SOIL SCIENCE

Vol. 108, No. 6
Printed in U.S.A.

PENETRATION OF CLAY BY ROOT HAIRS

R. A. CHAMPION AND K. P. BARLEY
Waite Agricultural Research Institute, Adelaide, Australia[1]

Received for publication February 24, 1969

Recent theoretical and experimental investigations show that root hairs are likely to be important in the uptake of less mobile nutrients. For example, for an ion species having an apparent diffusivity in the soil of 10^{-9} cm^2. sec^{-1}, theory predicts that depletion will scarcely extend beyond the tips of the root hairs in the first week of uptake (14). Autoradiographs of phosphate depletion in a highly buffered soil confirm that this is so (11).

The faces of peds are often altered by plasma concentrations and separations (3). Skins (cutans) occur widely, especially in illuviated horizons where the coating material is mainly translocated clay (4). Soileau, Jackson and McCracken (16) found that synthetic cutans of iron-kaolinite reduced the diffusion of potassium out of illite aggregates. In horizons where peds are highly developed, roots tend to be clustered in the macrovoids, especially if the peds are mechanically strong and the macrovoids are orientated vertically (6, 8). When this is so, the supply of less mobile nutrients from a ped is likely to depend on whether root hairs are able to penetrate its surface.

The present experiment was designed to investigate the ability of root hairs to penetrate resistant clay. The clay was remoulded to eliminate pores of root hair dimensions, and consolidated to different voids ratios[2] to vary its strength and compressibility.

MATERIALS AND METHODS

Preparation of Clay Cores

The clay was collected from the B horizon (45–75 cm.) of Urrbrae fine sandy loam. The following nutrients were added: KNO_3-N, 50 ppm; KH_2PO_4-P, 100 ppm. The relevant properties of the clay, measured after the addition of nutrients, are given in table 1. Litchfield (12) reported that the clay fraction consisted of kaolinite, illite and ferric oxide. Air dried clay was wetted to a gravimetric water content (w) = 42 per cent and kneaded for ten minutes in a kneading machine (Baker-Perkins, London, No. 491005). The water content was then raised to w = 53 per cent and kneading continued for a further five minutes. Samples of the saturated, remoulded clay were packed into 7.6 cm. internal diameter metal rings and loaded in uniaxial consolidometers. The method of consolidation followed that described by Akroyd (1). The initial load was one bar; the load was doubled at twelve hour intervals and the water was allowed to drain freely through porous stones. Twelve hours after the final increment of load, the consolidometer was unloaded in one step to 0.05 bar. Twelve hours later the cores were removed from the consolidometers, weighed and wrapped in aluminium foil to prevent loss of water. The cores contained a little entrapped air; the air-filled voids ratio was 0.019 ± 0.009.

Culture of Seedlings

Seeds of *Pisum sativum* L. var. White Brunswick were soaked in aerated water for six hours at 20° C and germinated in moist vermiculite. When the radicles were 1.5 cm. long the seedlings were planted.

[1] The paper is a contribution of the Department of Agronomy, Waite Agricultural Research Institute. The senior author was supported by an Australian Meat Research Committee Junior Studentship. We acknowledge the helpful advice given by Dr. A. D. Rovira and Mr. B. Cockraft.

[2] In mechanical studies it is convenient to use voids ratio e, rather than bulk density, ρ_b, as e is purely a measure of the compactness of the soil, whereas ρ_b is influenced not only by the degree of compaction but also by the particle density, ρ_p; these quantities are related by the equation $e = (\rho_p/\rho_b) - 1$. Similarly we use water-voids ratio, $e_w = \phi\rho_p/\rho_b$, where $\phi = w\cdot\rho_b/100$ is the volumetric water content, and air-voids ratio, $e_a = a\cdot\rho_p/\rho_b$, where a is the volumetric air content.

Radicles Grown On Clay Slopes

After the aluminium foil had been removed from the flat upper face, the cores were weighed and then inclined at a small angle to the vertical in containers. Five pea seedlings were placed on the top edge of each core with their radicles down the face—see fig. 1a. Two layers of (50 μ thick) polyethylene sheet were placed over the radicles and the exposed clay face. Wet sand was tamped firmly into each container to pack the polyethylene against the growing radicles and the core. The top of the container was covered with 12μ thick polyethylene film. The peas were grown for three days at 20° C in which time the radicles reached the bottom of the slopes. The sand and one layer of polyethylene were removed, the seeds and shoots were cut from the roots, and the cores were weighed with the roots in place. After removing the second layer of polyethylene, the roots were removed from the clay face under a dissecting microscope, and observations were made on the deformation of the clay by root hairs. Finally the cores were oven dried and weighed.

Radicles Penetrating a Clay Core

In this method, cores $\leqslant$ 25 mm. thick were used. After each core had been weighed, channels were made by pushing a 1 mm. rod through the foil into the clay to a depth of 3 mm. Tips of pea radicles were inserted in the channels (see fig. 1b). Five or more radicles were planted in each core. Wet sand was packed around the seedlings which were left to grow for three days at 20° C. The cores were kept in containers sealed with 12 μ polyethylene film. At harvest, each core was weighed and then broken apart to enable inspection of the walls of the channels made by the radicles.

In both procedures cores were rejected if w and hence e_w changed significantly during the growing period.

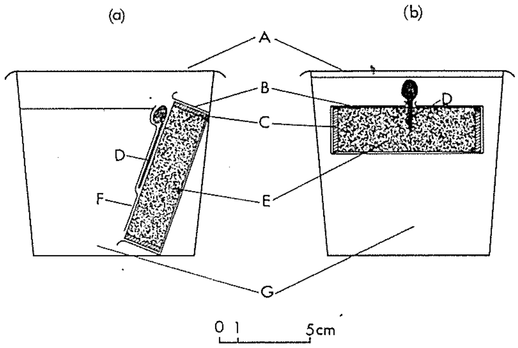

FIG. 1. Assemblies used to grow radicles (a) down clay slopes, (b) through clay cores. A polyethylene film; B aluminum foil; C consolidometer ring; D radicle; E clay core; F polyethylene diaphragm; and G wet sand.

TABLE 1
Properties of the Clay

Mechanical analysis	(%)	pH (1:5 suspension)	6.9
Coarse sand	0.4		
Fine sand	14.8	Exchangeable Ca (me. %)	15.5
Silt	17.5		
Clay	64.9	Total exchangeable cations (me. %)	34.1
Atterberg limits	(%)		
Plastic limit	26.4		
Liquid limit	83.0		
Particle density (g/cc)	2.64		

RESULTS

Growth Down Clay Slopes

A face view of a radicle growing down a clay slope is shown in fig. 2. Root hairs developed densely, attaining a length of 800 μ on the sides of the radicles, where they were unconfined due to arching of the polyethylene diaphragm over the radicle. After the radicles had been lifted gently from the cores, observations were made of the deformation of the subjacent clay. The radicles grooved the clay to a depth that depended on its density. The grooves were as deep as the radius of the radicle on the least dense clay, but were scarcely visible on the most dense. On the less dense clay perforations had been formed in the groove by the root hairs—see fig. 3a; but the hairs were unable to penetrate the denser clay, merely forming shallow indentations—see fig. 3b. Table 2 shows that the value of the water-filled voids ratio (e_w) limiting penetration lay between 1.08 and 1.11. The few deep perforations in cores 4 and 6 could perhaps be explained by local weaknesses in

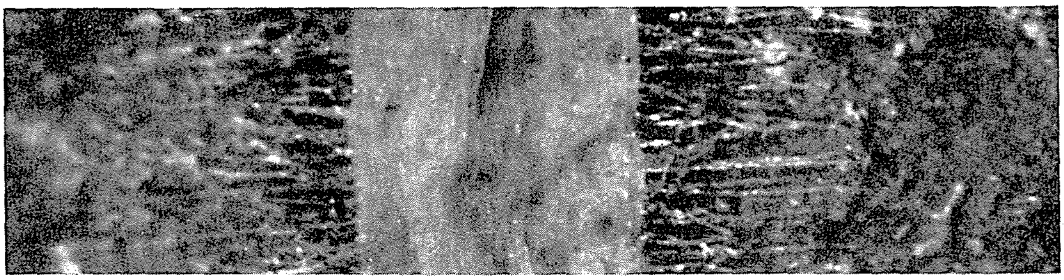

FIG. 2. Face view of radicle grown down clay slope (× 40).

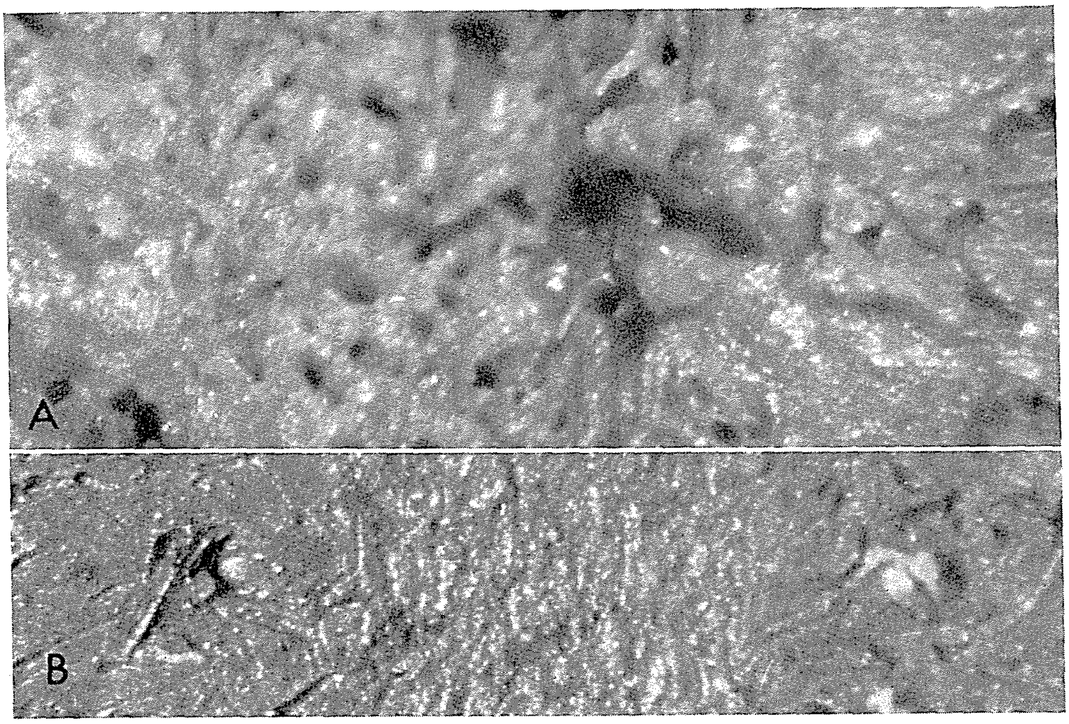

FIG. 3a. Deformation of clay slope showing fine detail; $e_w = 1.3$ (× 100).
FIG. 3b. Deformation of clay slope; $e_w = 0.9$ (× 40).

the clay. Even in the less dense clays the depth of perforation did not exceed 500 μ. The parallel striations visible in fig. 3a and fig. 4 probably represent the imprint made by files of epidermal cells.

Growth in Clay Cores

Clay was displaced upwards by general shear failure around the upper edge of each channel; further below the face of the core the channel would have been accommodated wholly by local consolidation (5). From penetrometer data it is known that point resistance, and hence local consolidation, attains a steady maximum after the apex of a probe has penetrated three diameters into the clay. As the diameter of the widest radicles was 1.5 mm., anomalous results may be expected within 5 mm. of the channel edge.[3] Table 3 shows that in the less dense cores, root hairs perforated the upper 15 mm. or more of the channel walls—see fig. 4. In the denser cores, perforation was re-

[3] When the clay undergoes general shear failure, e_w approaches a critical value, over-consolidated clays becoming less dense and lightly consolidated clays becoming more dense (14).

TABLE 2

Deformation of clay slopes by root hairs

Core	e_w	Density of Grooves & Perforations* >20μ	Density of Perforations* >20μ	Maximum Length of Hairs Penetrating Clay (μ)
1	0.71	+	−	20
2	0.93	+	−	20
3	0.98	+	−	20
4	1.00	++	+	50
5	1.00	+	−	20
6	1.01	++	+	50
7	1.03	+	−	20
8	1.08	++	−	20
9	1.11	++	+	300
10	1.17	++	+	500
11	1.22	++	+	100
12	1.24	++	++	300
13	1.26	++	+	100
14	1.35	++	++	300
15	1.40	++	+	200

* − none, + sparse, ++ dense.

stricted to the top few millimeter of the channel. If the top 5 mm. is excluded as being a mechanically anomalous zone, the limiting value of e_w lay between 1.11 and 1.14. With a few exceptions, root hairs did not develop more than 25 mm. down the channel.

DISCUSSION

As the radicles caused local consolidation, the voids ratio of the clay encountered by the hairs would have been less than the initial or bulk value. Crockroft[4] found that, when pea radicles were grown through the clay concerned, local consolidation reduced e_w adjacent to the channel by approximately 0.1. Thus the absolute value of e_w limiting root hair penetration, when radicles were grown through the cores, is likely to have been 1.0 and not 1.1. The value of e_w in the clay immediately beneath the radicles on the slopes is not known, but it is likely that less consolidation occurred on the slopes than in the cores, because the grooves would have been accommodated partly by general shear failure. This may explain why the apparent limiting value of e_w found with the slopes was slightly less than that found when radicles were grown through the cores.

The absolute limit of 1.0 agrees with the value of e_w found to limit the deep penetration of radicles into cores of remoulded clay (6). This may reflect a common osmotic origin of the growth pressure in the radicle and its root hairs.

As noted by Barley (2), for bodies as thin as root hairs, the force required to overcome skin friction is potentially far greater than the force required to deform the soil. In the growing root hair only the extreme hemispherical tip undergoes surface extension (10); this may perhaps be regarded as an adaptation that minimizes skin friction. In addition, the mucilage that covers the tip of the hair (15) may act as a lubricant. If we postulate that the deformation of clay by the growing tip of the hair can be represented as the spherical enlargement of a cavity by internal pressure, the pressure required may be found from the theory of Farrell and Greacen (7). Insufficient mechanical data are at present available to calculate this pressure for the clay used in this experiment. It is worth noting that not only strength parameters but compressibility coefficients also are required. General relations between these parameters, coefficients and e_w cannot be expected; the limiting value of e_w

TABLE 3

Deformation of walls of radicle channel by root hairs*

Core	e_w	Density of Perforations† at Depths: 5 mm.	10 mm.	15 mm.	Maximum depth of Channel Perforated. (mm)
1	0.88	−	−	−	1
2	0.89	−	−	−	0
3	0.95	−	−	−	2
4	1.08	−	−	−	2
5	1.10	+	+	−	12
6	1.11	+	−	−	5
7	1.11	+	+	−	9
8	1.14	++	+	+	17
9	1.25	++	+	+	25
10	1.40	++	+	+	20
11	1.49	++	+	+	23

* Radicles grown through clay cores.
† See footnote Table 2.

[4] Cockroft, B. 1968 The penetration of remoulded clays by fine probes and plant roots. Ph.D. Thesis, University of Adelaide.

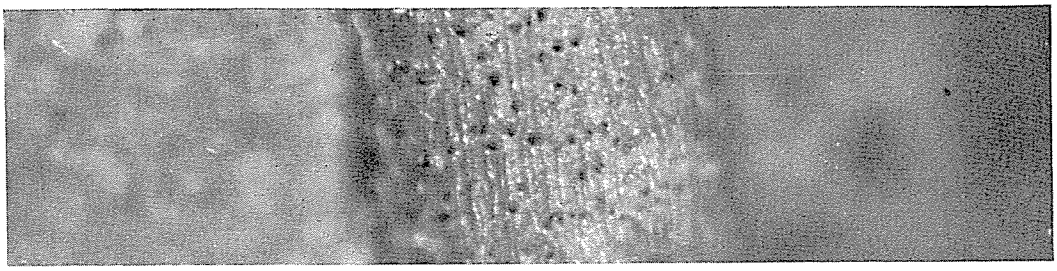

FIG. 4. Fracture face of clay core; $e_w = 1.2$, showing wall of root channel (× 40).

reported here applies only to the particular clay prepared in the manner specified.

As the experiments were conducted with saturated clay, the possible influence of aeration needs to be considered. The diffusion of oxygen through the clay to the radicles would have been very slow at all voids ratios, as the diffusivity of oxygen in water is 10^{-4} times that in air. Nevertheless striking differences in root hair penetration were observed at different voids ratios. Internal transfer of oxygen has been observed in pea radicles (10), but this supply diminishes with distance down the radicle. When radicles were grown through the cores in the present experiment, root hairs failed to develop more than 2 to 3 cm. below the surface, even in the least resistant clay. In deep cores the radicles themselves continued to elongate for several centimeters below the hair-bearing zone. Either some factor other than mechanical resistance, for example oxygen deficiency, operated in depth or, alternatively, hairs may have grown only on cells that were already present in the tip at the time of planting. In contrast to those grown in the cores, the radicles grown on the slopes were well aerated at their sides, where a gap occurred between the diaphragm and the clay. This gap was continuous with the atmosphere. As the limiting value of e_w found on the slopes was close to that found in the top 2 cm. of the cores, it seems unlikely that aeration can have influenced the results in this zone.

The clay used in these experiments was remoulded to eliminate voids of a size commensurate with the width of the hairs. In finely structured soils hairs may penetrate existing microvoids, and fine structure may often determine whether or not penetration occurs. Where the faces of peds are cutanized, microvoids are infrequent, and hairs must deform the clay to enter a ped.

SUMMARY

Growing root hairs are capable of deforming moderately resistant clays. When pea radicles were grown on or in a saturated remoulded clay, root hairs were able to penetrate when the initial voids ratio exceeded 1.1. Taking into account local consolidation by the radicle, the limiting voids ratio was close to 1.0. The mechanics of penetration by root hairs is discussed briefly.

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