ECOLOGY OF ALNUS GLUTINOSA (L.) GAERTN.

IV. ROOT SYSTEM

By D. N. McVEAN
(*The Nature Conservancy, Edinburgh*)

(*With two Figures in the Text*)

Some typical sapling root systems have already been described and mention made of a possible aeration mechanism (McVean, 1953). Figs. 1 and 2 show root systems at the end of the first and third season's growth on well-drained soil.

The composition of the gas contained in roots from below soil water-table was examined in February 1952. Roots were exposed and screw clips used to seal off lengths of about 5 in. (11.5 cm.). The roots were severed outside the clips and the severed portion quickly washed in clean water. Gas was then squeezed out with the fingers under glycerine-salt mixture and collected, by means of an inverted funnel, in a transparent plastic tube. The tube was then closed with clips and removed to the laboratory where gas analysis was usually carried out twenty-four hours later.

Analysis was carried out in a Timiriazeff Eudiometer (Darwin and Acton, 1925), glycerine salt being used instead of water in order to obtain estimates of the carbon dioxide content. (When the apparatus is filled with this mixture, some time must be allowed for the gas bubble to attain atmospheric pressure when the pressure of the piston is removed.) Absorption of oxygen was carried out in strong pyrogallol (10 grm. in 100 c.c. potassium hydroxide of specific gravity 1.5), and carbon dioxide in 10 per cent potassium hydroxide.

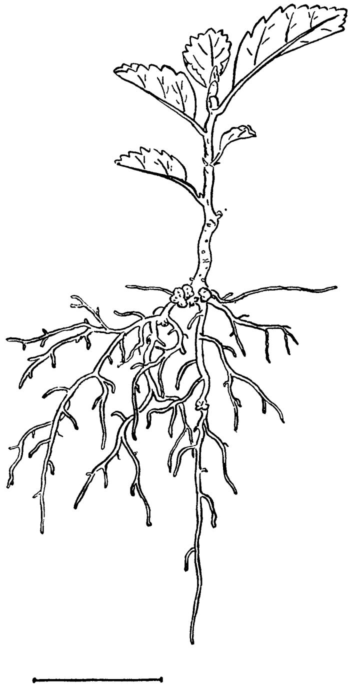

Fig. 1. Alder seedling after one season's growth in well-drained loam.

The apparatus could only be read with accuracy to 0.0025 c.c. and could only deal with 0.4 c.c. gas at one estimation so that atmospheric CO_2 could not be estimated as a check, and expired air was used instead. Results of the analysis are given in Table 1.

It was concluded that the composition of the root gas is O_2 – ca. 17 per cent, CO_2 – ca. 0.5 per cent, N. (by difference) – ca. 82.5 per cent, i.e. lower in oxygen and slightly richer in CO_2 than atmospheric air. Most of the CO_2 produced by root respiration probably enters solution.

These figures are not markedly different from the figures obtained by other workers, using more critical methods of analysis, for the submerged parts of herbaceous aquatics (Conway, 1937; Vallance and Coult, 1951).

The volume of the roots from which gas had been obtained was estimated by displacement and the gas found to occupy 8.5-10.0 per cent of the total. All extra-cambial tissues were then removed and the volume of the wood cylinder determined. The cortical tissues were found to comprise only 6 per cent of the root so that the gas obtained above cannot all be from the small cortical air spaces but must come largely from the xylem cylinder.

Table 1. *Composition of alder root gas*

Date	Gas	Volume of gas (c.c.) Original	After KOH	After pyrogallol	O_2 per cent	CO_2 per cent
16/2/52	Air	0.3600	–	0.2850	20.8	trace
,,	Root	0.3400	–	0.2800	17.6	–
,,	,,	0.2350	–	0.2000	14.8*	–
,,	,,	0.2100	–	0.1800	14.3*	–
,,	Air	0.3100	–	0.2500	19.3*	trace
22/2/52	,,	0.3425	–	0.2700	21.1	,,
,,	Expired air†	0.3950	0.3775	–	—	4.4
,,	Root	0.6225	0.6200	0.5125	17.3	0.4
27/2/52	,,	0.3750	0.3725	0.3100	16.7	0.6
,,	,,	0.2600	–	0.2150	17.3	–

* Old pyrogallol was used in the first series of analyses so that oxygen absorption fell away and the values are almost certainly too low.
† Breath held for as long as possible.

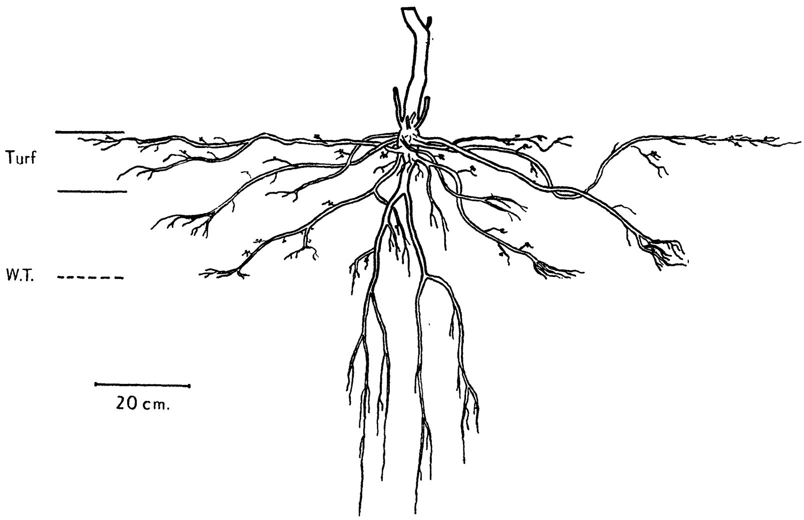

Fig. 2. Root system of three-year-old alder sapling on well-drained loam.

When the root is compressed the gas certainly appears to issue from the cut surface of the vessels. Gas can be obtained from all roots soft enough and of suitable diameter to be compressed between finger and thumb, i.e. all submerged roots except the finest root tips. Roots, and portions of roots, above the level of the normal water-table are generally too hard for this treatment but probably do not differ from the soft roots in their gas content.

It has already been pointed out that alder roots of all ages are sheathed by a reddish oxidized deposit in reducing soils.

The method of analysis was not sensitive enough to employ in testing for the presence of a diffusion gradient in the roots.

Arber (1920) points out that among legumes aerenchyma may be produced internally from a normal cambium, the air being contained in the xylem elements, e.g. in *Aeschynomene aspera*, a shrub which grows on the margins of lakes and streams in India. The wood of *Herminiera* (*Aeschynomene*) *elaphoxylon* has real perforations in its xylem elements so that there is free passage for gases.

Conway (1940), when considering the aeration system of plants which grow in wet soils, says: 'The situation seems less clear when one comes to consider the root systems of woody species which typically inhabit wet soils. It would be very interesting to have data on the oxygen supply available for the roots of such species as *Alnus glutinosa* and *Salix fragilis* – It is to these border-line cases that the centre of interest is bound to turn if we accept the idea that the internal aerating system of the extreme helophytes makes them independent of the oxygen concentration round their submerged parts.'

Conway also points out that, from the gas analysis work carried out by Romell and others, it is clear that there is a very sudden change in oxygen concentration within a narrow region of soil which delimits the zone of complete saturation (from 15 per cent oxygen to 1 per cent, the CO_2 values being correspondingly higher).

Certain chemical tests (McVean, 1953) confirmed that on Chippenham Fen the peat quickly became reducing once the region of the water-table was reached, and consequently that the region of the roots, from which gas was obtained for analysis, was surrounded by an actively reducing medium. McQuilken (1935) found roots of *Pinus rigida* extending several feet into saturated sandy soil, and branching extensively. Mycorrhizal development was present and these roots had no large air spaces or other anatomical variation of the type often found in submerged roots. *P. rigida* normally thrives on xeric sites.

Because of their well-developed surface and deep root systems alders are seldom wind thrown. There are a few wind-thrown trees in Woodwalton Fen, Huntingdonshire where an alderwood stands on well stratified and waterlogged *Sphagnum* peat. The surface roots have come away readily with the surface sheets of peat, and the tap roots have snapped under the strain.

Many of the older accounts lay stress on the danger that threatens the established alder through temporary or permanent changes in the local water-table. In fact, the alder is probably better protected against such eventualities than most other trees. Other species respond to a high water level by the production of surface roots only, and a sudden fall of water level leaves them exposed to the danger of drought. The deep roots of the alder can penetrate well below water level, and when this falls, supply the tree with deep-seated moisture that other species cannot utilize. The thriving alders round Fowlmere on the East Anglian Breckland are evidence of this, and it may be that the outstanding success of *A. glutinosa* as a pioneer species on spoil heaps (Whyte and Sisam, 1949) owes as much to this feature as to the existence of nitrogen fixing organisms in its roots nodules.

In an attempt to test the relative importance of different parts of the root system in supplying the tree with water during the summer months, some root-cutting experiments were carried out in 1950. After a short dry period in May and June the season was rather wet so that the surface soil never dried out as completely as had been hoped, though the water-table at Fowlmere was low and the mere was dry.

Sapling 1. (Fowlmere.) All surface roots were severed at the end of May.

On August 2nd it was apparent that growth had been all but stopped by the treatment, and the appearance of the tree was strikingly different from the neighbouring controls. Foliage was sparse and light green and yellow in colour. Many leaves showed marginal and interveinal scorching, were brittle and fell away at the touch. Catkin initials had been formed abundantly by the treated tree while controls had few or none. The tree showed every sign of general mineral deficiency, especially lack of nitrogen.

Sapling 2. (Fowlmere.) All deep-going roots, except a few branches of the surface system, were cut at the end of May.

In August all leaves, except those lately formed at the tips of the branches, were seen to be much smaller than those on the control trees. Extension growth of the branches had been slight and the sapling had lost the characteristic excurrent habit. Lateral shoots showed a tendency to outgrow the apical shoot of their branch.

Sapling 3. (Fowlmere.) All deep-going roots were cut at the end of May.

The small size of the proximal leaves was not so marked as on sapling 2, but the growth of the branch tips had been less, and many of the apices had withered off to be supplanted as leaders by the nearest lateral shoot. The excurrent habit had again been lost.

The number of roots cut in 2 and 3 was small compared with that in 1 and yet it is probable that, had a dry summer such as that of 1949 been experienced, the two saplings with cut tap roots would have been unable to survive on a site with so deep a water-table.

Howard (1925) has described the effect of monsoon rains on fruit tree growth at Indore, India. After the break of the rains the aerial growth of the custard apple, for example, becomes more rapid, leaves increasing in size, and internodes in length. His illustration of the different leaf sizes recalls the appearance of the branches of saplings 2 and 3 very strongly, and it would seem that the two situations are not dissimilar, the summer rains of 1950 compensating for the loss of deep-seated moisture. Howard also points out that the small size and light green colour of the hot-weather leaves, when surface roots are inactive, suggest a shortage of combined nitrogen in the deep soil layers. The root pruning of sapling 1 appears to have produced an essentially similar situation.

Sapling 4. (Chippenham, on the open clay drove.) All roots of the strong deep-going system were cut on a warm dry day at the end of May 1950 and wilting of all the young shoots took place within five minutes.

The plant subsequently recovered turgor and showed no further signs of injury.

Sapling 5. (Chippenham drove.) All surface roots severed on the same day as those of sapling 4, leaving the few deep roots.

Slight wilting was observed after two hours but recovery was rapid. The absence of any later signs of nitrogen deficiency can only be ascribed to the more general distribution of nodules than on sapling 1, especially to those round the crown of the plant, and to the higher nitrifying activity of the soil.

Root damage was approximately equal in the Fowlmere and Chippenham groups, but the latter did not show the same sharp differentiation between surface and tap roots, and the water-table was only 0.5 m. below the surface. The experiment at Fowlmere was repeated in the summer of 1951 when the mere was full of water and the water-table about 1 m. below the surface. All surface roots of two trees were cut and all the main tap roots of two others. It was noted at this time that the saplings root-pruned in the previous year were now growing normally.

The saplings were examined at the end of September. Those with cut surface roots had made little growth, and leaves were sparse, yellow and brittle, but catkin initials had not been produced. Those with cut tap roots were quite normal.

Although symptoms of nitrogen deficiency had again been produced in the first group some fundamental stimulus for the production of catkin initials appears to have been lacking since none of this sapling population produced initials in 1951.

The contrasting result from the second group in the two years shows that the tap roots were important to the sapling water supply when the surface soil was dry in 1950.

The results of the whole experiment thus tend to confirm the importance of the deep roots on dry sites, and that of nodules on soils of low nitrifying status.

EFFECT OF HIGH WATER-TABLES

The effect of rising water levels on the established tree may depend entirely on the rate at which this takes place. The alder generally reacts to a rise in water-table above the soil surface by the production of adventitious roots from the bole. These are richly branched, spongy like other submerged roots, and may penetrate the soil or remain floating in the water.

Clarke (1925) records that the original Fowlmere alders were planted when the water-table was low, and that abnormally high water levels about 1884 rose some 4 ft. (1.2 m.) up the stems. Many of the trees were killed and the remainder produced adventitious roots.

At Dernford Fen part of the alderwood is now almost continuously flooded, the water standing up to 1 m. up the boles of the trees at most times of the year. None of these trees has died though all are stunted and with many dead branches, masses of adventitious roots hanging free in the water or penetrating the mud.

In other parts of the Dernford wood water level is just below the surface during the period of most active growth. The thick, fleshy leading roots of the surface system then behave as though positively aerotropic by breaking through and growing along the top of the surface litter. At the same time nodule growth is particularly active, and the nodules, which are close to the surface and may attain the size of cricket balls, develop on their outside powdery lenticellular tissue which is light in colour and conspicuous in contrast to the normal appearance of the nodules at other seasons of the year. These phenomena have not been observed in the drier woods.

Howard (1925) again records something similar from Indore fruit trees. During the monsoons the water-table rises from 20 ft. (6 m.) down to within a short distance of the surface. Many deep roots then die and the surface roots grow to the surface within the shade cast by the canopy.

The evidence is thus good for the presence in alder of at least two physiological root types, the deep-going system which is capable of growth in a reducing medium, and the surface nutritional rootlets which require a higher oxygen tension in their surroundings and which bear the nodules. Completely flooded trees show by their stunted growth and dead branches that the root system is not functioning normally, but the extent to which the adult root system is killed by flooding is not known. Since nodules are not found far below normal water level inundated trees must lose most of the benefit of nitrogen fixation by their nodule organisms.

WATER LENTICELS

Hypertrophied lenticels were often observed on waterlogged seedlings and saplings, both in pot experiments and in the field. These occurred on stem base, surface roots and the surface of nodules which were often entirely covered by the loose tissue.

Hahn, Hartley and Rhoades (1920) describe the occurence of hypertrophied lenticels on young conifers in the presence of excess moisture. They report that such structures had previously been recorded from a number of dicotyledonous swamp plants, and that the conifer lenticels consist of pale yellow, loosely piled mounds of tissue, which often split stellately.

Water lenticels, splitting stellately, have also been reported on alder saplings in water culture (T. Ferguson, private communication).

There are two theories regarding the causes of lenticel proliferation: increased general sap pressure, and lowered oxygen tension with increased carbon dioxide concentration. Hahn *et al.* (1920) found that with both weak and strong conifer plants the conditions leading to hypertrophy, if prolonged, caused injury or death. Templeton (1926) found water lenticels on the roots of cotton plants in very wet soils, and, as a result of pot experiments, came to the conclusion that the second of the above theories is correct, the degree of hypertrophy being determined by the amount of oxygen available to the root.

The result of growing saplings with their roots in a reducing soil (Part III, 202) also supports this conclusion.

Water lenticels on stem root and nodule may increase the efficiency of the aeration system of the plant and assist the respiration of the nitrogen-fixing organisms. Bond (1952) suggests that the nodule rootlets of *Myrica* may perform a similar function.

SUMMARY

Analysis of the gas contained in alder roots from below soil water-table is described and the results shown to be comparable with those obtained by other workers on the submerged parts of herbaceous aquatics.

The gas is largely contained in the xylem elements as in the genus *Aeschynomene*.

The structure of the water lenticels on stems, roots and nodules is described and the suggestion made that they may play an important part in the root aeration mechanism of the species when growing on waterlogged sites.

Root-cutting experiments to test the importance of different parts of the root system in the water supply of the tree have shown that the deep tap roots may well account for the success of the established alder on sites of deep water-table. The importance of the surface system (with its nodules and mycorrhiza) in the nutrition of the tree on infertile soils was also demonstrated by this method.

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