

ROOT GROWTH OF *ACER PSEUDOPLATANUS* L. IN RELATION TO GRASS COVER AND NITROGEN DEFICIENCY

by

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(Received 5.11.'53)

CHAPTER I

INTRODUCTION AND EXPERIMENTAL METHODS

§ 1. Introduction

In the course of a study of grass and tree seedling interaction, information was required concerning the growth rates of roots of sycamore (*Acer pseudoplatanus* L.) under various environmental conditions. In this paper observations on the effects of a grass cover and deficient nitrogen on the development of sycamore seedlings are reported.

The study of growing roots presents obvious difficulties and no entirely satisfactory method has yet been evolved. Excavations are laborious and inadequate, in that they result in the destruction of the root system, thus preventing further recording. In addition, the small absorbing roots may be lost by such treatment. Destruction of the roots can be avoided by the use of water cultures for growing plants but, obviously, results obtained in this way can be applied to field conditions only with the greatest reserve. In a study of competition effects it has serious limitations.

Investigators, since the time of SACHS, have attempted to overcome these difficulties by constructing observation boxes in which the roots grow against a glass panel, which forms the front of the box. Thus, root growth can be observed without destroying the plants or removing them from their environment. BÜSGEN (4) and ENGLER (6) were among the earliest to use devices of this kind for the study of tree roots. DEAN (5) and SCHINDLER (17) both constructed large glass fronted observation boxes, but full reports of their results are lacking. At East Malling, ROGERS did much work on apple tree root systems, in large trenches sited close to the trees to be studied and equipped with small glass windows. A preliminary report on methods was published in 1934 (12) and a discussion of the results obtained over a 4-year period appeared in 1939 (14). ROGERS (13) also gives an extensive summary of the literature relating to root growth investigations.

At Wageningen, BLAAUW (3) constructed a large root-observation chamber in the grounds of this Laboratory, and used it for some qualitative studies of the roots of herbaceous plants. In common with numerous other workers with

such chambers, however, no full report of investigations has been published.

It seemed, nevertheless, that a study of tree roots growing in grass might profitably be undertaken in this observation chamber. The original intention was to perform a series of short-term experiments to determine the effect of withholding and then supplying various nutrients and water on the growth rate of sycamore roots. It was with this aim in view that the beds over the chamber were planted. It was found, however, that root growth rate could not be measured satisfactorily over short periods, and the experimental material was used for a semi-quantitative study of the growth of seedling roots under conditions of nitrogen deficiency and grass competition (cf. also § 9).

§ 2. Experimental Methods and Design

The root observation chamber has been described by BLAAUW (3). Briefly, it comprises an underground chamber, 2 m. high, $1\frac{1}{2}$ m. wide, and $3\frac{1}{2}$ m. long, built of ferro-concrete. The side walls consist of glass plates, 2 cm. thick, resting in rubber frames, and sloping at an angle of 70° . The top of the glass panel is 20 cms. below ground level and the bottom is divided, by ferro-concrete panels, into three seed beds each 1×2 m. On one side of the chamber, the bottoms of the beds are closed and each is fitted with a square concrete funnel extending to the base of the bed. This enables the water-table to be controlled by sub-irrigation. The other side does not have these facilities. The chamber is fitted with electric light and is entered by light-proof doors.

A factorial design of two nitrogen levels \times three grass levels was set out on the six plots (seed-beds) and four 3-year sycamore transplants were planted in each plot, close to the glass wall. The grass used was *Lolium perenne* L., perennial rye-grass. The choice of sycamore was dictated by the fact that it had been used in previous experiments and it was known to find difficulty in growing in grass; perennial rye-grass was used because it produces a dense mass of roots in a short period.

On March 8th, 1951, the seed-beds were filled with coarse gravel to a depth of 105 cms. and the remainder with washed quartz sand. Grass (all of one clone) was planted on four of the beds as follows: On two beds, 7 rows of 12 tufts were planted parallel to the glass face ($\frac{1}{2}$ -grass) and on the other two, 14 rows of 24 tufts per row (1-grass). Each tuft comprised about 4 tillers, and had resulted from single tillers planted in May, 1950. The remaining two beds were left grassless (0-grass). Four evenly-matched sycamore transplants were planted 15 cm. from the glass

Composition of nutrient solution used.

Solution I (Nitrogen deficient)	mg/litre	p.p.m.
MgSO ₄ ·7H ₂ O	355	Mg 35
KH ₂ PO ₄	522	K 150
		P 119
Ca (NO ₃) ₂ ·4H ₂ O	441	Ca 75
		N 52
<i>Traces:</i>		
Ferric citrate	0.03	
H ₃ BO ₃	0.003	
MnCl ₂ ·4H ₂ O	0.002	
ZnSO ₄ ·7H ₂ O	0.0002	
CuSO ₄ ·5H ₂ O	0.0001	
H ₂ MoO ₄ ·H ₂ O	0.001	
<i>Solution II (+ Nitrogen)</i>		
As solution I, plus: NH ₄ NO ₃	601	N 210

panels in all beds. Thus about half of each bed formed a plot measuring 1×1 m. In the remaining space in each bed, two reserve seedlings were planted.

All the plots were watered when necessary and every three days were given nutrient solution. Two solutions were employed, one containing all the essential elements, the other deficient in nitrogen, as indicated in the accompanying table.

In each case the solution was supplied at a rate of three litres every three days. Since the sub-irrigation facilities applied to three plots only, water and nutrient solution were applied from above ground. The water-table was maintained at the same level in all plots (130 ± 5 cms. below the surface).

By 2nd May, one seedling in each of the grassed, + nitrogen plots had died and these were replaced on that date. On June 4th the plots were examined again and shoot growth was measured, a leaf count made, and a leaf-colour assessment made by an independent observer. Slight damage to 2 trees on the grassless, nitrogen deficient plot by *Apatete aceris* L. was noticed and the caterpillars were removed.

Shoot growth was measured fortnightly throughout the season. Tree root growth was recorded by fortnightly tracings on to cellophane with a chinagraph pencil: at the end of the study these tracings were transferred to drawing paper and then photographed. Observations on the life-history of the root systems were made weekly, and similar records were kept of grass root growth. The abundance of grass roots in the upper parts of all the windows, however, made it impossible to make tracings of all visible grass roots as was done for the trees. It was decided, therefore, to trace three sample squares, 15×15 cms., on each window every fortnight. To bring out plot growth differences, the squares were sited at the lower levels; the first from 94 to 109 cms., the second, from 109 to 124 cms., and the third, from 124 to 139 cms. The lateral displacement of each square was determined randomly at each sampling. The microscope used for measuring root dimensions is equipped with a moving cross-wire and is theoretically accurate to 0.1μ . A 20 watt electric bulb only, was used to observe the roots, and exposure to this was less than forty minutes per week. This was done in view of ROGERS' (15) findings that direct exposure to light adversely affects root growth and increases the rate of suberization.

On 12th August, a mole entered two of the nitrogen deficient plots and deranged most of the roots against the glass panels. The study was, therefore, concluded on this date, the sycamore root systems washed out and roots and shoots oven-dried and weighed. It was, unfortunately, not possible to harvest the grass.

CHAPTER II

EXPERIMENTAL RESULTS

It is convenient first to describe the form of roots seen in the observation chambers, and then to deal with the effects of grass and nitrogen deficiency on root size, form of the root system and growth throughout the season.

§ 3. Appearance of the roots

a. Tree roots. All the roots visible against the glass panels were, in fact, laterals, but for purposes of description they have been divided into main roots and laterals. Main roots were easily distinguishable by their size and colour but there was no clear-cut difference between first-order and second-order laterals. Consequently, roots were only designated second-order laterals when they could be seen leaving first-order roots.

Main roots were white in colour and succulent. Tapering started about 1 cm. before the root cap and the root tip terminated in a mass of dead cells which were sloughed off as the root moved through the soil. Occasionally, larvae of a *Collembola* species and nematodes were observed at the root tips, apparently feeding on these dead cells. Few root hairs were recorded on these roots, but the figures cited later must be accepted with caution. In order that root systems should be exposed to the light as little as possible, a systematic search for root hairs was not made, and they were recorded only when seen in the course of root measurements.

Between the age of 2 to 4 weeks, suberization started. Root hairs shrivelled and the cortex turned brown. In some cases this colouration progressed from the basal end of the root down towards the tip and, in others, it appeared in patches throughout the length of the root which eventually joined up. It is presumed that at this stage the root was no longer capable of absorbing (18). After suberization, the cortex shrivelled and secondary thickening was put on.

First-order lateral roots were a translucent grey in colour and lacked a pronounced root cap. The root tip, however, was darker in colour than the body of the root and was opaque. Root hairs were abundant and grew in a zone about 0.5–2.0 cm. long just behind the root tip (Plate I). Suberization of laterals was seen only in the largest trees and seldom started before the age of 5 weeks. Usually (though by no means invariably) suberized roots persisted.

Second-order laterals were similar in appearance to first-order laterals, but they never persisted and were never suberized. This last observation is in contrast to that of ROGERS regarding rootlets of apple trees. He observed that the small laterals did not rot away until after suberization. First and second-order laterals were observed to emerge from both white and suberized roots, upwards of a fortnight after the development of the main roots.

Young root hairs were translucent and white in appearance, but turned yellow as they became older and shrivelled after about a week.

ROGERS records 'a copious exudation from the older root hairs', the precise nature of which he did not determine. A similar phenomenon was observed during the present study but on all root hairs, irrespective of age. During the course of some later experiments (20) photomicrographs of roots growing in a gravel culture were taken and the same observation was made. The globules on the root hairs can be seen in Plate I. There appears to be no real evidence for regarding these globules as root hair exudates, and no reason to suppose that they are not merely drops of water condensed on the root hair. ROGERS discards this suggestion on the grounds that, in the early stages, the globules form at the extreme ends of the root hairs; this, however, seems to be no real objection to the condensation theory, since in a mass of root hairs it seems probable that the tips are at a lower temperature than the bases (at any rate, if there is any air movement) and, therefore, most likely to condense water vapour.

It appeared from observations confined to lateral roots that root hairs formed when the growing root was about 0.6–0.8 mm. long. The young root elongates, however, at a faster rate than that of root hair formation. Thus, at 2 mm. in length, the terminal 1 mm. was clear of root hairs; at 6 mm., the root hair zone was about 3 mm. behind the root tip.

b. Grass roots. Main roots (including adventitious roots) and first-order laterals were observed. Both types were white in colour and opaque. Root hairs were abundant on all lateral roots, but especially so on those roots which grew into the gravel below the sand. The root hair zone extended from about 2 cm. behind the root tip to 4 cms, but the density of hairs was considerably less than in tree roots. Lateral roots, too, were abundant in the gravel region, especially at the junction of the sand and gravel. Grass roots did not, of course, suberize in the same way as the tree roots. It was noticed that at the age of about 2 weeks they became grey-brown in colour, but did not lose their root hairs.

§ 4. *The effect of a grass cover and a nitrogen deficiency on root dimensions*

From 12th–16th June, 1951, samples of all roots were measured; mean diameter (the mean of three measurements made at intervals along the root), mean diameter of suberized root, number of root hairs per cm. run in the root hair

zone, and length of root hairs (mean of five measurements) were recorded. These data are summarised in Table 1 for tree roots and in Table 2 for grass roots. Tree seedlings growing in the nitrogen deficient plots had smaller roots and a reduced density of root hairs. This last effect was also brought about by a grass cover. It will be noticed, too, that suberization was accompanied by a reduction in diameter of up to 50% and this is in accord with ROGERS' observations for apple tree roots.

Grass roots showed no apparent plot differences either in root size or density of root hairs.

TABLE I

The effect of grass and nitrogen level on tree root size. Mean dimensions of tree roots, recorded 12-16th June, 1951

Plot	Main Roots					Laterals		
	Number of roots measured	Mean diam. unsubs. mm.	Mean diam. subs. mm.	Number of root hairs per cm.	Mean length of r. hairs. cm.	Mean diam. mm.	Number of root hairs per cm.	Root hair length cm.
1-grass, N.Def.	2	0.80	0.40	110	0.31	0.26	302	0.29
1-grass, + N.	16	1.10	0.68	152	0.29	0.30	356	0.33
$\frac{1}{2}$ -grass, N.Def.	13	1.18	0.71	130	0.40	0.43	231	0.26
$\frac{1}{2}$ -grass, + N.	12	1.26	—	158	0.43	0.53	237	0.37
0-grass, N.Def.	20	0.89	0.45	141	0.35	0.37	183	0.31
0-grass, + N.	25	1.00	0.79	161	0.34	0.45	282	0.33
<i>Mean Plot*</i>								
1-grass	9.0	1.03	0.54	131	0.30	0.28	233	0.31
$\frac{1}{2}$ -grass	12.5	1.22	0.71	144	0.42	0.48	234	0.32
0-grass	22.5	0.95	0.62	151	0.33	0.41	326	0.32
N. Def.	11.7	0.96	0.52	127	0.35	0.35	239	0.28
+ N.	17.7	1.13	0.74	157	0.35	0.43	290	0.34

* The "mean plot" data give measures of the effects of grass and nitrogen respectively. Each of the values for grass levels is the mean of the two plots similarly treated with respect to grass, and without regard to the nitrogen treatments. The nitrogen mean plot values are means of 3 plots treated similarly with respect to nitrogen, and without regard to the grass levels.

§ 5. Growth of tree roots throughout the season

a. Root elongation and form. The grass roots on all plots had appeared against the glass panels by April 5th. — three weeks before any tree roots were visible. This was in spite of the tree seedlings having been planted with the bulk of their roots well below the level of the grass roots.

By June 14th, the date of the first root tracings, the panels below the grassed plots showed abundant grass roots to a depth of 116 cm. It had not been foreseen that any roots would

TABLE 2

The effect of a nitrogen deficiency on grass root size. Mean dimensions of grass roots, recorded 12th-16th June, 1951.

Plot	Number of roots measured	Main Roots			Laterals		
		Mean diam. mm.	Number of root hairs per cm.	Root hair length cm.	Mean diam. mm.	Number of root hairs per cm.	Root hair length cm.
1-grass, N. Def.	20	0.37	None seen	—	0.19	49	0.47
1-grass, + N.	20	0.42	None seen	—	0.19	54	1.05
$\frac{1}{2}$ -grass, N. Def.	20	0.43	32	0.28	0.28	59	0.94
$\frac{1}{2}$ -grass, + N.	20	0.40	38	0.28	0.18	63	0.88
<i>Mean plot</i>							
1-grass	20	0.40	—	—	0.19	52	0.76
$\frac{1}{2}$ -grass	20	0.42	35	0.28	0.23	61	0.91
N. Def.	20	0.40	32	0.28	0.24	54	0.71
+ N.	20	0.41	38	0.28	0.19	59	0.97

penetrate the gravel surface during one season, but unfortunately this had already occurred. Although it made the study of individual roots easier it was unfortunate in that the growth medium could not be regarded as constant; and observed differences between roots growing in sand and those in gravel were difficult to interpret. For example, it seemed that lateral roots and root hairs were more abundant in the gravel layer than in the soil. This may have been an illusion due to their not being visible in the sand; or it may have been a real difference, in which case there was no way of telling to what extent the vigour of the grass was enhanced by this increased absorbing surface. In no case did tree roots reach this depth.

Root tracings of the most extensive root system in each plot are represented in Figs. 1-6, and the principal measurements taken from the tracings are tabulated (Table 3); in Figs. 7 and 8 visible growth throughout the season is represented by mean total root length. In Tables 4 and 5, mean maximum rooting depths, mean lateral spread and the principal rooting depth, on the dates of the first and last tracings are tabulated.

Under the conditions of these experiments, length of visible root is a better index of growth than the number of roots; the latter is unreliable in that the same root may be counted several times, because of the tendency to grow away from the glass panel for a short distance and then reappear.

Turning to Figs. 7 and 8, it can be seen that the effect of a grass cover on root growth was more marked than that of nitrogen deficiency. Not only was the growth rate depressed but, with one exception, the period of active growth was shortened. On the grassless plots there was no sign of a diminishing growth rate by August 9th, whereas on most of the grass plots growth began to fall off by June 28th. It is seen that the full-grass + nitrogen plot displayed a higher growth rate than the corresponding half-grass plot. This appeared to be due, largely, to one tree which had replaced a dead one on 2nd May. Since it seemed

that the disproportionate contribution of this tree to the mean values might be due to its grass-free start, these values have also been plotted without it (broken line).

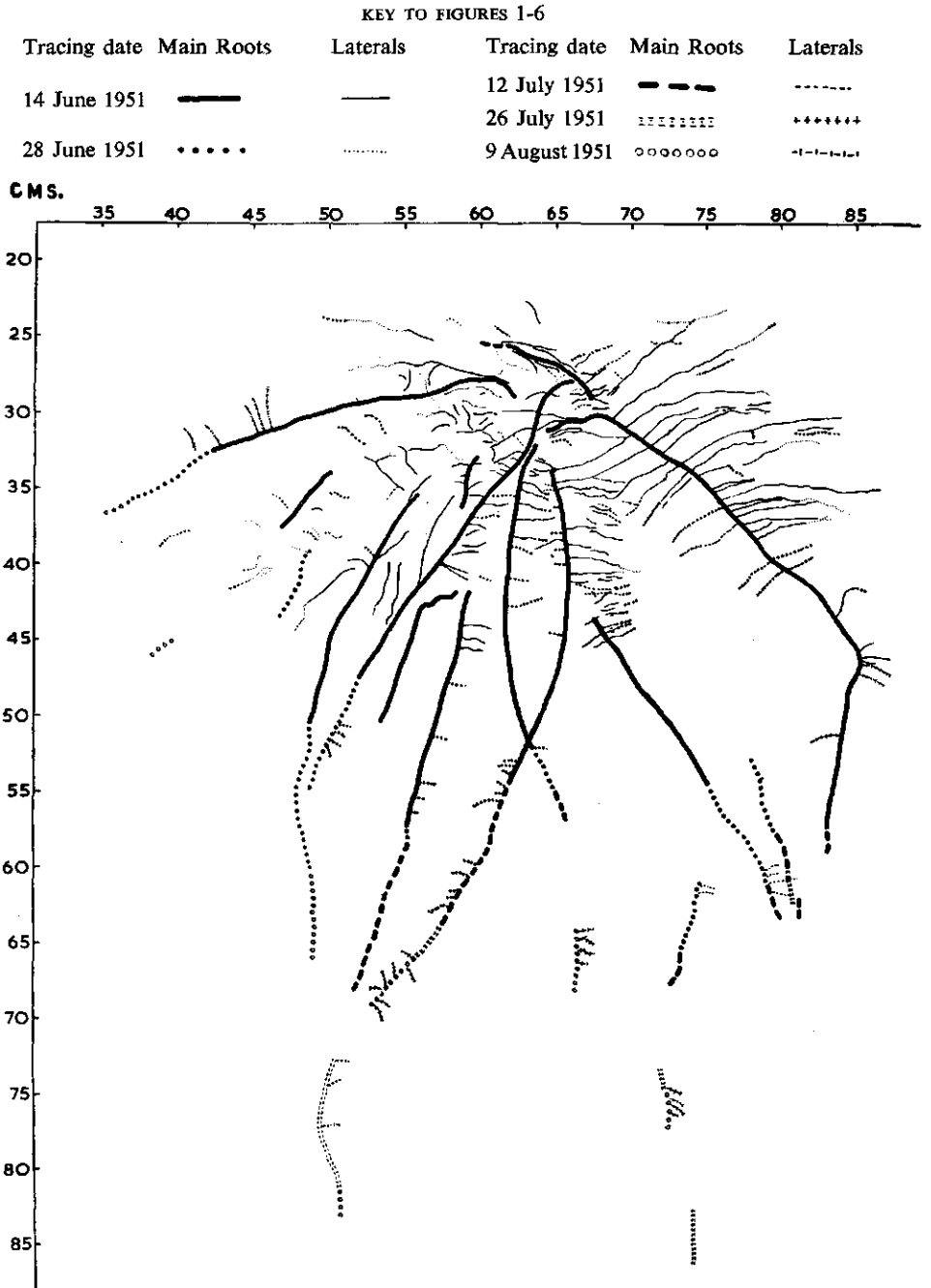
The effect of grass was of the same nature for both main roots and laterals, but it was more marked on laterals than on main roots (Table 3).

TABLE 3

Growth in length of sycamore roots as seen in the root observation chamber June 14 to August 9, 1951. Plot means in cms.

Plot		14.6.51	28.6.51	12.7.51	26.7.51	9.8.51
Full-grass, N. Deficient	Mains	2.0	3.1	4.8	12.4	15.4
	Laterals	2.1	3.0	3.6	4.1	4.5
	Total	4.1	6.1	8.4	16.5	19.9
Full-grass, + Nitrogen	Mains	38.8	71.6	81.6	89.7	94.3
	Laterals	10.9	21.2	26.4	34.5	34.5
	Total	49.7	92.8	108.0	124.2	128.8
Half-grass, N. Deficient	Mains	41.6	59.7	68.7	75.5	79.1
	Laterals	4.1	15.0	20.9	22.4	24.4
	Total	45.7	74.7	89.6	97.9	103.5
Half-grass, + Nitrogen	Mains	35.5	56.9	71.3	80.5	93.7
	Laterals	8.5	12.1	19.6	36.1	39.7
	Total	44.0	69.0	90.9	116.6	133.4
Grassless, N. Deficient	Mains	63.0	105.5	129.1	149.2	164.4
	Laterals	62.5	89.1	116.2	160.2	191.5
	Total	125.5	194.6	245.3	309.4	355.9
Grassless, + Nitrogen	Mains	91.3	121.1	138.1	158.9	170.5
	Laterals	108.6	146.4	168.7	207.2	227.3
	Total	199.9	267.5	306.8	366.1	397.8

Figs. 1-6. Photographs of the most extensive root tracing in each plot of the observation chamber, taken at the end of the experiment.



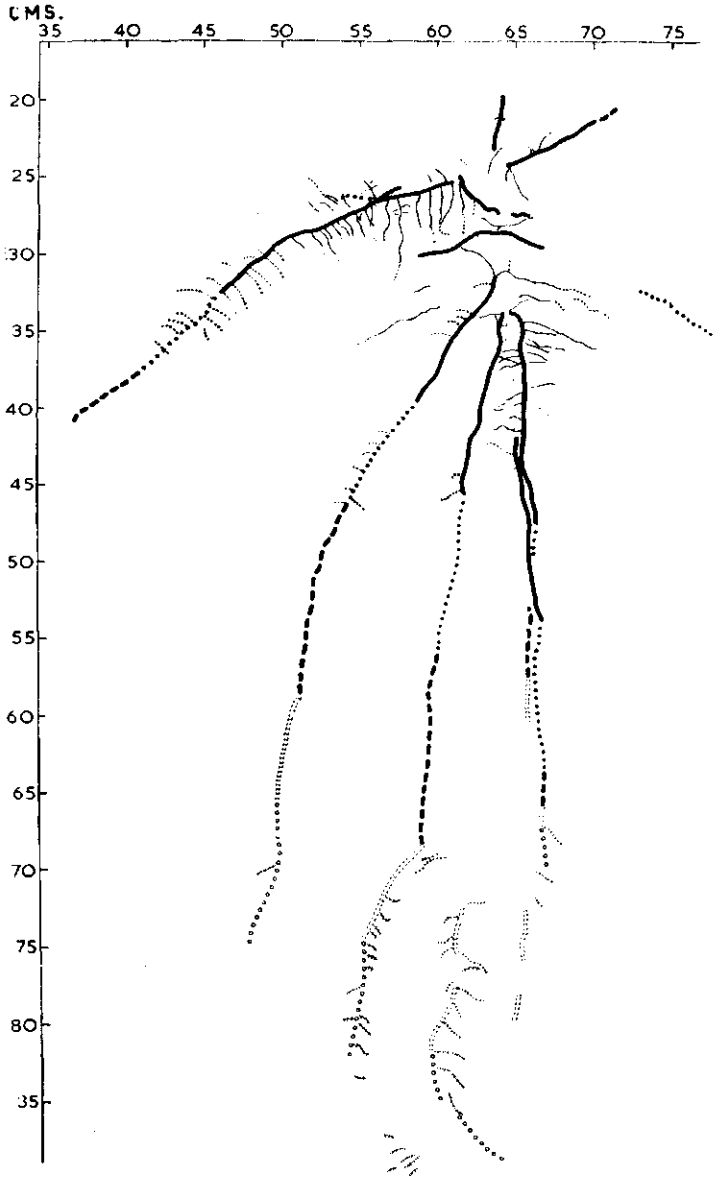


Fig. 2. Grassless, nitrogen deficient.

The influence of nitrogen level is less clear. On grass-free plots, the low nitrogen level had the effect of reducing the amount of growth, but there was no difference in rate of growth between the two levels. The effect of nitrogen deficiency, therefore, was either to depress the initial growth rate or to delay the start of active growth. On full-grass plots there was evidence that the first alternative was the correct one. The majority of the nitrogen deficiency effect was, on grass-free plots, on lateral roots. On full-grass plots a marked difference in main root growth at the two nitrogen levels was observed, but not in lateral root growth;

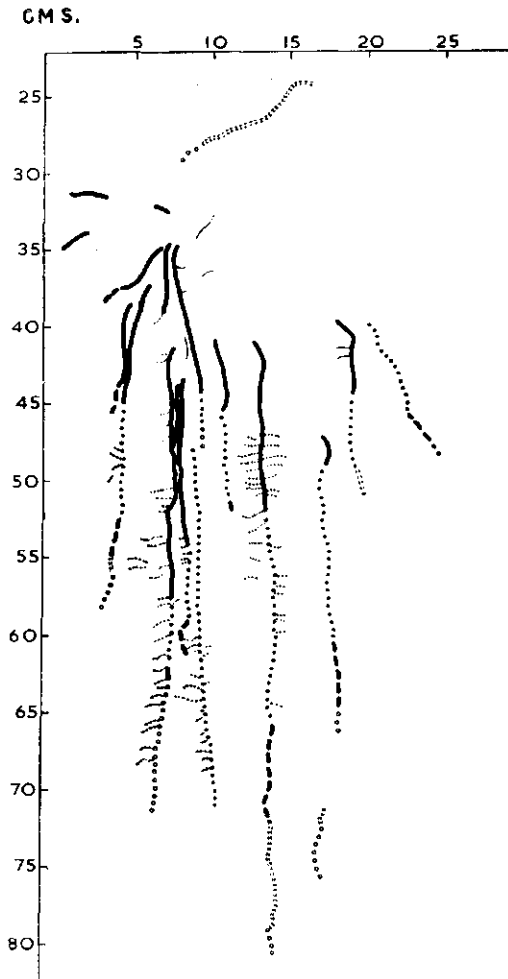


Fig. 3. Half-grass, + nitrogen.

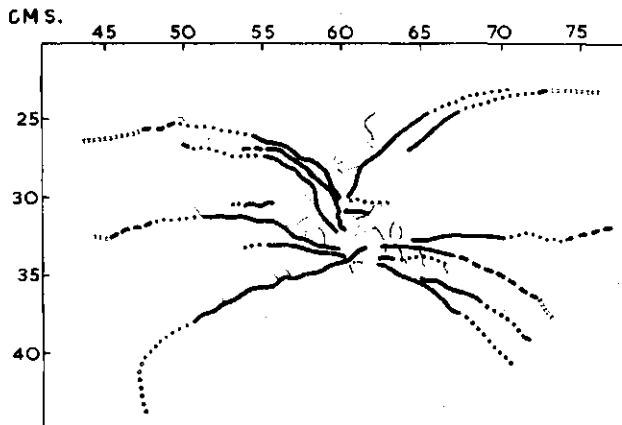


Fig. 4. Half-grass, nitrogen deficient.

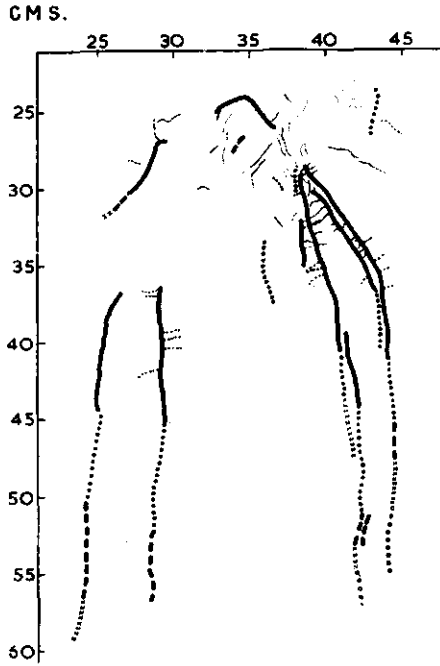


Fig. 5. Full-grass, + nitrogen.

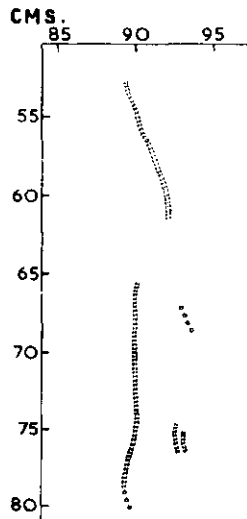


Fig. 6. Full-grass, nitrogen deficient.

on half-grass plots the influence was of the same nature for both main roots and laterals. It was found later that the influence of nitrogen on full-grass plots was not as great as that observed. Harvesting ¹⁾ showed that a much lower propor-

¹⁾ See Table 7.

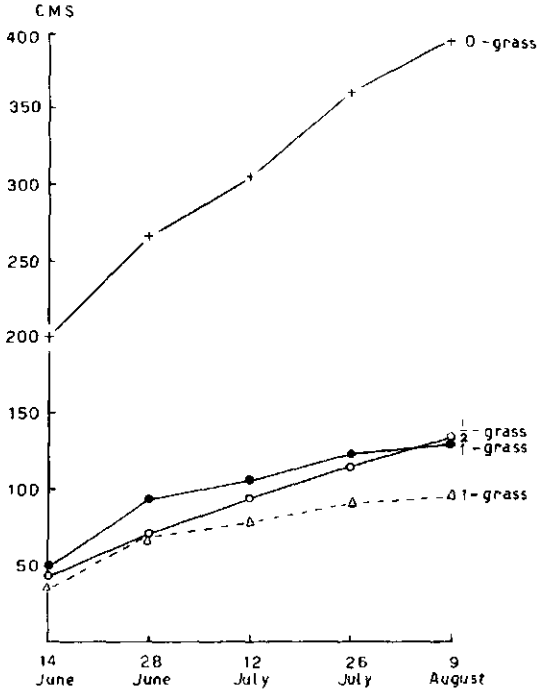


Fig. 7. The influence of grass level on the elongation of sycamore roots. Mean total root length as seen in the root observation chamber, 14 June-9 August. Plots with added nitrogen. + --- + = 0-grass; o --- o = 1/2-grass; • --- • = 1-grass; Δ --- Δ = 1-grass, less tree no 18.

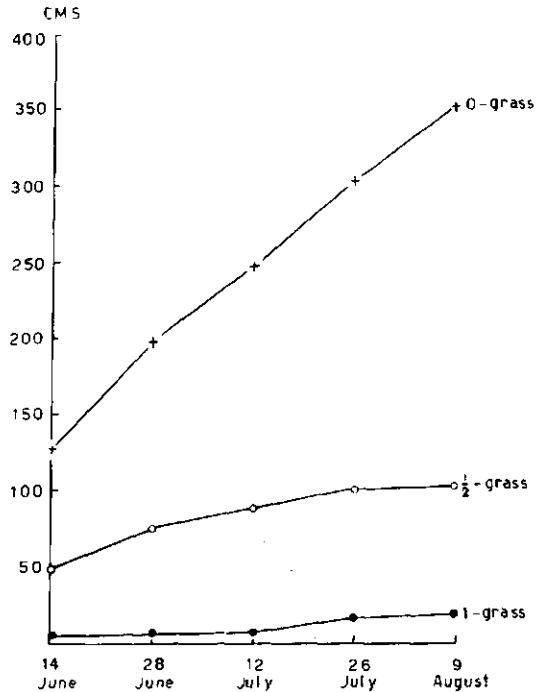


Fig. 8. The influence of grass level on the elongation of sycamore roots. Mean total root length as seen in the root observation chamber, 14 June-9 August. Plots deficient in nitrogen. + --- + = 0-grass; o --- o = 1/2-grass; • --- • = 1-grass.

tion of main roots was visible on the nitrogen deficient full-grass plot, than on any other plot. Thus, on both half-grass and full-grass plots the effect of nitrogen was probably of the same nature on both main roots and laterals.

No material differences between nitrogen levels were seen in any of the factors recorded in Tables 4 and 5. There was some relation between nitrogen level, maximum rooting depth and horizontal spread on June 14th, but by the end of the season such a relation had largely disappeared. Grass, on the other hand, consistently restricted rooting depth and lateral spread. The difference between full-grass and half-grass plots was less than that between half-grass and grassless plots.

TABLE 4

The effect of grass and nitrogen level on sycamore root system size. 14th June, 1951. Plot means in cms.

Plot	Max. depth main Roots	Max. depth laterals	Lateral spread all roots	Principal rooting depth main roots	Principal rooting depth laterals
1-grass, N. Def.	40.9	31.6	3.3	40	28
1-grass, + N.	52.0	46.1	12.1	44	42
$\frac{1}{2}$ -grass, N. Def.	31.1	45.9	13.4	42	43
$\frac{1}{2}$ -grass, + N.	39.6	45.5	13.7	39	41
$\frac{1}{4}$ -grass, N. Def.	49.3	42.2	18.4	36	33
0-grass, + N.	49.2	40.3	23.2	39	32
<i>Mean Plot</i>					
1-grass	46.5	38.9	7.7	42	43
$\frac{1}{2}$ -grass	35.4	45.7	13.6	41	42
0-grass	49.3	41.3	20.8	38	33
N. Def.	40.4	39.9	11.7	39	35
+ N.	46.9	44.0	16.3	41	38

b. The rate of suberization. Since the unsuberized part of the root is the result of past and current growth, the ratio $\frac{\text{unsuberized root length}}{\text{new growth}}$ gives an approximate measure, in terms of the recording interval, of the mean rate of suberization over the period of the experiment (14).

In Table 6, this ratio is shown against plots with the time in weeks. Each term of the ratio is the mean of four values (corresponding to the last four recording dates).

The rate of suberization was not markedly affected, apparently, by either grass or nitrogen level. The values in this Table are somewhat higher than those found by ROGERS for apple tree roots (14). Part of this difference may be due to differences in the time of exposure to light during measurements.

TABLE 5

The effect of grass and nitrogen level on sycamore root system size. 9th August, 1951. Plot means in cms.

Plot	Max. depth main roots	Max. depth laterals	Lateral spread all roots	Principal rooting depth main roots	Principal rooting depth laterals
1-grass, N. Def.	58.8	40.0	9.1	49	38
1-grass, + N.	63.8	55.2	14.2	45	44
$\frac{1}{2}$ -grass, N. Def.	61.2	62.2	17.7	43	44
$\frac{1}{2}$ -grass, + N.	63.8	55.2	14.2	45	44
0-grass, N. Def.	83.1	80.3	31.3	46	44
0-grass, + N.	79.4	77.6	30.3	45	37
<i>Mean Plot</i>					
1-grass	61.3	47.6	11.7	47	41
$\frac{1}{2}$ -grass	62.5	58.7	15.9	44	44
0-grass	81.3	79.0	30.8	46	40
N. Def.	67.7	60.8	16.0	46	42
+ N.	69.0	62.7	19.6	45	42

c. Harvesting data. It is apparent that unless the proportion of visible roots to actual roots is fairly constant for all plots, results obtained by this method of study are meaningless. A measure of the reliability of the method was obtained when the seedlings were harvested. Unfortunately, only main roots could be measured. The ratio $\frac{\text{mean length of actual main roots}}{\text{mean length of visible main roots}}$ is given in Table 7, together with oven-dry weights of all roots.

It can be seen that with regard to this ratio the values are fairly constant with the exception of the full-grass, nitrogen deficient plot and the grassless + nitrogen plot. The higher ratios for these two plots indicate that the observed values were too low, as compared with the other plots. The fact that root length on the full-grass, nitrogen deficient plot was under-estimated, reduces the effects of both grass and nitrogen deficiency as derived from the observation of visible roots; the fact that in the grassless, + nitrogen plot the root length was also underestimated increases these effects. The magnitude of the effects is such that it does not affect any of the conclusions reached.

The oven-dry weight data show similar plot differences to those of the final root tracing and suggest that same conclusion. Again, the full-grass, + nitrogen plot mean weight was unduly influenced by the dead tree replacement.

The ratio $\frac{\text{mean length}}{\text{mean dry weight}}$ is of interest since it compares length and dry weight as indices of growth. Table 7 shows that both nitrogen deficiency and a

TABLE 6

The effect of grass and nitrogen level on rate of suberization of sycamore roots. Ratio unsuberized root length / new growth and time of suberization. Main roots only.

Plot	Unsuberized root New growth	Suberization time in weeks
1-grass, N. Def.	1.26	2.52
1-grass, + N.	1.97	3.94
$\frac{1}{2}$ -grass, N. Def.	1.83	3.66
$\frac{1}{2}$ -grass, + N.	1.93	3.86
0-grass, N. Def.	2.07	4.14
0-grass, + N.	1.70	3.40
<i>Mean Plot</i>		
1-grass	1.62	3.24
$\frac{1}{2}$ -grass	1.88	3.76
0-grass	1.89	3.78
N. Def.	1.72	3.44
+ N.	1.87	3.74

TABLE 7

A comparison between actual and observed root length; and harvesting data. Plot means.¹

Plot	ML, MR (actual) ¹	Main Roots (actual)				Lateral Roots (actual)	All Roots (actual)
	ML, MR (observed)	Num- ber	Mean length cms.	Mean dry wt. gms.	Length Dry wt.	Mean dry wt. gms.	Total root dry wt. gms.
1-grass, N. Def.	7.22	5.50	118.9	0.86	138.26	1.51	2.37
1-grass, + N.	3.50	10.75	329.8	2.45	134.61	2.42	4.87
$\frac{1}{2}$ -grass, N. Def.	3.54	8.75	279.7	2.03	137.78	1.82	3.85
$\frac{1}{2}$ -grass, + N.	3.49	13.00	327.1	2.40	136.29	2.51	4.91
0-grass, N. Def.	3.39	15.75	558.0	6.49	85.98	4.56	11.05
0-grass, + N.	4.49	24.50	765.5	9.26	82.67	10.20	19.46

¹ ML, MR = mean length, main roots.

grass cover effect an increase in this ratio, which means that length is less affected by a grass cover and by a nitrogen deficiency than is dry weight – as has previously been demonstrated for shoots (2). However, in studies of root interaction, dry weight has a limited value; form and extent of the root system are equally, if not more, important.

To sum up, it would appear that the main effect of a nitrogen deficiency is to reduce the size of the root system, but not to affect its form. Grass, however, modifies size, form and rate and pattern of growth.

§ 6. Grass root growth

The data collected on the growth of grass roots throughout the season are summarised in Figs. 9, 10 and 11. No record of the number of roots in each panel is given since this would give a false impression of root growth. It was observed in the gravel layer that the grass roots meandered considerably. In the sand, this twisting could not be seen, but the large number of short root lengths visible in the panels suggested that it was present here, too, and that several of lengths seen belonged to the same root. Root number, therefore, was merely an index of twisting and since this did not appear to be associated with nitrogen level, it has not been given.

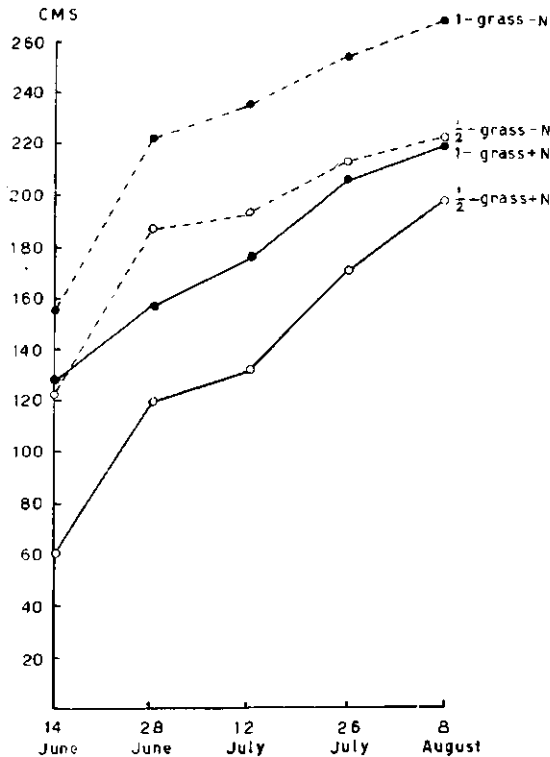


Fig. 9. The influence of nitrogen deficiency on the elongation of grass roots. Total length of roots in cm., visible in a 15×15 cm. square sited at depth 94–109 cm., in the root observation chamber, 14 June–8 August. ● = 1-grass; ○ = $\frac{1}{2}$ -grass. Broken line = nitrogen deficient; solid line = plus nitrogen.

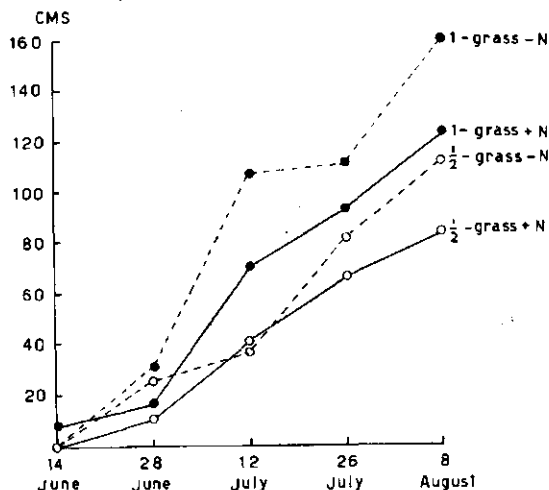


Fig. 10. The influence of nitrogen deficiency on the elongation of grass roots. Total length of roots in cm., visible in a 15×15 cm. square sited at depth 109-124. cm., in the root observation chamber, 14 June-8 August. • = 1-grass; o = $\frac{1}{2}$ -grass. Broken line = nitrogen deficient; solid line = plus nitrogen.

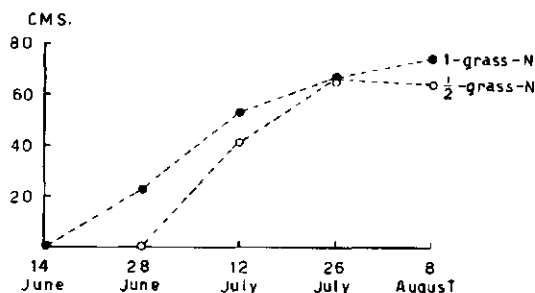


Fig. 11. The influence of nitrogen deficiency on the elongation of grass roots. Total length of roots in cm., visible in a 15×15 cm. square sited at depth 124-139 cm., in the root observation chamber, 14 June-8 August. • = 1-grass; o = $\frac{1}{2}$ -grass. Broken line = nitrogen deficient; solid line = plus nitrogen.

From Figs. 9, 10 and 11, it can be seen that at all levels there was a marked positive correlation between amount of root and nitrogen deficiency. Rates of growth of the nitrogen deficient roots were higher than those of the + nitrogen roots at the beginning of the season, but there was little difference by the end of the experiment. At the two uppermost levels, growth was still vigorous at this time, but at the lowest level - reached by nitrogen deficient roots only, in the tracings - the growth curve was beginning to flatten off.

Main roots formed the majority of the root length observed and, in general, their growth pattern followed that of the total. Differences in lateral root growth were conspicuously small, but the order of plots was again similar to that of total growth. Growth rates were lower than those of main roots, and fell off earlier.

Maximum rooting depth on all plots is tabulated in Table 8. Differences are

in accord with the growth curves in that maximum depth increased with decreasing nitrogen.

It seems, from these results, that the effect of nitrogen level on the extension of grass roots was exactly opposite to its effect on tree roots, in that grass root extension increased with reduced nitrogen. Further, a nitrogen deficiency did not reduce grass root dimensions or the proportion of laterals to main roots.

TABLE 8

The effect of nitrogen level on maximum rooting depth of grass roots, in cms. 12th June-7th August, 1951.

Plot	12.6.51	26.6.51	10.7.51	24.7.51	7.8.51
1-grass, N. Def.	116	122	148	149	150
1-grass, + N.	101	119	123	125	130
$\frac{1}{2}$ -grass, N. Def.	111	134	150 + *	-	-
$\frac{1}{2}$ -grass, + N.	90	96	131	132	136
<i>Mean Plot</i>					
1-grass	109	121	136	137	140
$\frac{1}{2}$ -grass	101	115	141	141	143
N. Def.	114	128	149	150	150
+ N.	96	108	127	129	133

* Deepest root beyond bottom of glass panel.

§ 7. Shoot growth

By June 5th, conspicuous differences were seen in the above-ground growth of the grass at the two nitrogen levels. That on the nitrogen deficient plots had short, narrow leaves of a pale green colour and was brittle to the touch; on the plots with nitrogen, however, growth was vigorous and the leaves dark green and succulent.

Plot differences between tree seedlings were less marked; seedlings on the nitrogen deficient plots had small light-green leaves with yellow-streaked petioles. Grassed trees were less vigorous with smaller leaves than non-grassed, but at the higher nitrogen level, they did not display other signs of nitrogen deficiency. It became apparent later that all grassed trees were suffering from a lack of nitrogen, (as indicated by stunting and discolouration of leaves and petioles), but the symptoms had not developed at this stage.

On 30th August, a leaf count was made and the length and breadth of the four largest leaves measured. The distance from the ground to the first leaf was also measured. Deficient nitrogen depressed leaf number and size, but not to the same extent as did the grass cover. Grass, moreover, suppressed the development of leaves which formed below the grass level. This appears to be a shade effect. Since, on the grassed plots, suppression was complete to nearly half the total height, the effect may be a serious one.

Leading shoot growth curves are shown in Figs. 12 and 13. It can be seen that shoot growth is not a sensitive index of growth. On June 4th differences between plots were slight. At both nitrogen levels grass-free trees were taller than grassed but the slight differences between half-grass and full-grass trees unexpectedly favoured the latter. In all cases, nitrogen deficient trees were shorter than trees on the plots with nitrogen. Normal shoot growth had ceased at this date in all plots, and subsequent growth came from lammas shoots only. With the exception of tree number 18 (full-grass, + nitrogen) lammas shoots were confined to the grass-free, + nitrogen plot. It appears, therefore, that, under the conditions of this experiment, lammas shoot formation depended, either directly or indirectly, on nitrogen supply.

In Table 9, oven-dry weights of leaves and stems are presented. The plot differences again bring out the limitation of height as an index of growth.

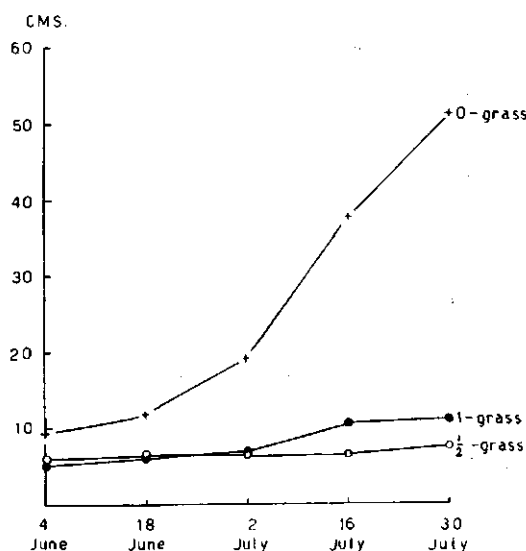


Fig. 12. The influence of grass level on shoot elongation of sycamore transplants growing in the root observation chamber. Mean shoot length in cm., 4 June-30 July. *Plots with added nitrogen.* + --- + = 0-grass; o --- o = $\frac{1}{2}$ -grass; • --- • = 1-grass.

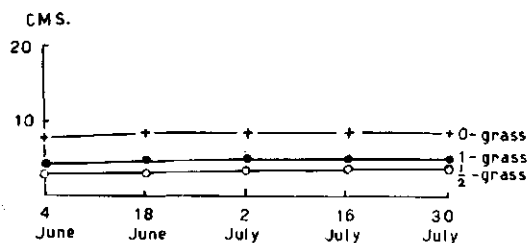


Fig. 13. The influence of grass level on shoot elongation of sycamore transplants growing in the root observation chamber. Mean shoot length in cm., 4 June-30 July. *Plots deficient in nitrogen.* + --- + = 0-grass; o --- o = $\frac{1}{2}$ -grass; • --- • = 1-grass.

TABLE 9

The effect of grass level and nitrogen deficiency on the dry weight of sycamore shoots, and on root/shoot ratio. Oven-dry weight in gms. Means of 4 trees.

Plot	Leaves	Stem	Total	Root wt. Shoot wt.
1-grass, N. Def.	1.05	7.79	8.84	0.268
1-grass, + N.	8.67	22.35	31.02	0.157
$\frac{1}{2}$ -grass, N. Def.	3.47	18.28	21.75	0.177
$\frac{1}{2}$ -grass, + N.	10.10	26.82	36.92	0.133
0-grass, N. Def.	10.21	52.66	62.87	0.176
0-grass, + N.	55.33	124.79	160.12	0.125
Mean Plot				
1-grass	4.86	15.07	19.93	0.213
$\frac{1}{2}$ -grass	6.79	22.55	29.34	0.155
0-grass	32.77	88.73	111.50	0.151
N. Def.	4.91	39.37	31.15	0.207
+ N.	24.70	57.99	76.02	0.138

§ 8. *The ratio of root growth to shoot growth in sycamore seedlings*

The last column of Table 9 gives the mean root/shoot ratio by plots. The effect of a nitrogen deficiency was to increase root growth relative to shoot growth and this agrees with the findings of ALDRICHE-BLAKE (2) and others. The effect of grass was also to increase root growth relative to shoot growth, though this increase was less marked than that brought about by nitrogen deficiency.

CHAPTER III

DISCUSSION AND SUMMARY

§ 9. *Some remarks on the value of root observation chambers*

Some of the results of this study must be regarded with caution in view of certain unsatisfactory features of the observation chamber. As has already been stated, the original intention of performing short-term experiments had to be abandoned because of the impossibility of measuring root growth over short periods. Measurements were made at two-hourly intervals with a horizontal microscope from a base-line marked on the glass with a writing diamond. It was found, however, that the thickness of the glass and the difficulty of focussing on the sloping glass wall introduced considerable errors. For complete accuracy, the microscope had to remain in position from one reading to the next and, thus, comparisons of root growth of grass and trees over the same period of time could not be made. Further, successive measurements on the same root

gave such variable results that any attempt to correlate them with environmental conditions failed.

The impossibility of adequately controlling or interpreting the environmental conditions in root observation chambers outside is, perhaps, the most unsatisfactory feature of such chambers. As a result of our experiences, the use of the Wageningen root chamber for short term studies of root growth has now been abandoned in favour of experimentation in the relatively constant and well-defined environment of the laboratory (20, 10, 11).

Another drawback of root observation chambers is the obvious one that only a part of a root system is visible against the glass and, until the material is harvested at the end of the experiment, the investigator has no indication of whether what is seen is representative of actual root growth. In the present case, comparisons between visible and actual root length were satisfactory with the exception of the extreme plots, but it is by no means certain that the relationship held throughout the period of the experiments.

It is clear, then, that root chambers do not provide a completely satisfactory means of studying root growth. As has been pointed out, they are generally too large for adequate control of the environment and too small for experiments over which a suitable statistical control can be established. Nevertheless, that they are valuable for both qualitative and semi-quantitative study has been demonstrated by ROGERS (14).

§ 10. *Discussion of the experimental results*

Considering the results obtained in the present study, it appears that, in general, the life history of the absorbing roots of sycamore seedlings closely follows that of apple tree roots as described by ROGERS (14). The experiment has demonstrated, realistically, the importance of nitrogen in the nutrition of both trees and grass, but it suggests that there is a definite difference between the two species in reaction to nitrogen deficiency. Thus, from a comparison of Figs. 7-8 with 9-11, it appears that nitrogen deficiency depressed the growth of tree seedling roots but increased that of grass roots. There is little support for this observation about grass roots in literature. HARRISON (8, 9) and GODLEWSKI (7), found a similar response to nitrogen deficiency, but most investigators (see, for example, RUSSELL (16)) record an opposite effect.

If a deficiency of nitrogen does in fact increase the growth of grass roots, then the advantages afforded to grass, in competing with trees for nutrients and moisture, are spectacular. As has been stated, however, it was feasible to measure samples of grass root growth only; and it may be that the observed effect of a nitrogen deficiency was not a real one. Nevertheless, even if this is so, there is abundant evidence that sycamore seedlings are ill-equipped to compete with grass.

It has been demonstrated that active root growth of perennial rye-grass starts considerably earlier than that of sycamore (§ 5a). This aspect of the grass effect might well repay further investigation and extension to other grass and tree species. If it is a general phenomenon, then it is clear that grass has a marked advantage over planted seedlings at a highly critical stage in their establishment.

It is also clear that root growth of grass is more rapid than that of sycamore; and that the total absorbing surface of grass roots is considerably more extensive in the same volume of soil. It is not suggested that the picture seen in the observation chambers is typical of an established grass cover, since this picture

resulted from newly-planted grass. In fact, observations elsewhere suggest that, in established grasslands, rooting is largely confined to the surface layers of the soil. Nevertheless, the grass roots appear to utilise fully the available rooting space and the grass effect on tree seedlings must be due, largely, to superior competitive ability. A factor that may have some significance is that, under the experimental conditions, the absorbing life of sycamore rootlets was considerably less than that of grass roots. Although the latter turned brown with age, they retained their root hairs and, presumably, were still capable of absorbing.

Evidence is also provided that height increment is not a satisfactory basis for comparative growth studies of young trees. ADAMS (1) and SHIRLEY (19) have drawn attention to the limitations of this widely used method of assessing tree growth. The latter points out that 'first year growth in height of newly planted conifers is made largely at the expense of food stored during the preceding year and, therefore, it cannot be used as an index of the excellence of the growing conditions'. Further, it is clear that if light conditions are modified (as indeed they are, by grass), height increment will not be related to absolute growth. SHIRLEY found that a reduction in light intensity from full daylight to 21% of full daylight was accompanied by dry weight reductions of 83% on trenched plots and 93% on untrenched plots; the corresponding height reductions, however, were only 39% and 54%.

The inhibiting effect of grass on the growth of trees has been ascribed to a variety of factors ranging from straightforward competition to the production of hypothetical toxic substances. While it cannot be claimed that the work reported here has established the fundamental nature of grass/tree interaction it seems evident that, whatever other factors may be involved, competition, in particular for nitrogen, must play a major part.

§ 11. Summary

Observations are reported on the effects of a grass cover and nitrogen deficiency on the development of sycamore (*Acer pseudoplatanus* L.) transplants growing in a root observation chamber. The following conclusions were drawn.

1. The presence of grass (*Lolium perenne* L.) depresses root growth rate, shortens the period of active growth, reduces the density of root hairs, and restricts both rooting depth and lateral spread of sycamore roots. Shoot growth, leaf development and lammas shoot formation are inhibited.

2. A deficiency of nitrogen reduces the size and growth of sycamore roots, but increases the elongation of grass roots. Shoot growth and leaf development of both sycamore and grass are inhibited.

3. Active growth of grass roots starts some three weeks earlier in the spring than that of sycamore roots, and is considerably more rapid.

4. The absorbing surface of grass roots is greater than that of sycamore roots in the same volume of soil. The absorbing life of grass root hairs is longer.

5. Both nitrogen deficiency and grass increase the ratio $\frac{\text{root dry weight}}{\text{shoot dry weight}}$ in sycamore transplants.

6. Height increment is not a sensitive index of dry matter production in sycamore transplants.

Under the conditions of this experiment the effects of grass were more marked than those of nitrogen deficiency.

The value of root observation chambers is discussed, and the conclusion is drawn that for short-term growth measurements they are considerably less satisfactory than the controlled environment of a laboratory.

Acknowledgements

This work was carried out under the direction of Prof. Dr E. C. WASSINK, to whom I am greatly indebted. I should also like to acknowledge financial help in the form of a scholarship from the Government of the Netherlands.

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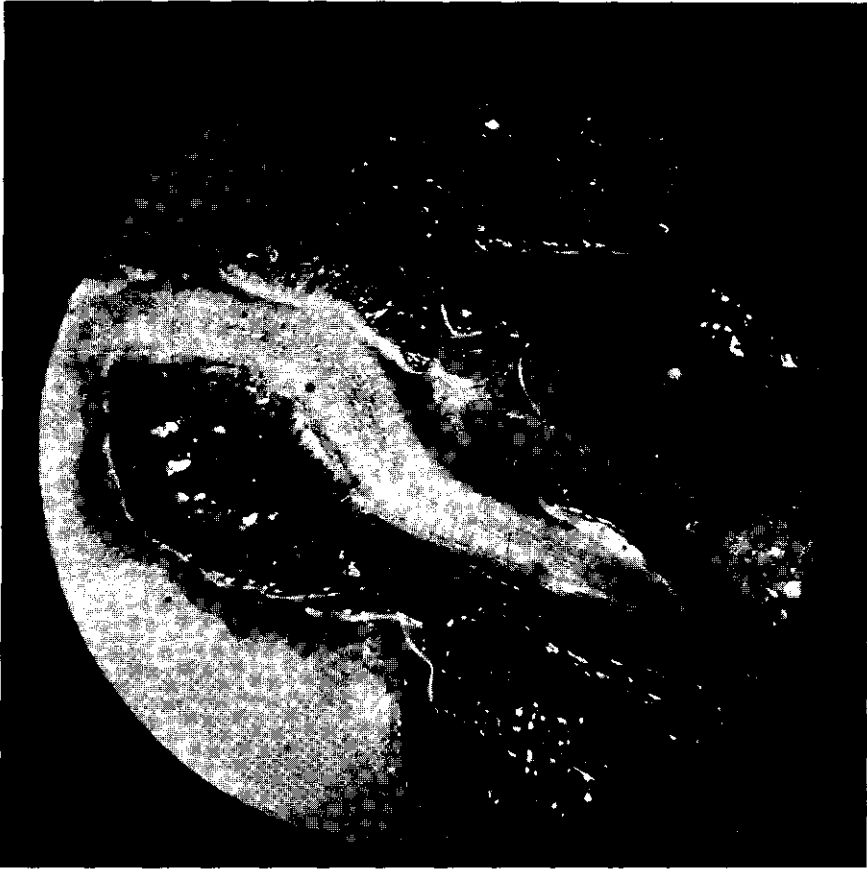


Plate I. Photomicrograph of a lateral root of sycamore. Experiments described in (20). Note root hair zone and moisture globules. Magnification $\times 30$.