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THE RELATIONSHIPS BETWEEN CUMULATIVE SOLAR RADIATION AND THE DRY WEIGHT INCREASE OF NURSERY-GROWN WHITE PINE AND RED PINE SEEDLINGS

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CAREFULLY controlled cultural experiments in which nutrition and solar radiation were varied simultaneously indicate that there is a high degree of correlation between the total radiant energy received during the growing period and the dry weight increase of white and Scots pine seedlings (Mitchell, 1934; Gast, 1937). On the basis of data from various experiments in different years (Gast, Fig. 14) the yields of seedlings grown in relatively favorable nutrient environments appear to be linearly related to the logarithm of the cumulative radiation. A similar relationship was observed in the response to varying radiation intensities of white pine seedlings grown under nursery conditions at the Black Rock Forest experimental nursery during the summer of 1934 (Mitchell, 1936). The 1936 experiment at the same nursery, although primarily concerned with seedling nutrition, afforded opportunity for further study under field conditions of the relationships between cumulative radiation and seedling growth. In the 1936 study, the results of which are reported in this paper, both red pine and white pine seedlings were grown for one season in seedbeds exposed to each of the following radiation intensities: 30, 57, 78 and 100 percent of full sunlight. Details of the experiment are described in the following section.

METHODS

The substrate used in the 1936 nursery experiment consisted of a mixture of sand, humus and clay contained in specially constructed seedbed frames, previously described (Mitchell, Finn and Rosendahl, 1937). Although this prepared soil was relatively low in mineral nutrients, its physical properties were as good or slightly better than the average nursery soil. Thorough mixing assured uniformity.

The eight beds which comprised that part of the 1936 nursery experiment pertinent to the present discussion were seeded on May 1, four to white pine (*Pinus strobus* L.) and four to red pine (*Pinus resinosa* Ait.). The mean reserve dry weights of the two lots of seed used were: 9.97 mg. for white pine, and 5.17 mg. for red pine. Germination started about May 15 and all seed coats were shed by May 27. The seedlings were watered daily during dry periods, and were weeded at three-week intervals.

All beds were supplied finely ground rock phosphate at the rate of 250 grams per five square feet. This fertilizer was mixed with the soil previous to seeding. In addition, each bed received 1.3 g. KCl, 0.9 g. $CaCl_2 \cdot 6H_2O$, 7.5 g. $MgSO_4 \cdot 7H_2O$ and 0.2 g. $FeCl_3$ per five square feet of seedbed. These chemicals were applied in solution and in two equal treatments, one on June 26 and one on July 27. There was only one difference in fertilization: each of the white pine beds was supplied dried blood at the rate of 32 g. per five square feet, whereas those beds seeded to red pine received no dried blood or any other nitrogen-bearing compound. This differential in nutrition was deemed necessary as a precaution against damping off, to which heavily fertilized red pine are particularly susceptible (Mitchell, 1939).

On October 19, 146 days from the time the seed coats were shed, representative samples were taken from each bed. Each seedling was washed in a small stream of water to remove soil particles, measured, cut into two portions (root and shoot) for ratio determinations, each part placed in a labeled glassine envelope, dried at 70°C. and weighed to ± 0.1 milligram. Data on root, shoot and total dry weights are summarized in Table 1.

The intensity of radiation was varied by means of brass wire cloth screens of different transmission factors. Screens of the same specifications used in the 1934 experiment (Mitchell, 1936) were employed in the present study, and they were similarly supported above the beds with skeleton frameworks made of strap iron. Wire screens which reduced the radiation to 26, 48 and 74 percent of full sunlight were placed over three of the beds seeded to white pine and three of those seeded to red pine. The other two beds, one seeded to each species, were covered from the time of planting until two weeks after the seed coats were shed with screens which reduced the radiation by about 50 percent; thereafter they were exposed to full sunlight. The early-season shading of the "full light" beds is essential, at least for white pine seedlings, since this species is subject to injury if exposed to full sunlight during and immediately following germination (Mitchell, 1934).

As in previous studies, measurements of total solar radiation (visible plus infra-red) were made with Eppley Weather Bureau type Pyrheliometers registering on a Leeds and Northrup two-point recording potentiometer (Micromax, equipped with special integrating device). One pyrheliometer was placed at the plant level in a "full light" bed, where it remained during the entire summer. Another pyrheliometer was alternated between the various other beds as a check on the radiation transmitted by the different screens. Data on the cumulative solar radiation received by the different beds, expressed as kilogram calories per square

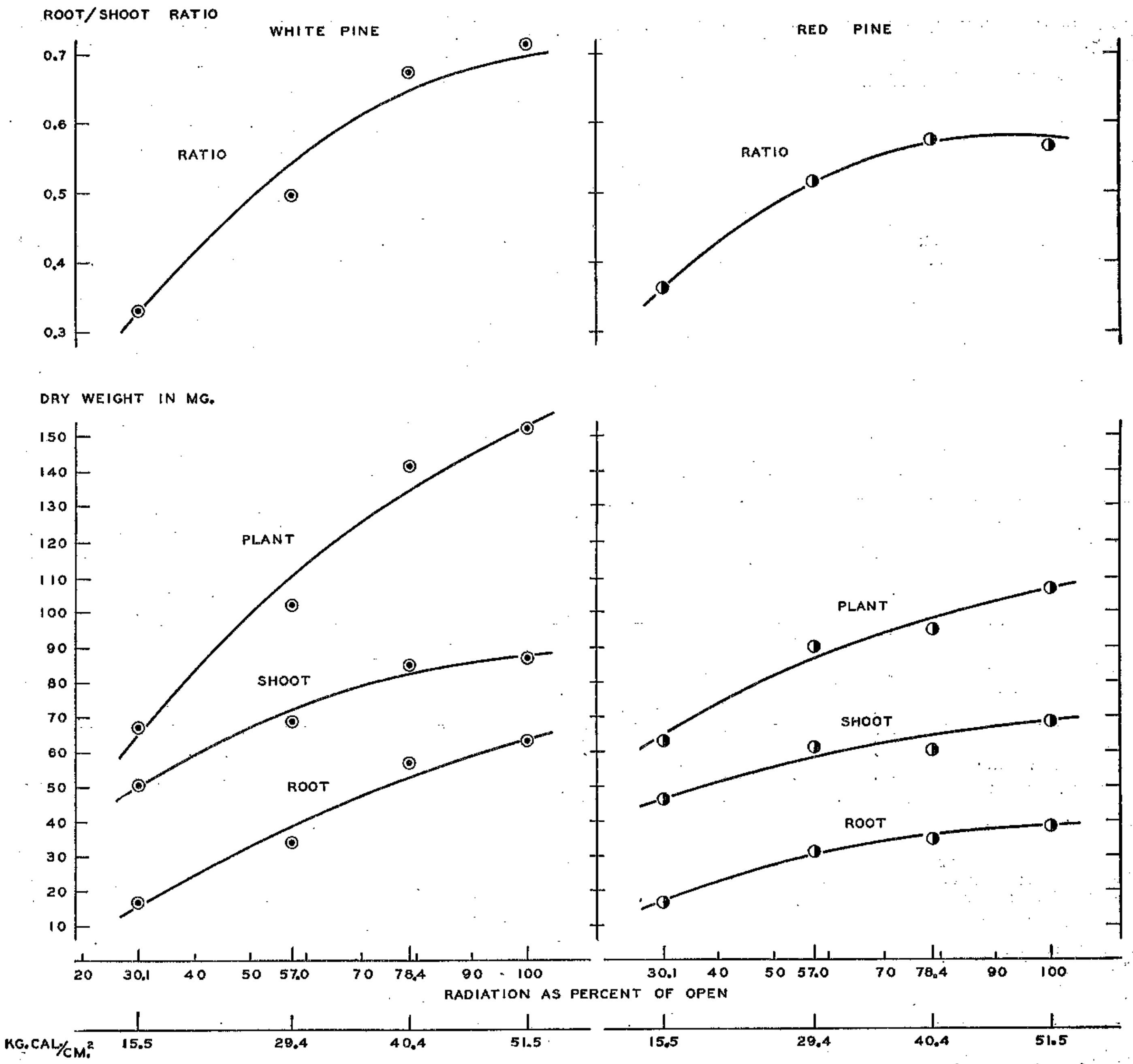

FIG. 1.—The effect of varied solar radiation upon the total dry weights, root weights, shoot weights and root/shoot ratios of nursery-grown red pine and white pine seedlings.

centimeter, are entered in column 2 of Table 1. Radiation values for the various beds, expressed as percentages of the "full light" beds, are entered in column 3 of the same table. These percentages are not identical with the transmission factors for the different screens because the radiation received by the "open" beds was reduced by 50 percent until two weeks after the seed coats were shed.

DISCUSSION

As shown in Fig. 1, the total yields (root weight and shoot weight) of white pine and red pine seedlings increased with increments of solar radiation over the entire range of intensities studied. It is evident, however, that in each case the response to increments of radiation above 50 percent of full sunlight was less than to increases through the lower range of intensities.

Although it is not so apparent from the root and shoot weights plotted separately in Fig. 1, the root/shoot ratio curves show that increments of solar radiation have a relatively greater stimulating effect upon root than shoot development. Seedlings of both species which received only 15.5 kilogram calories per square centimeter of radiant energy during the growing season—that is, approximately 30 percent of the radiation to which those in the "full light" beds were exposed—are very inferior as regards balance between root and shoot to plants which received from 75 to 100 percent of full sunlight.

The height growth as well as the needle length and number of both species varied inversely as the radiation intensity. At first glance and previous to lifting, the taller, longer-needled plants produced in the beds which received but 30 percent of full sunlight gave an illusion of size and thriftiness which closer inspection and weighings proved false. Although taller, the heavily shaded seedlings were spindling, succulent, comparatively light, poorly balanced (root/shoot ratio) and otherwise less desirable as seedbed or transplant stock than those exposed to the higher radiation intensities. These observations, which are in agreement with the results of previous studies, supply further proof of the limited usefulness of height measurements as a basis for comparing the "growth" of variously treated 1- to 3-year-old coniferous seedlings (Mitchell, 1936).

In Fig. 2 the red pine and white pine yield data from the present experiment are shown plotted on arithmetic axes over logarithmic values of cumulative solar radiation. Data from the 1934 experiment, previously reported (Mitchell, 1936), are included in this figure for purposes of comparison. These seedlings were harvested 100 days from the time the seed coats were shed, whereas the 1936 experiment continued for 146 days. It is significant that in each case the correlation between cumulative radiation and the dry weight increase of nursery-grown seedlings takes the form of a linear increase—the same relationship as that discovered for plants grown in the somewhat artificial environment of the carefully controlled nutrient-sand culture experiments (Gast, Fig. 14). This similarity of response is further evidence of the validity of the arithmetic: logarithmic correlation between seedling yield and solar radiation, a relation which was noted in previous reports (Gast, 1937; Mitchell, 1936).

Available data indicate that the response of several species of pine to increased radiation is conditioned, and therefore frequently limited, by nutritional factors. In carefully controlled experiments where solar radiation and nutrition were varied simultaneously, it was found that increments of radiation above 30 to 50 percent of full sunlight had little or no effect upon seedlings grown in very infertile soils, or in nutrient-sand cultures of low nutrient availability. But in more favorable nutrient environments, yields increased with increments of radiation up to full sunlight (Mitchell, 1934; Gast, 1937). Thus, the difference in the slope of the regression lines representing the 1934 and 1936 white pine data, as shown in Fig. 2, can probably be explained on the basis of nutrition. The prepared soil of the 1936 experiment was naturally more fertile than that used in 1934, and the former was further improved by the addition of chemical fertilizers. Although both were sufficiently fertile so that the yields of seedlings grown therein were linearly correlated with cumulative radiation up to full sunlight, the difference in fertility is reflected in the greater yield increment, per unit of radiation increase, of seedlings grown in the better soil.

TABLE 1

The total weights, root weights, shoot weights and root/shoot ratios of red pine and white pine seedlings grown for one season in nursery beds under varied radiation intensities.

Species	Solar Radiation: Kg. Cal. per Sq. Cm.[1]	Solar Radiation: As % of "Full Light"	Size of Sample	Dry Wt. of Roots in Mg.	Dry Wt. of Shoots in Mg.	Root/Shoot Ratio	Total Dry Wt. of Plants in Mg.[2]: Experimentally Determined	Total Dry Wt. of Plants in Mg.[2]: Calculated[3]	Correlation Coefficient	Standard Error of Estimate
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)		
Red Pine (*Pinus resinosa* Ait.)	15.5	30.1	45	16.6	45.9	0.36	62.5 ± 3.6[4]	64.2	.60	± 20.3
	29.4	57.0	39	31.1	60.8	0.51	91.9 ± 3.7	86.8		
	40.4	78.4	47	34.5	60.1	0.57	94.6 ± 3.5	98.0		
	51.5	100.0	173	38.6	68.0	0.57	106.6 ± 3.8	106.6		
White Pine (*Pinus strobus* L.)	15.5	30.1	64	16.7	50.6	0.33	67.3 ± 3.7	64.5	.80	± 28.3
	29.4	57.0	68	34.0	68.4	0.50	102.4 ± 4.7	111.4		
	40.4	78.4	51	57.1	84.8	0.67	141.9 ± 6.3	134.7		
	51.5	100.0	65	63.1	88.6	0.71	151.7 ± 6.9	152.6		

[1] Cumulative radiation received on a fixed horizontal surface (Eppley Weather Bureau type pyrheliometer) from the time the seedlings shed their seed coats on May 27 until they were harvested 146 days later.

[2] Red pine seedlings are from seeds with a mean fresh weight of 9.52 mg. (reserve dry weight = 5.17 mg.); the white pine are from seeds with a mean fresh weight of 17.03 mg. (reserve dry weight = 9.97 mg.).

[3] The average relationship between cumulative radiation and the yield of red pine seedlings is expressed by the equation $y = 81.39\ x - 32.69$, in which y = the yield in milligrams, and x = the logarithm of the cumulative radiation expressed as kg. cal. per sq. cm. For the white pine relationship, the equation is $y = 169.0\ x - 136.7$. Both regression lines are plotted in Fig. 2.

[4] Standard error of mean.

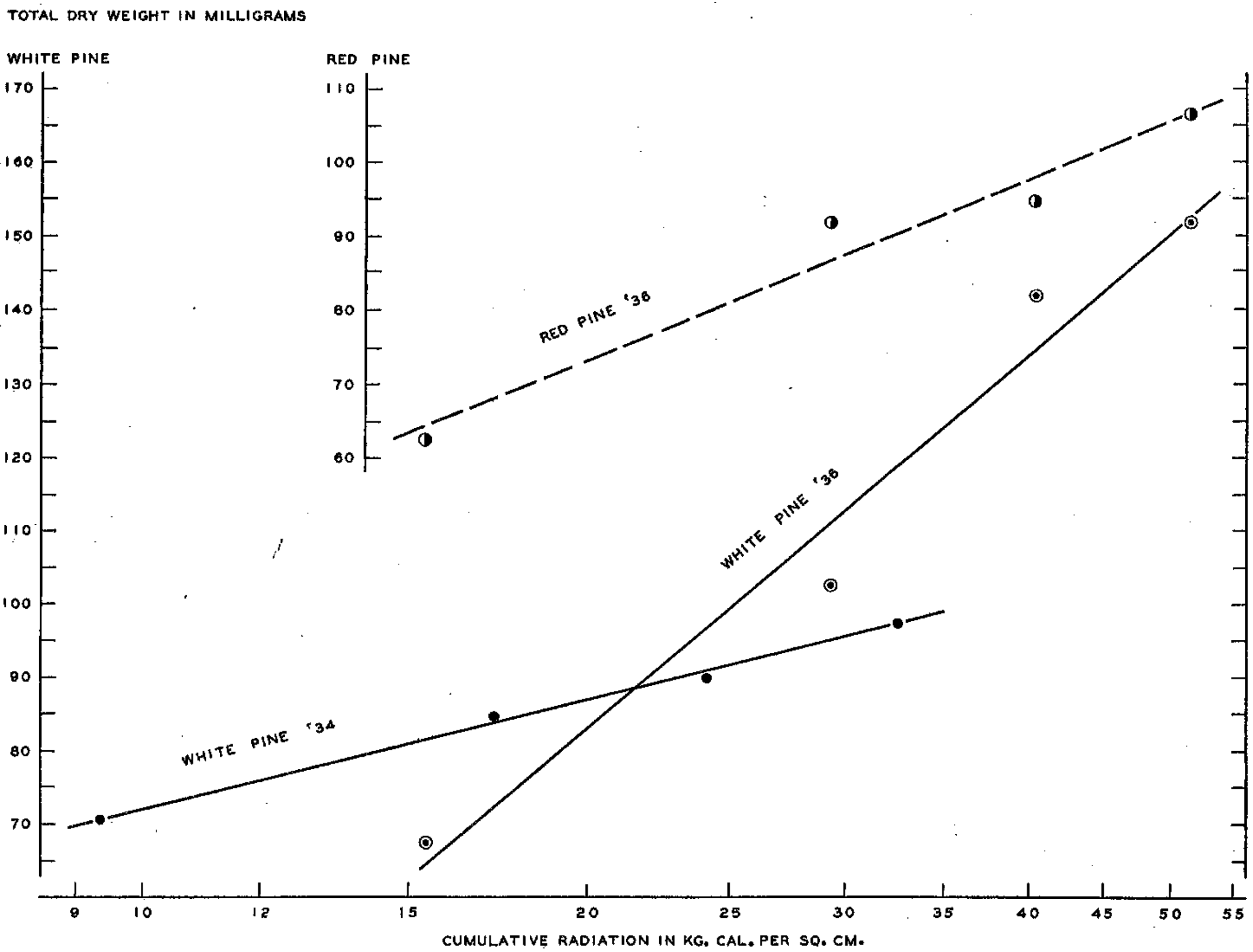

FIG. 2.—The relationships between cumulative solar radiation and the yields of nursery-grown red pine and white pine seedlings. Radiation on logarithmic and yields on arithmetic axes.

The 1934 data (from Table 1, Mitchell, 1936) are expressed as from seeds of the same reserve dry weight as those used in the 1936 experiment. Soil and length of growing period differed (see text).

It will be observed (Fig. 2) that there is a significant difference in the slope of the regression lines representing the average relationships between yield and radiation for the 1936 white pine and red pine seedlings. The relatively greater response of the white pine seedlings to equal increments of radiation is probably due more to nutritional factors than to differences in the efficiency of the two species in their use of radiation. As discussed earlier in this report, the white pine seedlings were supplied nitrogen as dried blood, whereas the red pine received no nitrogen other than that contained in the soil. It is true that the two species may, and probably do, differ in their light requirements. However, because of the difference in nitrogen supply, no reliable data on this subject can be obtained from the present experiment. For such comparisons, the two species would have to be grown in parallel series of radiation intensities under otherwise identical conditions of soil, nutrition, and other factors influencing yield.

As shown in Fig. 2, the dry weights of white pine seedlings which received a total of 15.5 kg. cal. of radiant energy during the 1936 growing season are considerably lower than for seedlings exposed to the same cumulative radiation during the 1934 experiment, and somewhat lower than the 1934 seedlings which received a total of only 9.4 kg. cal. These differences are the reverse of what might be expected in view of the observed correlations between seedling growth and cumulative radiation. They are especially contradictory since, as previously discussed, the soil used in 1936 was the more fertile, correction was made for the difference in seed size, and cultural methods and conditions of moisture supply, drainage and aëration were essentially the same for the two growing seasons.

There are several possible explanations of this apparent discrepancy. The most probable is that suggested to the writers by Dr. Gast, who pointed out certain effects which may be attributed to changes in the *quality* of the radiation to which seedlings were exposed during the two experiments. The evidence favoring such an explanation may be summarized as follows. Although conclusive meteorological information is lacking, the results of Gast's studies (1937 and personal communication) give preliminary evidence that, during cloudy weather, there is relatively more absorption of infra-red than visible radiation. During the 1936 growing season there was much less precipitation, and hence less cloudy weather, than for a comparable period in 1934—or any other year from 1932 to 1939. This is proven by records of rainfall, diameter increment data from trees on sample plots, notes on cloudiness, and relative fluctuations in total solar radiation, which was measured and recorded continuously during each summer.[1] Although not in themselves conclusive, these observations are interpreted as indicating a smaller ratio of infra-red to visible radiation during the *relatively* cloudy summer of 1934 than during the unusually clear summer of 1936.

For additional evidence of such a difference in the quality of radiation, attention is directed to comparative data on seedlings from the two experiments, especially the root/shoot ratios, as summarized in Table 2.

TABLE 2

Comparison of white pine data from the 1934 and 1936 experiments.[1]

Experiment	Cumulative Radiation as Kg. Cal. per Sq. Cm.	Total Dry Wt. in Mg.[2]	$\frac{\text{Root}}{\text{Shoot}}$ Ratio	Nitrogen Content in Mg.
1934	*9.4*	*70.5*	*0.52*	*1.14*
1934	15.5 [3]	82.0 [3]	0.68 [3]	1.20 [3]
1934	*17.3*	*84.4*	*0.72*	*1.29*
1936	15.5	67.3	0.33	1.08

[1] The 1934 data are from Table 1, Mitchell, 1936; the 1936 data are from Table 1 of this report.

[2] All yields are expressed as from seed with a reserve dry weight of 9.97 mg.

[3] Since no seedlings of the 1934 experiment were exposed to exactly 15.5 kg. cal. of radiant energy (the amount received by the 1936 seedlings in the 30 percent light bed), these data were estimated from the curves of average relationship shown in Figs. 1 and 2 of the report on the 1934 experiment.

The root/shoot ratios of the 1934 seedlings are considerably larger than those of seedlings exposed during 1936 to the same total radiation (15.5 kg. cal.). Available data indicate that root development in relation to the shoot tends to vary inversely as the infra-red/visible radiation ratio. For example, Gast (*loc. cit.*) found that Scots pine (*Pinus silvestris* L.) seedlings exposed to solar radiation containing a full complement of infra-red had significantly lower root/shoot ratios than seedlings grown under a water screen which removed 97 percent of the infra-red longer than wave length λ 1.0 μ. In view of this finding it seems reasonable to attribute the larger root/shoot ratios of the 1934 seedlings to a change in the quality of radiation—that is, a greater absorption of infra-red during 1934 than during the unusually clear summer of 1936. The difference in root/shoot ratio, which can be explained in this way, is sufficient to account for the apparent discrepancy in the total yields. Large roots in relation to the shoots usually indicate a greater absorbing surface, greater mineral nutrient intake and hence a greater yield. This is confirmed in the present instance by the fact that the 1934 seedlings, although grown in the *poorer soil,* absorbed significantly more nitrogen and weighed considerably more than the 1936 seedlings exposed to the same total radiation. It is believed that the comparative data on root/shoot ratios, total yields, nitrogen contents and relative cloudiness strongly favor a difference in the infra-red/visible radiation ratio as the most probable explanation of the apparent discrepancy in yields. Although the evidence supporting this conclusion is fairly convincing, it is too incomplete to be conclusive. This fact emphasizes the need for more information regarding the complementary effects of infra-red and visible radiation on the physiology of plants.

From the viewpoint of investigators interested in experimental technique it is significant that, on the whole, the weights of seedlings from the 1934 white pine experiment tend to deviate less from the calculated curve of average relationship than do the 1936 white pine or red pine yields (Fig. 2). The superior precision of the 1934 results, which is also reflected in the standard errors of the mean yields (Table 1, Mitchell, 1936), can be attributed, in a large degree, to the fact that the seed-size factor was subject to more exact control during the 1934 study. The seeds used in 1934 were separated, by individual weighing, into 1-milligram fresh-weight classes. Since only seed from two of these classes were planted, the maximum possible deviation from the mean seed weight was $\pm$1.0 milligram. At the end of the experiment yields of seedlings from the two seed classes were converted to a common basis with correction factors, previously discussed, and were expressed as from seed of a single 1-mg. fresh-weight class. In the 1936 experiment no attempt was made to control seed size, which varied according to the frequency distribution characteristic of the species and the sample. In the case of white pine, for example, the seed lot used included seeds which were as much as 6.0 mg. larger or smaller than the mean. Thus the largest and smallest seeds differed by about 12 milligrams, which is sufficient to account for variations of 30 percent in the dry weights of the resulting seedlings (Mitchell, 1939). Deviations of this magnitude necessarily affect the precision of experimental data, especially when the number of observations is limited.

[1] On cloudy days the graphs of solar radiation show numerous fluctuations as clouds obscure the sun, whereas on clear days a smooth, somewhat bell-shaped curve is recorded.

CONCLUSIONS

Data from the present experiment indicate that for white pine and red pine there is an arithmetic: logarithmic correlation between seedling yields and cumulative solar radiation. This relationship, which takes the form of a linear proportion, is valid under certain conditions of mineral nutrition, and when the radiant energy measurement used is that of total radiation. These observations are in complete accord with the results of previous studies with various species of *Pinus*.

Seedlings exposed to full sunlight during the greater part of the growing season are not only heavier (total dry weight) but have better root systems and a more favorable root/shoot ratio than plants grown in lower light intensities.

Evidence is presented that the root/shoot ratios and the yields of seedlings grown in different years in the same locality may be influenced by climatic factors which change the *quality* of solar radiation by altering the ratio of infra-red to visible radiation. Seedlings grown during a sunny summer in a soil of high fertility may be smaller than those grown during a relatively cloudy summer in a soil of lower fertility, even though both receive the same cumulative radiation intensity. An explanation of this paradox is suggested.

REFERENCES

Gast, P. R. 1937. Studies on the Development of Conifers in Raw Humus. Meddel. fr. Statens Skogsförsöksanstalt (Sweden) 29:587-682.

Mitchell, H. L. 1934. Pot Culture Tests of Forest Soil Fertility. Black Rock Forest Bul. 5.

Mitchell, H. L. 1936. The Effect of Varied Solar Radiation upon the Growth, Development and Nutrient Content of White Pine Seedlings Grown under Nursery Conditions. Black Rock Forest Papers 1:15-22.

——— Finn, R. F. and Rosendahl, R. O. 1937. The Relation Between Mycorrhizae and the Growth and Nutrient Absorption of Coniferous Seedlings in Nursery Beds. Black Rock Forest Papers 1:57-73.

——— 1939. The Growth and Nutrition of White Pine (*Pinus Strobus* L.) Seedlings in Cultures with Varying Nitrogen, Phosphorus, Potassium and Calcium. Black Rock Forest Bul. 9.