

## EFFECT OF SEED WEIGHT AND SEED ORIGIN ON THE EARLY DEVELOPMENT OF EASTERN WHITE PINE

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*With one plate and two text-figures*

ALTHOUGH the effect of seed size on the growth and yield of grains and other crop plants has been frequently and intensively studied, little is known about this effect on trees, particularly over a period of more than one growing season. The present experiment was designed to give precise information concerning the effect of seed weight and seed origin on the growth and development of eastern white pine (*Pinus strobus* L.) seedlings over a three-year period. Such information on the factors influencing the growth of an important timber tree is not only of value in amplifying and clarifying existing knowledge of the development and growth behavior of trees, but is also of practical importance, both to the forester growing planting stock, and to the botanist utilizing tree seedlings in precise experiments.

### PREVIOUS WORK

Numerous investigations of the relation between seed weight and plant size have been undertaken, mostly on fast-growing, short-lived plants. Investigators have found that seed weight significantly affects plant size during the early stages of plant development. Considerable disagreement exists, however, as to whether this effect of seed weight persists or whether it diminishes in importance, even ultimately disappearing (9).

Seed weight tests involving forest trees have been summarized by Champion (4) and Baldwin (3). Although many of these tests were on a small scale and their results inconclusive when judged by modern statistical standards, they substantially agree that seedling size is influenced by seed size for at least one year. In the few experiments carried on for more than one year, height rather than weight has generally been used as a measure of growth. Furthermore, in several studies, ultimate plant size was related to first-year plant size instead of to seed size. The accumulated evidence, nevertheless, indicates that differences in growth due to varying original seed size tend to disappear within a few years.

In most of the reported tests, the average weight of a group of seeds has been used rather than the weight of individual seeds. McComb (6), however, weighed acorns of chestnut oak (*Quercus montana*) to the nearest

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The soil bed near the headquarters of the Harvard Forest consisted of six inches of gravel for drainage overlain by twelve inches of a mixture of equal parts of nursery soil, sand, and peat, sifted and thoroughly mixed. The sand culture consisted of washed quartz sand ten inches deep in an unpainted galvanized metal box, and was subirrigated three times daily by nutrient solution. The solution used contained 250 parts per million of nitrogen and phosphorus, 125 ppm of potassium and calcium, 100 ppm of magnesium, and 3.4 ppm of iron (ferric citrate) as recommended by Gast (unpublished).

The seed were planted  $1\frac{1}{2}$  inches apart in rows spaced at intervals of  $1\frac{5}{8}$  inches. Seed location was randomized within rows, and the location of the three rows of each seed lot was randomized within the bed.

At the close of each growing season, approximately one-third of the plants was cut off at the ground line, and both fresh and oven-dry weights obtained. As a result of this annual harvest, the remaining plants were left relatively free to grow during the ensuing season. In order to obtain an adequate sample of certain lots that had germinated poorly, all plants of these lots were harvested before the end of the experiment. Thus, lot 4 was completely harvested at the end of the first growing season, and lots 3, 8, and 9 at the end of the second season. Only one harvest was made from the sand culture, as the remaining plants died during the second season due to neglect caused by the illness of the author.

All data were subjected to statistical analysis after methods outlined by Snedecor (10). In particular, analysis of covariance was extensively adopted.

The terms "significant" and "highly significant" are used in the text only in their statistical sense. A significant difference indicates that the probability is less than one out of twenty ( $P = 0.05$ ) that the difference is due to chance; whereas for a highly significant difference, this probability is less than one out of one hundred ( $P = 0.01$ ).

#### PERCENT GERMINATION

Petri dish germination tests of 100 unweighed seed from each lot were made on unstratified seed, seed stratified one month, and seed stratified two months. These tests, as well as the germination records of the weighed seed in the sand and soil beds, show clearcut differences in viability between the different seed lots. Stratification of  $36^{\circ}\text{F}$ . improved germination in all but one lot (no. 4).

Seed weight also influenced percent germination. The mean weight of the 756 seed that germinated was 17.07 mg., whereas that of the seed that did not germinate was 15.57 mg., a highly significant difference of 1.50 mg. This relationship apparently held true for all seed lots, although too few seed failed to germinate in some lots to permit conclusive tests.

Since empty seed had been eliminated during the weighing process, it would appear that heavy white pine seed germinate better than light seed of the same origin. This conclusion is borne out by investigators working with other forest trees (3).

## TIME OF GERMINATION

Not only do heavy seed germinate better than light seed, but they also germinate quicker. This is shown in Table 2. The seed that germinated 11–12 days after planting (on July 7 and 8) averaged 17.49 mg. On succeeding days, the mean weight of newly germinated seed decreased until, for the period following July 18 (22 days after planting), the mean weight reached a low of 14.26 mg.

TABLE 2.

RELATION OF SEED WEIGHT TO TIME OF GERMINATION

| Days after planting | No. of seed germinated | Mean dry seed weight in milligrams |
|---------------------|------------------------|------------------------------------|
| 11–12               | 134                    | 17.49                              |
| 13–14               | 160                    | 16.96                              |
| 15–16               | 217                    | 15.94                              |
| 17–18               | 84                     | 15.61                              |
| 19–20               | 63                     | 15.30                              |
| 21–22               | 55                     | 15.57                              |
| 23+                 | 43                     | 14.26                              |

The mean date of germination did not vary significantly between the sand and the soil. The period of germination was confined to nine days in the sand culture but lasted sixteen days for most lots in the soil bed, a few seed germinating as late as the second year.

The different lots varied slightly in their mean date of germination, but no correlation was noted between mean date of germination and either mean seed weight of lot or the locality from which the lot was collected. Lots 5 and 7 germinated earliest (July 9) and lots 3 and 9 the latest (July 16 and July 14).

## ABNORMAL DEVELOPMENT

Of the 756 seed that germinated, 31, or 4 percent, developed abnormally. All but a few of these died before the end of the first growing season.

The most common type of abnormality was the failure of primary needles to grow after their appearance (12 plants). In two additional plants, the terminal shoots never appeared and the plants soon died.

An abnormality typical of lot 8 was the development of dwarf seedlings from light weight seed. Other types of unusual development, each observed twice, were the failure of the stem to grow in height although the cotyledons developed normally close to the ground, and the inability of the young plant to shed the seed coat, a failure ultimately causing death. Other plants merely developed poorly and ultimately died without any external deformity or attack by insects or fungi.

As the root systems of these abnormal plants were not examined, it is not known whether or not abnormal shoot development was related to abnormal root development.



## INSECTS AND DISEASES

Despite disinfectants and other precautions, 35 plants were killed during the first season by insect and disease attack, and nearly as many additional during the next three years.

The nursery disease "damping off" accounted for at least 26 plants during the first few weeks of the first season. An indeterminate additional number undoubtedly damped off during germination before the plant reached the surface. No particular lot seemed to be more susceptible to the disease than any other.

The other external causes of mortality in the first growing season were drought and beetle damage to tender shoots immediately after germination. Two suspected species were identified by the Division of Forest Insect Investigations, Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture, as *Dysidius mutus* Say and *Anisodactylus merula* Germ., both members of the family Carabidae, the ground beetles.

Subsequent mortality was caused by damping off fungi, basal stem girdling by the pales weevil (*Hylobius pales* Boh.), winter consumption of two-year-old seedlings by field mice, and cold injury during the winter of 1942-43.

Mortality during the first growing season from all causes, both internal and external, was correlated with seed weight, the heavier seed having the higher survival. This relationship was true within the individual lots as well as for all lots taken together. The mean seed weight of the 66 plants that died was 14.30 mg., or 2.81 mg. less than the mean seed weight of all plants.

## GROWTH OF SEEDLINGS

Each year, the effect of seed dry weight and seed origin on the dry weight of the shoot was studied by analysis of covariance. These analyses differed only in that fewer seed lots were available for sampling in the successive years, and more plants were sampled from each seed lot in each succeeding year (21 in 1943 as against 12 in 1941).

Seed weight was correlated with the size of the resulting plant each year. The regression of shoot weight on seed weight was linear and highly significant in all cases. In each succeeding year, however, the correlation coefficient between seed weight and shoot weight decreased; being 0.73 after the first year, 0.44 after the second, and 0.36 after the third. Thus the evidence is unmistakable that the effect of seed weight on plant weight becomes of less importance as the tree grows older.

External factors such as competition and soil nutrition were relatively uniform. Hence this growing lack of correlation between seed and plant size would appear to be due not to the external conditions of the experiment, but rather to hereditary, physiological, and other internal factors.

As heavy seed tended to germinate earlier than light seed (Table 2), the growing season of plants from heavy seed was materially longer than that of plants from light seed. The effect of this condition was to accentuate differences in size at the end of the first season; that is, the slope of the



regression of shoot weight on seed weight was greatest for one-year-old plants. Such an influence, however, should not affect the correlation coefficient for the regression.

The significance of the downward trend of the correlation coefficients is strengthened by the consistent values of other statistical measures in the three different years. In all cases, variations in mean seed weight and mean shoot weight between seed lots were highly significant and of a similar order of magnitude. Mean shoot weights of the different lots adjusted for variations in mean seed weights were of comparable significance each year. The implication is that hereditary differences in growth rates between the different seed lots were of similar magnitude each year. They did not tend to diminish or become more pronounced as the seedlings aged.

Although the individual seed weights were correlated with the shoot weights of resulting plants, the mean seed weights of the different lots were but poorly correlated with their respective shoot weights. (Statistically, the error of estimate of the regression of mean shoot weight on mean seed weight between the different lots was highly significant throughout). The individual lots, then, not only differed inherently in their mean growth rates, but also this difference was independent of the mean seed weight of the lot. The effects of seed weight and seed origin on growth are not interrelated.

The reduction in error due to the regression of shoot weight on seed weight was highly significant at all times. When this regression was calculated for individual seed lots, it was found in no case to differ from the regression based on the entire experiment. The relationship between seed weight and shoot weight, then, is a true species relationship and does not differ as between different seed origins within the species, at least in the case of white pine.

To compare the relative efficiency of the different samplings, the standard error of estimate of lot mean shoot weights was expressed as a percent of the overall mean shoot weight. This measure, an expression of the precision of the mean shoot weights of the different lots, was comparable for the three years, ranging from 4.6 percent to 6.9 percent.

As the shoot weight of a plant depends upon both its seed weight and its growth rate, the effect of varying seed weight must be removed if the actual growth of the various lots is to be determined. This calculation was made by adjusting the mean shoot weights of the different lots to the weights that might have been expected had all the plants developed from seed of the same weight (16.00 mg.). The adjustment utilized the regression of shoot weight on seed weight derived from the same data, and followed methods outlined by Snedecor (10). The use of this single correcting formula is quite legitimate, as the overall regression did not differ significantly from the regression for any one lot (10).

In Table 3 are given for each year of the experiment the adjusted shoot weights of the various lots arranged in approximate order of decreasing growth rates. The effect of seed weight is demonstrated by a comparison of the unadjusted and adjusted shoot weights for the first year. Actual

TABLE 3.  
MEAN SHOOT WEIGHTS OF LOTS BY YEARS

| Lot               | Mean shoot weight in milligrams |  |                            |                           |
|-------------------|---------------------------------|--|----------------------------|---------------------------|
|                   | Unadjusted<br>first<br>year     | Adjusted <sup>1</sup><br>first<br>year | Adjusted<br>second<br>year | Adjusted<br>third<br>year |
| 7 . . . . .       | 79                              | 78                                     | 1019                       | 4790                      |
| 1 . . . . .       | 62                              | 77                                     | 1013                       | 4440                      |
| 5 . . . . .       | 95                              | 72                                     | 918                        | 4310                      |
| 10 . . . . .      | 99                              | 73                                     | 688                        | 3640                      |
| 4 . . . . .       | 71                              | 69                                     | —                          | —                         |
| 6 . . . . .       | 53                              | 69                                     | 898                        | 3310                      |
| 2 . . . . .       | 59                              | 67                                     | 799                        | 3610                      |
| 3 . . . . .       | 55                              | 61                                     | 818                        | —                         |
| 9 . . . . .       | 73                              | 67                                     | 651                        | —                         |
| 8 . . . . .       | 49                              | 59                                     | 676                        | —                         |
| Average . . . . . | 71                              | 69                                     | 831                        | 4020                      |

<sup>1</sup>Adjusted to a mean dry weight of 16.00 mg., thus removing the effect of varying seed weights between lots.

mean shoot weights of the different lots varied from 49 to 99 mg.; but after the effect of seed weight had been removed, this variation was reduced to from 59 mg. to 78 mg. Much of the apparent variation in plant size between lots is, therefore, due to mere differences in seed weight rather than to actual differences in growth rate. Also, the largest plants (lots 5 and 10) did not grow as fast as lots 7 and 1, but merely started with larger seed. It is obviously necessary to take seed weight variations into account in growth studies of tree seedlings, as has been previously pointed out by Gast (5) and Mitchell (7, 8).

Differences in growth between lots were generally consistent, as between years. Lot 7 was the fastest growing in all three seasons, lot 1 following closely each year. The other lots were more or less consistent in their growth.

Little difference in growth rate between localities is apparent. Seed lots collected from Massachusetts (Harvard Forest) and from New York (Pack Forest) show similar growth. Lots from the White Mountains of New Hampshire are possibly slower growing. This difference may be due to the higher latitudes and altitudes from which the seed were collected. Not enough lots were tested, however, to permit accurate generalizations.

EFFECT OF GROWING MEDIUM

The discussion of growth thus far has been limited to data obtained from the soil bed. The same seed lots were also grown in a subirrigated sand culture.

In the sand bed, the plants were much larger at the end of the first year than were those grown in soil (87 mg. as against 69 mg.). Fewer plants were sampled from the sand, with the result that the data obtained were much less precise than those for the soil grown plants. As a result, the



sand values are less precise and less significant. For instance, the correlation coefficient between seed weight and shoot weight was 0.53 for the sand and 0.73 for the soil. All trends and relationships, however, held for the sand grown plants as well as for plants from the soil bed.

The regression of shoot weight on seed weight for both the sand and soil beds is shown graphically in *Figure 1*. The crooked lines represent the actual data grouped by classes. Both regressions follow similar trends despite the differences in fertility of the two media.

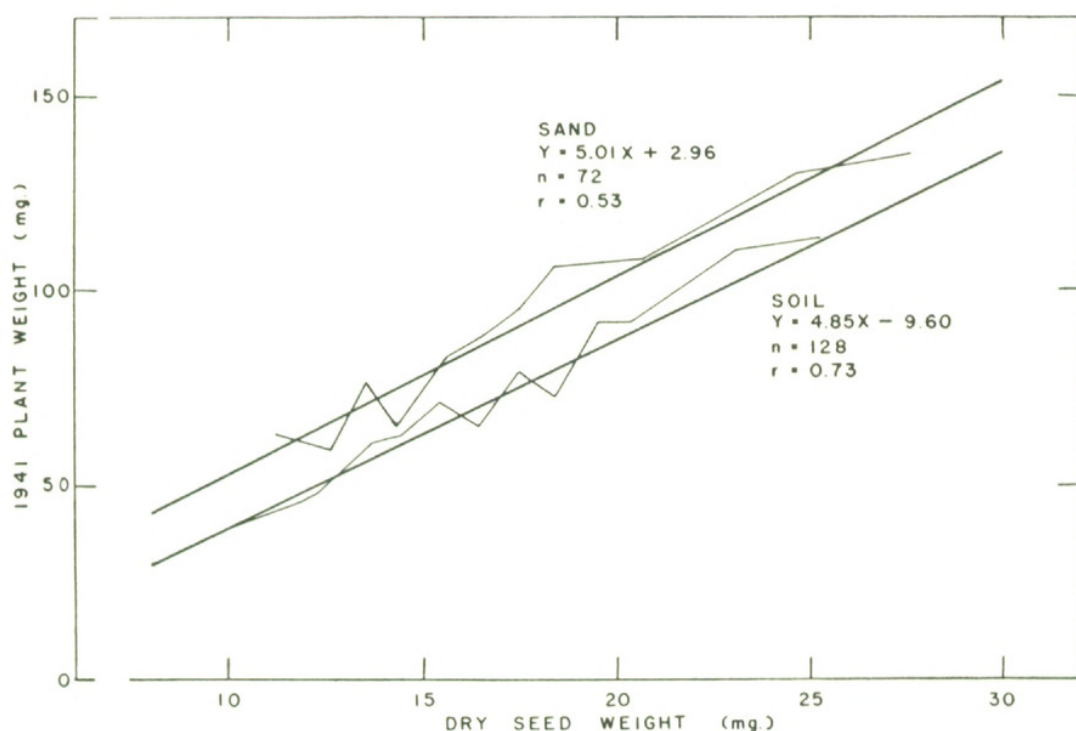


FIG. 1. The effect of seed weight on shoot weight in sand and soil beds.

Although the nutrient sand culture trials gave less precise results (due to poorer sampling) than did the soil bed trials, the evidence is that the effects of seed weight and seed origin on early growth hold for plants grown under varying nutrient conditions.

#### HEIGHT AS A MEASURE OF GROWTH

During the first two years of growth, the heights of white pine seedlings vary but little. Height is not a reliable measure of growth during this period. At the close of the third year in the present study, however, heights varied considerably. At this time, the effect of seed weight and seed origin on the height of white pine seedlings was studied by analysis of covariance. Trends and relationships were found to be generally the same as when shoot weight was used as a measure of growth, but values were of much less significance. For instance, the correlation coefficient between seed weight and height was 0.22, a barely significant value. The mean heights of the individual seed lots ranged from 5.1 to 7.7 inches.

Height is obviously not a satisfactory measure of growth when pine



seedlings are but three years old. It may, however, be an adequate growth measure of older trees. In hardwoods and other plants where the initial growth is largely linear, height is, in some respects, a satisfactory measure of growth as early as the first year (6).

#### RESERVE DRY WEIGHT

The seed coat makes up a considerable proportion of the weight of a seed. Since it is shed soon after germination, it does not nourish the seedling. If the dry weight of the seed coat is subtracted from the dry weight of the entire seed, a value is obtained which closely approximates the dry weight of the food reserves in the seed. This value has been variously described as "effective weight" (7) and "reserve dry weight" (5). Such a value is obviously more closely related to subsequent growth than is the dry weight of the entire seed. Nevertheless, the calculation of the reserve dry weight for each seed would appear to be unnecessary wherever it is directly proportional to seed weight.

To test this proportionality, seed coats were collected after germination, oven-dried, and weighed to the nearest hundredth of a milligram. When the reserve dry weight values thus obtained were plotted against seed dry weight, these two factors were found to be highly correlated. This relationship is shown in *Figure 2*, where the two parallel lines define the area in which practically all the 753 individual plotted points fell. Furthermore, similar regressions for each of the ten seed lots showed similar slopes and

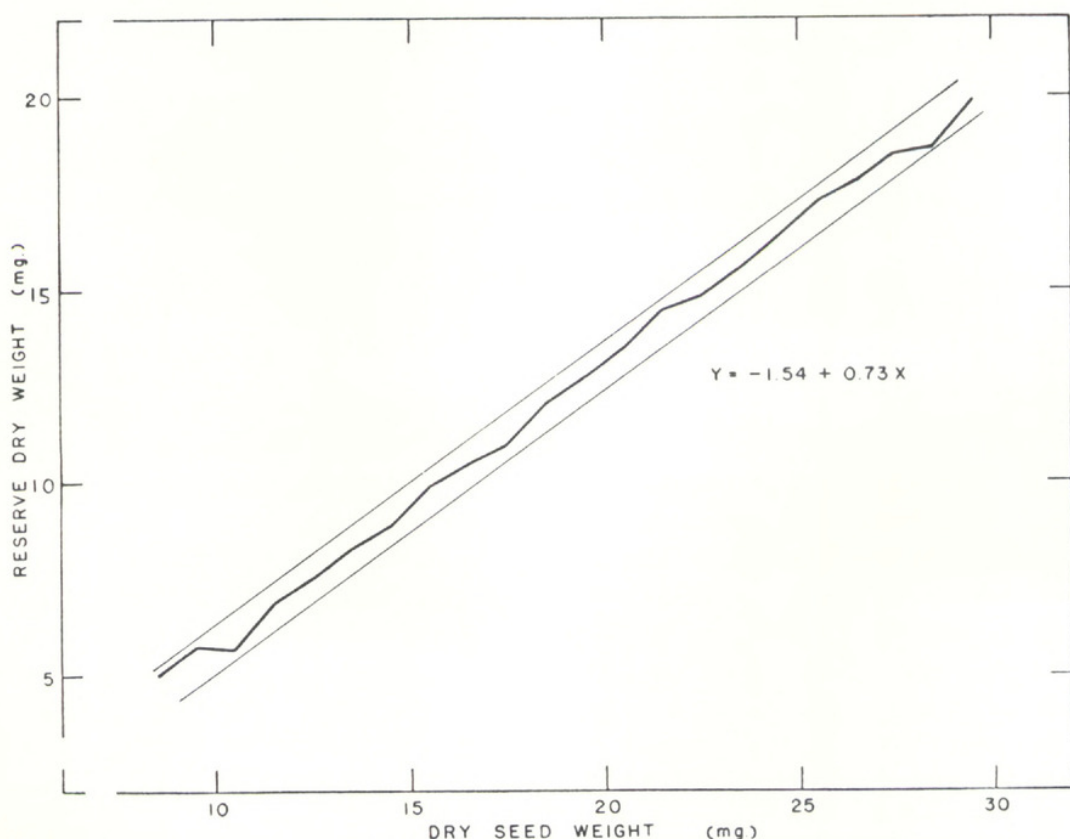


FIG. 2. Relation between reserve dry weight and seed dry weight.

elevations. Reserve dry weight, therefore, is not only highly proportional to seed dry weight, but this relationship also does not vary among various seed origins. The only cases where reserve dry weight was not proportional to seed dry weight occurred in partially filled seed. Several of these seed apparently gave rise to some of the abnormal plants discussed earlier.

Mitchell (7) previously had found reserve dry weight proportional to seed dry weight. The lack of proportionality found in the same data by Gast (5) appears to be due to his use of theoretically smoothed data rather than the actual values.

Twice in the present study parallel analyses of covariance were run, one analysis utilizing seed dry weight and the other, reserve dry weight. On both occasions, the correlation between reserve dry weight and shoot weight failed to differ significantly from the correlation between seed dry weight and shoot weight. Other values and relationships similarly held in the parallel tests. Furthermore, the regression of shoot weight on reserve dry weight was demonstrated to be identical with the regression of shoot weight on seed dry weight by converting the two regressions to similar terms. Since the results obtained from these parallel analyses did not differ significantly, no additional precision was obtained when reserve dry weights were used.

Reserve dry weight, then, is more closely related to subsequent growth because it closely approximates the weight of the food reserves in the seed. On the other hand, it is not necessarily more closely correlated with shoot weight than is seed dry weight. Because of the high degree of proportionality between reserve dry weight and seed dry weight, the calculation of the former is unnecessary, and the use of the latter is just as satisfactory in seed weight studies involving a single species. The use of reserve dry weights, however, is desirable when different species are to be compared, and in special cases such as when the seeds are known to be partially empty.

#### COMPOUND INTEREST GROWTH

Many formalized mathematical growth laws have been advanced to explain various growth data. A law frequently applied to growth of tree seedlings is the compound interest law (5). Various investigators have presented evidence to show that the size of pine seedlings at the end of the first growing season is roughly determined by the weight of the seed (initial capital) and the total effect of environmental and hereditary factors (interest rate). This follows the compound interest formula:

$$V_n = V_o (1.0p)^n$$

in which  $V_n$  is the accumulated capital;  $V_o$ , the initial capital;  $p$ , the interest rate; and  $n$ , the number of compounding intervals.

The argument has been advanced that, during a period of juvenile development, a plant increases in size at a constant rate of interest in close agreement with the compound interest law. From the above formula, it can readily be seen that the interest rate is measured by the ratio of accumulated capital to initial capital, provided that the compounding periods are of equal length. It follows that this ratio will remain constant for each



succeeding growing season if the plant is growing at a constant compound interest rate. Using the shoot weight at the end of the season as  $V_n$  and the weight at the start of the season as  $V_o$ , we find that the resulting ratios express the number of times that the plant increased in shoot weight during each growing season. Thus, the shoots of the white pine seedlings in the present experiment attained a size at the end of the first growing season roughly 8.5 times greater than that part of the dry food reserve of the seed which, on the basis of the shoot-root ratios immediately after germination, could be assumed to have gone into shoot growth (80 percent). During the second season, the shoots increased 12.2 times in weight, and, during the third, 4.5 times. This wide variation in the rate of growth from year to year, particularly the marked decrease during the third year, indicates that white pine seedlings do not consistently increase in shoot weight at a constant compound interest rate during the first three years of growth.

#### SEED ORIGIN

That seed origin affects the growth of white pine seedlings has already been demonstrated. Not only is seed origin important in its relation to growth, but it also affects other phases of the early development of white pine. It influences both the moisture content and habit of the resulting plants.

At the close of the first growing season, the moisture content of all harvested plants was calculated from their fresh and oven-dry weights. Analysis of covariance revealed that moisture content was completely unrelated to seed weight but that it was influenced both by seed origin and medium of growth.

Plants grown in the sand contained an average of  $63.9 \pm 0.05$  percent moisture, whereas those grown in the soil bed contained an average of only  $60.2 \pm 0.03$  percent moisture, a highly significant difference that was consistent for all lots.

The various seed lots differed in moisture content to a highly significant degree. Lot 3 had the highest moisture content (65.0 percent in sand and 61.8 percent in soil); while lot 2, also originating from the Harvard Forest, had the smallest amount of moisture (62.6 percent in sand and 59.7 percent in soil). The moisture contents of the various lots, while differing considerably, were apparently not related to the regions in which the seed originated, although the sampling from the different regions was insufficient to permit a generalization.

By the end of the second year, differences in appearance between the various seed origins had become quite apparent. These differences were due primarily to variations in needle length, the number of developed laterals, and the spasmodic occurrence of lammas shoots, secondary shoots formed after a mid-season period of dormancy.

To illustrate these differences in form, the largest, median, and smallest plants of each lot were photographed. In *Plate I*, the two fastest growing lots (7 and 1) are illustrated in the top row; the two lots with the largest seed (5 and 10) are in the middle row; and two of the slower growing lots



(6 and 2) are in the bottom row. The long needles and comparative absence of secondary growth give lots 5 and 10 a form quite distinct from that of lots 6 and 7, where the needles are relatively short and well-developed lammas shoots conspicuous.

At the end of the third growing season, few lammas shoots were observed (the late summer was quite dry); but variations in needle length and in the number of laterals resulted in distinct differences in appearance between the various lots. Needles were longest in lots 1 and 5 and shortest in lots 6 and 10. Many more laterals had developed on plants in lot 5 than in lot 1, the other lots having an intermediate number.

These differences in appearance are quite distinct, although somewhat difficult to measure quantitatively. They are obviously related to seed origin and apparently little affected by variation in seed weight.

#### SUMMARY

In order to study the effect of seed weight and seed origin on the early development of eastern white pine (*Pinus strobus* L.), one hundred seeds of each of ten different origins were weighed individually and grown under uniform conditions. At the close of each of the first three growing seasons, plants were removed, weighed, and their shoot dry weights statistically related to both seed weight and origin.

Heavy seed germinated better, germinated earlier, and survived in a higher proportion than did light seed from the same lot. Seed origin also affected germination and survival.

Shoot weight at the end of the first year was closely correlated to seed weight. As the plants grew older, however, the effect of seed weight on shoot weight diminished, but was still highly significant at the end of the third year. This relationship was the same for all the seed origins. Furthermore, the effect of seed weight on shoot weight was the same whether the plants were grown in a sand culture of high fertility or in a soil bed of moderate fertility. This result suggests that the effect of seed weight is independent of the nutrition of the seedlings.

Each seed lot consisted of seed of a single origin — seed collected from a single mother tree. The variation in growth between these lots was generally consistent from year to year and was highly significant at all times.

The effects of seed weight and seed origin on growth are not interrelated; that is, the mean seed weight of a lot gives no indication of the growth rate of that lot.

Much of the apparent variation in plant size between lots is caused by differences in seed weight rather than by differences in growth. The largest plants are not necessarily the fastest growing, but may merely have originated from the largest seeds. The influence of seed weight must be removed to bring out true differences in growth rate. This adjustment can be made by utilizing the regression of plant weight on seed weight derived from the same data.

The height of three-year-old pine seedlings is not a satisfactory measure of their growth.



Although the reserve dry weight of a seed is more closely related to subsequent growth than is seed dry weight, its use in the present experiment resulted in no increase in correlation between seed and shoot weight because of the high correlation between seed dry weight and reserve dry weight.

Shoot growth over a three year period failed to follow a constant compound interest rate of growth.

Plants grown in the nutrient sand culture contained more moisture than those grown in soil. Moisture content varied according to seed origin, but was independent of seed weight.

As early as the second year, differences in appearance between the various seed lots became noticeable. These differences resulted primarily from variations in needle length, the number of laterals, and the occurrence of lammas shoots.

Briefly, seed weight is related to germination, survival, and the early size of the plant. The correlation between weight and shoot weight diminishes as the plant ages, but is still noticeable after three years. Seed origin is related to germination, appearance, moisture content, and seedling growth. The influence of seed origin on plant size is as strong at the end of the third as at the end of the first growing season, in marked contrast to the constantly diminishing influence of seed weight. Both seed weight and seed origin, then, influence markedly the early development of eastern white pine.

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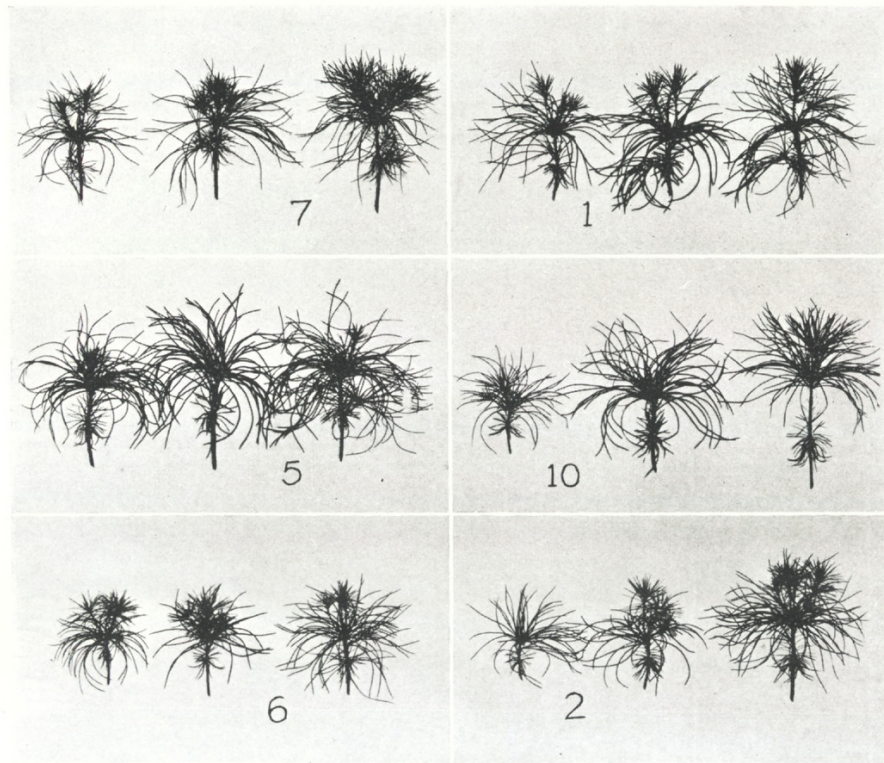
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#### EXPLANATION OF PLATE I

Silhouettes of the smallest, median, and largest plants of selected lots at the end of the second year.

HARVARD FOREST,  
PETERSHAM, MASS.





SEED WEIGHT AND SEED ORIGIN



Spurr, Stephen H. 1944. "Effect of Seed Weight and Seed Origin on the Early Development of Eastern White Pine." *Journal of the Arnold Arboretum* 25(4), 467–480. <https://doi.org/10.5962/p.185507>.

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