

ON THE ROLE OF THE ACORN IN ROOT GROWTH OF AMERICAN OAK SEEDLINGS

by

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(Received 30.8.'56)

INTRODUCTION

Many investigations into the influence of light and shade upon plant growth have demonstrated that when photosynthesis is curtailed, root elongation is limited to a greater extent than shoot growth (4, 8, 9). The reason advanced for this phenomenon is that, since the site of utilisation of carbohydrates in the root system is at a greater distance from the centre of production than is that in the shoot, the root system will respond to a shortage in production before the shoot. Such an explanation implies that root growth depends on contemporary photosynthates and that storage products in the roots are in some way unavailable for root growth – a supposition for which little evidence has been adduced. An alternative explanation is that the shoot system has an advantage over the root system in competing for available reserves, but again, we have no evidence about this. We do not know whether the response is immediate, resulting in a gradual decrease in root growth, or whether the original rate of utilisation of carbohydrates is maintained until available supplies are exhausted, so that eventually there is a sudden stoppage of root growth.

In an attempt to answer this last question, in some experiments, with first-year seedlings of *Acer pseudoplatanus* L. and *Quercus borealis maxima* (MARSH) ASHE the influence on root elongation rate of varying the light intensity over the shoot system was determined over short periods (10). It appeared that the root growth rate of *Acer* was directly determined by light intensity (and by inference, photosynthesis); at each light intensity the roots assumed a definite growth rate. When this rate was plotted against the light intensity over the shoots, a curve closely resembling a curve of photosynthesis and light intensity resulted. *Quercus*, however, showed no sign of such dependence; at all light intensities, the root elongation rate was the same. The results indicated specific differences in reaction to a reduced light intensity, but the duration of the experiments was insufficient for conclusions about the connection between carbohydrate synthesis and root growth in *Quercus*, and a more extensive investigation seemed desirable.

In the present paper experiments are described in which a limitation in pho-

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tosynthesis was imposed for an indefinite period and the effect on root elongation studied. The results of these experiments prompted an investigation into the role of the cotyledons in root growth.

MATERIAL AND CULTURAL METHODS

The experiments were made with first-year seedlings of *Quercus borealis maxima* (MARSH) ASHE in various stages of development. A more detailed description of the cultural methods employed is given elsewhere (10, 6).

Briefly, seeds were germinated in white silica sand, in either pottery flats, 25 × 25 × 7 cm (deep), or wooden boxes 20 × 20 × 20 cm. After shoot emergence, the following nutrient solution was supplied at a rate of about 200 ccm every 3 days.

MgSO ₄ ·7H ₂ O	0.36 g/l.
KH ₂ PO ₄	0.53 g/l.
Ca(NO ₃) ₂ ·4H ₂ O	0.445 g/l.
NH ₄ NO ₃	0.61 g/l.

Trace elements

Ferric citrate	0.03 mg/l.
H ₃ BO ₃	0.003 mg/l.
MnCl ₂ ·4H ₂ O	0.002 mg/l.
ZnSO ₄ ·7H ₂ O	0.0002 mg/l.
CuSO ₄ ·5H ₂ O	0.0001 mg/l.
H ₂ MoO ₄ ·H ₂ O	0.0001 mg/l.

The trace element solution is that of OLSEN (5).

Between germination and transfer to the experimental environment, the seedlings remained in a north-facing double-walled greenhouse at a temperature of 20° ± 2.5°C and under natural daylight. When the natural daylength fell below 16 hours, supplementary illumination from a single 40-watt fluorescent tube ("daylight" type) at an intensity of 200 lux at the uppermost leaf surface was given, to extend the photoperiod to 16 hours. When 1 complete whorl of leaves had developed, the seedlings were transferred to a more easily controlled environment and remained under conditions of constant temperature (20° ± 1½°C), light intensity (5000 lux) and relative humidity (60-75%) for a period of at least 3 weeks before any experimental treatments were started.

Most of the experiments involved the measurement of root elongation rates under various treatments. For this purpose, seedlings, on removal from the greenhouse, were transplanted into glass root tubes, one seedling to each tube. These tubes were 50 cm long and 4½ cm in diameter, and were drawn out to a diameter of 1 cm at the base. A plug of glass wool was placed in the bottom of each tube and the remainder filled with clean gravel. They were kept in light-proof boxes, 60 cm long × 45 cm wide × 65 cm deep, 12 tubes to a box. The tubes fitted into circular holes cut into the top of the box, while the narrow section at the base of each tube extended through the bottom of the box, enabling rubber tubing to be attached for purposes of sub-irrigation. Twice daily, the tubes were saturated with nutrient solution of the same composition as that supplied before transplanting.

The seedling roots grew against the sides of the glass tubes and could be examined through a microscope. Root growth was measured by marking a base line on the tube with a glass pencil and measuring the distance from one edge of this line to the root tip by means of a horizontal microscope.

EXPERIMENTAL METHODS AND RESULTS

In general, each series of experiments arose out of the results of the preceding set and it is logical, therefore, to treat methods and results together.

The first series aimed at elucidating the relation between plant size and root elongation rate, when photosynthesis is curtailed. Seedlings, varying in size from those having a single whorl of leaves to those having 3 whorls, were grown at a light intensity of 5000 lux and daily measurements of root elongation were started. When the growth rate was relatively constant, the light intensity was

reduced to 200 lux and the measurements continued until root growth stopped and the roots began to suberise. In an attempt to distinguish between the influence of plant weight and that of leaf area, some seedlings were partially defoliated. It was possible, in this way, to compare seedlings having widely different weights but about the same leaf area, and those having about the same weight but very different leaf areas. In the first six experiments, the material used was as follows:

- Expt. 1 - Seedlings with 1 whorl of fully-expanded leaves.
- Expt. 2 - Seedlings with 1½ whorls of fully-expanded leaves.
- Expt. 3 - Seedlings with 2 whorls of fully-expanded leaves.
- Expt. 4 - Seedlings with 2 whorls of fully-expanded leaves, defoliated to 1 whorl.
- Expt. 5 - Seedlings with 3 whorls of fully-expanded leaves.
- Expt. 6 - Seedlings with 3 whorls of fully-expanded leaves, defoliated to 1 whorl.

The leaves remaining on the seedlings after defoliation were the youngest. The seedlings used in Expt. 2 (1½ whorls of leaves) had one whorl of fully-expanded leaves and a terminal bud which started to swell just after the beginning of the experiment.

All the seedlings used in these experiments had been transplanted with the acorns attached to the plant and, due to the differences in development, the acorns were in varying stages of exhaustion at the beginning of the experiments. It seemed possible, therefore, that differences in response to continuous low light might be due, in part, to an effect of the acorn. To test whether there is, in fact, any influence of the acorn, 4 experiments were performed in which the acorns were removed one week before measurements of root growth began. The development stages were as follows:

- Expt. 7 - Seedlings with 1 whorl of fully-expanded leaves.
- Expt. 8 - Seedlings with 1½ whorls of fully-expanded leaves.
- Expt. 9 - Seedlings with 2 whorls of fully-expanded leaves.
- Expt. 10 - Seedlings with 3 whorls of fully-expanded leaves.

Root measurements in these last experiments were made either once or twice daily. For all experiments about 7 roots from each seedling were chosen and measured once daily until they stopped growing and began to suberize. By this time, no growing roots could be found on any seedling under these conditions. The seedlings were then harvested, leaf areas were measured and dry weights of roots, stems and leaves determined separately.

It is proposed to treat all ten experiments together since, in a number of ways, the results of the last four reinforce those of the first six.

Results of these experiments can be seen in Figs. 1 to 7 and Table 1. In the figures, the mean hourly root growth rate is plotted against time for three of the six size classes. For considerations of space and because each growth curve followed essentially the same pattern, representative examples only have been presented for the first six experiments. In Table 1, the dry weight data and reaction times etc. are shown.

Each value in the table is the mean of the 3 seedlings treated similarly in each experiment. Column (8) in Table 1 gives the mean lateral root growth rate (hourly) during the period when it is relatively steady i.e. from the change in light intensity until the point at which a reduction in rate was first noticed. This method of deriving a measure of the growth rate is somewhat subjective, but it appeared to be the best available. To include all measured values would give a false impression of the growth level since the value obtained would be influenced by the length of the periods during which the growth rate was declining, which periods were not of the same duration in every case.

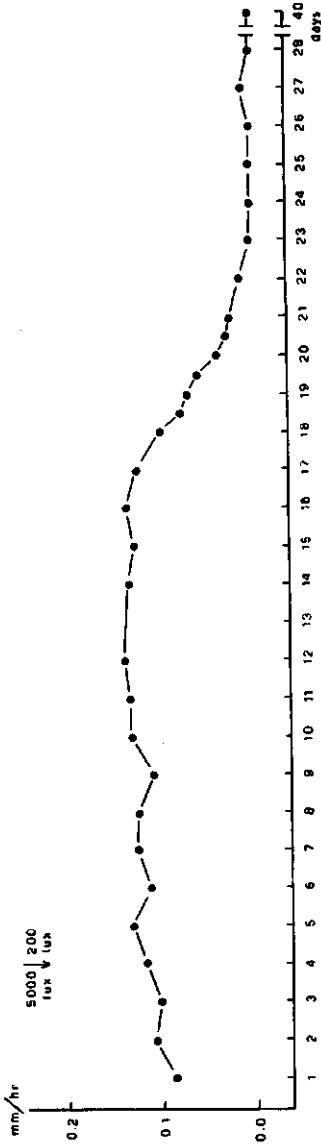


FIG. 1. *Quercus borealis*. The course of root growth in seedlings with 1 whorl of fully-expanded leaves, on transfer from a light intensity of 5000 lux to 200 lux for an indefinite period. Seedlings with acorns attached

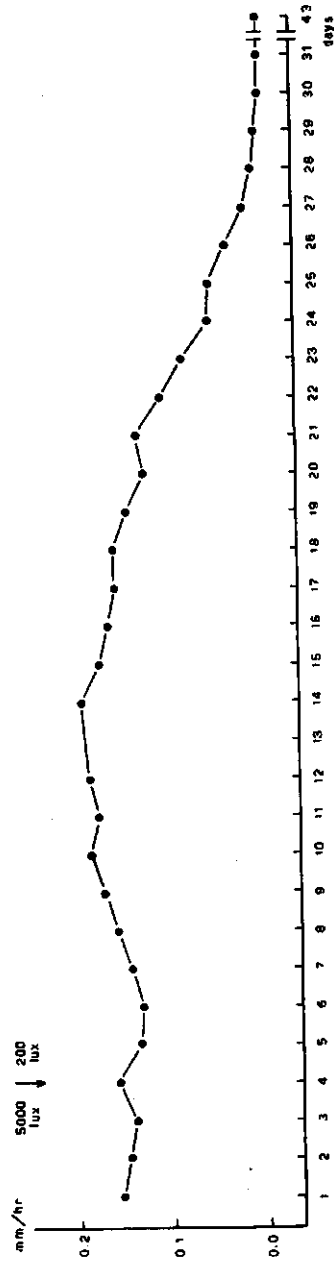


FIG. 2. *Quercus borealis*. The course of root growth in seedlings with 2 whorls of fully-expanded leaves, on transfer from a light intensity of 5000 lux to 200 lux for an indefinite period. Seedlings with acorns attached

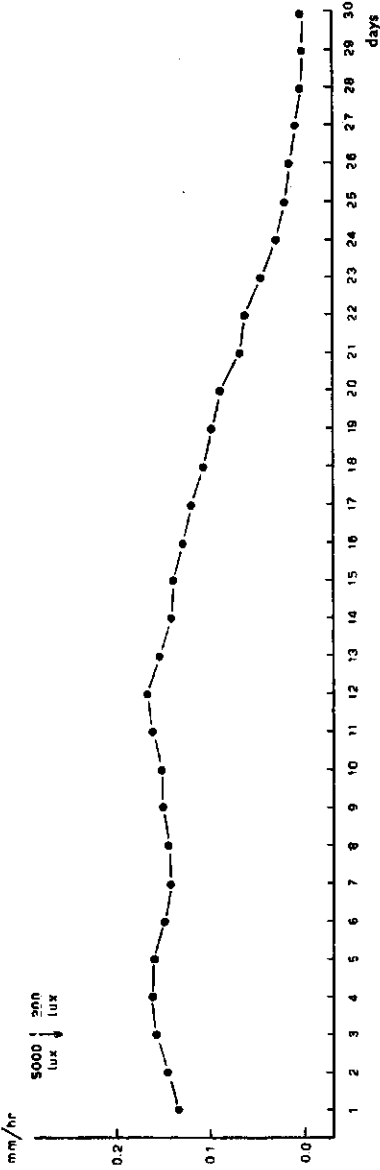


FIG. 3. *Quercus borealis*. The course of root growth in seedlings with 2 whorls of fully-expanded leaves defoliated to 1 whorl, on transfer from a light intensity of 5000 lux to 200 lux for an indefinite period. Seedlings with acorns attached

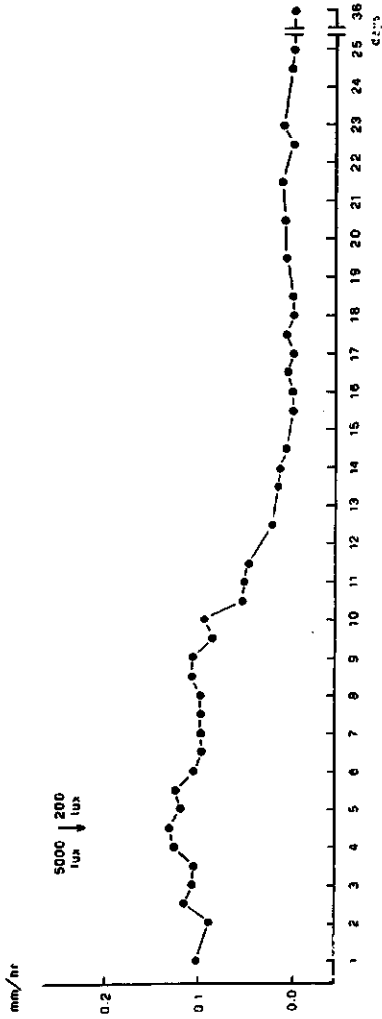


FIG. 4. *Quercus borealis*. The course of root growth in seedlings with 1 whorl of fully-expanded leaves, on transfer from a light intensity of 5000 lux to 200 lux for an indefinite period. Seedlings with acorns detached

Column (9) gives the number of days from the first rise in growth after the beginning of the experiments to the point at which 50% of the lateral roots being measured had stopped growing.

Column (7) contains stem-plus-root weights. In view of the fact that, just before the experiments began, half the seedlings were partially defoliated, it was not considered advisable to include leaf weights in this measure since to do so would give a false picture of plant size.

It will be noted that no "mean growth rate" values have been calculated for Expt. 8 (seedlings with $1\frac{1}{2}$ whorls of leaves). This is because a steady growth rate was never attained for a period long enough to give such values any meaning.

TABLE 1. *Quercus borealis*. Data relating to plant size and reaction to low light intensity in Experiments 1-10. For explanation, see text. All values are means of 3 seedlings

Experiment No.	Total leaf area (cm ²)	Final dry weights (gms.)					Mean root growth rate to 1st drop (mm/hr)	Days to 50% stopped
		Leaves	Stem	Roots	Acorn	Plant (less leaves and acorn)		
1	2	3	4	5	6	7	8	9
1	126.7	1.08	0.91	1.01	0.38	1.92	0.105	15.8
2	151.5	1.29	1.28	1.33	0.28	2.61	0.126	18.3
3	243.8	2.84	1.42	1.63	0.14	3.04	0.151	22.0
4	104.3	0.99	1.25	1.48	0.11	2.73	0.147	20.0
5	351.7	3.47	1.75	1.75	0.08	3.50	0.198	24.3
6	140.0	1.26	1.67	1.90	0.08	3.56	0.192	24.7
7	144.9	1.50	0.91	1.18		2.09	0.102	6.0
8	157.3	1.15	1.07	1.20		2.26	-	8.7
9	250.3	2.69	1.14	1.57		2.71	0.156	10.0
10	354.6	3.19	1.66	1.92		3.58	0.182	25.0

Figs. 1 to 3 show representative results for the first six experiments. In each case, acorns were attached to the seedlings. All these curves have essentially the same pattern but there are differences in both level and duration of root growth which can be correlated with plant size. In all the curves, the effect of a reduction in light intensity over the shoot from 5000-200 lux was an ultimate reduction in root growth rate which became evident after periods varying between 15 and 25 days, according to plant dry weight (Table 1). The rate of root growth before the reduction varied between 0.015 and 0.198 mm/hr, again depending on plant weight.

That the level of growth and reaction to low light intensity are not correlated with leaf area can be seen from Table 1. For example, the seedlings in Experiments 5 and 6 had very different leaf areas (respectively 351.7 and 140.0 cm²), but showed approximately the same mean root growth rate (0.198 and 0.192 mm/hr.) and reaction time (24.3 and 24.7 days).

Results of the 4 experiments made with seedlings from which the acorns had been removed are presented graphically in Figs. 4 to 7. It can be seen that, with the exception of Fig. 5 (seedlings with $1\frac{1}{2}$ whorls of leaves), the pattern of the curves is the same as in the previous experiments. The level of root growth is not markedly affected by the removal of the acorns but a big influence of the acorn on reaction time is apparent. Thus, in experiments 7 to 9 the time of reaction to a low light intensity varies between 5 and 13 days. Only in the last experiment (plants with 3 whorls of fully-expanded leaves) does the reaction time approach that of similar plants with acorns.

The behaviour of plants with one whorl of fully-expanded leaves plus an expanding terminal bud was unexpected (fig. 5). In this figure, the term "bud swelling" refers to the first signs of expansion of the bud, visible to the naked eye. By "leaves expanding" is meant the point at which the newly developed leaves are about 1 cm long, judged by eye. Bud expansion

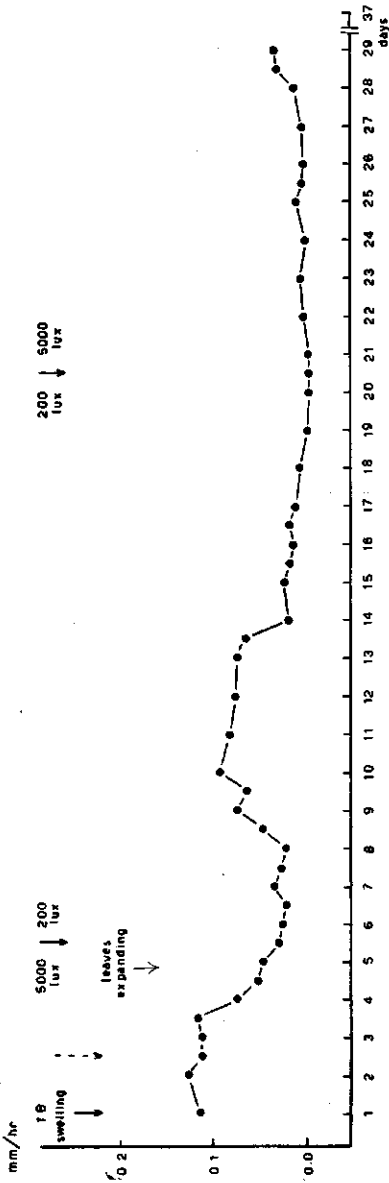


FIG. 5. *Quercus borealis*. The course of root growth in seedlings with 1½ whorls of fully-expanded leaves, on transfer from a light intensity of 5000 lux to 200 lux for an indefinite period. Seedlings with acorns detached. Dotted arrow: see text

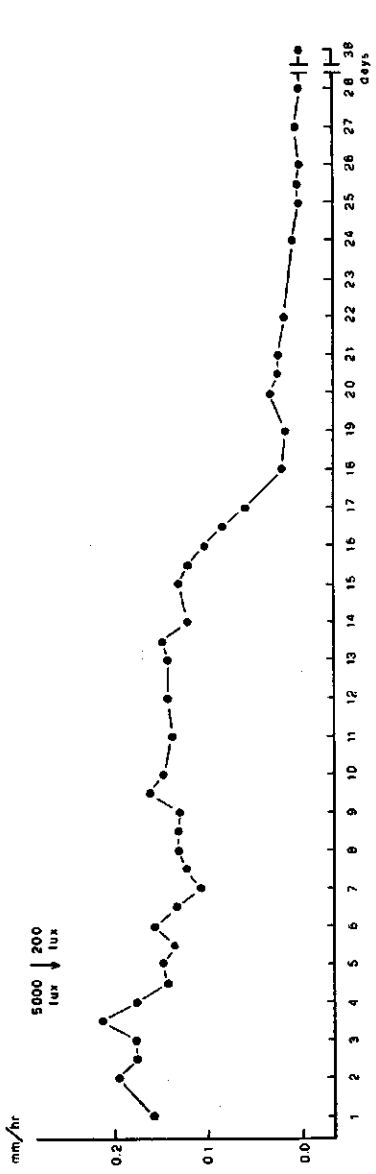


FIG. 6. *Quercus borealis*. The course of root growth in seedlings with 2 whorls of fully-expanded leaves, on transfer from a light intensity of 5000 lux to 200 lux for an indefinite period. Seedlings with acorns detached

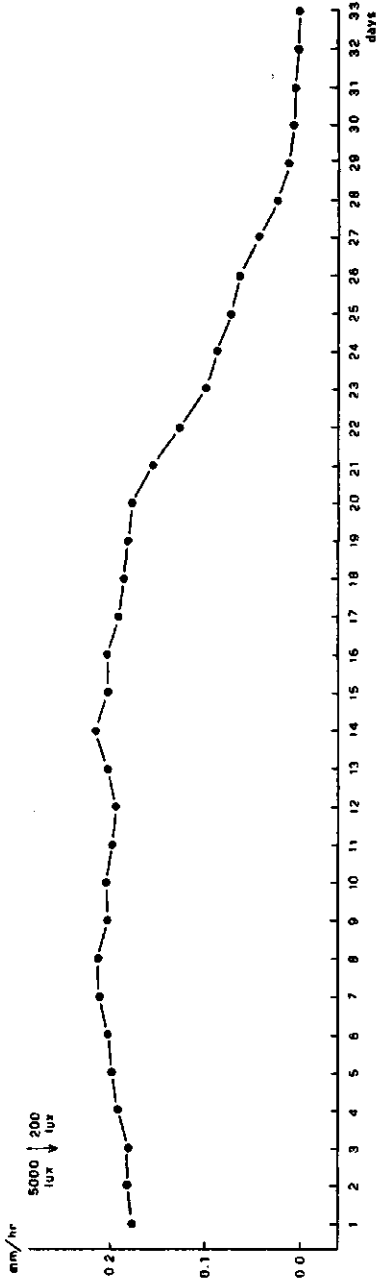


FIG. 7. *Quercus borealis*. The course of root growth in seedlings with 3 whorls of fully-expanded leaves, on transfer from a light intensity of 5000 lux to 200 lux for an indefinite period. Seedlings with acorns detached

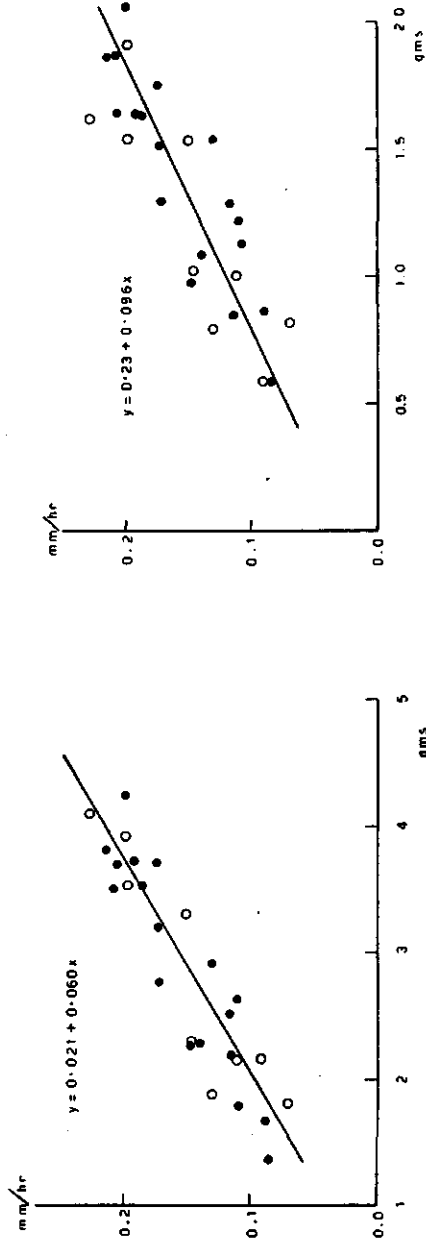


FIG. 8. *Quercus borealis*. The relation between mean lateral root growth rate and plant dry weight; data from Experiments 1-10. Seedlings with acorns detached are indicated by O

appears to be accompanied by a reduction in growth rate of both main and lateral roots. The point marked by the dotted arrow in fig. 5 shows the point at which unfolding as distinct from swelling was first visible. Thirty-six hours later the growth rate began to fall, and, after a further 2 days, reached a level at some 12% of the original. The reduction in light intensity was made while the growth rate was falling, $5\frac{1}{2}$ days after the beginning of the measurements. Three days later the root growth rate began to rise and, $1\frac{1}{2}$ days later, reached a point about 10% below the original level at 5000 lux. This level, however, was maintained for only 3 days, and root growth then fell off rapidly until it stopped altogether. A repetition of this experiment gave essentially the same result and it must be concluded that the observed effect is a real one.

The relations between dry weight and growth level and reaction time in the two sets of experiments are illustrated in Figs. 8 to 13. Individual seedlings have been treated separately. Circles indicate values derived from seedlings from which the acorns were removed, while the dots represent plants which retained their cotyledons.

Figures in which mean growth rate is a component do not include the experiment with seedlings at the stage of $1\frac{1}{2}$ leaf whorls and with acorns detached.

In Fig. 8, mean lateral root growth rates have been plotted against plant dry weight (i.e. stem-plus-root weight); there is a linear relation between these variables (significance level $> 0.1\%$). In Figs. 9 and 10, stem and root dry weights are separated. In both cases there is a very highly significant linear relation with root growth level (Table 2) but it is closer in the case of root weight ($F = 108.05$) than in that of stem weight ($F = 66.83$).

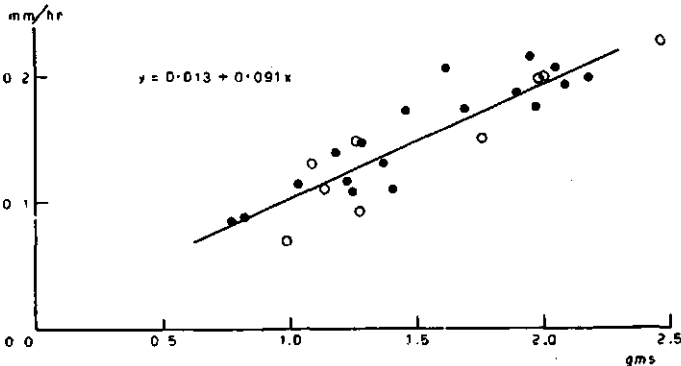


FIG. 10. *Quercus borealis*. The relation between mean lateral root growth rate and root dry weight; data from Experiments 1-10. Seedlings with acorns detached are indicated by O

Figures 11, 12 and 13 illustrate the relation between dry weight and the length of time before half the lateral roots being measured had stopped growing. In the figures the seedlings with 3 whorls of leaves and without acorns, have been marked thus \ominus . In each figure the points can be divided into two distinct groups according to whether or not the acorn was detached. It is clear that, within each group, there are significant linear relations between the components of plant dry weight and reaction time. These relations, however, are not as clear in the seedlings with acorns detached as in the intact plants; and this appears to be largely due to a single seedling which had a much higher plant dry weight than any of the others included in the figures. The values given by this seedling have been ringed in Figs. 11 to 13; if they are excluded, the linearity between plant weight and duration of growth in the plants without acorns becomes more obvious. In any case, the relations are statistically significant (Table 2).

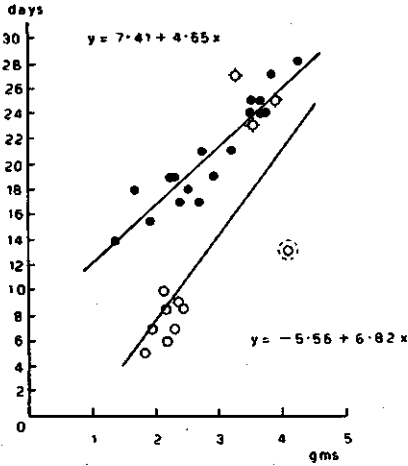


FIG. 12. *Quercus borealis*. The relation between duration of growth and stem dry weight; data from Experiments 1-10. For explanation of symbols, see text.

FIG. 11. *Quercus borealis*. The relation between duration of growth and plant dry weight; data from Experiments 1-10. For explanation of symbols, see text

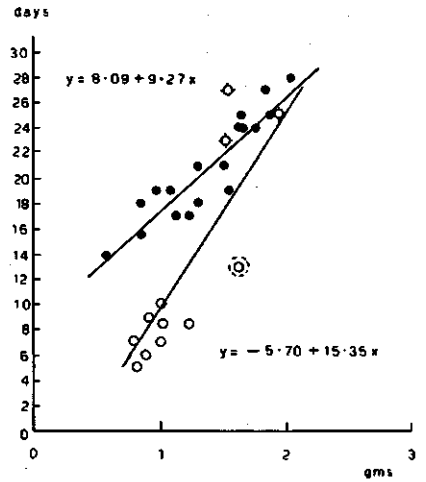


FIG. 13. *Quercus borealis*. The relation between duration of growth and root dry weight; data from Experiments 1-10. For explanation of symbols, see text

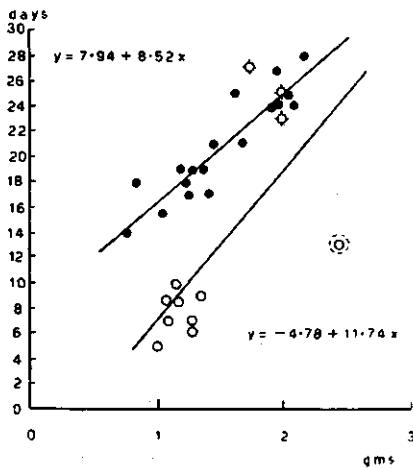


TABLE 2. *Quercus borealis*. Variance ratios (F) and regression equations for the relationships derived from Experiments 1-10

Variables	Plant dry wt.	Stem dry wt.	Root dry wt.	Leaf area
Mean root growth rate	F = 244.000 (D.F., 1 and 25) Y = -0.021 + 0.060X	F = 66.83 (D.F., 1 and 25) Y = 0.023 + 0.096X	F = 108.05 (D.F., 1 and 25) Y = 0.013 + 0.091X	F = 4.419 (D.F., 1 and 16)* Y = 0.111 + 0.00023X
Days to 50% roots stopped (Acorn attached)	F = 120.50 (D.F., 1 and 16) Y = 7.41 + 4.64X	F = 95.80 (D.F., 1 and 16) Y = 8.09 + 9.269X	F = 77.13 (D.F., 1 and 16) Y = 7.94 + 8.523X	F = 4.74 (D.F., 1 and 7)** Y = 0.070 + 0.00034X
Days to 50% roots stopped (Acorn detached)	F = 14.82 (D.F., 1 and 10) Y = -5.56 + 6.818X	F = 20.39 (D.F., 1 and 10) Y = -5.70 + 15.352X	F = 9.75 (D.F., 1 and 10) Y = -4.78 + 11.742X	F = 45.54 (D.F., 1 and 10) Y = -4.88 + 0.076X

* Seedlings with acorns attached

** Seedlings with acorns detached

There was no significant relation between leaf area and root growth rate in either set of experiments, but, in the series not specifically designed to test the influence of leaf area (i.e. those in which the acorns were removed from the seedlings), the relation is almost significant ($F = 4.74$ for 1 and 7 D.F.). With regard to reaction time, there is a significant linear relation with leaf area in both sets of experiments. In the first series, however, it is barely so ($F = 4.843$ for 1 and 16 D.F.); whereas in the series not specifically designed to test the influence of leaf area, the relation is very highly significant ($F = 45.538$ for 1 and 10 D.F.).

Unlike in *Acer saccharinum* (7), there is little difference in the regression coefficients (Table 2) for the relations involving stem and root dry weight. Only in Figs. 12 and 13 is there a noticeable difference in slope and, in this case, increases in stem weight have a greater effect on duration of root growth than do increases in root weight.

Another feature brought out by Table 2 is the fact that, in all the relations involving seedlings with acorns detached, the regression coefficients are higher than in the corresponding relations established for seedlings which retained their cotyledons.

With one exception, the results of the experiments described above are straightforward and provide no great difficulties in the way of interpretation. The exception is the one in which seedlings with expanding terminal buds were used. As has already been said, it appeared that, in the absence of the cotyledons, the expansion of the terminal bud results in a reduction in root growth, followed by an increase when a low light intensity is imposed. When the acorn remained attached to the plant, no such changes were observed. It seemed of interest to extend these observations, in an attempt to confirm this influence of bud expansion. In the next 4 experiments, the root growth of seedlings in different stages of shoot development was compared at a light intensity of 5000 lux and a temperature of $20^{\circ} \pm 1.0^{\circ}\text{C}$. In order to eliminate any influence of light intensity changes, the intensity of 5000 lux was maintained throughout the experiments. The development stages were as follows:

Expt. 11 - Seedlings with $1\frac{1}{2}$ whorls, cotyledons attached.

Expt. 12 - Seedlings with $1\frac{1}{2}$ whorls, cotyledons removed ca. 1 week before the experiment.

Expt. 13 - Seedlings with $2\frac{1}{2}$ whorls, cotyledons attached.

Expt. 14 - Seedlings with $2\frac{1}{2}$ whorls, cotyledons removed ca. 1 week before the experiment.

In each experiment, 3 seedlings were used. In Figs. 14 to 17, mean hourly root growth rates are plotted against the time in days, expansion of the bud and leaves being indicated by arrows.

It will be noticed that the time scale is relative to the time of visible bud swelling and not to the beginning of the experiment as has been the case in previous figures. This was done for the following reason. Owing to a shortage of plants, it was not possible to obtain seedlings in exactly the development stage required. Thus, the terminal buds of the seedlings used did not all expand on the same day and, if the effect of bud expansion is to be illustrated by means of averages based on all seedlings, this is clearly an undesirable condition. Therefore, all measurements relating to the day when bud swelling was first observed were pooled for the purpose of deriving mean values, and the other values fitted accordingly. The time scale is, thus, relative to the time of visible bud swelling.

Comparing Figs. 14 and 15, it is clear that removing the cotyledons when only 1 whorl of fully-expanded leaves is present markedly modifies the reaction to the expansion of the terminal bud. When the acorn is present (Fig. 14), bud expansion has no significant effect on root growth rate; when the acorn has been

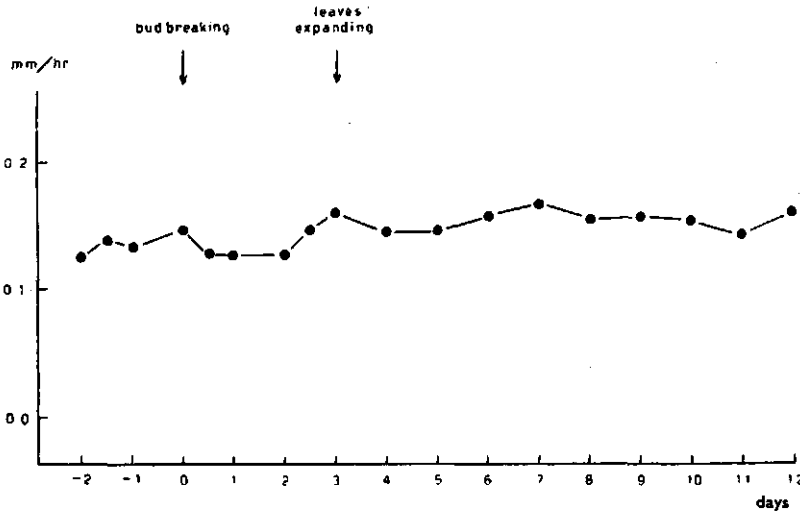


FIG. 14. *Quercus borealis*. The effect of bud expansion on root growth of seedlings with $1\frac{1}{2}$ whorls of fully-expanded leaves, at 5000 lux. Seedlings with acorns attached. The time scale is relative to the time of visible bud swelling

removed, however, (Fig. 15), bud swelling is accompanied by a fall in root growth rate to zero, but, some 10 days after the first visible signs of bud swelling, the original growth rate has been resumed. The cotyledons, thus, seem to act as a "buffer" between shoot expansion and root growth.

When seedlings with 2 fully-expanded leaf whorls were used (Figs. 16 and 17), growth rates were somewhat erratic. In spite of this, it can be seen that the expansion of the terminal bud has no significant effect on root growth whether the acorn remains attached or not. At the stage of 2 leaf whorls, therefore, the

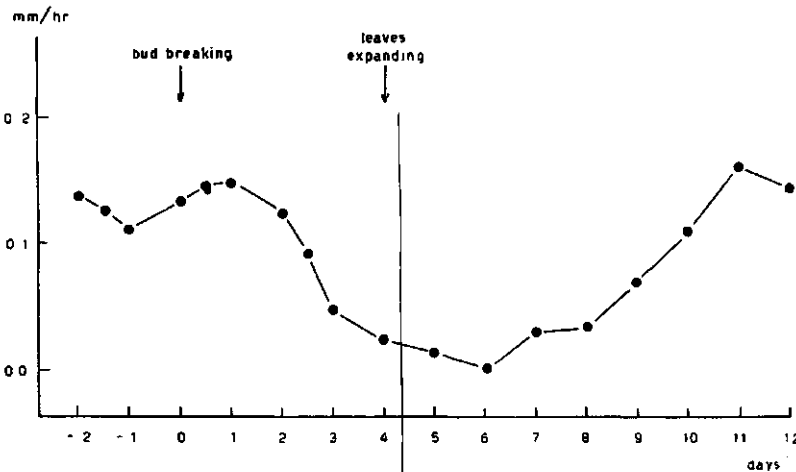


FIG. 15. *Quercus borealis*. The effect of bud expansion on root growth of seedlings with $1\frac{1}{2}$ whorls of fully-expanded leaves, at 5000 lux. Seedlings with acorns detached. The time scale is relative to the time of visible bud swelling

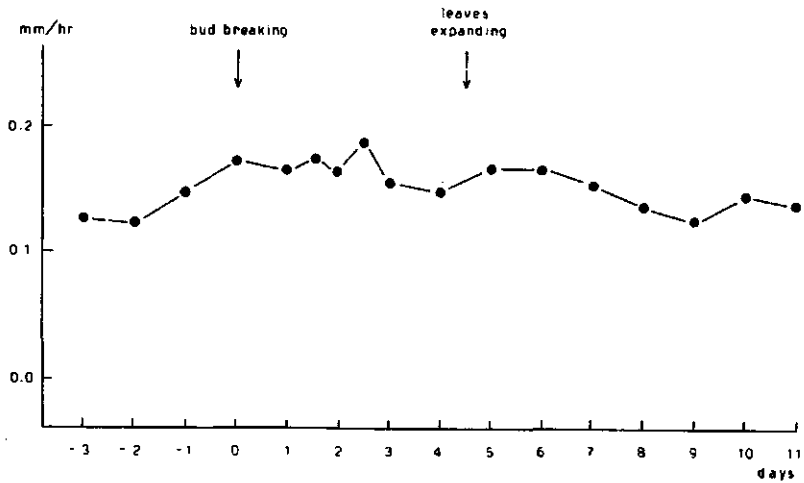


FIG. 16. *Quercus borealis*. The effect of bud expansion on root growth of seedlings with $2\frac{1}{2}$ whorls of fully-expanded leaves, at 5000 lux. Seedlings with acorns attached. The time scale is relative to the time of visible bud swelling

“buffering activity” of the acorn is no longer required to maintain the normal growth rate.

It will be remembered from the experiment in which a low light intensity was imposed just after the expansion of the first terminal bud (Fig. 5), that the root growth rate began to increase about 5 days after bud expansion. In Expt. 12 just described in which a light intensity of 5000 lux was maintained throughout, there was no obvious rise in growth rate before 9 days after bud expansion. The reduction in light intensity, thus, had the effect of reducing the length of the period of

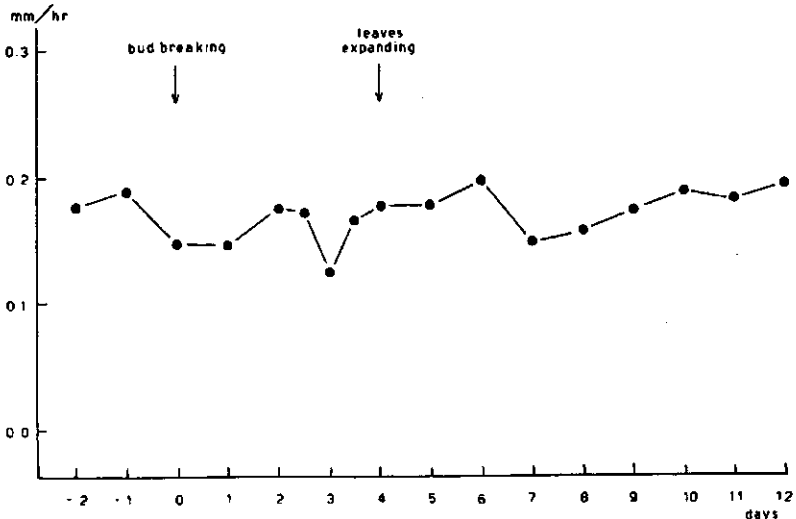


FIG. 17. *Quercus borealis*. The effect of bud expansion on root growth of seedlings with $2\frac{1}{2}$ whorls of fully-expanded leaves, at 5000 lux. Seedlings with acorns detached. The time scale is relative to the time of visible bud swelling

low growth rate resulting from bud expansion in the absence of the acorn. A repetition of the low light experiment confirmed this result and, at the same time, offered an explanation of the reduced duration of low root growth rate. It was found that when seedlings with expanding terminal buds are exposed to a light intensity of 200 lux, leaf expansion stops and does not begin again until a relatively high intensity is resumed. It can be argued that this cessation of leaf expansion will result in an increase in the carbohydrates available for other growth activities in the plant. When root growth is limited by a lack of carbohydrates (as is probably the case with very young seedlings under a low light intensity and without cotyledons) this increase may well result in a temporary increase in growth rate, as was observed in Expt.8.

DISCUSSION

These experiments demonstrate that, physiologically, the differences between *Quercus borealis* and *Acer spp.* are not as great as was at first supposed (10, 7). Although there is no direct relation between photosynthesis and root growth in *Quercus*, the indirect relation via reserve carbohydrates is similar in both species. Thus, in *Quercus* too, there is a linear relation between dry weight and both level and duration of lateral root growth. Again, rate of growth is more closely correlated with root dry weight than with stem weight; but, with regard to duration of growth, the correlations are closest and the regression slopes steepest in the case of stem dry weight.

The most interesting of the experiments, however, are those in which the importance of the acorn was studied. It seems that, under a prolonged low light intensity, the cotyledons play no part in determining the *rate* of root growth but, when seedlings have not expanded more than 2 leaf whorls, they have a big influence on the *duration* of growth. This influence is quantitative, and varies inversely with the dry weight of the seedlings from which the acorns have been removed. Since increase in plant dry weight is accompanied by exhaustion of the acorn, it follows that the influence of the acorn diminishes as it becomes exhausted and it seems reasonable to suppose, that its influence is exercised through the provision of carbohydrates. However, since it has also been concluded that the rate of growth is directly related to the level of reserve carbohydrates, it is not clear why the acorn should have no effect on rate of growth. This apparent inconsistency can be explained if it is assumed that when unfavourable conditions are imposed, the root first exhausts the available reserves in the plant, before broaching those in the acorn. The *level* of growth would then depend solely on the extent of the plant reserves, while the *duration* of growth would be determined by both the plant and the amount contributed by the acorn.

There is evidence, also, that, as might be expected, the carbohydrates of the root system are more readily available for root growth than those of the shoot; this may be concluded from the closer correlation between root growth rate and root weight (Fig. 9) than between root growth rate and shoot weight (Fig. 10). With regard to the duration of growth, however, the relation is closest in the case of shoot weight; and this is in accord with the suggestion that, for root growth, the reserves of the root system are more readily available than those of the shoot. If it is supposed that the root system first exhausts its own reserves before broaching those of the shoot, then the *level* of growth will depend primarily upon reserves in the root, while the *duration* of growth will be determined primarily by the contribution from the shoot system. An alternative explanation

is that, in these experiments, the rate of root growth was limited not by carbohydrate supply but by some other factor not supplied by the acorn. If this were so, however, one would not expect to find such a close relation between root growth rate and plant dry weight.

The following hypothesis would account for the observations reported. *Root growth in first-year seedlings of Quercus borealis depends upon the level of reserve carbohydrates in the root system. When conditions unfavourable for the replenishment of reserves are imposed, available reserves in the root system are first of all exhausted before those in the shoot system are broached; when the shoot system can no longer contribute to root growth, reserves in the acorn are tapped.*

From the experiments specifically designed to test the influence of leaf area on rate and duration of root growth it is clear that there is no obvious relation between these variables (Table 2). In the experiments not so designed, there is evidence of a linear relation between leaf area and both rate and duration of growth. This relation is, of course, indirect and only to be expected. The amount of reserve carbohydrates in a plant is determined by its leaf area; any variable directly related to reserve carbohydrates (e.g. root growth rate and duration) will, therefore, bear an indirect relation to leaf area.

The experiments with seedlings with expanding buds contain several features of interest. It seems that during the expansion of the second leaf whorl, the acorn acts as a buffer between shoot and root growth. Removal of the acorn at this stage results in a reduction in root growth rate, but has no obvious effect on leaf expansion. It follows that leaf growth results from carbohydrates outside the acorn, while root growth at this stage depends upon carbohydrates supplied by the acorn. Now it has already been argued that the root only uses reserves in the acorn when those in the plant are not available. If this is a correct assumption, it follows that shoot expansion effects a change-over from plant reserves to acorn reserves for root growth. It seems, thus, that, as far as reserves in the plant are concerned, the shoot has some priority over their use.

During the expansion of the third leaf whorl, removal of the acorn has no effect on root growth rate. This is unlikely to be because the reserves in the acorn are exhausted, since at the stage of 2 leaf whorls the acorn still has a marked effect on the duration of root growth under continuous low light. More probably the reserves in the plant are sufficient both to maintain the normal rate of root growth and to support shoot growth and leaf expansion; and the buffering activity of the acorn is no longer apparent.

These observations are in accord with the very limited amount of work which has been done previously on the influence of the acorn on the growth of *Quercus* seedlings. For example, KORSTIAN (3) studied the effect on survival and early growth of removing acorns of *Quercus alba* and *Quercus montana* at different stages after germination. This treatment adversely affected root growth relatively more than shoot growth. Thus, removal of the acorn after the leaves had been unfolded for 8 days had virtually no effect on subsequent height increment; and shoot dry weight increment was affected very much less than increase in root dry weight. This finding can be explained by assuming that, in the absence of the acorn, the shoot can successfully compete with the root system for available reserves. EYTINGEN (2) reported upon experiments of NESTEROV who also concluded that the acorn affects root growth more than shoot growth.

The suggestion that reserves in the acorn are only broached when reserves in the plant are no longer readily available and that the acorn may act as a 'buffer',

is in accordance with previous work (1, 3). It is known, for instance, that acorn size is of greatest importance in determining seedlings survival and early growth when conditions are unfavourable to photosynthesis. For seedlings germinated in a grass cover, for instance, survival may be directly correlated with acorn size; for seedlings growing on favourable sites, however, no such relation exists (3). Again, in a grass cover, the exhaustion of the acorn is both rapid and complete; on open sites, on the other hand, complete exhaustion may never occur and the acorn may decay long before it has been fully utilised by the seedling.

SUMMARY

This paper describes a study of root elongation rates in first-year seedlings of *Quercus borealis maxima* (MARSH) ASHE, raised under conditions of constant temperature (20°C), light intensity (5000 lux), daylength (16 hours per cycle) and relative humidity (69–75%), and then subjected to a light intensity of 200 lux. This reduction in light intensity resulted in a reduction in root growth rate between 15 and 25 days after the intensity change. Both the rate and duration of growth are linearly related to plant dry weight. Experiments with partially defoliated seedlings demonstrated that there is no direct relation between these variables and leaf area.

In a few experiments, seedlings were grown under a light intensity of 200 lux and the effect of removing the acorn was studied. Removal of the cotyledons had no effect on the rate of root elongation, but the duration of growth was reduced by up to 10 days, the extent of the reduction varying inversely with seedling dry weight. Root growth rate under these conditions was more closely related to root dry weight than to shoot dry weight, but duration of growth was most closely correlated with shoot weight. These observations can be explained by assuming that root growth depends primarily upon the level of reserve carbohydrates in the root system; when conditions unfavourable for the replenishment of reserves are imposed, available reserves in the root system are first exhausted before those in the shoot are broached; and when the shoot system can no longer contribute to root growth, reserves in the acorn are tapped.

It was observed that, at a light intensity of 5000 lux and in seedlings which have lost their cotyledons, the expansion of the second leaf whorl is accompanied by a fall in root growth rate; no such drop was recorded in seedlings with cotyledons intact. From this it was concluded that the shoot can successfully compete with the root system for available reserves, and that the acorn can act as a buffer between leaf expansion and root elongation. During the expansion of future leaf whorls no changes in root elongation rate occurred and the buffering capacity of the acorn appears to be no longer necessary.

It was also found that a change in light intensity from 5000–200 lux during the expansion of the second leaf whorl results in a temporary increase in root growth rate. The reduction in light intensity also inhibits leaf expansion and, presumably, this cessation of leaf expansion results in an increase in the availability of carbohydrates for root growth.

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