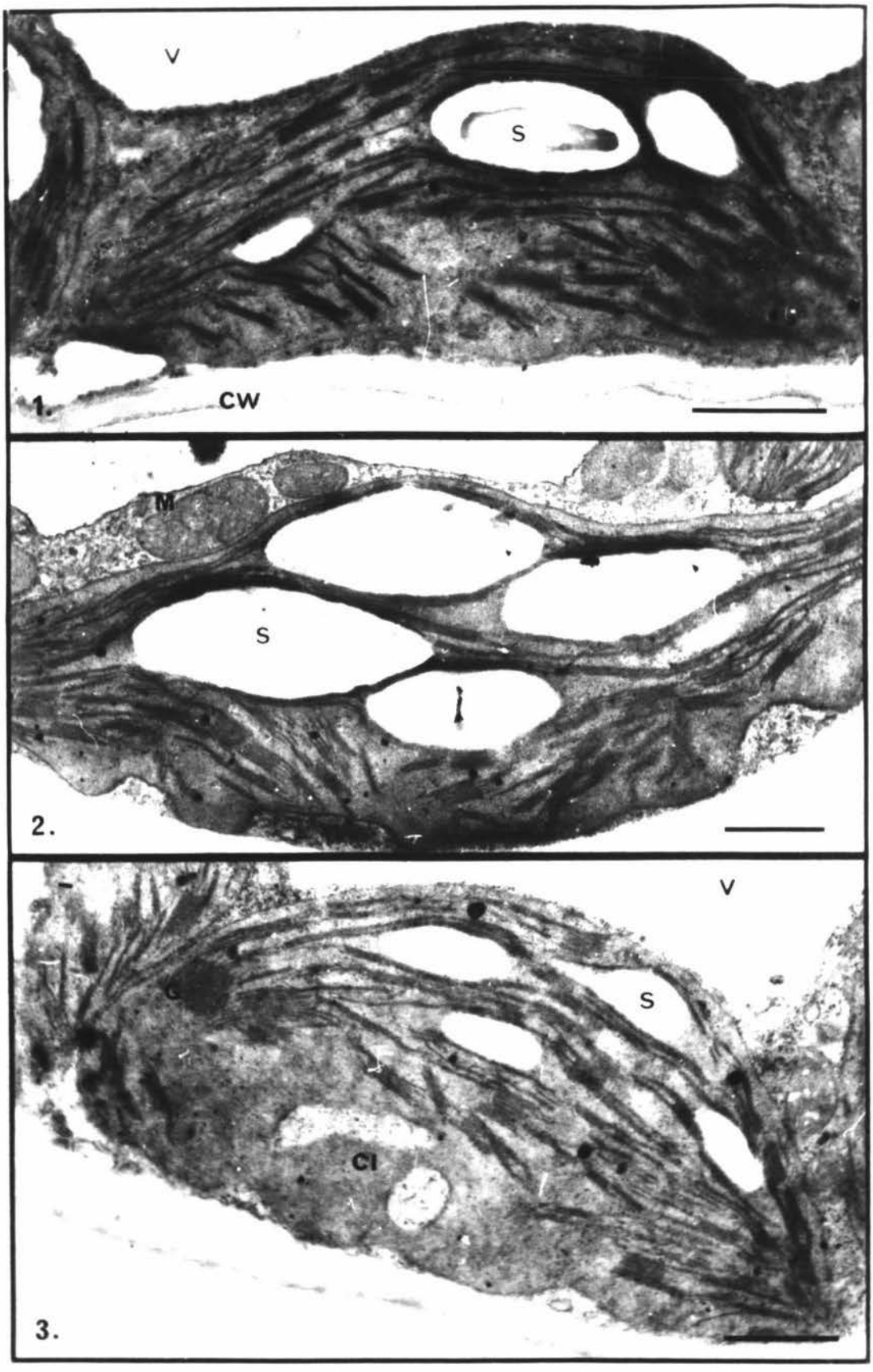


Fig. EM 4. (1. 706·2, 2. 705·23, 3. 692·13)

SOYBEAN. High light.

Lower palisade mesophyll.

1. Blue biased, 2. Balanced, 3. Red biased.



g. EM 8. (1.704·22, 2.698·29, 3.705·24)

SOYBEAN. Low light.

Spongy mesophyll.

1. Blue biased, 2. Balanced, 3. Red biased.

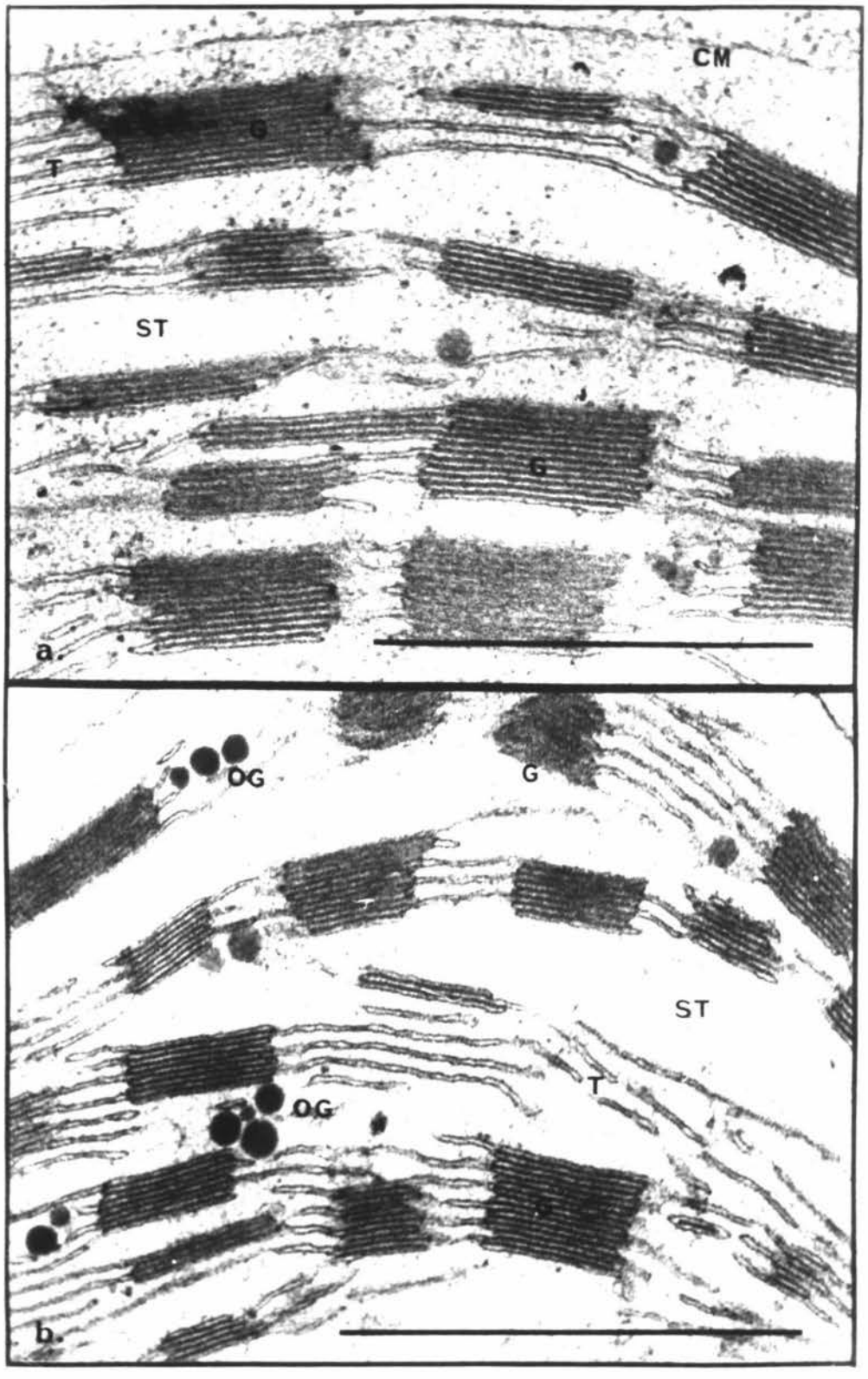


Fig. EM 9. (a. 695·32, b. 693·14)

WHITE CLOVER. a. Palisade mesophyll.
b. Spongy mesophyll.
(Blue biased, high light).

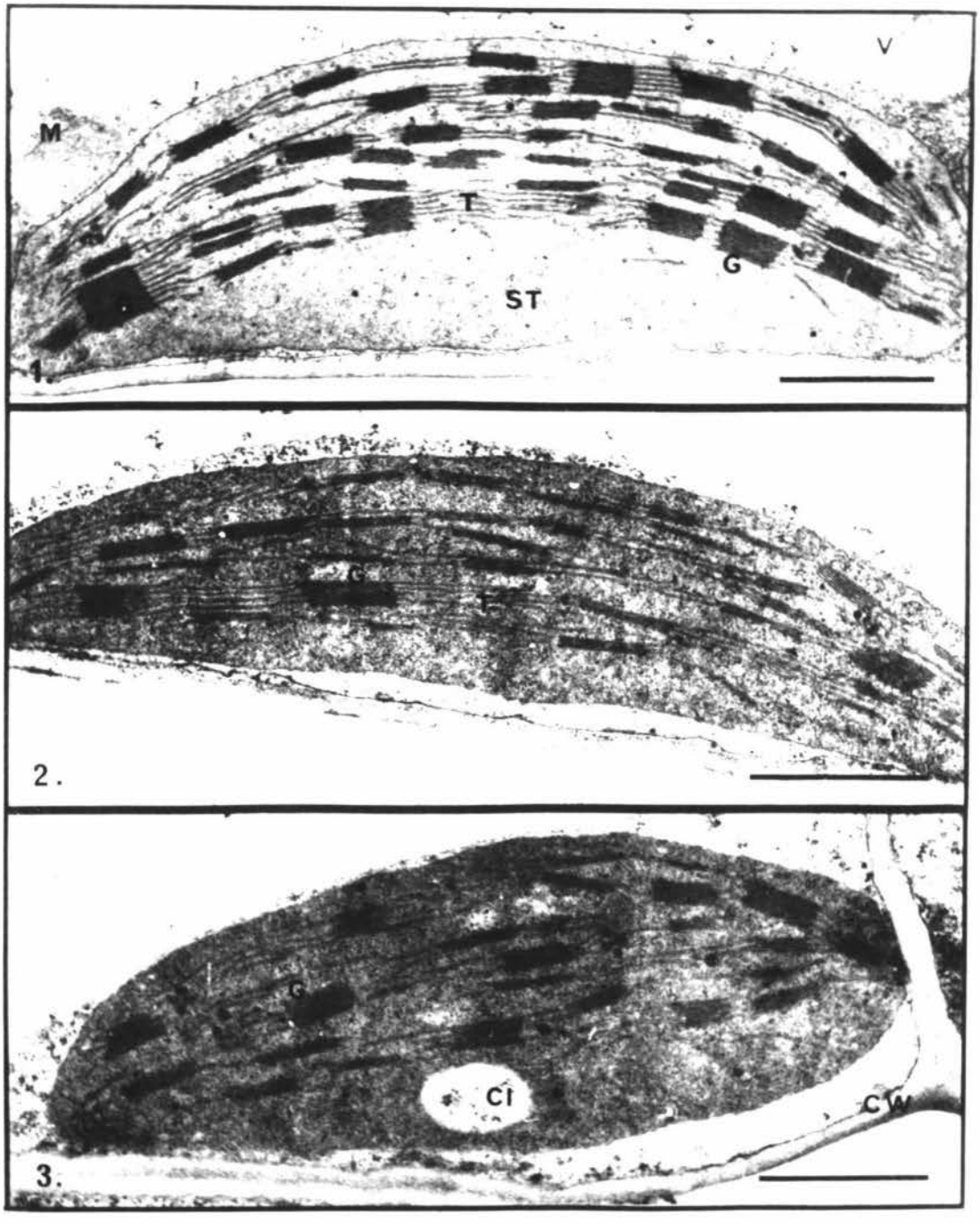


Fig. EM 10. (1. 695·31, 2. 696·5, 3. 693·22)

WHITE CLOVER. High light.

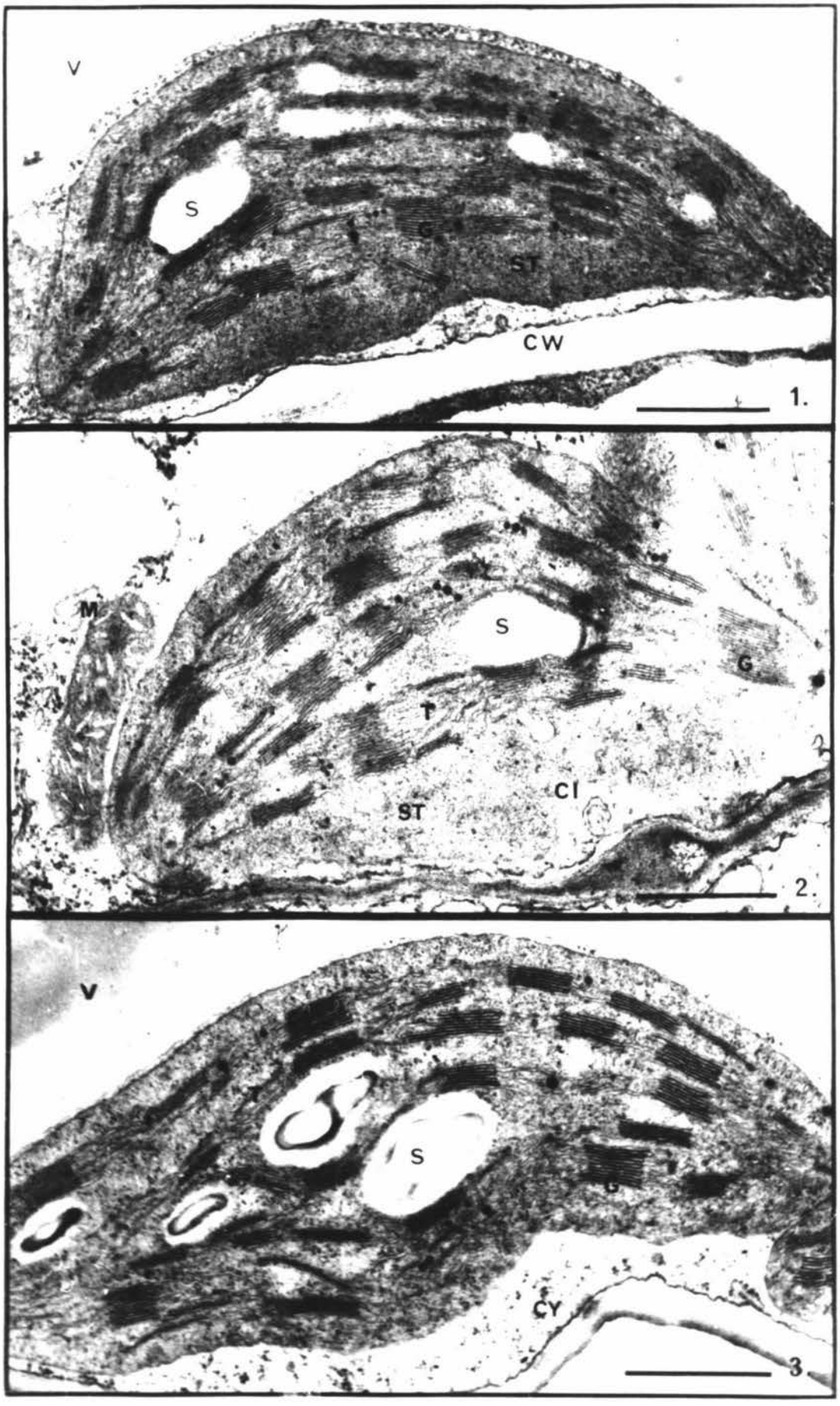
Palisade mesophyll.

1. Blue biased.

2. Balanced.

3. Red biased.

Fig. EM 13. (1. 699·22, 3. 700·22,
WHITE CLOVER. Low light. 2. 699·2)
Spongy mesophyll.
1. Blue biased, 2. Balanced, 3. Red biased.



Appendix 6.

Solar Radiation

Characteristics

Table 24

Distribution of Standard Solar Radiation Curve (%)

(Data adapted from Moon, P., "Proposed Standard Solar-Radiation Curves for Engineering use". Journal of the Franklin Institute, 230 (1940): 583-617)

Solar Irradiation at Sea Level with Surface Perpendicular to Sun's Rays, M = 2

	%		%		%
400 - 410	1.6	500 - 510	3.5	600 - 610	3.3
410 - 420	2.0	510 - 520	3.4	610 - 620	3.3
420 - 430	2.2	520 - 530	3.4	620 - 630	3.4
430 - 440	2.4	530 - 540	3.4	630 - 640	3.4
440 - 450	2.8	540 - 550	3.4	640 - 650	3.4
450 - 460	3.0	550 - 560	3.4	650 - 660	3.4
460 - 470	3.2	560 - 570	3.4	660 - 670	3.3
470 - 480	3.3	570 - 580	3.4	670 - 680	3.3
480 - 490	3.4	580 - 590	3.4	680 - 690	3.1
490 - 500	3.5	590 - 600	3.3	690 - 700	3.0
				700 - 710	3.2
				710 - 720	2.7

Table 25

Spectral Distribution of Solar Energy and Amount

Air Mass	Equivalent Sun Angle	Rel. Amt. of Radn. in Wavelength Bands (Incl. Allowance for Alteration due to Longer Path).			
		400-500 nm	500-600 nm	600-700 nm	700-800 nm
1	90^{o}	131	151	129	108
			411		
2	30^{o}	92	118	116	90
			326		
3	19.3^{o}	62	96	96	78
			254		
5	11.3^{o}	32	60	72	61
			164		

Table 26

Proportional Distribution of Spectral Energy for Various Air Masses and Equivalent Sun Angles on Basis of Amount in 400-700 nm Range = 100

Air Mass	Equiv. Sun Angle	Wavelength Band				
		400-500	500-600	600-700	400-700	700-800
1	90^{o}	31.9	36.7	31.4	100	26.2
2	30^{o}	28.2	36.2	35.6	100	27.7
3	19.3^{o}	24.4	37.8	37.8	100	30.7
5	11.3^{o}	19.5	36.6	43.9	100	37.2

Table 27

Relative Solar Irradiance, Luminous Efficiency, and Colour Temperature at Sea Level for Various Air-mass Values. (Adapted from Moon, 1940, Table IV)

From "Radiation Biology", Vol. III A. Hollaender, Page 155.

Air Mass Solar Angle	0	1 90°	2 30°	3 19.3°	4 14.3°	5 11.3°
Wave length, nm	Percentage of Total Irradiance					
290-400	7	4	3	2	1	1
400-700	41	46	45	43	41	38
700-1100	28	33	36	38	40	42
1100-1500	12	10	9	9	9	9
1500-	12	7	7	8	9	10
Total	100	100	100	100	100	100
Total Irradiance[a] $W\ m^{-2}$	1320[b]	930	740	610	510	430
Lumens w^{-2}	93	105	106	103	98	93
ft-c $g\text{-}cal^{-1}\ min^{-1}\ cm^{-2}$	6000	6800	6850	6650	6300	6000
Colour temperature, ^{o}K	6200	5500	5100	4700	4300	4100

a Multiply by 100 for microwatts per square centimeter and by 0.0014 for calories per minute per square centimeter.

b Value of solar constant.

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