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ROOT GROWTH AROUND BARRIERS

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ABSTRACT

Horizontally growing root tips from red maple trees (*Acer rubrum* L.), when grown through a holder and then deflected laterally by a barrier, curve back toward their original direction as they grow beyond the barrier. The amount of recurvature increases as the angle of the barrier is increased up to a barrier angle of 60° but decreases only slightly as barrier length is increased from 1 to 7 cm. The stimulus to recurve beyond the barrier appears to be the initial physical bending that produces asymmetry both in the root tip and in the bent portion. Comparable behavior of horizontal root tips under natural conditions tends to produce long, straight roots radiating from the stem.

Introduction

Horizontal woody roots of red maple (*Acer rubrum* L.) radiate from the base of the stem and are remarkably straight over distances up to 25 m despite frequent small bends where the root tip apparently grew around obstacles in the soil. The over-all straightness suggests that the tip had tended to return to its original direction of growth after having been deflected by the obstacles (LYFORD and WILSON, 1964). NOLL (1894) observed the tendency of secondary roots of *Lupinus* seedlings to return to the original radial direction away from the primary root after being deflected and called this tendency "exotropy." DARWIN (1898) described similar behavior in the primary root of a *Vicia faba* seedling. Several workers in the 1890's, concerned primarily with plagiotropism in roots, reported that exotropy disappeared when seedlings were rotated on a klinostat (RUFELT, 1962). ZEHENDNER (1924) confirmed NOLL's observations on unrotated roots. In general, exotropy has been infrequently studied and poorly documented. The present study utilizes a technique for growing red maple roots under semicontrolled conditions while attached to mature trees to observe and measure the growth response of horizontal roots whose growth is displaced laterally by artificial barriers.

Material and methods

Roots used were induced to grow *in loco* from forest-grown red maple trees (*Acer rubrum* L.) growing in moist to wet soils at the Harvard Forest, Petersham, Massachusetts. The roots of comparable trees have been described previously (LYFORD and WILSON, 1964; WILSON, 1964). The experimental procedure as used in June, 1965, can be outlined as follows: (*a*) Horizontal woody roots 1–2 cm in diameter are severed a few meters from the stem of a tree; (*b*) about 10 cm of the end attached to the stem is wrapped in moist soil; (*c*) within about 2 weeks several new root tips 1–2 mm in diameter grow out horizontally from just behind the cut end, elongating at a rate of 1–2 cm per day; (*d*) the woody root is affixed to a horizontal board so that the new roots grow on the surface of the board in or on a thin (about 3 mm) layer of moist soil obtained from the local *A* horizon. The boards are protected by a shed built over them.

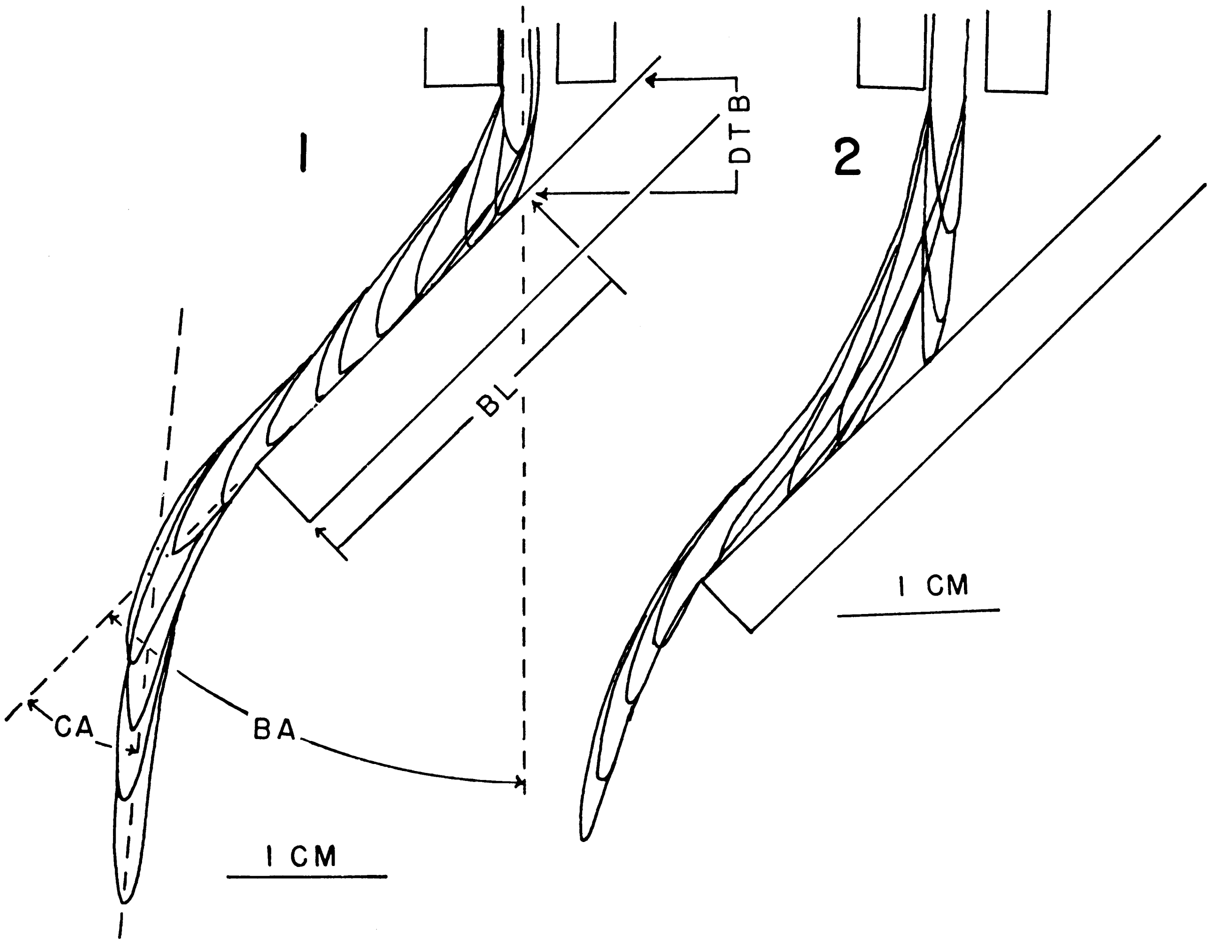
For each experiment a root tip is placed in a horizontal holder made of paraffin-coated Masonite fiberboard. Each holder consists of a trough in which the root is placed and a barrier (fig. 1). The distance from the end of the trough to the barrier is 0.5–2.5 cm, the length of the barrier (measured from the extrapolated midline of the trough) is 1–10 cm, and the angle the barrier makes with the trough is 15°–90°.

During an experiment, the root grows out of the trough, hits the barrier, and grows around it (figs. 1, 2). The flat bottom of the holder keeps the plane of growth horizontal. The amount of recurvature of the root after it reaches the end of the barrier (fig. 1, correction angle) is measured with a protractor from a photograph. Each correction angle in figures 3 and 4 is the maximum angle in the first 2 cm beyond the barrier.

Results

If unimpeded by barriers, the roots grew straight in the direction of the long axis of the root tip. When straight, rapidly growing roots were bent 10 cm behind the tip (where cortical cells were no longer turgid) so that the tip pointed at 45°, 90°, or 180° to the original direction, in all cases the tip continued to grow straight in the new direction at an undiminished rate. Thus, exotropic curvature was not elicited by merely changing the orientation of the tip with respect to the rest of the root system.

The 64 roots grown in holders (so that a barrier deflected the growing tip from the direction imposed by the trough) all recurved when the tips grew beyond the end of the barrier, thus exhibiting an exotropic response. There was no apparent difference in recurvature between roots that grew on top of the soil and were occasionally photographed and those that grew always covered by 3–4 mm of soil. Furthermore, there was no difference in the correction angle at distances between the trough and the barrier of 0.5–2.5 cm with a barrier angle of 45° and barrier length of 2 cm. Therefore, a distance of 0.5 cm was adopted for subsequent experiments.



FIGS. 1, 2.—Superimposed tracings from series of photographs taken at approximately 8-hr intervals of roots growing around barriers. Fig. 1, distance to barrier from trough (DTB) = 0.5 cm, barrier length (BL) = 2 cm, barrier angle (BA) = 45°, correction angle (CA) = 43°. Fig. 2, same as fig. 1, but DTB = 1.5 cm, CA = 29°.

When a barrier length of 2 cm was used, the magnitude of the correction angle was related to the barrier angle (fig. 3). The correction angle increased as the barrier angle was increased from 15° to 60°, and the root completely compensated for the imposed deflection at barrier angles up to about 30°.

When a barrier angle of 45° was used, there was a slight decrease in correction angle as barrier length was increased from 1 to 7 cm (fig. 4). In an experiment with a 10-cm barrier, the root had a correction angle of 21° (fig. 5). Thus there appeared to be little tendency for the root to become trained to the direction of the barrier in these experiments.

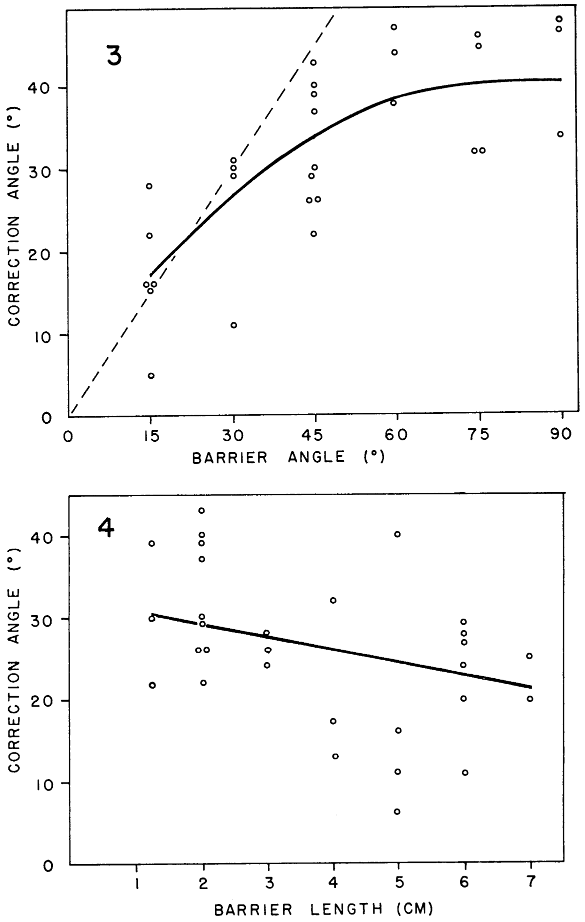
Two kinds of curvature occurred during growth around barriers. The first kind was a physical bending of the portion of the root between the barrier and the trough as the tip skidded along the barrier. At a distance of 0.5 cm from the trough to a 45° barrier, the tip skidded about 5 mm, but at a distance of 1 cm or more the tip skidded to the end of a 2-cm barrier (figs. 1, 2). While the tip was skidding along the barrier, the orientation of the tip gradually changed until, if the barrier was long enough, it grew parallel to and against the barrier. In several cases the root tip appeared to be laterally asymmetrical when growing parallel to the barrier, as though the tip was tending to grow at an angle to the barrier. The second kind of curvature occurred when the roots grew beyond the end of the barrier. Here the tip portion of the root grew back toward the original direction so that there was no physical bending, just curved growth (figs. 1, 2).

Growth around a 90° barrier presented the roots with special problems. After hitting the barrier, the root tips did not skid to one side but grew down until they hit the bottom of the holder and then turned to grow along the barrier. In about half of the cases the tip died before turning, but those that did turn then grew normally and showed exotropic recurvature (fig. 6). Lateral roots usually developed on the outside of the bent portion of both these roots and those growing around a 75° barrier. In an unsuccessful attempt to grow a root in a **U** shape so that it would turn 180°, lateral roots were formed on the outside of the bent portion as the growth of the main root slowed and stopped.

Discussion

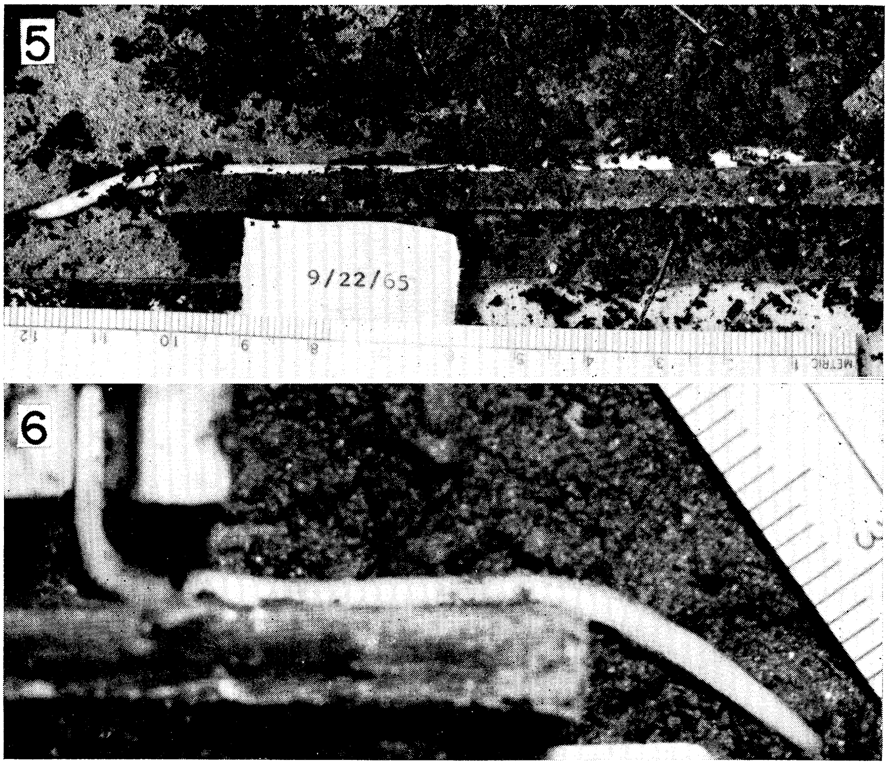
It is clear that horizontal red maple roots tend to return to the original direction of growth after having been deflected by a barrier. This tendency can be called exotropy, although the reference direction is not, as suggested by Noll (1894) and Zehendner (1924), determined by the location of the primary root but, rather, by the direction of the elongating portion of the root tip at the time of deflection. Because the root tip does not always completely correct its orientation after a change in direction, a 25-m red maple root is not completely straight (Lyford and Wilson, 1964); but if there were many small obstacles that deflected the tip randomly to the right or left, then the root would tend to grow radially away from the stem. As Noll has stated, by maintaining the radial direction of horizontal roots, exotropy results in efficient exploitation of the soil by a root system.

There are several possibilities for the mechanism of exotropic curvature, but without further data they must all remain speculative. One possibility is that bending of the root induces lateral transport of



Figs. 3, 4.—Variation in correction angle (CA) with changing barrier lengths (BL) and barrier angles (BA). Each point is value for single experiment. Fig. 3, BL = 2 cm, DTB (distance to barrier) = 0.5 cm, dotted line is CA = BA, equation for least-squares curve is $Y = 5.44 + 0.858X - 0.005X^2$. Fig. 4, BA = 45°, DTB = 0.5 cm, equation for least-squares line is $Y = 32.30 - 1.59X$.

auxin to the convex side, which then both causes the observed lateral root formation and beyond the barrier inhibits growth on the same side of the root to produce exotropic recurvature. Lateral transport of root-forming substances in bent roots has been shown by DE HAAN (1936). A second possibility is that the bending sets up longitudinal pressure differences in the cortex of the two sides of the root. These differences could be maintained as the root grows along the barrier until they are nullified by curved growth beyond the barrier. A third possibility is that exotropy is actually positive haptotropism, that is, response to contact as described by DARWIN (1898) and BENNET-CLARK, YOUNIS, and ESNAULT (1959), and independent of the bending of the root. A fourth possibility is that horizontal root orientation is maintained by some kind of internal correlation mechanism of the sort described by WESTING (1965) for lateral branches under the heading of "pleuronasty."



FIGS. 5, 6.—Photographs of roots showing exotropic curvatures. Scale divisions are in millimeters. Fig. 5, BA = 45°, DTB = 0.5 cm, BL = 10 cm, CA = 21°. Fig. 6, BA = 90°, DTB = 0.5 cm, BL = 2 cm, CA = 34°.

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