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Review

Root growth movements: Waving and skewing

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ABSTRACT

Roots anchor a plant in the soil, acquire nutrition and respond to environmental cues. Roots perform these functions using intricate movements and a variety of pathways have been implicated in mediating their growth patterns. These include endogenous genetic factors, perception of multiple environmental stimuli, signaling pathways interacting with hormonal dynamics and cellular processes of rapid cell elongation. In this review we attempt to consolidate our understanding of two specific types of root movements, waving and skewing, that arise on the surface of growth media, and how they are regulated by various genes and factors. These include crucial factors that are part of a complex nexus of processes including polar auxin transport and cytoskeletal dynamics. This knowledge can be extrapolated in the future for engineering plants with root architecture better suited for different soil and growth conditions such as abiotic stresses or even extended spaceflight. Technological innovations and interdisciplinary approaches promise to allow the tracking of root movements on a much finer scale, thus helping to expedite the discovery of more nodes in the regulation of root waving and skewing and movement in general.

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1. Introduction

Roots are hidden parts of plants usually growing downward and branching inside the soil in an intricate and dynamic fashion. They help anchor the plant and acquire nutrients while also sensing the soil milieu, which in turn mediates overall plant physiological responses to its environment. As a seed germinates, the movement of roots into the substratum is controlled by both genetic and environmental cues. This seemingly simple process is actually a complex phenomenon as the root integrates cues from gravity, touch, light, nutrition and other environmental conditions that regulate its movement and architecture.

The development of roots has been investigated for many decades and substantial progress has been made in understanding root structure and developmental physiology [1]. Roots grow by the concerted action of rapid cell division and subsequent rapid elongation of the newly formed cells in the elongation zone. These processes are under the control of hormones, structural proteins and a dynamic cellular trafficking machinery to provide new materials for the elongating root. The root also has complex cross-talking signaling pathways that perceive and respond to diverse environmental cues such as light, gravity, mechanical obstacles, moisture and nutrient gradients, allowing an optimal growth trajectory [1–6].

Charles Darwin was a pioneer in systematically documenting plant movements in his book, *The Power of Movement in Plants*

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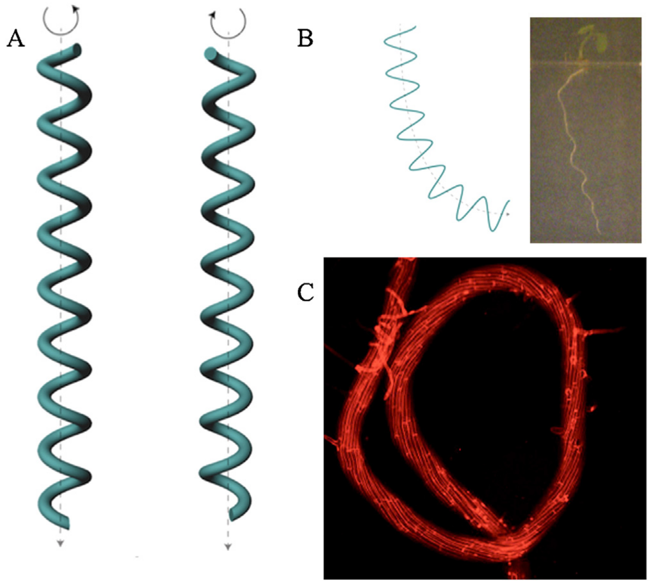

Fig. 1. Helical motion of roots, root waving and skewing. (A) Diagram depicting the helical circumnutation of a root. The spiral motion around an imaginary axis can be clockwise (right-handed) or counterclockwise (left-handed) when looking down toward the direction of root growth. (B) *Left panel* – Cartoon depicting the waving and skewing of the root as it grows on a slanted hard growth medium. *Right panel* – Root of *Arabidopsis thaliana* grown on a slanted hard growth medium showing skewing and waving. (C) Confocal image of a propidium iodide-stained root coil showing marked epidermal cell file rotation.

[7]. Before beginning a specific discussion on root waving and skewing, it is imperative to understand the types of movement in plants. Though sedentary, terrestrial plants show different classes of movement, arising due to unequal expansion in different regions of a plant organ [7,8]. Tropistic movements occur in response to a directional cue. For example, roots are usually negatively phototropic (move away from light) and positively gravitropic (grow toward gravity). Nastic movements also occur in response to external factors but are independent of their position, e.g. the closing of leaves at night. Nutations refer to movement mainly controlled by an internal mechanism, and circumnutation specifically refers to an autonomous circular nutation that results in an elliptical, circular or irregular motion of the plant organ around an imaginary axis in the direction of growth (Fig. 1A). For an in-depth historical perspective and understanding on tropisms and circumnutation, see Refs. [8–11]. These various forms of movements usually occur together; for example, it has been shown that gravity amplifies the circumnutatory response in *Arabidopsis thaliana* [12]. Hence the movement of roots comes about by a combination of tropistic responses to gravity, touch, moisture and light and circumnutation, though further studies are needed across different species to build a better model of how these processes interact. It should also be noted that even though plants with delicate roots like *Arabidopsis* show a slight circumnutation of the tip as they grow, other plant species with considerably thicker roots do not show this characteristic circumnutation.

In this review we will discuss specifically two classes of movements, waving and skewing, that are essentially surface-dependent movements of roots growing on slanted impenetrable (high agar concentration) growth media. Most of the studies have been performed with the model plant *A. thaliana*, which has helped shape our understanding of how roots move. However, the movement of the delicate roots of *Arabidopsis* and how they react to mechanical obstacles and other cues could be very different from more robust roots of other bigger plants. Hence, though helpful as a model organism for uncovering basic mechanisms of root movement, true understanding of movement in other species is an urgent need. In addition, although analysis of waving and skewing is a good model to understand the dynamics of root growth and movement, the actual movement of a root in the soil is very different and any parallels drawn need confirmation in the latter system.

2. Waving and skewing: “root” cause

The cultivation of *Arabidopsis* seedlings on a slanted impenetrable medium (high agar density of 1.5–2%) leads to the appearance of waving and skewing. Though they have been studied for quite some time now, a universally accepted model does not exist. Two models have been put forward to explain the presence of waving and skewing of roots of plants grown on agar plates.

Model 1. One model explains waving and skewing as a result of touch, gravity and circumnutation [9]. According to this model, the growing root tip is forced down due to gravity on a slanted impenetrable medium, causing it to respond to touch (thigmotropism). The interaction of touch and gravity, coupled with the inherent tendency of the root tip to circumnutate with a fixed handedness, leads to a characteristic deviation from the vertical (skewing) and formation of sinusoidal wave-like patterns (waving) (Fig. 1B). The waves arise due to spiral growth of the circumnutating root tip with alternating reversals in its handedness midway into each wave due to the effect of thigmotropism. The skewing can be explained based on the inherent handedness with which the root grows. If the roots are left-handed, the left-handed turns are larger compared to the right-handed ones and the root gradually skews to the right.

Model 2. Alternatively, another interesting model explains skewing and waving as a result of physical interaction of the root tip with the growth media [13]. According to this model, the slanted growth medium frictionally impedes the root tip's movement, while the elongation zone keeps growing. This causes a distinct nontropic curved deflection of the root to one direction until the root tip is impeded again. The process repeats to give rise to waves. This model for waving along with the inherent circumnutating tendency might explain the skewing of the roots.

Similar root trajectory observations were made by Darwin with roots of various plant species [7]. Hence these two phenomena are mechanistically explained by an interaction between thigmotropism, gravitropism, circumnutation and physical root-media interactions [8,13,14]. It should be noted that waving and skewing are surface dependent phenomenon that do not appear when a root grows embedded in the growth medium or in liquid medium since uniform touch/pressure exists around the growing root.

Skewing is defined as rightward or leftward when looking through the medium (from the back of the plate) and waves are usually quantified by their frequency and amplitude. An endogenous chirality can explain why the roots tend to slant in a certain direction. This endogenous nature of root slanting is clear from studies in microgravity where in the absence of gravity, roots have an exaggerated skewing [15]. It is also interesting to note that the *Arabidopsis* accession Cvi shows a naturally exaggerated root skew compared to other ecotypes, possibly because of its habitat of growth on rocky walls [16].

Skewing is directly proportional to the slant angle of the medium, presumably due to increase in the force of contact between the root tip and the medium during growth [17]. During these movements, epidermal cell files of the roots also show a twist referred to as cell file rotation, which may be due to the effect of mechanical impedance on elongation of the root. This rotation occurs due to differential rates of anisotropic expansion between outer and inner cell layers of an elongating root, with the outer epidermal cell files twisting thus offsetting the elongation lag between the two layers [18]. Cell file rotation becomes more

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