MODIFICATION AND MEASUREMENT OF SUN, SKY AND TERRESTRIAL RADIATION FOR ECO-PHYSIOLOGICAL STUDIES

by

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INTRODUCTION

Attempts to obtain maximum production from crop and pasture, orchard and forest land under arid and semi-arid conditions encounter physiological problems probably in many instances not unlike those met in the latitudes more distant from the equator. In mesophytic areas research on the genetically controlled reaction of plant to nutrition and environment has had important consequences. This research has resulted in enormously increased productivity; the yields obtained by use of the best current agronomic practices markedly surpass the yields based on the empirical practices of even the most observant farmers and foresters. Basic new physiological knowledge gained from systematic experiment has been put to use.

As yet, only a beginning has been made toward an understanding of the effects on plant yields of the quality and intensity of the light environment. Some species of plants thrive under light intensities which are too low for other species to survive. The species capable of growth in the shadow of an almost complete canopy of taller plants and trees are classified as "tolerant" (of shade). The "intolerant" species require moderately high levels of light intensity to survive. An indication of the tolerance of 183 species of herbaceous plants, trees and shrubs is given in Tables 388 and 389 of the *Handbook of Biological Data* (Spector, editor, 1956).

The cutting practices to be used for harvesting a mature forest stand look forward to the regeneration of a new young stand. These practices must be adjusted to the tolerance of the seedlings of the tree species to be favoured. For an intolerant species more of the canopy must be removed by cutting more trees at the time when a crop of seed may be anticipated.

FIELD EXPERIMENTS, 1923-1928

A series of studies of the light requirements of the seedlings of intolerant New England white pine (*Pinus strobus* L.) was started in 1923 (Gast, 1930). In 1925 the light intensities were measured under forest canopies beneath which were 11-year-old white pine seedlings. Three areas were chosen for study. In an area from which few trees had been removed the canopy was estimated as 85 per cent of full. Under it the light intensity was measured by different pyranometers during the period from 12 May to 13 September. These measurements indicated that the light intensity (total = visible + infrared) was 27 per cent of that in the open area not shaded by trees. Under this canopy the 11-year-old seedlings had just managed to survive; their average height was only 11 inches. From the second, the "open" area, the mature trees had been removed three years earlier. In the third area, where the canopy was estimated as 40 per cent of full coverage, the intensity was measured as 57 per cent of the intensity in the open. The increase in intensity from 27 per cent to 57 per cent notably increased the growth rate. It was concluded that an intensity of at least 27 per cent of full light is necessary for the growth of seedling white pine trees at a rate minimal for survival.

This type of experiment is an example of the observations taken during ecological field studies for description of the environment. Similar measurements by various investigators are quoted by Sauberer and Härtel (1959).

THE "SEMI-FIELD" TECHNIQUE

To verify the conclusions of this field study other experiments were devised. Studies of this sort may be distinguished as "semi-field" experiments. They are quite different from the wholly controlled, artificial environment of the phytotron. Thus in the "semi-field" experiments the natural sunlight is used but it is modified by screens which alter both the intensity and the quality of the irradiation.

Methodology of Plant Eco-physiology: Proceedings of the Montpellier Symposium.
Méthodologie de l'éco-physiologie végétale: Actes du colloque de Montpellier. Unesco 1965.

As in the case of the typical ecological study under the wholly natural conditions just cited, continuous measurements of the environment are necessary for correlation with the biological effects.

Other field tests during the period from 1923 to 1928 indicated that the effect of light could not be dissociated from the nutrition of the seedlings. The availability of nitrogen is changed when the temperature of the soil is raised by thinning of the canopy. The severance of the tree roots when the trees are cut changes the soil biology. To study questions of nutrition simultaneously with light intensity and quality the "semi-field" technique is convenient and efficient.

SEMI-FIELD TESTS: FIRST EXPERIMENT 1930

The first semi-field tests using natural light modified by screens were performed at the Swedish Forest Research Institution in 1930 (Gast, 1937). In this study the effects of varied light intensities, light quality and soils with differing nutrition on the growth of seedling European Scots pine (*Pinus sylvestris* L.) were examined.

For the modification of light intensity wood strips were used to construct three compartments in a Möller house (*Plates 2, 3* and *4*). The wood strips were spaced so as to transmit one-half, one-quarter and one-eighth of the light transmitted by the glass. The irradiation intensities in the compartments came close to the intended values. As measured by a horizontally mounted 180° pyranometer (see Drummond, page 15) the intensity under the glass alone (area not shaded by a lath screen) was 50 per cent. The compartment intensities, as percentage of sunlight in the open, were 22 per cent, 11 per cent and 6 per cent. Fans (*Plate 3*) operated at reduced speed gave a gentle air circulation through the compartments.

To modify the quality of the radiation a water-filter was placed over some of the plants in the "50 per cent" area (*Plate 4*). A tray with a glass bottom was filled with water to a depth of 10 cm. This absorbed the infra-red radiation longer than approximately 1 micron. (The exact transmission is uncertain; this is again referred to in a later section "Transmission of Radiation by a Water-Filter".) Under the water tray the intensity was measured as 27 per cent of the radiation in the open. Of the radiation passing through the glass of the Möller house the water tray absorbed 46 per cent. It can only be assumed, since no measurements were made of the irradiation in the region from 0.4 to 0.7 micron, that intensities for the visible region were approximately the same under the water tray and in the unshaded area adjacent to it. As components of sunlight a value of 54 per cent is a reasonable estimate for the spectral region $0.3 < \lambda > 1.0\ \mu$ and 46 per cent for the region $1 < \lambda > 3\ \mu$.

The soils used in this experiment differed in potential nitrogen availability—from previous studies they were known to have different rates for nitrogen mobilization. The soils were combined with sand to give a porous mixture. The pots containing the soils were embedded in sand to stabilize the soil temperature (*Plates 3* and *4*).

SEMI-FIELD TESTS: SERIES 1931-1939

The seedlings grown during the first test in 1930 were analysed for nitrogen. The concentration of nitrogen in the plant (expressed as percentage of the dry weight) provided an efficient index as to nitrogen availability. An adequate supply of nitrogen is essential to the full utilization of the available light. Less nitrogen than the amount required to maintain the optimum internal concentration limited the growth at the higher light intensities.

That the internal concentration could be used to appraise the optimal nutritional levels of nutrients other than nitrogen seemed worth testing. To explore this possibility a series of studies was conducted to determine the concentrations of nitrogen, phosphorous, potassium and calcium in the seedlings variously supplied with these nutrients. The plants were grown in what are now called hydroponic cultures—the plants are rooted in sand which is periodically flooded with a solution of the salts comprising the nutrient mixture. For each nutrient element a graded series of concentrations is needed.

From the analyses for nitrogen, phosphorous, potassium and calcium in the graded series of weights of plants grown in the graded series of nutrient solutions were obtained conclusions as to the internal concentration (gramme element/gramme dry weight) optimal for growth. Such is the method of foliar diagnosis as it was used in these studies.

Gradual modification of the techniques for most efficient manipulation of the large number of plants involved in these tests was to be expected. In the earlier experiments unglazed clay pots were placed in pails the insides of which were painted with tar (*Plates 7, 9* and *10*). Later special glazed earthenware pots with a bottom opening were used (*Plate 8*). (Plastic containers now available can be used to advantage as suggested by Dr. J. Wehrmann, in a private communication.) The sand was a mixture of two sizes of quartz sand (at least 99 per cent SiO_2); it was cleaned before use with a dilute $HCl\text{-}H_2SO_4$ mixture and then with ordinary water until no mineral acid could be detected. The nutrient solutions were stored in jugs placed in a dark chamber underneath the pots; they were flushed from below into the pots to a height sufficient to dampen the top of the sand by pumping air into the tops of the jugs (*Plates 8* and *9*).

Instead of the lath screens used in 1930, in all later experiments bronze-wire-cloth screen was used to modify the light intensity (*Plates 5, 6* and *8*). The bronze screen is preferred because the flecks of light and shade are small and the illuminated and shaded areas of the plants alternate more frequently. The screen is formed as a hemi-cylinder with a comparatively small radius and a long axis. The frame holding the pots is so oriented that the long axis of the screen is north-south. A constant transmission at all hours of the day results. Since the irradiation under the screen was measured, the changing declination of sun created no difficulty—but if desirable, the screen could be adjusted by tilting the long axis so that any change in transmission is minimized.

The seedlings were grown from seeds sorted for size and in any one pot seedlings from only one size of seed were grown. At any given time during vegetative growth the weights of the seedlings are proportionate to the "capital"—the initial dry weight—of the plant at the beginning of the measured growth. This is an example of one of the details which must be followed through in order to attain precision in this type of experiment. In practice, the weights of the plants are corrected to a common normal initial "capital" weight. The seeds sorted into weight classes were germinated in separate flats (*Plate 10*). Immediately the seed coat (testa) was shed, samples of seedlings and seed coats from each weight class were taken and their dry weights determined. The ratios between the weights of the seedlings grown for any specific period (e.g., 9, 90, 180 days) were the same as the ratios of the seed weight classes from which the plants were grown. An adjustment factor can be derived to correct the dry weights of the seedlings grown from any seed weight class to a "normal" value (Aldrich-Blake, 1930, 1932, 1935; Gast, 1937; Mitchell, 1934, 1939).

This summary account omits many details of techniques described in the referenced papers. Following this earlier work on pine seedling nutrition came the studies, among others, by Björkman (1940, 1942, 1944, 1956), Tamm (1954, 1955) and Ingestad (1957, 1959, 1960). Gradually these pilot experiments on nutrition of seedlings in hydroponic cultures were extended to studies of fertilized experimental plots in forest stands (Mitchell and Chandler, 1939). A bibliography of studies of tree nutrition and foliage analysis both in hydroponic cultures and in nature can be compiled from the references cited above, supplemented by Tamm and Carbonnier (1961), Wehrman (1959) and others.

NUTRITIONAL LEVELS

The concentration levels of macronutrients in the plant tissues which are associated with maximum vegetative growth are still being studied, as the references just cited indicate. (Note that where plant productivity is measured by the harvest of grain and fruit, a nutritional level which produces the maximum vegetative growth may only in part be responsible for maximum productivity; it may be a contributing but not controlling condition. For during the flowering and fruiting phases nutritional levels differing from those of the vegetative phase may be optimal for maximum productivity. The advantages of using only the vegetative phase for "preliminary" semi-field tests seem obvious; in subsequent experiments the variations in the yields of the fruiting phase with changing environment may be studied with better understanding.)

During their early growth, tree seedlings are limited to the vegetative phase of development. During this phase the same internal concentrations of nitrogen, potassium and phosphorus appear to provide for maximal growth of pine seedlings rooted either in hydroponic ionic solution cultures or in natural soils. A mnemonic "rule of three" is close to correct. That is, for nitrogen 3 per cent N of dry weight gives the best growth. For potassium, one-third of 3 per cent, equal to 1 per cent K (not K_2O) is apparently close to the optimum. For phosphorus, one-third of 1 per cent, equal to 0.3 per cent P (not P_2O_5) is most favourable.

Adequate levels of the internal concentrations of calcium and the micronutrients are tentatively known (Ingestad, 1960).

FORMALIZATION OF GROWTH/NUTRITION RELATION

The weight of the seedlings in relation to the supply of macronutrients is amenable to mathematical formalization. The effect of nitrogen, potassium and phosphorus on dry weight can be expressed quantitatively by an appropriate Mitscherlich type of equation; i.e., as a factor (nutrition) is increased there is an exponential increase in yield up to a maximum; then further increases in the factor cause an exponential decrease from the maximum. The effect of the complex of individually varying factors can be expressed by a multiple equation where the total resultant is the product of each of the Mitscherlich components taken separately—in other words, summation of the individual factors can be expressed by a logarithmic form of the Mitscherlich equation (Gast, 1937; Mitchell, 1934, 1939).

LIGHT AND GROWTH

The intolerant pine seedlings (white pine and Scots pine) grown for approximately ninety days fully used the maximum light available in the open in the northeastern United States. The seedling dry weights were exactly proportionate to the cumulative sunlight as measured by a 180° Eppley pyrheliometer (pyranometer) within the error of the sunlight record (about 3 per cent). Such full use of "open" (100 per cent) sunlight will be obtained, however, only if the macro-

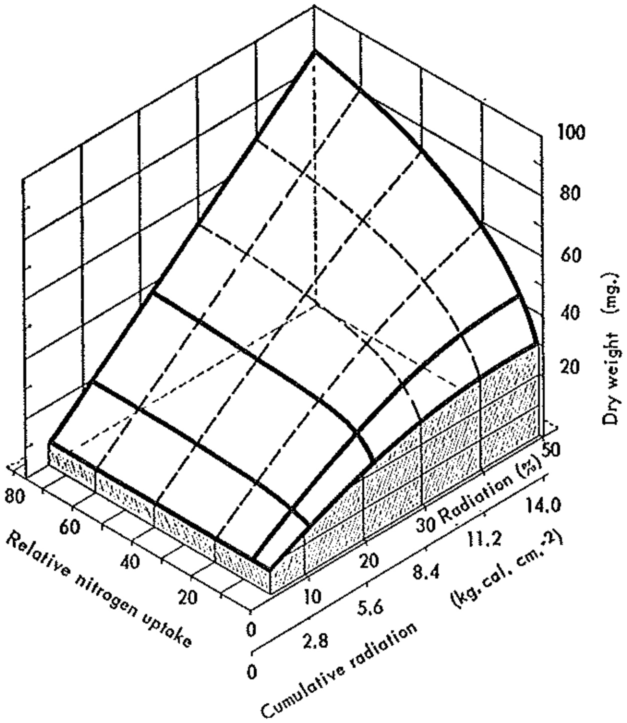

FIG. 1. The dry weights of three-month Scots pine seedlings as affected by radiation and nitrogen availability. Seedling weights normalized to 4.8 mg. fresh seed weight. Radiation scaled as percentage of open, and in kg.cal. by 180° pyranometer. Nitrogen availability calibrated by hydroponic cultures. (After Gast, 1937, Fig. 20.)

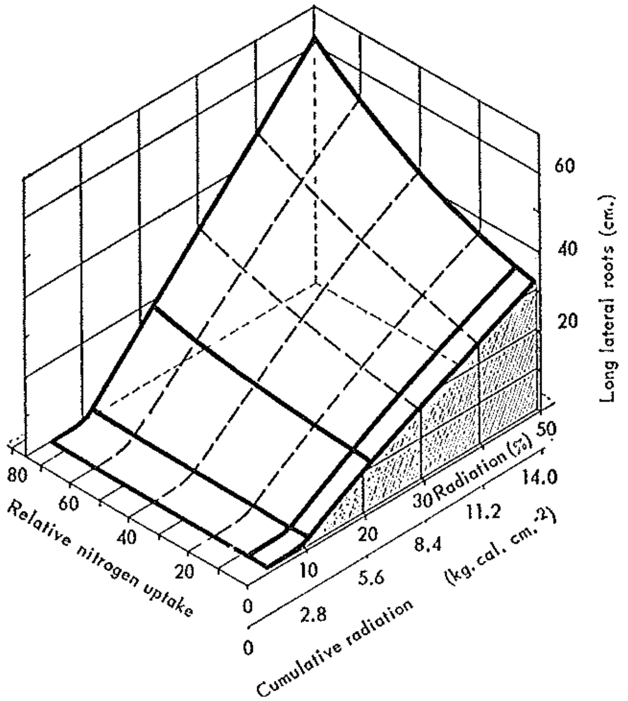

FIG. 2. Lengths of long lateral roots of seedlings as in Fig. 1 (After Gast, 1937, Fig. 21.)

and micronutrient concentrations are maintained at the optimal concentrations referred to above.

The results of the experiment in Sweden in 1930 are reported in three figures. In Figure 1 the relation between light (50, 22, 11, and 6 per cent values) and nitrogen nutrition is correlated with the dry weight of the seedlings. In Figure 2 the correlation is with the length of the long roots which increase with increasing light intensity. In Figure 3 the correlation is with the shoot/root ratio.

As calibrated by the later hydroponic experiments, the nitrogen available from the three different soils was in the proportions 76 : 8 : 2 (shown as heavy lines). The intermediate values (light dashed lines) which indicate the shape of the curved surface were interpolated from the hydroponic experiments of later years.

From 1931 to 1934 seedlings were grown in hydroponic cultures both in the open and under screens for reduction of the irradiation intensity. The dry weight of the seedlings increased with increasing intensities up to the intensity of full—"open"—sunlight. That is, later experiments showed that under conditions of the highest nitrogen availability of Figure 1 where the internal concentration of nitrogen in the seedlings is close to 3 per cent, the linear relationship can be extrapolated as a straight line up to twice the light intensity shown

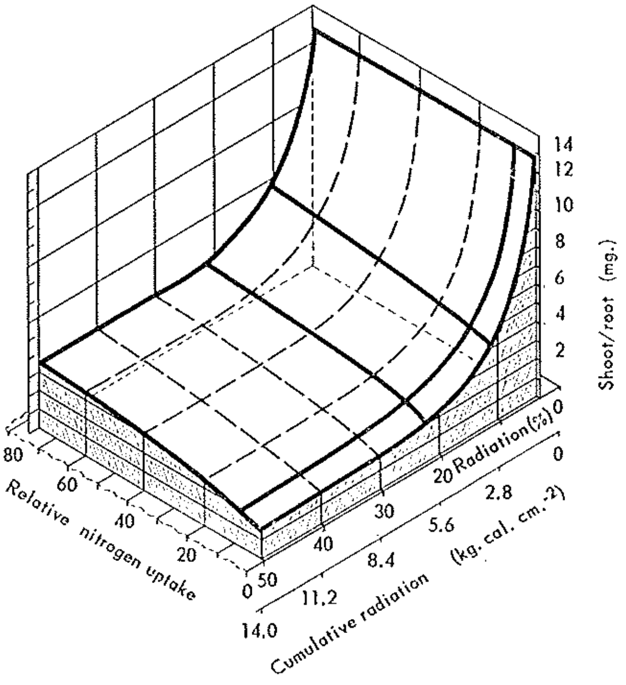

FIG. 3. The shoot/root ratios of seedlings as in Figures 1 and 2, but note that in this figure the direction of the cumulative radiation scale is reversed. (After Gast, 1937, Fig. 22.)

in the figure—100 per cent—equal to 28 kg.cal. cm^{-2}. In the case of white pine the growth is proportionate to the sunlight intensity up to 40 kg.cal. cm.^{-2} (46.5 watt hours cm.^{-2}) summed over a three-month growth period (Gast, 1937).

The accuracy of the correlation between the vegetative growth and sunlight is illustrated by the experience of Mitchell (1934, p. 66-67, 1936, 1939) at Cornwall. White pine seedlings were grown in full sunlight as measured by a 180° pyrheliometer (*Plates 6* and *8*). After several weeks of cloudy weather in the middle of the growing season it was noted that the seedlings sampled at the beginning of September were underweight in the light of previous experience. Due to the cloudy weather the cumulative irradiation was low. An additional growth period of a few weeks of sunny warm weather brought both cumulative irradiation and yield in dry weight up to expectation.

LIGHT AND SHOOT/ROOT RATIOS

The experiments in the period 1930-1938 made clear the reasons why the intolerant species of pine required approximately 30 per cent of full light for survival under a canopy of older trees.

In Figure 2 it is seen that the growth of the long lateral roots is proportionate to the irradiation, even at low levels of nitrogen availability. But if the weights of the shoots and the roots are compared (Fig. 3), it is seen that as the light intensity decreases below 30 per cent of open the relative weights of the roots decrease markedly in relation to the shoots. (Note that for convenience in representing the surface in Figure 3 the scale of the radiation axis is shown as increasing from right to left, instead of from left to right as in Figures 1 and 2).

The large change in the shoot/root ratio as the light intensity decreases below 30 per cent, as disclosed in the hydroponic cultures, correlates with evidence from the forest observations that 30 per cent is the minimum for the survival of seedling trees under an older stand. A full discussion of the significance of the 30 per cent light intensity requires a review of the mycotrophic habit.

THE MYCOTROPHIC HABIT

Evidence for the importance of the mycotrophic habit may be cited from an experiment by Hatch (1937, p. 100). A sample of soil was collected from a prairie area. The site was so distant from a forest stand that there was no possibility that it contained any fungi which could infect pine tree roots to form mycorrhizae. Seedlings cultured in this soil both with and without the addition of fungal inoculum are shown in Figure 4. The marked increase in growth and in nitrogen content of the plants grown symbiotically is notable (see Table 1).

TABLE 1. Weights and nutrient content of seedlings grown in prairie soil. (After Hatch, 1937, Table IX)

	Inoculated		Uninoculated	
	mg.	% dry weight	mg.	% dry weight
Average dry weight	404.6		320.7	
Nitrogen	5.00	1.24	2.69	0.84
Phosphorus	0.79	0.20	0.24	0.07
Potassium	3.00	0.74	1.38	0.43

The comparative morphologies of roots cultured in three different nutrient media are shown in *Plate 11.* Type A are from a hydroponic culture with a moderately high concentration of nutrients. In a lower concentration of complete nutrients in hydroponic culture and occasionally in "natural soils", root-hairs are formed on the short lateral roots (type B). The normal type of infected short lateral roots forming mycorrhizae is shown as type C. Such "true" mycorrhizae are found in cultures of a forest soil containing both organic matter and inoculum of mycorrhizal fungi. The sections through the roots which are "true" mycorrhizae (type C) show the cellular enlargement characteristic of the reaction of the root cells to the intra-penetrating growth by the hyphae of mycorrhizal-forming fungi. For comparison with type C are included sections through the "pseudo-mycorrhizal" roots in type A, and the rare lateral roots covered with root-hairs in type B. (Hatch, 1937). The mycorrhizal roots increase the surface for the uptake of nutrients from the soil. The increased surface follows from the increased volume

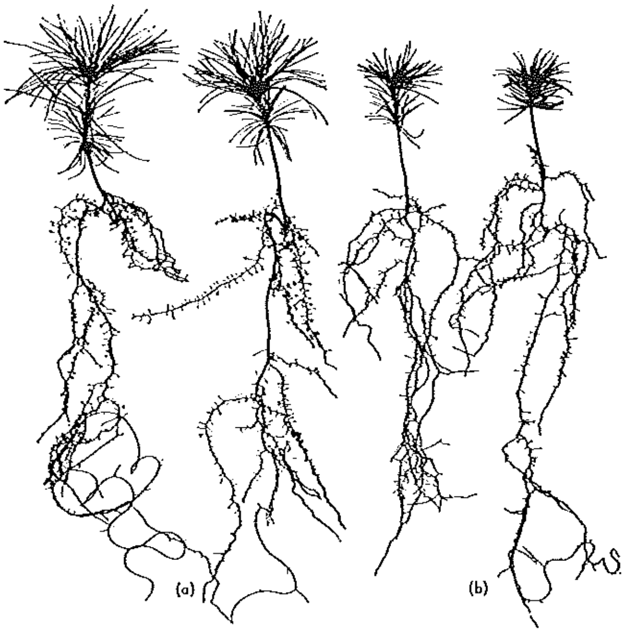

FIG. 4. White pine seedlings raised in prairie soil: (a) inoculated; (b) uninoculated. (After Hatch, 1937, Table IX.)

covered by the mantle of fungal hyphae and, in addition, the extension of the hyphae into the surrounding soil. Both increase in surface and in metabolic kinetics are believed to account for the increased growth and mineral uptake, leading to an increased nutrient content of plants equipped with true mycorrhizal roots over those with "pseudo-mycorrhizal" roots. In natural soils the plant roots are but sparsely furnished with root-hairs and these are found only near the tips of the "long laterals".

A deficiency of easily available nitrogen, phosphorus, potassium and calcium in a natural soil otherwise adequately supplied with macronutrients will, if the inoculum is present, stimulate the development of the mycotrophic habit. Whether or not a deficiency in micronutrients will also promote the appearance of true mycorrhizae has not, it is believed, been tested.

It appears, then, that by use of the hydroponic culture a condition different from that existing in natural soils can be created. In the case of plants in natural soils the efficiency of the mycorrhizal hyphae in assisting uptake of exchange-bound nutrient ions becomes significant. When the nutrients are present as free ions, as in the hydroponic solution media, the factor of mycotrophy is eliminated.

But where present the mycorrhizal roots are more efficient than pseudo-mycorrhizal roots in the uptake of mineral nutrients. Melin and Nilsson have produced clear evidence for this favourable influence of mycorrhizae by the use of labelled elements: P^{32} (1950, 1954), N^{15} (1953), Na^{22} (1955*a*), Ca^{45} (1955*b*).

The literature on mycorrhizae and the mycotrophic habit is extensive; the reports cited above are but a small part of the total. A large, related but separate literature treats of symbiosis with bacteria, and the symbiotic phenomena in roots harbouring simultaneously bacteria and fungi. The growth of the whole plant is in all instances affected by the supply of photosynthate to the roots, and by formative influences such as night temperature (Mes, 1959*a*, 1959*b*). Again, irradiation as a part of the plant environment enters by indirection as a significant factor, as indicated by experiments with the water-filter.

In connexion with a succinct yet adequate discussion of mycotrophy Björkman (1942) cites all relevant literature, and this is brought up to date by his 1956 report. Björkman seems to de-emphasize a possible role of the fungal hyphae which the writer considers important. This is the likelihood that by ion exchange a hypha can acquire nutrient ions from the surface of a soil particle to which the nutrient ion is bound. The writer (unpublished) attempted to use ion-exchange resins (commercial "Permutit", etc.) to synthesize a balanced nutrient substrate which would release into the "soil" solution a minimum of free ions. Further work with ion-exchange resins, concentrated ion-exchange clays (montmorillonite, kaolinite), "humus" concentrates and vermiculite should be undertaken.

MINIMAL LIGHT INTENSITIES

An analysis is now possible of the factors entering into a requirement of about 30 per cent of natural sunlight as a minimum for the growth of intolerant pine seedlings. At less than 30 per cent irradiation the photosynthate is retained mostly in the shoot at expense of the root. Large shoot/root ratios result. Pine seedlings growing under natural forest conditions are obligate symbionts—the macronutrients are never present at the relatively high solute concentrations of the hydroponic cultures. Failing an adequate supply of carbohydrate, as in the instance of seedlings with high shoot/root ratios, the mycorrhizae are starved. They are no longer efficient in the uptake of macronutrients. The seedlings suffer from a deficiency of the mineral nutrients due to an inadequate root system.

So much is clear; but a further question remains to be explored. It is noted that severance of the roots of mature trees which enter into a small plot will promote growth of plants within the plot. The biotic conditions in the soil within the plot are changed. There is less drain on the available water. But the possibility of antibiotic competition must not be disregarded. The mycorrhizae on the roots of the trees with the foliage in full sunlight may well be capable of excreting antibiotic substances which would inhibit the development of mycorrhizal fungi on shaded seedlings inadequately supplied with carbohydrate. The mycorrhizae on the roots of seedlings growing under less than 30 per cent irradiation would be subject to such starvation. Contemplated but never tried were experiments to study competition between the mycorrhizae on roots of plants with the tops in the contrasting conditions of high and low intensities of irradiation; in semi-field tests the desired contrasts could be arranged by the use of shades.

The test just suggested would serve to increase our understanding of the complex situations under which tree seedlings are established or fail to survive according to the light intensities following removal of overshadowing trees of the higher canopy. The effect of reduction of the carbohydrate to the roots on the development of mycorrhizae was demonstrated by Björkman (1944) in an ingeniously simple experiment. By constricting the stems of seedlings with wire the flow of carbohydrate to the roots was slowed and the inhibition of mycorrhizal development resulted. Melin and Nilsson (1957) by the use of C^{14}-labelled photosynthate found that the C^{14} and its conversion products are rapidly transported to the root tips and to the mycorrhizal mantles.

The connexions between the formative influences of low versus high light intensities and the mycotrophic habit are clear for intolerant seedlings growing in low light intensities—less than 30 per cent of the open—under the canopies of older trees. The information necessary for a similar analysis of tolerant species is not in hand. To acquire this information it would be helpful to use the screens and the water-filter. These same techniques would be of use in examining differences in the role of mycotrophy in tolerant and intolerant species which depend on this phenomenon for the uptake of mineral nutrients.

Another instance of the formative effect of diminished infra-red irradiation is an experiment by Gast and Hatch (Hatch, 1937, p. 72). Plants grown under a water-filter developed twice as many mycorrhizal short roots as did the plants grown under wire-cloth screens which transmitted respectively 11, 24, 48 and 85 per cent of full sunlight. Some objective measure of the extent of mycorrhizal development is required. Such a measure may be the percentage of short roots which exhibit coral-like branching and enlargement. This is not always infallible. Although the effect of light intensity on the mycorrhizal development was anticipated (Gast, 1937, p. 661-665), we did not discover the evidence for the influence of light (Hatch, 1937, p. 70-73, Table III) which was observed by Björkman (1940, 1942) under almost the same experimental conditions except for the soils. The critical factors which differed as between the two sets of experiments are still not clear.

TEMPERATURE AND GROWTH

In a complex physiology such as the mycotrophic habit implies, the possibility always exists that other factors of the environment may become important. Temperature is such a factor. For the tomato (*Lycopersicon esculentum*) as the day temperature increases a decreasing night temperature is more productive as found by Went (1957) in a study of the interaction of temperature and the photoperiod.

This finding contrasts with the results from a study of the growth of the symbiotic velvet bean (*Stizolobium deeringianum*) observed in a series of cultures from 1954 to 1958 (Mes, 1959*a*). This bean grows symbiotically with nodules of *Rhizobium sp.* on the roots. There is no evidence of photoperiodic control during the vegetative phase of growth; variations in length of light period from 12 to 16 hours were without effect. At low night temperatures the rhizobia were apparently inefficient and nitrogen starvation of the beans resulted. Higher night temperatures, 18°C. as compared with 10°C., increased the dry weight by 40 per cent (if a "starter" increment of nutrient nitrogen was added) or by 116 per cent (in the absence of "starter" nitrogen). The results cited in Table 2 are from but one of several experiments giving the same evidence. The higher night temperatures in every way favoured the plant growth and development. In the velvet bean, contrary to the finding for the tomato, there is apparently a higher rate of translocation of sugar from shoot to root. The indirect evidence for this is the higher rate of nitrogen fixation in the root nodules, plausibly due to a more ample carbohydrate supply. The higher nitrogen level of 2.6 per cent of dry weight promotes better growth than does a content of 1.6 per cent.

Table 2. Effect of night temperature on the growth, development and nitrogen assimilation in the velvet bean (*Stizolobium deeringianum*). (After Mes, 1959, Table 1[1])

	Temperature	
	Day 27°C. Night 18°C.	Day 27°C. Night 10°C.
Dry weight per plant (grammes)	5.4	2.5
Ratio: dry weight of shoot to dry weight of root	4.8	1.8
Nitrogen		
Percentage of dry weight	2.6	1.6
Total per plant (mg.)	138	40
Nodules (*Rhizobium sp.*)		
Number per plant	13	12
Dry weight per plant (mg.)	239	143
Dry weight per nodule (mg.)	18.4	12
Nitrogen assimilated		
Per nodule (mg.)	8.3	0.8
Per mg. dry weight of nodule (mg.)	0.45	0.07

[1] Experiment 3. Period of growth: 18 December 1957 to 18 March 1958. No nitrogen added to growth medium. Values are means obtained from five pots with five plants each.

LIGHT QUALITY

The seedlings grown under the water-filter were irradiated with 50 per cent sunlight from which the infra-red longer than about 1 μ had been removed. Significant differences in growth and development resulted. The irradiation as measured by a 180° pyrheliometer (or pyranometer) was 27 per cent of the sunlight in the open. The formative effects on plant development are shown in Figures 5, 6 and 7. These are Figures 1, 2 and 3 modified by insertion of a vertical plane at the 27 per cent point for "cumulative radiation". The intercepts of the plane with the curved surface in each of the figures indicate the expected values of weight, length of long lateral roots or shoot/root ratio if the light quality had been the same as for the graded series of light intensities. The differences in the heights of the planes above or below the intercept line show the deviations of the found from the expected values.

Note, however, that the curved surface of Figure 1 is plotted against the values of total radiation as measured by a pyranometer. If the seedling weights were

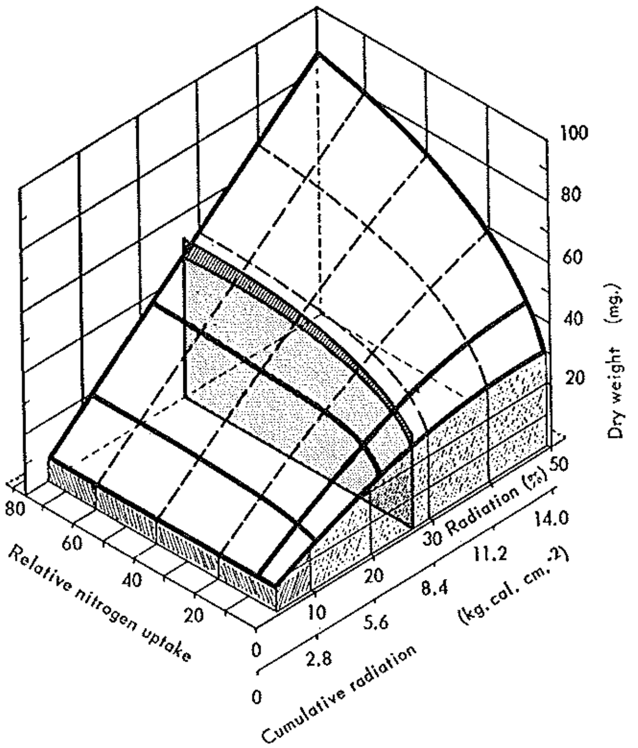

FIG. 5. Effect of water-filter (10 cm. deep) on seedling weights. Vertical plane inserted at 27 per cent irradiation intensity (cumulative radiation 7.6 kg. cal. $cm.^{-2}$) under water (cf. Fig. 1).

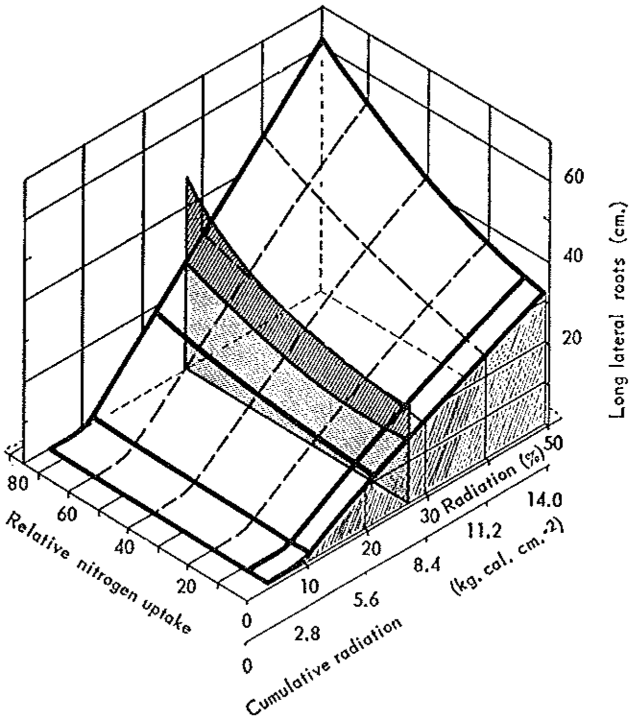

FIG. 6. Effect of water-filter on lengths of long lateral roots (cf. Figs. 1 and 2).

to be correlated with the visible components of the irradiation they should be approximately the same under the water-filter as outside it. (Under the water-screen, it is true, part of the infra-red $0.8 < \lambda > 1\ \mu$ component was included.)

Alternatively, consider the evidence in another way. The radiation outside the water-filter ($0.3 < \lambda > 1\ \mu$ plus $1 < \lambda > 3\ \mu$) is 185 per cent of that under the water-filter ($0.3 < \lambda > 1\ \mu$). This extra 85 per cent ($1 < \lambda > 3\ \mu$) gives, in plants grown at the highest nitrogen level, a 70 per cent increase in seedling weight.

The superficial conclusion would be that if the visible irradiance is about 50 per cent of that in the open, then a supplement of infra-red increases the weights of the seedlings, the increase being proportional to the intensity of the added infra-red. (Note that the irradiation is measured as the heat content, not as the flux of photons.) This explanation is probably too simple. The development of the plants differs as the quality of the light is changed. Root growth is favoured in the absence of the infra-red absorbed by the water-filter. In the smaller plants under the water-filter the vertical plane (27 per cent) of Figure 6 rises considerably above the normal surface. The shoot/root ratio is correspondingly smaller (Fig. 7). Parallel to the

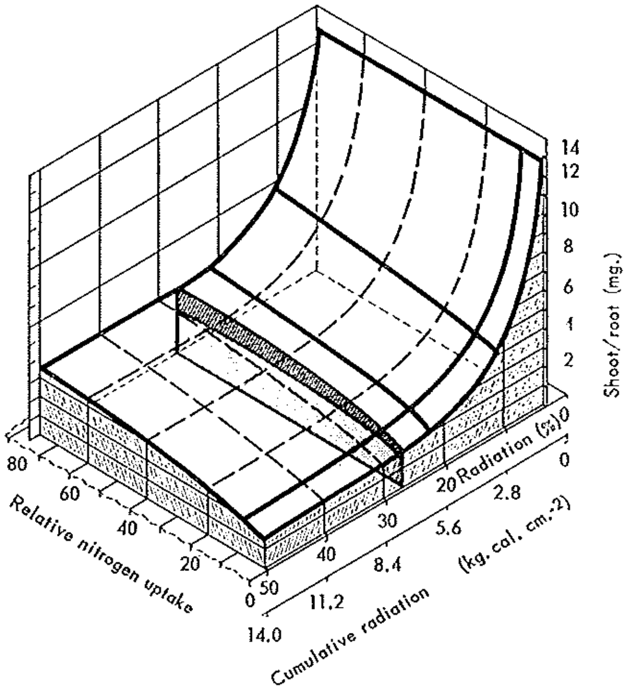

FIG. 7. Effect of water-filter on shoot/root ratios of seedlings (cf. Figs. 1 and 3).

increase in root development is an apparent enhancement in root efficiency. The plants under the water-filter contained the largest content of nitrogen (3.3 per cent) of any grown in the soil of highest nitrogen availability.

However, the régime of day-time infra-red irradiation was not the only environmental factor which was changed. The water-filters were left in position over the plants during the night. Cooling by a transfer of heat by radiation from the plants to the cooler night sky was inhibited. This was possible only in the "open" experiments of 1931-1934 in Petersham (*Plates 5* and *6*). Under the Möller house in the 1930 experiments (*Plates 3*, *4* and *5*) the glass roof would prevent radiational cooling of the plants outside the water-filter. To this extent the experiments in 1930 provided controls lacking in the 1931-1934 experiments. In the latter there were no tests to provide a comparison between (a) plants grown under a water-filter continuously for 24 hours, and (b) plants grown under a water-filter present during the day but removed at night.

The possible effect of night temperature has been clearly demonstrated by the work on the velvet bean cited above. To the extent that the experiments with pine seedlings are inconclusive they point out the requirement for measurements of the radiative loss of heat from the plants. Such are especially important in dry climates where the low water content of the atmosphere favours rapid radiative cooling at night. Both the environmental temperature and the radiative cooling which affects it must be continuously monitored. A water-screen placed over the plants during the dark hours would effectively reduce radiative cooling. Thus it should be possible by careful observations to distinguish between the foliage temperatures—and resulting physiological effects—brought about by convective transfer of heat to the ambient air and radiative cooling outward from the foliage through a dry atmosphere.

PLANT PHOTORESPONSES

Studies devoted to the clarification of photoperiodism and the effect of light on seed germination have led to the discovery that light was involved in many more chemical reactions within the plant than the formation of chlorophyll, consequent photosynthesis and a tropic orientation of stems and leaves. It now appears that some twenty-odd plant responses are due to photoreactions. In addition to the formation of chlorophyll, light is responsible for the formation of the carotenoids (flavin) and anthocyanin. The latest pigment to be intensively studied is phytochrome. Success in concentrating it (Butler, Norris, Siegelman and Hendricks, 1959) may be expected to lead soon to elucidation of its exact chemical nature. Both auxin and the "new" growth regulators can be influenced by light. Thus limited evidence indicates that under photocontrol are such diverse effects as protochlorophyll regeneration, epinasty, leaf abscission, Casparian strip formation, phylloidy of tracts, succulency, sex expression, plastid generation. In this list Hendricks (1959) includes also responses of parts of plants not exposed to light which can only be affected by photo-induced regulators: bulb formation, rhizome production and root development.

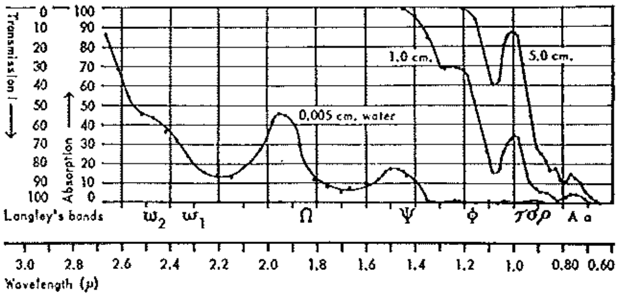

FIG. 8. Transmission of liquid water through indicated depths. (After Gast, 1930, Fig. 2.)

The preceding analyses serve only to suggest the extraordinary range of photoresponses which the ecologist must consider. Recent accounts of the status of these studies are summarized in Withrow (editor, 1959), and Machlis and Briggs (editors, 1960, 1961). But in connexion with the interpretation of the effects of a water-filter more details about phytochrome should be recalled. It exists in two forms, P^{660} and P^{730}. The P^{660} form absorbs red light and is converted to the P^{730} form believed to induce a biological response. The P^{730} form absorbs far-red and is converted to the inactive P^{660} form. The P^{730} form kept in the dark reverts to the P^{660} form (Hendricks 1959). The action spectrum for photolability is seen in the lower part of Figure 9.

One might suggest that the effect of the water-filter as described above is associated with the interconversion of phytochrome between P^{730} and P^{660}. But the water screen of 5 cm. depth transmits about 15 per cent in the region of $\lambda < 0.8\ \mu$ (Fig. 8). (Note that the accuracy of this transmission of the water-filter may be questioned, as discussed in another section of this article). Hence one questions whether or not the interconversion of phytochrome by differing intensities of λ-660 mμ and λ-730 mμ may not be too simple an explanation.

Another possibly more plausible explanation as to the effect of the water-screen follows from experiments by Hendricks (1959). He found that the germination of *Lepidium* seed was better when the red radiation ($\lambda \simeq 0.66\ \mu$ max.) was supplemented by "full" sunlight for 8 to 64 seconds, whereas sunlight filtered through 5 cm. water was less effective in promoting germination (Table 3). To quote from his discussion: "A newly

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[1] Here numbered Table 3.

TABLE 3. Effect of exposure to sunlight on germination of *Lepidium virginicum* seed. Seeds were returned to darkness and shifted from 15° to 25°C after exposure to radiation. Average results from four lots of 100 seeds each. (After Hendricks, 1959, Table III)

Duration of exposure to full sunlight (sec.)	Percentage germination with 4 min. prior exposure to red radiation		Percentage germination without prior exposure	
	Unfiltered radiation	5 cm. H_2O filter	Unfiltered radiation	5 cm. H_2O filter
0	64	78	0	0
1	42	53	21	
2	51	56	27	17
4	53	60	29	
8	85	53	30	25
16	87	60	36	
32	93	59	48	28
64	93	71	62	

recognized effect of radiation at high flux density that probably is important to growth of plants in sunlight, as well as to several other photobiological responses, is illustrated by results in Table III. [1]

"An explanation is that the high radiant flux is supplying activation energy that in the molecular surroundings of the point of absorption is not in equilibrium with the black-body radiation. This affects, to a degree dependent upon the radiant flux, the balance of those reactions having slow turnover rates in the vital system. The reversible photoreaction samples this general condition through its dependence on the hydrogen-transferring systems. Upon removal to darkness, the pigment balance is fixed at the condition attained in the high radiant flux. In general, the systems seem to shift toward high amounts of A as shown in the following reaction (2)[1]—they become relatively more sensitive to red radiation:

$$\text{(2)}\quad P^{660}H^2 + A \underset{\text{7200 -- 7400 Å max}}{\overset{\text{6500 -- 6600 Å max}}{\rightleftharpoons}} P^{730} + AH^2.\text{''}$$

(and in darkness)

This explanation can be phrased in another way. It is known that photons with energies below the critical value for completion of a photochemical reaction can so excite the reactive molecules that the photons with energies above the threshold values are more effective. The concept advanced by Hendricks can be restated in terms of the energies of the photons (or "quanta") given in electronvolt (eV) units.

Photons with an energy of 0.41 eV form the flux of radiation of wavelength of 3 μ. For successively shorter wavelengths the connoted photons have the energies listed:

λ (μ)	eV	λ (μ)	eV
2.0	0.62	0.80	1.55
1.5	0.83	0.76	1.63
1.1	1.13	0.69	1.80
0.9	1.38	0.60	2.07

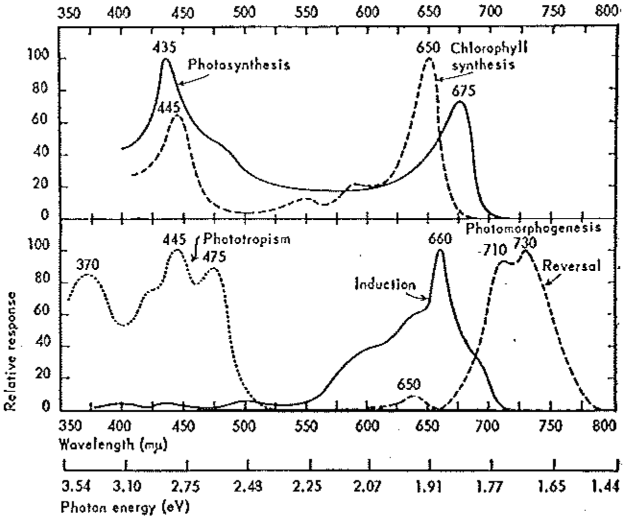

FIG. 9. Action spectra of five principal plant photochemical reactions: photosynthesis and chlorophyll synthesis in the upper section: in the lower, phototropic response and the interconversion from P^{730} to P^{660} and vice versa. All curves normalized to 100 for maximum relative response. Authorities for data are given by Withrow (1959, Fig. 5).

Using the language of photons and the action spectra for the interconversion of phytochrome (Fig. 9) the above explanation may be restated as follows. Irradiation with photons of 1.63 to 1.80 eV converts P^{730} to P^{660}. Irradiation with photons of 1.38 to 1.55 eV so "activates" the P^{660} molecule that exposure to photons with energies of 1.80 to 2.07 eV converts it to P^{730} and germination is induced.

In addition to the formative effect of far-red radiation, it is seemingly also effective in photosynthesis. Emerson and Rabinowitch (1960) discovered that the far-red radiation could increase the evolution of oxygen from water. The far-red region of $\lambda > 0.7$ μ (photon energy < 1.77 eV) by itself is inactive. Although absorbed, the energy of these photons does not accomplish photosynthesis. But as a supplement to photons with energies > 1.82 eV ($\lambda < 0.68$ μ) the far-red radiation becomes fully effective. Two quantitative conversions are postulated (Calvin, 1962). Gaffron (1962), although Franck would differ, suggests an interplay between two excitation levels in two differently bound chlorophyll *a* moieties. There is a suggestion from the results with the water-filter that the infra-red similarly supplemented the visible in increasing the growth of the pine seedlings.

In all the above discussion of photoresponse by the plant is an evident neglect of the variation in absorption of spectrally different energies. If reflection by foliage is taken in account, it is difficult to credit the infra-red with all the increase in yield for plants grown in full

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[1] In quoting this equation P^{660} and P^{730} have been substituted for "pigment" in the original by Hendricks.

sunlight as compared with the size under the water-filter.

It is clear from what has been said about the variety of possible effects of the water-filter that it was not used to the greatest advantage in the experiments which have been described. Not only did it change the quality of the light but it altered the night environment by inhibiting the outward flux of long wavelength infra-red—terrestrial radiation. The demonstrated responses of the plant could arise through a variety of mechanisms. Careful scheduling of the interposition of the water-filter in the radiation fluxes of both day and night are required.

TRANSMISSION OF RADIATION BY A WATER-FILTER

A tray of water is useful as a filter to absorb infra-red radiation. Presumably the transmitted energy could be estimated from absorption coefficients. The values for the coefficients determined by Aschkinass (1895) and by Driesch (1924) are more conveniently listed for reference in the *International Critical Tables* (Washburn, editor, 1930).

The values for the coefficients given by these two investigators (and their determinations are the only data which have been located) are not in close agreement. For this paper some new measurements were recently undertaken. It then became clear that every water tray used for a filter requires an *ad hoc* determination of its transmission.

As an illustrative guide of only approximate accuracy the transmissions shown in Figure 8 may be used. These were calculated for depths of 0.005 cm., 1 cm. and 5.0 cm. using the coefficients of Aschkinass. It is clear that 1 cm. completely absorbs radiation $\lambda > 1.4\,\mu$ and that 10 cm. would absorb $\lambda > 1.0\,\mu$. In the region $1.0 < \lambda > 0.7\,\mu$ it is difficult to calculate in advance the transmission of a glass-bottomed tray. The presence or absence of a glass cover will affect the transmission; and around the edge of the zone of transmitted light there will be anomalous spectral radiation. Only the central zone of transmitted light will be spectrally homogenous.

Where a water-filter is used for modification of the spectral quality of the irradiation environment of plants there is apparently no alternative to the direct measurement of the transmission of the filter. A series of observations will be required to determine the effect of the particular design of the water tray and the influence of the changing position of the sun in the sky, i.e., the effect of the angle of incidence of the solar beam on the top surface of the water-filter. The writer only rather recently appreciated the need for such observations; he certainly did not in the period 1929 to 1935. But even if he had, the equipment would not have been available, since only recently have convenient spectrographs been devised.

The transmissivity in the infra-red of distilled water differs from that of a dilute solution of colourless ions; a solution of $CuSO_4$ so dilute that no blue colour is evident when a white background is viewed through 20 cm. will show, as compared with distilled water, a relatively large absorption in the region $0.7 < \lambda > 1.0\,\mu$.

Spectrographs convenient for the measurements, which are here suggested as necessary, are under development. For instance, the interferometric instrument should be perfected by 1964. But the basic interferometer and the required accessory equipment may for several years continue to be expensive.

PLANE VERSUS SPHERICAL PYRANOMETER

Whether a spherical or a horizontal plane pyrheliometer (pyranometer) is to be preferred for plant ecological studies is periodically raised as a question for discussion. Several investigators (Gast, 1930; Miller, 1934) have proposed that the absorbing surfaces of pyrheliometers be made spherical for the measurement of radiation affecting plants (Figs. 10 and 11 and *Plate 12*). The problem is by experiment to discover whether the spherical or the 180° pyranometer is better for such measurements.

For the meteorologist the flat absorber is the only acceptable shape. The quantity measured is called the intensity of the "global" or "sun plus sky" radiation. It was noted above that if the hemi-cylindrical screen is used to produce a series of graded intensities, then the horizontal flat surface pyranometer is adequate for highly precise results for the correlation between the cumulative radiation over a given period and the increase in dry weight of experimental plants over the same period.

An experiment which would emphasize the difference in the records between a spherical and a 180° pyranometer could be undertaken with the use of a metal-cloth screen such as is shown in *Plate 8*. Assume that such a screen, transmitting 25 per cent radiation, is placed over the plants—and pyranometers—at 09·30 hours and removed at 14·30 hours. It would reduce the radiation reaching the plants and the pyrheliometers by 75 per cent during the 5-hour period centred at noon. During the "open" periods in early morning and late afternoon when the screen was not present the summated intensities shown by the spherical and the 180° pyranometer would show the greatest difference since the "cosine effect" on the horizontally mounted pyranometer would then be larger.

To examine the difference quantitatively we can use the 12 hours recorded by the Eppley Laboratory at Newport, R.I., on a day with a practically cloudless sky, 25 March 1962.

A 180° pyranometer was mounted on a polar axis (*Plates 13* and *14*). This is an unorthodox use of the 180° pyranometer and is not to be recommended as a routine

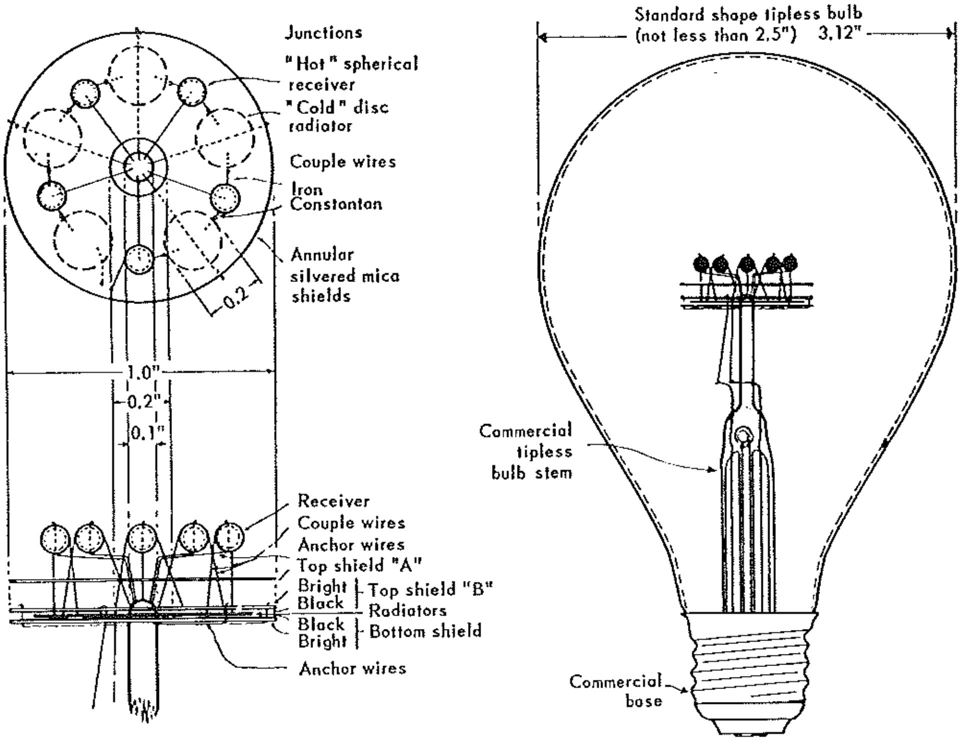

FIG. 10. Design for a spherical pyrheliometer (pyranometer) (after Gast, 1930, Fig. 7). The shields of mica, variously silvered or coated, serve to intercept the radiation and thus keep cool the "cold junction" of the five junctions of the thermopile. They also change the radiation environment of the black ("hot") junctions. (Cf. *Plate 12.*)

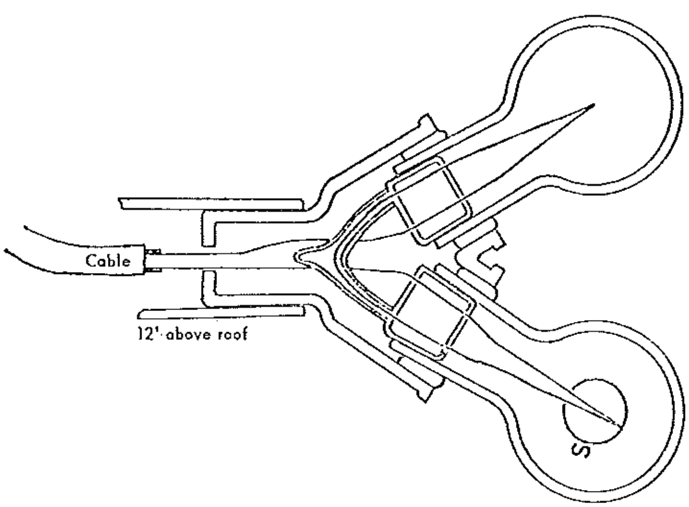

FIG. 11. Spherical pyranometer (Miller, 1937, Fig. 1). The single spherical black junction S is placed in one bulb, in the second is the single cold junction with a very small surface area compared with S. We do not concur with the discussion (Miller 1942, p. 325) of the noon-time displacement of the Eppley record; it is suspected that the plane receiver of the 180° pyrheliometer was not positioned to be exactly horizontal.

procedure for climatological records. (Part of the radiation reflected from the ground may be registered near sunrise and sunset and, at the same time, half the sky radiance is not registered; also, the calibration of the pyranometer in a non-horizontal position may not be constant due to changed convection currents inside the bulb.) However, in earlier studies (unpublished), the records from spherical pyranometers and an equatorially mounted pyranometer were found to agree within ±8 per cent. Probably most of the discrepancy can be attributed to failure of the spherical design to record as of exactly equal value, as it should, the radiation from every point in the sky (Fig. 12). One advantage of a 180° pyranometer on a polar axis is that the plane pyranometer is much easier to calibrate—but, as mentioned above, the calibration is rendered slightly uncertain by the possible loss in exact calibration in the tilted instrument.

However, the records shown in Figure 13 seem sufficiently accurate for this discussion. In addition to the record of the global radiation from a horizontal pyranometer (A) and the record from a 180° pyranometer mounted equatorially on a polar axis (B) is given the record from a "normal incidence" pyrheliometer (C). The latter two instruments record the "direct" solar irradiance as of normal incidence. But in addition to the direct sunlight and skylight within a field of 2.9°

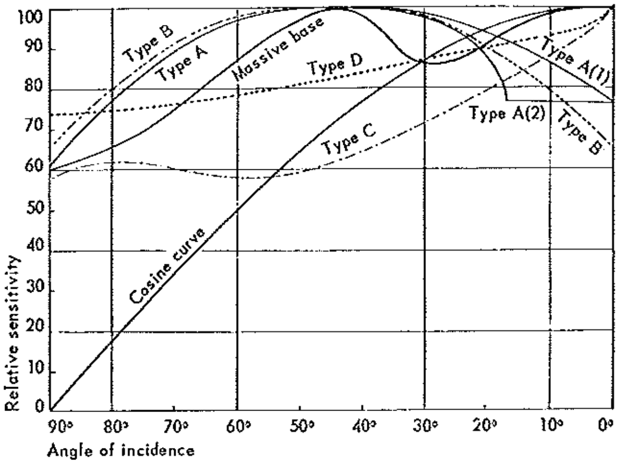

FIG. 12. Relative directional sensitivity of the types of spherical pyranometers shown in Fig. 10. The most nearly satisfactory is type D. (The "massive base" type was unsatisfactory in time response, hence discarded; described in Gast, 1930, pp. 27-30.) The "cosine curve" shows the variation in the record of a beam of radiation of constant intensity with the change in angle of incidence on a plane pyranometer. (After Gast, 1930, Fig. 9.)

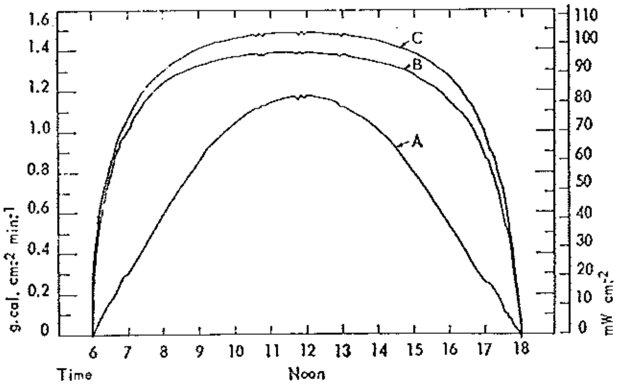

FIG. 13. Radiation measurements by three radiometers at Newport, R.I., on 25 March 1962; for description of records A, B, C, see footnotes to Table 4.

from the centre of the sun registered by a normal incidence pyrheliometer (curve B), the "normal" 180° pyranometer which follows the sun also registers the skylight from the field of 90° from the centre of the sun (curve C). The intensities recorded by curve C exceed those of B by the intensity of the skylight. Assume that the two 180° pyranometers are shaded by a wire-cloth screen for the period from two and a half hours before noon to two and a half hours after. The values or irradiation measured would then be as listed in Table 4, part B. The equatorially mounted ("normal") 180° pyranometer would record 571 g.cal. cm.$^{-2}$: that is, 63 per cent of the 905 g.cal. cm.$^{-2}$ recorded in the "open" (unshaded) condition. For the horizontally mounted 180° pyranometer the homologous values are 286 g.cal. cm.$^{-2}$, 54 per cent of 533 g.cal. cm.$^{-2}$.

TABLE 4. Radiation measurements by three radiometers[1] at Newport, R.I., on 25 March 1962 for specified times

Period	Radiometer I (g.cal. cm.$^{-2}$)	Radiometer II (g.cal. cm.$^{-2}$)	Radiometer III (g.cal. cm.$^{-2}$)
Part A. Full light throughout day ("open")			
06.00-09.30	223	240	108
09.30-12.00	209	223	166
12.00-14.30	205	221	164
14.30-18.00	202	221	95
Total for day	839	905	533
Part B. Shaded from 09.30 to 14.30 hours			
06.00-09.30		240	108
09.30-12.00		55[2]	42[2]
12.00-14.30		55[2]	41[2]
14.30-18.00		221	95
Total for day		571	286
% Ratio of shaded to " open "		63 %	54 %

1. Radiometer I: normal incidence, 6° aperture pyrheliometer, mounted on equatorial axis to follow the sun (cf. Fig. 12, curve B); radiometer II: 180° pyranometer (pyrheliometer) mounted on equatorial axis so that surface is normal to rays from sun (cf. Fig. 12, curve C); radiometer III: 180° pyranometer (pyrheliometer), mounted horizontally (cf. Fig. 12, curve A).
2. Computed intensity if shade with 25 per cent transmission is over both of the two pyranometers from 09.30 to 14.30 hours.

On cloudy days, the values would all be less, as would also be the difference between the 63 per cent and the 54 per cent recorded on a clear day. And of course the irradiation would be the sum of that for all days during which the plants are grown. The single day in Table 4 is used only as an example for the derivation of numerical values.

A supplementary set of plants for determination of the exact relation between plant yield and irradiation during any given test period would be desirable. This set of controls would consist of the plants grown in a series of compartments: one unshaded, or "open", and the rest covered with cloth screens transmitting respectively—to designate two possible series—70, 60 and 50 per cent, or 70, 55 and 40 per cent (produced by screens like those in *Plate 8*). These screens would remain over the plants continuously during daylight hours. The exact relation between yield (plant weight) and cumulative irradiation for the conditions of the experiment would be derived from this set of plant weights. In the experiments with the pine seedlings, it will be recalled, the relation between weights and cumulative irradiation was found to be linear. With other plants it may turn out to be quadratic.

If the average of the weights of the plants grown under the noon-time shade were close to 63 per cent of those grown in full sunlight, then one would conclude that the spherical pyranometer is the better instrument for estimating the relation between irradiation and the type of plant used in the experiment. If the relative average weights of the plants were closer to 54 per cent, then contrariwise the plane horizontal pyranometer is better. The reason for growing the plants under the series of calibrating shades would be to ensure that the relation between growth and irradiation is known. Actually one interpolates between weights determined by the shaded plants. Of course it is understood that the above two values, 63 per cent and 54 per cent, are numerical values taken as an example, using the data for a single day from Table 4. In any actual experiment, cumulative records would be used. These would be obtained over the experimental growing period by the use of three instruments: (a) a spherical pyranometer; (b) at option, a 180° pyranometer equatorially mounted; and (c) a horizontally mounted 180° pyranometer.

The difference between 63 per cent and 54 per cent is not large. But in our experience with pine seedlings it is about three times the standard error in carefully conducted experiments and could therefore be significant and could lead to conclusions as to preferred design of pyranometers.

But from a practical point of view it would seem that the above analysis does not justify the use of the spherical pyranometer for work in plant ecology. On the basis of this examination we may conclude that the application of the cosine law to the measurement of irradiation has but a relatively small effect on the choice between the plane and the spherical designs. As long as the same type of pyranometer (horizontally mounted 180°, equatorially mounted 180° or spherical) is used for recording the irradiation intensity, the plant yields should be proportionate. If the above analysis is valid, the general use of the 180° pyranometer, mounted horizontally as customary in meteorological practice, is to be recommended for ecological studies. The technique of calibration is well understood. Technical ingenuity can be depended on some day so to cheapen the cost that the ecologist can afford to buy as many pyranometers and associated recorders as he may need (Goodell, 1962).

FIELD EXPERIMENTS WITH CONTROLLED CONDITIONS

The term "semi-field experiments" as used above was applied to studies involving (a) natural sunlight, (b) pot cultures, (c) foliage analysis. The natural sunlight was modified by shades, wire-mesh screens were used to change the level of intensity without change in quality, or a water-filter was used to change the quality. The level of the irradiance was continuously recorded as a microclimatic factor. In the pot cultures the plants were rooted in "natural soil" samples or in sand periodically flooded with nutrient solutions ("hydroponic cultures"). By foliage analysis the internal levels of macronutrients were determined. (Although possible, no analyses were made for micronutrients.) Differences between optimum and actual levels were used to indicate the factor—light or a nutrient—which limited the yield; the Mitscherlich relation provided the analytical tool.

If the accuracy in the control of nutrition afforded by the technique of pot culture is not required, plants may be grown under shades in field plots. The productivity of crop plants as different as coffee and barley have been so examined. The largest yields were found under full sunlight. An early study on coffee was reported by Guiscafre-Arrillaga and Gomez (1942), and a more recent one by Montoya, Sylvain and Umaña (1961). Kamel (1959) has recorded the comparative yields of barley and mangold under shades and in full sunlight.

CONCLUSIONS

Experience with seedlings of forest trees in growth experiments has established that irradiation ("full spectrum": $0.3 < \lambda > 2.5\ \mu$) intensities and increase in dry weight show high correlation. Failure to achieve perfect correlation seems to be caused as much by error in the measurement of the irradiation intensity as by the error in the measurement of the plant yields, or genetic or other uncontrolled variance in the seedlings. These conclusions are predicated on careful control of the plant nutrition and all other technical details of the experiments. To cite but a single instance, corrections are required for the "normalization" of the "growth capital" at the beginning of the experimental period; for example, if tree seedlings are used for experimental material the "growth capital" can be correlated with the weights of the seeds. By the use of wire-cloth screens a preselected, graded series of irradiation intensities can be arranged; pyranometers placed under the screens provide measurements of the cumulative absolute intensities of the irradiation to which the plants are exposed during the growth period. The reasons for the discrepancies between anticipated and actual yields of the plants grown in the "full" spectrum ($0.3 < \lambda > 3\ \mu$) and the "limited" spectrum ($0.3 < \lambda > 1.0\ \mu$) under the water-filter are not clear. Several possibilities can be suggested. There is the possibility that supplementing the visible by infra-red ($0.8 < \lambda > 2.5\ \mu$) may contribute to the energy for photosynthesis or otherwise promote assimilation of the photosynthate. Since the water-filters remained over the plants during the night, cooling by outward radiation of the infra-red ($1 < \lambda > 30 < 60\ \mu$) was prevented. The higher "effective" (and sensible) temperatures of the above-ground parts of the plants during the night hours might well have exerted a formative influence. It is also possible, since the exact quality of the light transmitted by the various types of water-filters is unknown, that alternating levels of intensities of the red ($0.58 < \lambda > 0.68\ \mu$) and far-red ($0.68 < \lambda > 0.77\ \mu$) exert formative effects by interconversion of phytochrome. A 180° (plane) pyranometer, horizontally exposed, seems well adapted for measuring the intensity of irradiation as an environmental factor. This conclusion is based on deductive comparisons which stress the differences between the effects of angle of incidence in the records of spherical and plane pyranometers. Experimental studies of the "effective temperatures" of plants as correlated with terrestrial radiation in the spectral region $3 < \lambda > 30 < 60\ \mu$ seem long overdue.

APPENDIX : RADIOMETRIC QUANTITIES FOR THE INFRA-RED

Symbol	*Name*	*Description*	*Unit*
U	Radiant energy		joule
u	Radiant energy density		joule cm.$^{-3}$
P	Radiant power	Rate of transfer of radiant energy	watt
W	Radiant emittance	Radiant power per unit area emitted from a surface	W cm.$^{-2}$
H	Irradiance	Radiant power per unit area incident upon a surface	W cm.$^{-2}$
J	Radiant intensity	Radiant power per unit solid angle from a source	W sterad.$^{-1}$
N	Radiance	Radiant power per unit solid angle per unit area from a source	W sterad.$^{-1}$ cm.$^{-2}$
P_λ	Spectral radiant power	Radiant power per unit wavelength interval	W μ^{-1}
W_λ	Spectral radiant emittance	Radiant emittance per unit wavelength interval	W cm.$^{-2}$ μ^{-1}
H_λ	Spectral irradiance	Irradiance per unit wavelength interval	W cm.$^{-2}$ μ^{-1}
J_λ	Spectral radiant intensity	Radiant intensity per unit wavelength interval	W sterad.$^{-1}$ μ^{-1}
N_λ	Spectral radiance	Radiance per unit wavelength interval	W sterad.$^{-1}$ cm.$^{-2}$ μ^{-1}
ϵ	Radiant emissivity	Ratio of "emitted" radiant power to the radiant power from a black body at the same temperature	
α	Radiant absorptance	Ratio of "absorbed" radiant power to incident radiant power	
ρ	Radiant reflectance	Ratio of "reflected" radiant power to incident radiant power	
τ	Radiant transmittance	Ratio of "transmitted" radiant power to incident radiant power	
λ	Wavelength		cm., μ (micron) mμ (millimicron) Å (Ångström)

1 cm. $= 1 \times 10^4 \mu = 1 \times 10^7$ mμ $= 1 \times 10^8$ Å

RÉSUMÉ

Modification et mesure du rayonnement solaire, céleste et terrestre pour des études éco-physiologiques (P. R. Gast)

Les différentes étapes de la croissance et du développement des végétaux sont influencées à des degrés divers par la qualité et l'intensité du milieu radiatif. Ce milieu comprend le rayonnement solaire et céleste pour la bande spectrale comprise entre 0,3 μ environ et 60 μ environ. Le rayonement céleste compris entre 3 μ et 60 μ environ (rayonnement « nocturne » ou « terrestre ») est la cause, pendant les heures diurnes, d'un gain thermique; la nuit, il abaisse par perte radiative la température ambiante. Pour mesurer la totalité du milieu radiatif, il faut employer divers types de radiomètre. On peut étudier les effets du rayonnement, grâce à : *a*) des zones expérimentales de grandes dimensions permettant de véritables expériences « sur le terrain »; *b*) des expériences pilotes effectuées dans des conditions partiellement contrôlées, semblables à celles du terrain; *c*) des phytotrons. Ces expériences exigent des radiomètres, généralement assez coûteux. Pour orienter les études ultérieures, on se sert de certains résultats expérimentaux concernant la morphogénèse et les rendements végétaux dans des conditions de nutrition et en milieu radiatif contrôlées.

DISCUSSION

M. Evenari. I want to draw special attention to the far-red effect which has been mentioned. One most possibly deals here with the well-known red-far-red reaction which apparently affected photosynthesis indirectly, perhaps by increasing the efficiency of the photosynthetic apparatus. I would like to state in general that special attention should be paid in measurements of global radiation to the area of red and far-red as this spectral region influences basically morphogenesis and, through this, photosynthesis and net assimilation rate.

P. R. Gast. Mr. Evenari has indeed raised a question of great importance in the study of the whole plant as distinguished from the study of the efficiency of photosynthesis as a single plant physiological-biochemical-process. I believe that the work which I have described raises more questions than it answers.

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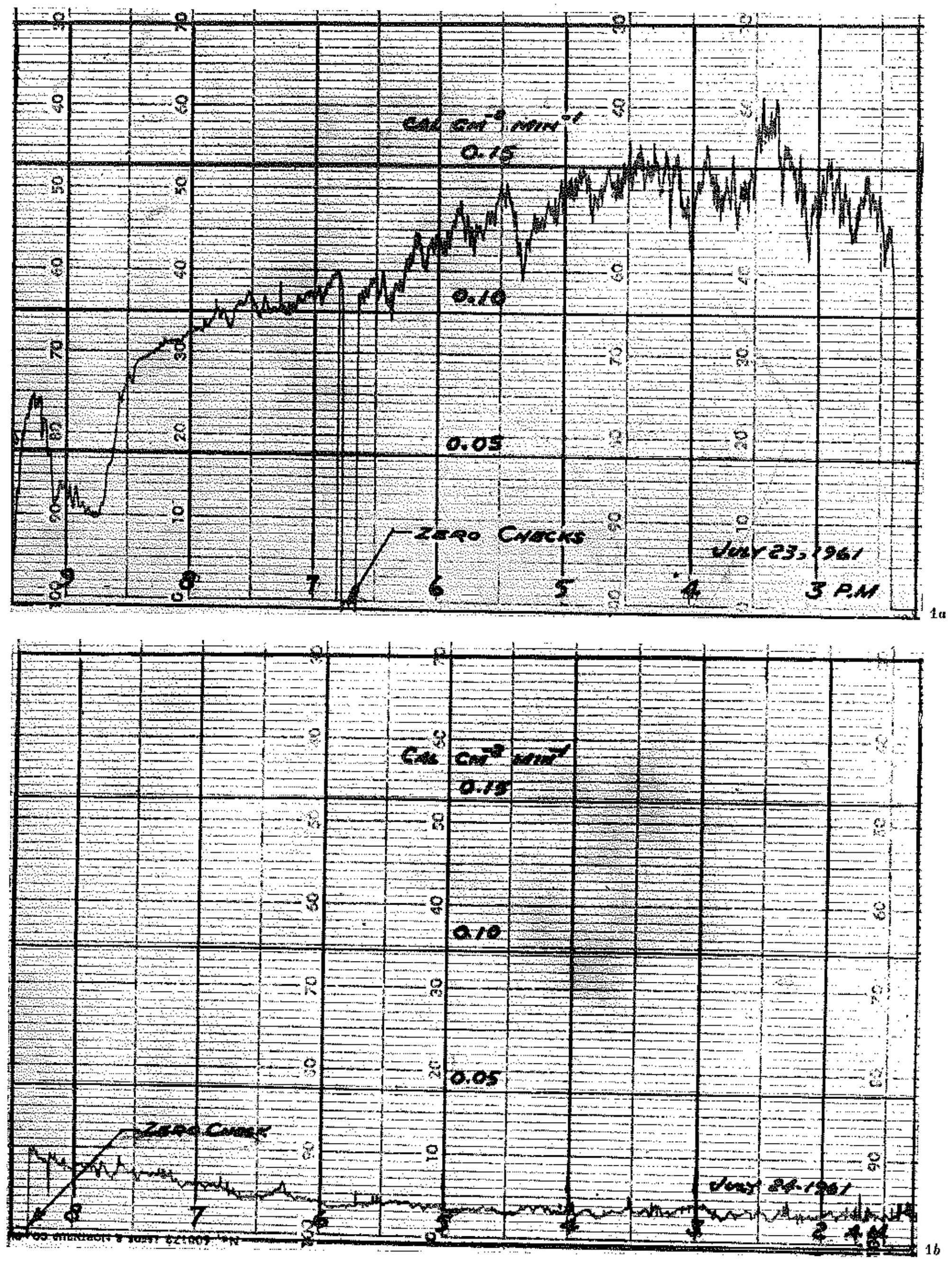

Plate 1

Typical records obtained of the long-wave radiative energy exchange between an artificial black surface (radiometer receiver) and the atmosphere during (a) day-time fine weather conditions with cumulus cloud and (b) night-time heavily overcast sky conditions. (After Drummond.)

Plate 8

Petersham, Mass., 1934. A preferred arrangement of the bronze wire-cloth hemicylindrical screens on the top of a wooden frame. The long axis of the screen is north-south, and a long overhang projects well beyond the southernmost plants. On the ground in front of the frames are the doors which darken the jug compartment. In the right foreground are (left) a glazed pot and jug arrangement as used for hydroponic cultures—by air pressure the sand can be flushed with solution in jug, to which it returns when pressure is released; (right) a similar glazed pot and bottle as used in the soil-sand and clay-sand cultures; the drainage into the bottle is returned to top of the pot. In the rear are the "Cello-Glass" screens used for protection against rain. When the pots are in position in the frames the areas around them are packed with sphagnum moss to stabilize the temperature: this is similar to the earlier method of embedding in sand. (After Gast, 1937, Fig. 9.)

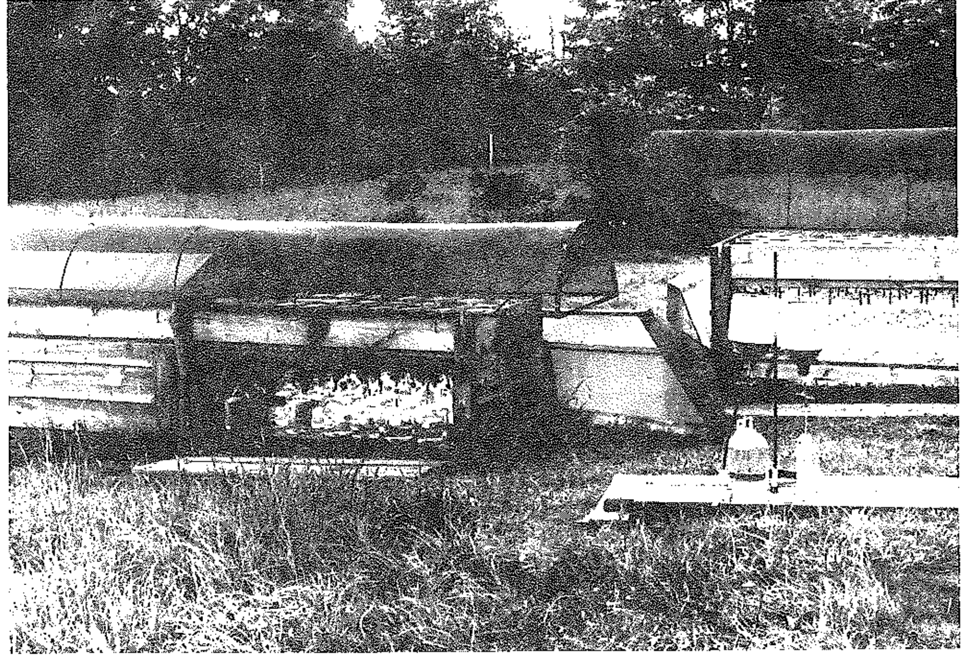

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Plate 9

Hydroponic cultures at Cornwall in 1932-1934. The unglazed pot and pail arrangement antedate the glazed pot technique. By connecting air pressure to several jugs they can be pumped simultaneously. Cloth shades darken the jug compartment. A photo cell and 180° pyranometer are mounted in near box. (After Mitchell, 1934, Plate III.)

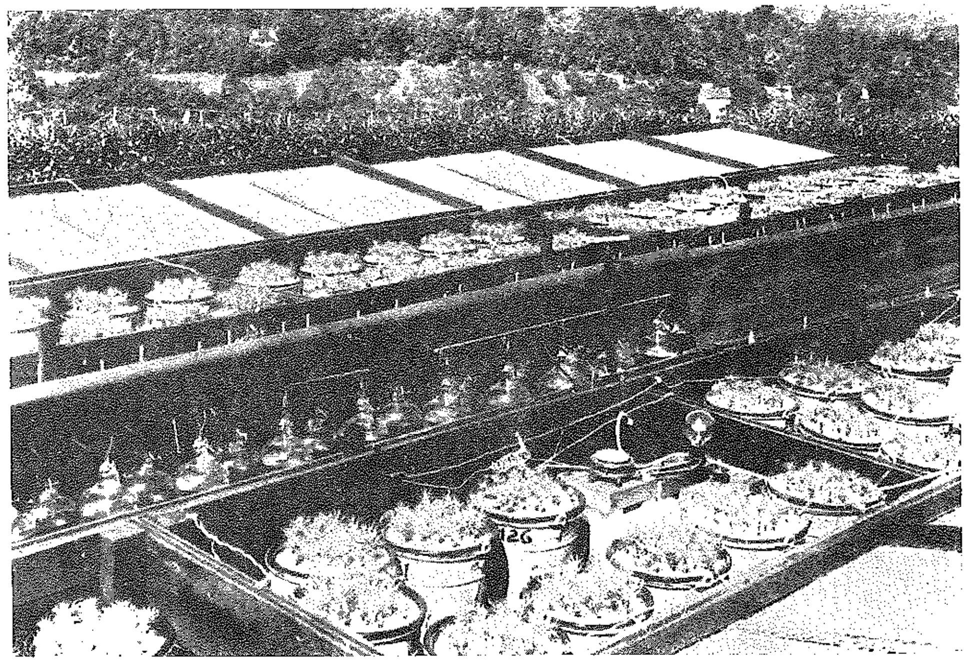

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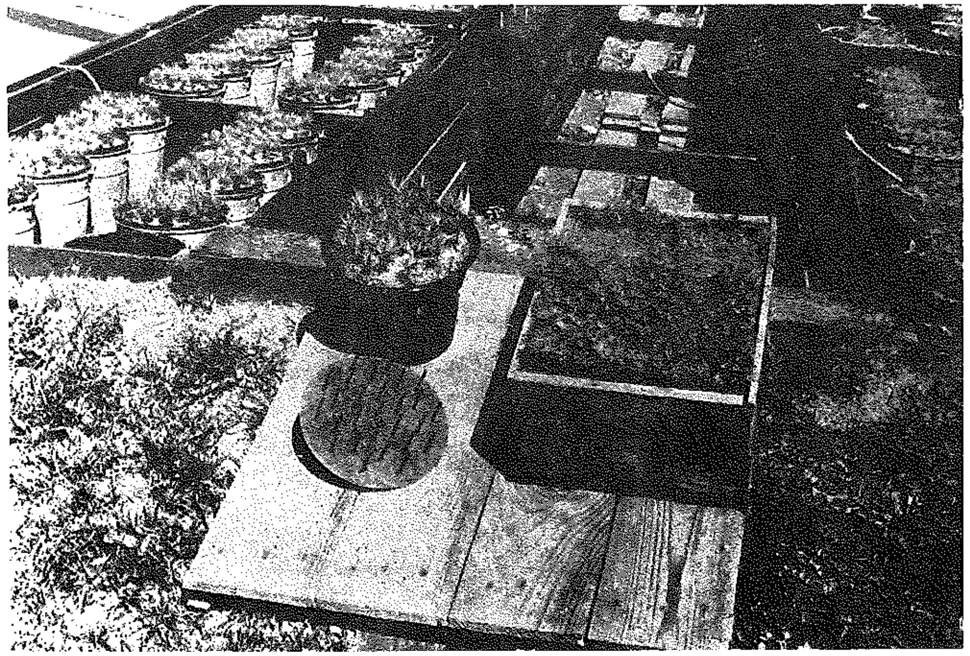
Plate 10

Transplanting procedures. The seeds are started in flat on right; by use of the planting dibble in front, the spacing between plants is equalized when they are transplanted into sand in the unglazed clay pot. (After Mitchell, 1934, Plate II.)



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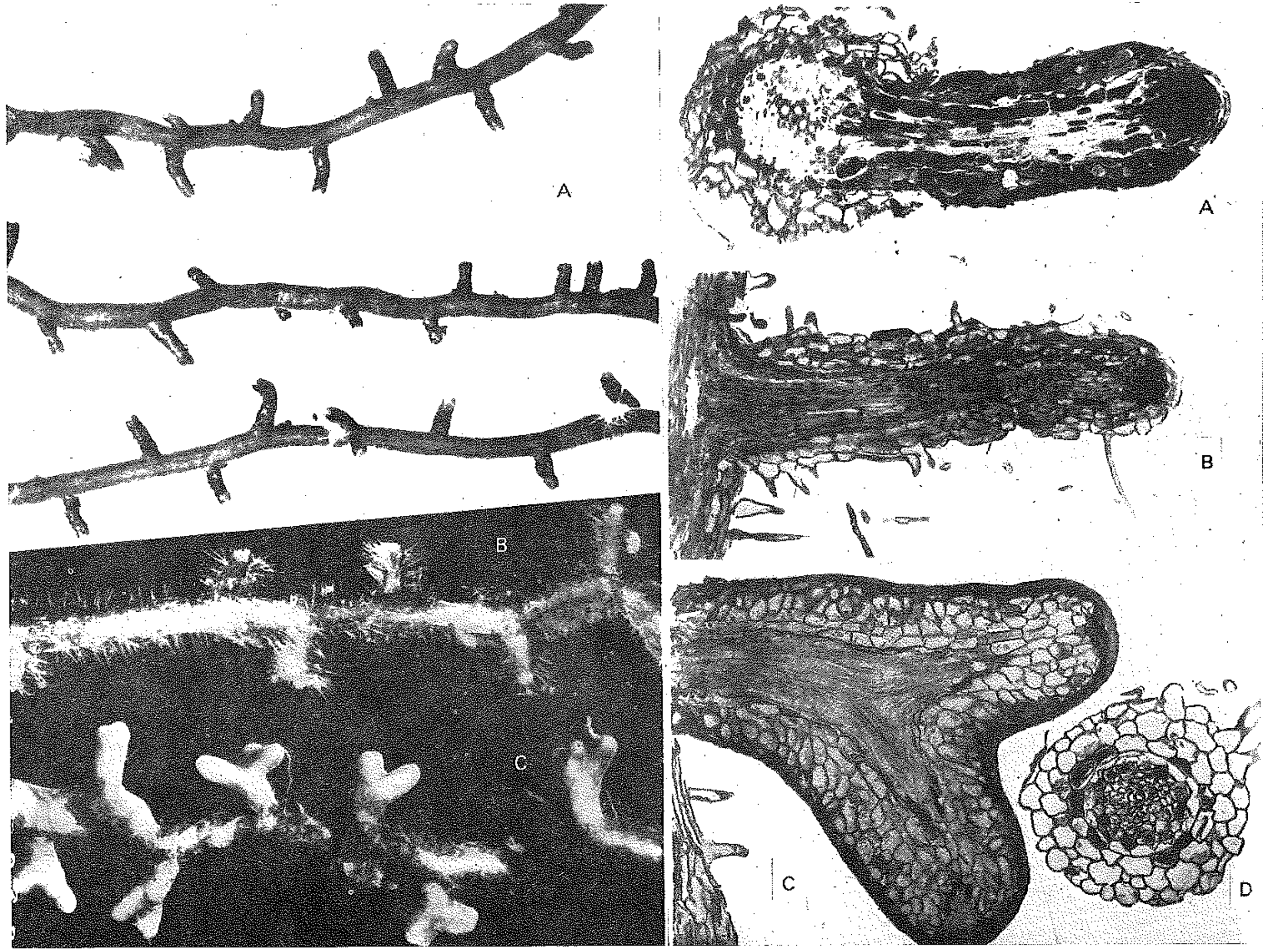


Plate 11
Forms of seedling pine roots.

Left:

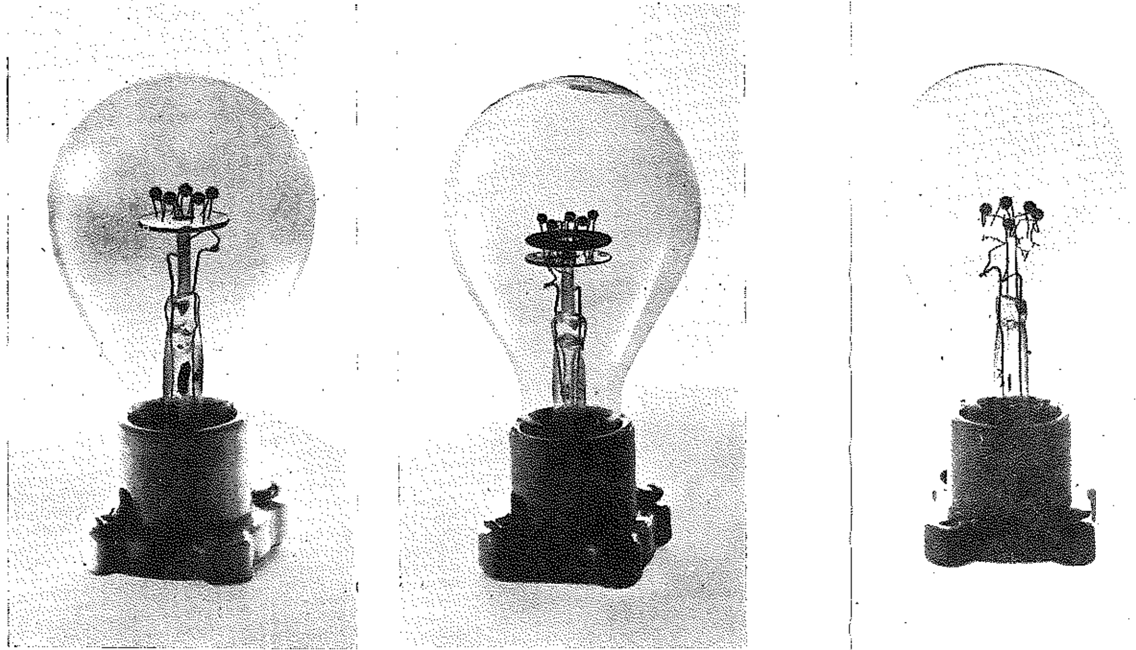
(A) pseudo-mycorrhizal short roots on long lateral roots of *P. silvestris;*
(B) uninfected short roots with root hairs on long lateral roots of *P. strobus* grown in sterile culture;
(C) mycorrhizal short roots on long lateral roots of *P. strobus* grown in pure culture with *Lactarius deliciosus.*

Right:

(A) longitudinal section of a short root from left;
(B) longitudinal (not medial) section of a short root from left;
(C) longitudinal (not medial) section of short root on left, note mantle and intercellular net of fungal hyphae, hypertrophy of root cells;
(D) Transverse section of short root of *P. silvestris*, enlarged 2 × the longitudinal sections. (After Hatch and Doak, 1933, Plates 58 and 59.)

Plate 12

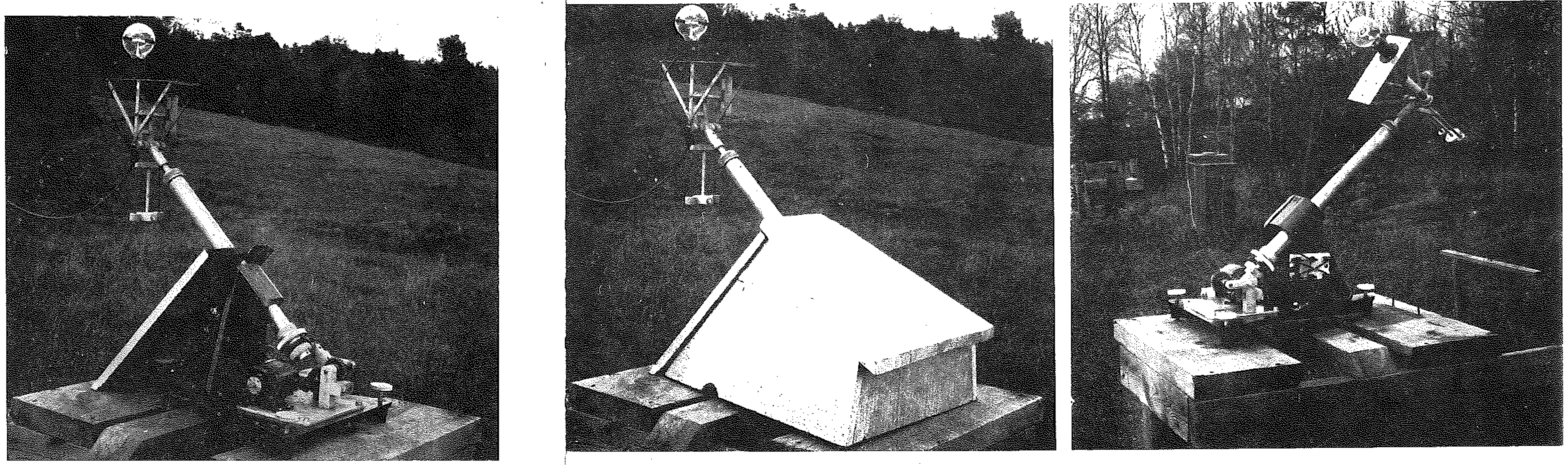
Three models of spherical pyranometers. Left: Type A does not use top shield "A" (as labelled in Fig. 10), the shield "B" is silvered. Type D (not shown) which showed the best relative directional response (see Fig. 12), is the same as type A but the shield "B" is coated with MgO smoke over the upper surface. Middle: Type C was constructed with a top shield "A" which was blackened with carbon smoke. Right: Type B has spherical receivers for the "hot" junctions which are covered with carbon smoke and the "cold" junctions which are coated with MgO smoke. (Retouched photographs after Gast, 1930, Fig. 8.)



12 *a*, *b*, *c*

Plate 13

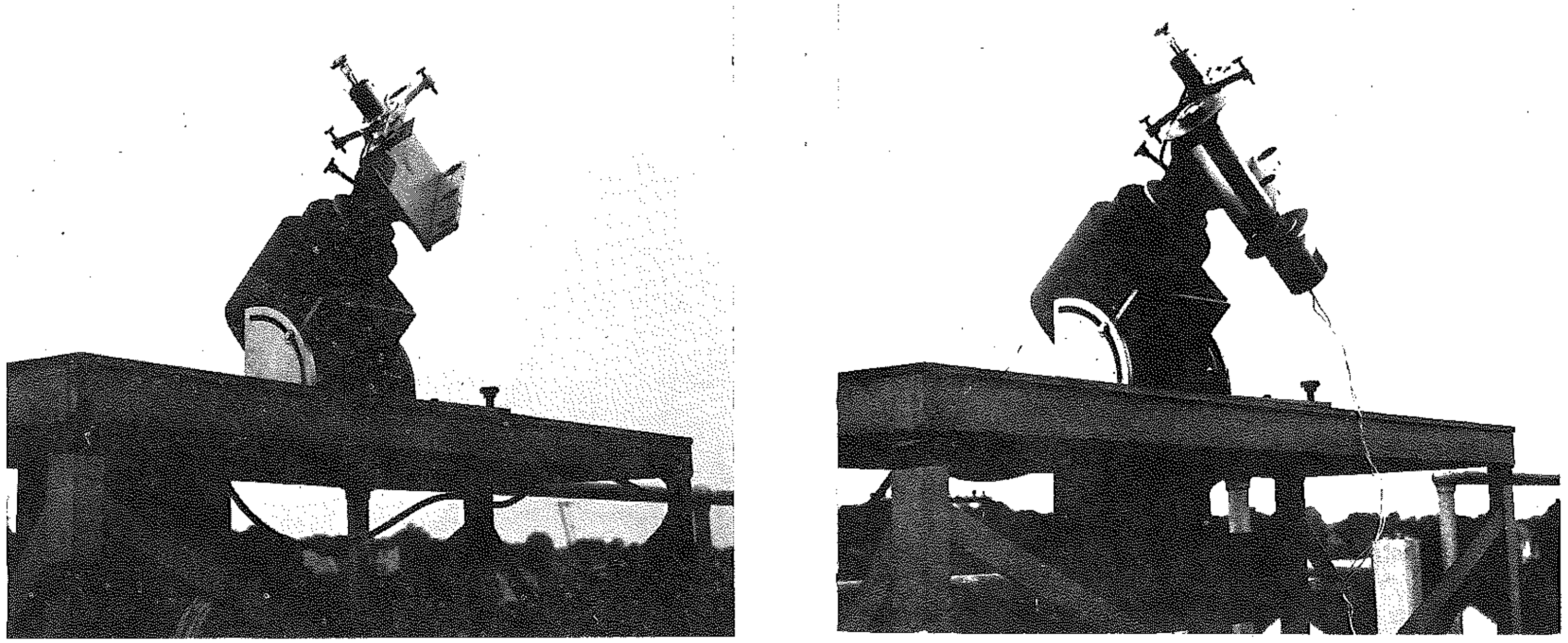
A 180° pyranometer on polar axis (equatorially mounted) continuously maintaining plane surface of receiver normal to rays from sun. Used in 1933 to derive a record for comparison with that from a spherical pyrheliometer (pyranometer), type D (cf. *Plate 12*).



13 *a*, *b*, *c*

Plate 14

Left: a 180° pyranometer on new design of polar axis. Right: the normal incidence pyrheliometer and pyranometer mounted together on polar axis.



14 *a*, *b*