

# Journal of Comparative Psychology

## The Coding of Object Thickness in Plants: When Roots Matter

Silvia Guerra, Bianca Bonato, Qiuran Wang, Francesco Ceccarini, Alessandro Peressotti, Francesca Peressotti, Walter Baccinelli, Maria Bulgheroni, and Umberto Castiello

Online First Publication, August 19, 2021. <http://dx.doi.org/10.1037/com0000289>

### CITATION

Guerra, S., Bonato, B., Wang, Q., Ceccarini, F., Peressotti, A., Peressotti, F., Baccinelli, W., Bulgheroni, M., & Castiello, U. (2021, August 19). The Coding of Object Thickness in Plants: When Roots Matter. *Journal of Comparative Psychology*. Advance online publication. <http://dx.doi.org/10.1037/com0000289>

# The Coding of Object Thickness in Plants: When Roots Matter

Silvia Guerra<sup>1</sup>, Bianca Bonato<sup>1</sup>, Qiuran Wang<sup>1</sup>, Francesco Ceccarini<sup>1</sup>, Alessandro Peressotti<sup>2</sup>,  
Francesca Peressotti<sup>3</sup>, Walter Baccinelli<sup>4</sup>, Maria Bulgheroni<sup>4</sup>, and Umberto Castiello<sup>1</sup>

<sup>1</sup> Department of General Psychology, University of Padova

<sup>2</sup> Department of Agricultural, Food, Environmental and Animal Sciences, University of Udine

<sup>3</sup> Department of Developmental Psychology and Socialisation, University of Padova

<sup>4</sup> Ab.Acus S.r.l., Milan, Italy


Tendrils are clasping structures used by climbing plants to anchor and support their vines that coil around suitable hosts to achieve the greatest exposure to sunlight. Although recent evidence suggests that climbing plants are able to sense the presence of a potential stimulus in the environment and to plan the tendrils' movements depending on properties such as its thickness, the mechanisms underlying thickness sensing in climbing plants have yet to be uncovered. The current research set out to use three-dimensional kinematical analysis to investigate if and in what way the root system contributed to thickness sensing. Experiment 1 was designed to confirm that the movement of the tendrils of pea plants (*Pisum sativum* L.) is planned and controlled on the basis of stimulus thickness when the stimulus is inserted into the substrate. Experiment 2 was designed to investigate what happens when the stimulus is lifted to the ground so as to impede the root system from sensing it. The results confirmed that tendrils' kinematics depend on thickness when the stimulus is available to the root system but not when it is unavailable to it. These findings suggest that the root system plays a pivotal role in sensing the presence and the thickness of a stimulus and that the information perceived affects the planning and the execution of the climbing plants' reach-to-grasp movements.


**Keywords:** reach-to-grasp movement, plants' movement, kinematics, plant behavior, plant cognition

**Supplemental materials:** <https://doi.org/10.1037/com0000289.supp>

Scientists have long been intrigued by the specialized adaptations of climbing plants that enable them to compete for necessary resources such as sunlight (Niklas, 2011). Charles Darwin (1875) first categorized climbing plants depending on their mode of attachment that can be classified as twining, hook and leaf-bearing, tendril-bearing, and root climbing. Climbing plants, in fact, employ a diversity of strategies to make use of trees, bluffs, and even human-created vertical structures to seek the way to the greatest amount of sunlight.


The study of climbing plant behavior is based on Darwin's observations on the oscillatory movements of exploring stems and tendrils (i.e., *circumnutation*; Darwin, 1875). Since Darwin's time, a plethora of studies have investigated the underlying mechanisms of the stimulus searching and attachment behaviors of climbing plants at the anatomical (Tronchet, 1945, 1946), biomechanical (Gerbode et al., 2012; Putz & Holbrook, 1992), physiological (Bauer et al., 2011; Jaffe & Galston, 1968; Stolarz, 2009), and cellular (Bowling & Vaughn, 2009; Weiler et al., 1993) levels.

Alessandro Peressotti  <https://orcid.org/0000-0001-8804-7935>

Francesca Peressotti  <https://orcid.org/0000-0002-2425-9231>

Walter Baccinelli  <https://orcid.org/0000-0001-8888-4792>

Maria Bulgheroni  <https://orcid.org/0000-0001-8484-9834>

Umberto Castiello  <https://orcid.org/0000-0003-0629-1286>

The present work was carried out within the scope of the research program Dipartimenti di Eccellenza (art.1, commi 314–337 legge 232/2016), which was supported by a Grant from MIUR (Ministry of Education, University and Research) to the Department of General Psychology, University of Padova.

Silvia Guerra served as a lead for conceptualization and data curation, and also served in a supporting role for writing (original draft) and

contributed equally to writing (review and editing). Bianca Bonato contributed equally to data curation. Qiuran Wang contributed equally to data curation. Francesco Ceccarini contributed equally to data curation. Alessandro Peressotti contributed equally to conceptualization and writing (review and editing). Francesca Peressotti contributed equally to conceptualization and writing (review and editing). Walter Baccinelli served as a lead for software. Maria Bulgheroni served as a lead for software. Umberto Castiello served as a lead for conceptualization, supervision, writing (original draft and review and editing) and contributed equally to methodology.

The authors declare no competing interests.

Correspondence concerning this article should be addressed to Silvia Guerra, Dipartimento di Psicologia Generale, Università degli studi di Padova, Via Venezia 8, 3513, Padova, Italy. Email: [silvia.guerra.5@phd.unipd.it](mailto:silvia.guerra.5@phd.unipd.it)

Despite the prolonged fascination with climbing plants, we know surprisingly little about how climbers make “decisions” with regard to stimulus searching and attachment behaviors. When Darwin (1875) conducted simple experiments indoors, he noted that vines are not only able to locate their supports and grow toward them but can even show aversion toward some of them. He first described this effect with regard to *Bignonia capreolata* L. tendrils that initially seized and then let go of sticks that were inappropriate in terms of size (Darwin, 1875). Darwin (1875) also observed that when the *B. capreolata* L. tendrils came into contact with a stimulus (i.e., a stick), they were able to bend and curl around it. If, instead, because of its thickness or excessive smoothness a stimulus was perceived as “inadequate,” after initially seizing it, the tendrils let go of it. A similar phenomenon was observed when herbaceous twining vines came into contact with a very thick trunk. Instead of winding around the tree trunk, they wound around themselves. As far as annual vines were concerned, Darwin (1875) commented that, independently of diameter constraints, it would have been maladaptive for the vines to wrap around thick, hence large, trees, as they would improbably reach higher light levels by the end of the growing season.

The cases cited above provide a degree of support to speculative claims that some climbing plants are able to modify their *circumnutation* patterns to a greater or lesser extent depending on features of the stimulus targets with respect to what would be expected by chance movement (Raja et al., 2020; Tronchet, 1946, 1977). Experimental evidence demonstrating that this might indeed be the case has been forthcoming from recent studies that used kinematic analysis to characterize the movements of the tendrils of pea plants (*Pisum sativum* L.) that appeared to be modulated depending on the features of the stimulus (Ceccarini et al., 2020, 2021; Guerra et al., 2019; for a review, see Castiello, 2021). Guerra and colleagues (2019), for example, recently demonstrated that pea plants (*P. sativum* L.) are able to perceive a stimulus and to modulate the kinematics of the tendrils’ aperture depending on its thickness. The aperture of the tendrils refers to the maximum distance between the tips of two tendrils reached during movements leaning toward a stimulus. The average and the maximum velocity of the tendrils were found to be higher for thinner stimuli compared with thicker ones. In temporal terms, it took more time for the tendrils to reach peak velocity and maximum aperture, calculated as percentages of the movement’s duration, when the stimuli were thinner. Likewise, the maximum distance between the tendrils was significantly greater for the thinner with respect to thicker stimuli (Guerra et al., 2019).

Another study has moreover provided evidence indicating that the movement of pea plants (*P. sativum* L.) obeys the speed–accuracy trade-off (Woodworth, 1899) principle. Speed–accuracy trade-off is a property of aimed movements present in a wide range of species, from insects to primates (Chittka et al., 2009). Studies investigating the revolving movement of the tips of the shoots of climbing plants reaching to grasp a stimulus found that pea plants (*P. sativum* L.) are able to process the properties of the stimulus even before any above-ground organ of the plant (e.g., tendrils, apex) makes mechanical contact with the stimulus, and, just as animals, they are able to modulate movement velocity strategically depending on the difficulty of the task at hand. One study recently reported that the average and the maximum tendril velocities were faster when the plants needed to reach and grasp a thinner rather

than a thicker stimulus (Ceccarini et al., 2020). These results are in line with previous evidence highlighting the “preference” of climbing plants for thinner over thicker stimuli (Carrasco-Urra & Gianoli, 2009; Darwin, 1875; Goriely & Neukirch, 2006; Putz & Holbrook, 1992). Reaching to grasp thick stimuli (i.e., those with larger diameters) is usually considered more “difficult” because it is more energy consuming compared with grasping thinner ones. In fact, it implies that the plant not only needs to increase the length of its tendrils to efficiently wrap itself around the stimulus (Rowe et al., 2006) but also has to strengthen tensional forces to counteract gravity (Gianoli, 2015; Sousa-Baena et al., 2021).

The hypothesis that climbing plants may have evolved a growth accuracy mechanism to improve the precision of their movement and if/how it may differ from the one used by animals has also been investigated (Ceccarini et al., 2021). This study results demonstrated that plants correct their movement in flight and strategically increase the production of secondary submovements when the task requires more accuracy, just as human beings do (Meyer et al., 1988; Novak et al., 2002). Altogether these findings indicate that plants are capable of extracting the “graspable” properties of the stimulus that permits them to select the most opportune movement and behavior to reach more light. In other words, plants have a tendency for tendril movement speed to covary with tendril movement accuracy (Ceccarini et al., 2020, 2021), something that would point in the direction of higher level processing. Climbing plants seem to plan actions in terms of their perceivable consequences such as selecting, planning, and initiating, suggesting that such activities are mediated by action–effect anticipations (Calvo & Friston, 2017). This leads to the hypothesis that plants may be endowed with purposeful, anticipatory behavior.

The mechanisms underlying thickness coding by plants remain obscure (Ceccarini et al., 2020, 2021; Guerra et al., 2019). A variety of hypotheses based on plants’ exceptional perception abilities have been put forward. Some recent reports have, for example, demonstrated that proprioception in plants is mediated by the long actin filaments in elongating fiber cells, which, acting as a bending tensile sensor, perceive the plant’s posture (Hamant & Moullia, 2016). These findings have been corroborated by studies on *Arabidopsis* mutants defective in actins (specifically ACTIN-8), which exhibit peculiar reactions, such as hyperbending and sustained oscillations of the stem in response to gravity, tilting, or other external perturbations (e.g., light stimuli; Okamoto et al., 2015). Proprioception may allow climbing plants to perceive the position of their tendrils and contribute to generating the necessary feedback information required for adjusting their aperture to the stimulus’ thickness. In addition to proprioception, plants have at their disposal a great variety of other sensory modalities (Karban, 2015), including vision (Crepey & Casal, 2015), acoustic perception (Gagliano et al., 2012), and chemosensory perception (Weidenhamer, 2016).

To begin with, climbing plants seem to have evolved a *plant-specific vision system* that processes the intrinsic and extrinsic properties of the stimulus. The findings of several studies suggest that the upper and subepidermis parts of a leaf comprise cells acting as *ocelli*, eye-like structures, allowing plants to gather visual information about their environment (Baluška & Mancuso, 2016). Support for this concept has been produced by studies investigating *Boquila trifoliolata* (Carrasco-Urra & Gianoli, 2009), which modifies the appearance of its leaves according to the host plant and perfectly

mimics the colors, shapes, sizes, orientations, and petiole lengths of the leaves. Crucially, the plant leaf mimicry occurs even without direct contact between the *Boquilla trifoliolata* vine and the host tree it is mimicking, a finding that supports the idea that plants are capable not only of sensing but also of decoding visual inputs (Carrasco-Urra & Gianoli, 2009). Given these visual capabilities, plants may correct the trajectory of their tendrils using visual information.

Plants can also use *echolocation* to acquire information about a stimulus. Recent reports have, in fact, shown that plants gain information about their surroundings by emitting sonic clicks and perceiving the returning echoes (Gagliano et al., 2012). This *bio sonar* presumably provides information about the stimulus' position and directs the tendrils toward the object to be grasped. Finally, plants may acquire information about the stimulus using *chemoreception of volatiles*. It is well known that plants release airborne chemicals that can convey ecologically relevant information about the stimuli with which they are interacting (Karban, 2015). Some parasitic plants, such as the *Cuscuta pentagona* Engelm, for example, localize host plants via airborne chemicals (Runyon et al., 2006).

Although these sensory mechanisms are all concerned with the aerial sector of plants, the roots and in particular their extreme tip (i.e., root cap) may also be involved in thickness sensing. The cap seems to be able to respond to numerous signals (e.g., gravity, touch, humidity), assess them, and dynamically control the direction of root growth (Hammond & White, 2011; Trewavas, 2017). Root caps, which make up a large part of a plant's body, are interconnected via vascular strands with their polarly transported auxin. A great deal of plant decision-making can be ascribed to the root cap system (Baluška et al., 2004, 2009). Consider the highly sophisticated responses of roots, such as gravitropisms and thigmotropism (Baluška et al., 2007; Braam, 2005). Roots, for instance, stop developing downward when they encounter a physical obstacle and instead begin to grow horizontally. Roots seem to be able to respond to stimuli and periodically try to move downward, remaining horizontal if unable to respond gravitropically (Massa & Gilroy, 2003).

Roots have also shown salt-avoidance behavior (Li & Zhang, 2008). As salinity interacts with the gravitropic response of shoots, plants are forced to assess the overall integrated signal to optimize shoot growth under abnormal saline conditions. It has been reported that phenotypic plasticity is the result of overall signal integration and not of a fixed graviresponse (Barlow, 2010; Trewavas, 2005).

It is however still unknown that signals are chiefly involved in obstacle perception, although the touch sensor is the most likely candidate given its immediate physical interaction with the obstacle. It is also unknown which component(s) or organelles in the root cells are utilized to perceive a mechanical force, and how they convert a physical touch signal to the auxin system. Auxins are a class of plant hormones that play a cardinal role in coordinating many growth and behavioral processes in plant life cycles and are essential for plant body development. There is also evidence that obstacle avoidance may rely on root exudates, the cocktail of compounds that are secreted by roots, at the root cap (Semchenko et al., 2008). Root recognition and navigation around physical obstacles is in fact prevented when activated charcoal, which absorbs many compounds, is inserted into the substrate (Mahall & Callaway, 1992).

In the light of all of these considerations, the research question addressed by the current study is: Are roots able to sense the thickness of a potentially available stimulus?

To test this, following in the footsteps of our previous studies (Ceccarini et al., 2020, 2021; Guerra et al., 2019), we performed two experiments in which kinematics was used to characterize the movement of *circumnutation* of the tendrils of a climbing plant (*P. sativum* L.) as they approach a stimulus. In Experiment 1, we set out to replicate the kinematical effects observed when stimuli of different thicknesses are available to the root system (Ceccarini et al., 2020, 2021; Guerra et al., 2019). One group of plants was tested with a "Thick" stimulus (3 cm diameter); another with a "Thin" one (1.2 cm diameter). In line with previous findings (Guerra et al., 2019), we expected the peaks of the average and maximum velocities of the tendrils to be higher for the thinner stimulus with respect to the thicker ones and the times it took the tendrils to reach the peak velocity and the maximum aperture to be later for the thinner with respect to the thicker ones. Finally, we expected the maximum distance between the tendrils to be significantly greater for the thinner with respect to the thicker stimuli. Experiment 2 was a replication of Experiment 1 except that the stimulus was lifted to the ground by means of an ad hoc apparatus. This manipulation allowed investigating the pattern of tendrils movement when the stimulus is unavailable to the root system. We hypothesized that (a) if the root system *plays a pivotal role* in determining tendril shaping during growth, then kinematical scaling of the velocity and aperture of the tendrils depending on the thickness of a stimulus is affected when the stimulus is not in the ground because that information is not available to the root system; (b) if the root system *does not play a pivotal role* in determining the tendril shaping during growth, then the kinematical scaling depending on the thickness of a stimulus should take place even in the case in which the stimulus is unavailable to the root system as thickness information could be coded by an aerial component of the plants (e.g., tendrils or the apex).

## Materials and Method

### Subjects

Ten and 21 snow peas (*P. sativum* var. *saccharatum* cv Carouby de Maussane) were chosen as the study plants for the Experiments 1 and 2, respectively (see Table 1). Healthy-looking pea seeds were selected, potted, and kept at the conditions outlined below. The plants were randomly assigned to the two experimental conditions.

### Stimuli

For Experiment 1, the stimuli were 60 cm in height wooden poles, either with a 3 cm diameter (the "thick" stimulus) or with a 1.2 cm diameter (the "thin" stimulus; Figure 1a). For Experiment 2, the very same stimuli were used, but they were lifted to the ground by means of an ad hoc apparatus (Figure 1b). For both experiments the stimulus was positioned at a distance of 12 cm from the plant's first unifoliate leaf (see Figure 1).

**Table 1**  
*Sample Description*

Stimulus	Thick	Thin
	Experiment 1	
No.	5	5
Distance	12 cm	12 cm
Germination period	6 d ( $\pm 1.6$ ; range 5–10)	6 d ( $\pm 0.4$ ; range 4–6)
Age	22 d ( $\pm 1.4$ ; range 19–23)	15 d ( $\pm 3.2$ ; range 14–26)
	Experiment 2	
Stimulus	Thick	Thin
No.	10	11
Distance	12 cm	12 cm
Germination period	5.5 d ( $\pm 1.5$ ; range 4–9)	6 d ( $\pm 1$ ; range 4–8)
Age	19.5 d ( $\pm 6$ ; range 11–31)	18 d ( $\pm 4$ ; range 14–37)

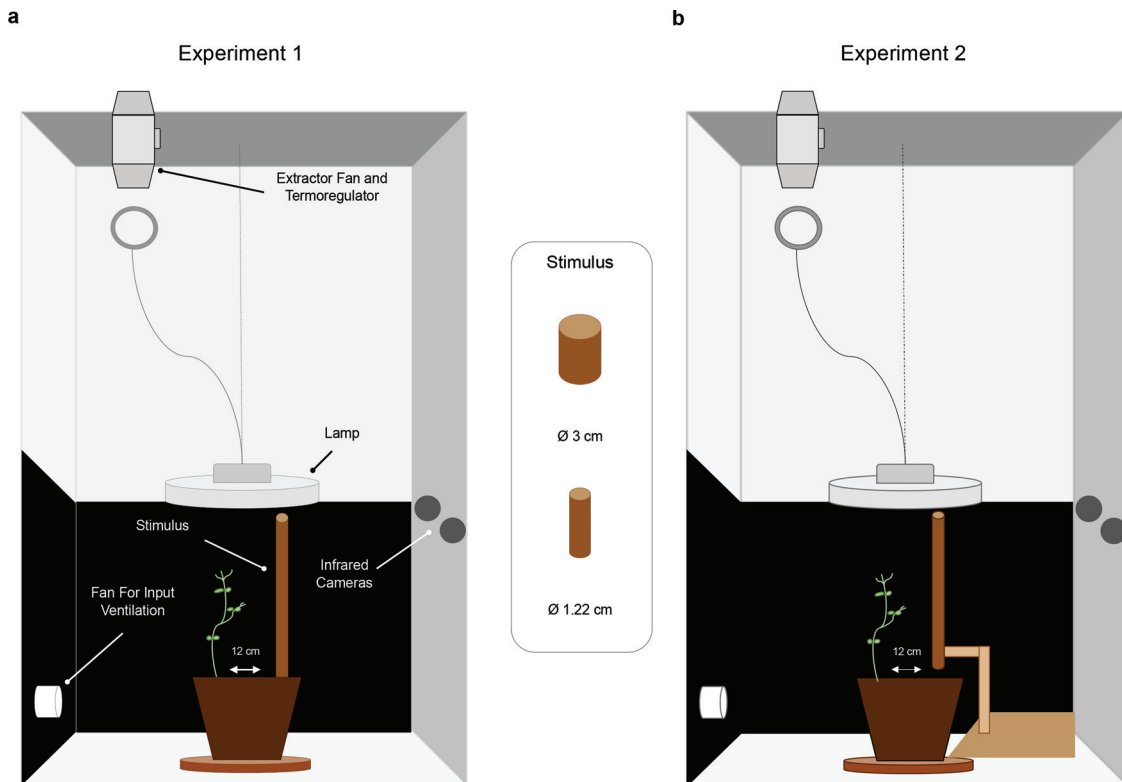
*Note.* Germination period and age, which are expressed in days, refer to the median, whereas median absolute deviation is noted in parentheses.

### Germination and Growth Conditions

Cylindrical pots (D 30 cm height 14 cm) were filled with silica sand (type 16SS, dimension .8/1.2 mm, weight 1.4). At the beginning of each experiment, the pots were watered and fertilized using a half-strength solution culture (Murashige and Skoog Basal Salt Micronutrient Solution; 10 $\times$ , liquid, plant cell culture tested; Sigma Life Science). The pots were then watered with tap water as needed 3 times a week. One seed per pot was placed at a distance of 8 cm from the pot's border and sowed at a depth of 2.5 cm. Each pot was then enclosed in growth chamber (Cultibox SG

combi 80  $\times$  80  $\times$  160 cm) so that the seeds could germinate and grow in controlled environmental conditions. The chamber air temperature was set at 26°C; the extractor fan was equipped with a thermo-regulator (TT125; 125 mm diameter; max 280 MC/H vents) and there was an input-ventilation fan (Blauberg Tubo 100–102 m<sup>3</sup>/h). The two-fan combination allowed for a steady air flow rate into the growth chamber with a mean air residence time of 60 s. The fan was placed so that air movement did not affect the plants' movements. Plants were grown with an 11.25-hr photoperiod (5.45 a.m. to 5 p.m.) under a cool white led lamp (V-TAC innovative LED lighting, VT-911-100W, Des Moines, IA, USA or

**Figure 1**  
*Graphical Representation Shows the Setup for (a) Experiment 1 and (b) Experiment 2*



*Note.* For Experiment 2, the stimulus is raised above ground. See the online article for the color version of this figure.



100W Samsung UFO 145 lm/W—LIFUD) that was positioned 50 cm above each seedling. Photosynthetic Photon Flux Density at 50 cm under the lamp in correspondence of the seedling was 350  $\mu\text{molph m}^{-2} \text{s}^{-1}$  (quantum sensor LI-190R, Lincoln, NE, USA). Reflective Mylar film of chamber walls allowed for better uniformity in light distribution. The experimental methodology was applied to the single plants that were grown individually in a growing chamber.

## Video Recording and Data Analysis

For each growth chamber, a pair of RGB-infrared cameras (i.e., IP 2.1 Mpx outdoor varifocal IR 1080P) were placed 110 cm above the ground, spaced at a distance of 45 cm to record stereo images of the plant. The cameras were connected via Ethernet cables to a 10-port wireless router (i.e., D-link Dsr-250n) connected via Wi-Fi to a PC and the frame acquisition and saving process were controlled by CamRecorder software (Ab.Acus s.r.l., Milan, Italy). To maximize the contrast between the peas' anatomical landmarks (e.g., the tendrils) and the background, black felt velvet was fixed on some sectors of the walls of the boxes and the wooden stimuli were darkened with charcoal. The intrinsic, extrinsic, and the lens distortion parameters of each camera were estimated using a Matlab Camera Calibrator app. Depth extraction from the single images was carried out by taking 20 pictures of a chessboard (squares' side 18 mm, 10 columns, seven rows) from multiple angles and distances in natural nondirect light conditions. For stereo calibration, the same chessboard used for the single camera calibration process was placed in the middle of the growth chamber. The photos were then taken by the two cameras to extract the stereo calibration parameters. In accordance with the experimental protocol, a frame was synchronously acquired every 3 min (frequency .0056 Hz) by the cameras. An ad hoc software (Ab.Acus s.r.l., Milan, Italy) developed by Matlab was used to position the markers, track their position frame-by-frame on the images acquired by the two cameras to reconstruct the three-dimensional trajectory of each marker.

The tendrils developing from the selected node were studied. In those cases in which the plant grasped the stimulus, the coiled leaf was analyzed. When no grasping occurred, the first node, counting from the bottom of the plant, characterized by two or three tendrils was examined. The initial frame was defined as the frame in which the tendrils of the considered leaf were visible from the apex. The end of plant movement was defined as the frame in which the tendrils of the leaf started to coil around the stimulus or a frame in which the tendrils remained apart. The markers on the anatomical landmarks of interest, namely the apex, the node below the tendrils, and the tips of the tendrils were inserted posthoc (see Figure 2). The markers were also positioned on the stimulus (i.e., on both the lowest and the highest point of the stimulus), the bottom of the stem, the second leaf and the internode as reference points.

The tracking procedures were at first performed automatically throughout the time course of the movement sequence using the Kanade–Lucas–Tomasi algorithm on the frames acquired by each camera, after distortion removal. The tracking was manually verified by the experimenter, who checked the position of the markers frame-by-frame. The three-dimensional trajectory of each tracked marker was computed by triangulating the two-dimensional trajectories obtained from the two cameras (Figure 2b and 2c). The

dependent variables specifically tailored to test our experimental hypothesis on the basis of previous evidence (Guerra et al., 2019) were: (a) the spatial trajectories of the landmarks considered; (b) the average and the maximum velocity of the tendrils during *circumnutation*; (c) the time it took for maximum tendril velocity to be reached; (d) the maximum aperture of the tendrils corresponding to the maximum distance reached by the tip of the tendrils during the approach phase; (e) the time it took for the maximum aperture of the tendrils to be reached.

Statistical tests were carried out to compare the median values of each of the dependent measures considered across all of the conditions using the Wilcoxon rank sum test (one-tailed). In addition to *W*-statistic and the *p*-value, we report the effect's size calculated as  $r = z/\sqrt{N}$ , in which *z* is the *z*-score and *N* is the total number of observations (Rosenthal, 1991). All statistical analyses were carried out using the computing environment R (R Core Team, 2013) software and the function *wilcox.test*. The procedures for video recording and the statistical analyses apply to all the experiments carried out during the study.

## Results

### Qualitative Results

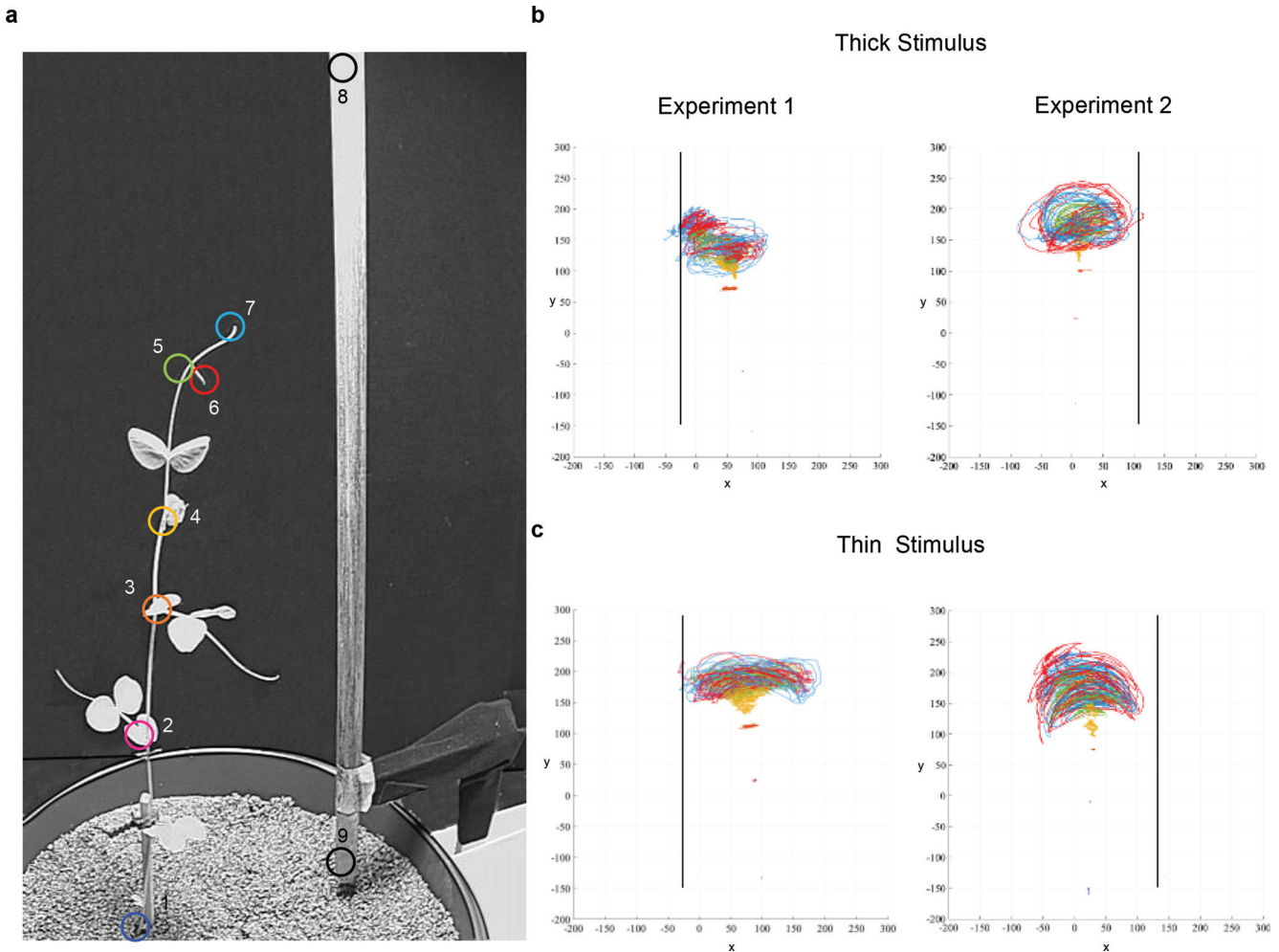
All the plant organs (i.e., the apex, the node below the tendrils, and the tendrils) showed a growing movement pattern characterized by *circumnutation* (please refer to Figure 2b and 2c). The growing movement appeared to be driven by the plant's intent to find a stimulus in the environment. In Experiment 1, once the plant perceived the stimulus, it started to move toward it and the tendrils began a choreography to grasp the stimulus (please refer to Video S1 in the online supplemental materials). A similar behavior was observed also in Experiment 2 but only when the tendrils touched the stimulus accidentally. In this case, plants quickly modified their trajectories and started moving toward it until they reached it (please refer to Figure 2b). Noticeably, this occurred only for the thicker stimulus (please refer to Video S2 in the online supplemental materials). When the stimulus was thinner, the plants continued to move toward the light because, given the reduced dimension of the thin stimulus, it might be impossible for them to touch it accidentally (please refer to Figure 2c and Video S2 in the online supplemental materials). The search patterns exhibited by the plants seemed systematic rather than random and might be equated to the systematic spiral search pattern that has been described for animals such as ants (Pfeffer et al., 2015). Future research will be able to increase our knowledge on this fascinating parallel and, in particular, on the nature of the movement and functional response of plants in different environmental conditions.

### Kinematical Results

As shown in Table 2, the dependent variables considered for the thinner and thicker stimuli were significantly different in Experiment 1. The average and the maximum tendril velocities were significantly higher for the thinner with respect to the thicker conditions. The time at which the maximum tendril velocity was reached earlier for the thicker than the thinner condition. The maximum tendril aperture, corresponding to the maximum distance reached by the tips of the tendrils during the approach phase, was

**Figure 2**

The Landmarks Considered and Examples of the Spatial Trajectories for Experiments 1 and 2. (a) The Landmarks Considered Were: the Base of the Stem (1), The Second Leaf (2), The Internode (3), The Apex (4), The Node Below the Tendrils (5), The Tip of the Tendrils (6, 7), and The Stimulus (8, 9). The Colors of the Circles Correspond to the Colors of the Trajectories Shown in the Right-Side Panel. (b) The Trajectories for all the Landmarks for the “Thick” Stimulus Condition in Experiments 1 and 2 are Shown. (c) The Trajectories for all the Landmarks for the “Thin” Stimulus Condition in Experiments 1 and 2 are Shown



*Note.* The axes  $x$  and  $y$  refer to the sagittal and vertical axis in mm, respectively. See the online article for the color version of this figure.

wider for the thinner than the thicker conditions. The time at which the maximum distance was reached was earlier for the thicker than the thinner condition. These results confirm that when the roots can access the stimulus, physically or possibly via exudates, the plant is able to perceive it and to plan movements depending on its size (Ceccarini et al., 2020, 2021; Guerra et al., 2019). In Experiment 2, no significant differences for the dependent variables considered were found (see Table 2). Presumably, when the roots cannot access the stimulus, physically or via root exudates, the plant is unable to perceive it or to plan movements appropriate to the stimulus' size.

### General Discussion

The current study set out to investigate how the root system of pea plants (*P. sativum* L.) contributes to perceiving and responding

to stimuli (i.e., pole supports) of different sizes. The results indicate that if the roots do not have access to the stimulus, the plant does not modulate its tendrils' response to different thicknesses. Instead, when the stimulus is available to the root system, the plant perceives and responds to different stimulus thicknesses (Experiment 1; Ceccarini et al., 2020, 2021; Guerra et al., 2019). In fact, study results showed that the plant not only acknowledged the presence of the stimulus but also scaled the kinematics of the tendrils depending on the stimulus' thickness. The average and maximum tendril velocities were higher for the thinner than the thicker stimulus. In temporal terms, it took longer for the tendrils to reach peak velocity and maximum aperture, both calculated as a percentage of movement duration, for the thinner than the thicker stimulus. Likewise, the maximum distance between the tendrils was significantly greater for the thinner than thicker stimulus. These findings signify that thanks to their root systems, climbing plants

**Table 2**  
Kinematical and Statistical Values for Experiments 1 and 2

Thick vs. thin stimulus	Median		W	p	r
	Thick	Thin			
Experiment 1					
Average tendril velocity (mm/min)	1.24	2.91	200	0.002	0.69
Maximum tendril velocity (mm/min)	5.24	17.25	218	0.001	0.73
Time of maximum tendril velocity (%)	64.21	90.2	156	0.037	0.38
Maximum tendril aperture (mm)	51.31	76.83	161	0.022	0.41
Time of maximum tendril aperture (%)	41.61	76.32	156	0.037	0.38
Experiment 2					
Average tendrils velocity (mm/min)	2.38	2.23	798	0.839	0.02
Maximum tendril velocity (mm/min)	10.62	11.75	739	0.449	0.08
Time of maximum tendril velocity (%)	39.40	47.29	814	0.958	0.01
Maximum tendril aperture (mm)	42.20	48.20	311	0.135	0.20
Time of maximum tendril aperture (%)	58.84	88.58	359	0.467	0.10

Note. % = percentage of movement duration.

have the ability to extract the “graspable” properties of a stimulus and then to plan and implement appropriate beneficial behavior. Just as animals, climbing plants seem to rely on sensorial mechanisms to reach a stimulus. Thus, contrary to what was previously thought, they drive their tendrils using more than just the contact sense (Darwin, 1875; Jaffe, 1979).

Notably, if the roots are unable to access the stimulus, the plant is left in the dark so to speak. It would seem, in fact, that the mechanisms of the aerial part of the plant are unable on their own or in concert to provide the plant with thickness information. Without information from the roots, the plants appeared disorientated and the radius of the shoot movement increased as if it were searching for a potential support. Yet when the tendrils touched the stimulus accidentally, they quickly modified their trajectories and started moving toward it stretching out to touch it. These findings agree with other descriptions of the movement of tendrils (Darwin, 1875; Jaffe, 1979; Jaffe & Galston, 1968). Tendrils first present a slow rotation through space (i.e., they circumnutate) until they make contact with a stimulus. The *circumnutation* then ceases as the tendril begins to coil around the stimulus (Jaffe, 1979; Jaffe & Galston, 1968). If the stimulus is inaccessible to touch, as in the case of a thin stimulus, then the tendrils remain straight.

The key functions of the roots are to acquire nutrients and water and to provide anchorage for the plant. Indeed, the vast majority of studies have focused on foraging strategies by the roots and their behavioral responses to multiple environmental cues such as the heterogeneous soil environment and the presence of other factors such as competitors (reviewed by Cahill & McNickle, 2011; Hodge, 2004, 2009). More recently, however, roots' ability to monitor and integrate numerous parameters simultaneously and to “translate” these sensory “experiences” into complex motoric responses has been described (Gandar, 1983; Massa & Gilroy, 2003; Semchenko et al., 2008). For instance, growing root apices can, under appropriate circumstances, perform crawling-like searching movements (Baluška et al., 2009; Edelmann & Roth, 2006) that closely resemble the behavior of lower metazoans such as corals and jellyfish (Darwin & Darwin, 1880; see also Barlow, 2006; Kutschera & Niklas, 2009). A similarity between roots and lower animals (i.e., the so-called “root-brain hypothesis”) was proposed by Charles Darwin and his son Francis. They observed that

roots tend to avoid inanimate obstacles, a behavior that is more dominant than the root's tendency to develop geotropically (Darwin & Darwin, 1880). They also noted that when the tip of *Vicia* roots came into contact with a thin glass plate at a steep angle, it modified its morphology and growth direction. Another similar example refers to the tip of the radicle that can distinguish between harder and softer objects pressed upon it. If the tip perceives the air to be moister on one of the sides, it transmits the information to the upper adjoining part, which bends toward the source of moisture. In almost every case, the movements reported seemed to be driven by a goal (Darwin & Darwin, 1880). In other words, the fate and the morphology of roots seem to be determined by complex interactions with various environmental factors such as potential physical obstructions and objects in the soil. When they make contact with physical obstacles, roots tend to grow toward areas of least resistance (Clark et al., 2003; Kozłowski, 1999). Circumventing physical obstacles could be critical for the plant's survival and performance, especially in rocky environments or when the soil is compacted. Wilson (1967), who was one of the first to investigate the pattern of woody root growth in maple trees in the presence of artificial barriers, showed that tree roots tended to return to their original growth point when they detected an obstacle. It has subsequently, been demonstrated that in *Arabidopsis thaliana* there are six genes involved in the stimulus–response interaction. In other words, the interaction between obstacles and the root cap affects the geotropic response that eventually reorients the roots leading them to grow along obstacles (Okada & Shimura, 1990).

Although it has long been known that roots have the ability to circumvent obstacles (Darwin & Darwin, 1880; Montagu et al., 1998; Simojoki, 2001), the mechanism underlying the obstacle avoidance response by roots is poorly understood. The root bending response, which does not seem to be just a passive response to an obstacle, appears to depend on a complex process. Evidence suggests that root obstacle avoidance is driven by the accumulation of root exudates at the root cap (Semchenko et al., 2008). It has recently been demonstrated that the bending of a root away from an obstacle involves active signal transduction and depends on both the mediated auxin transport and the PIN-FORMED (PIN)-mediated auxin transport and the transport inhibitor response 1/auxin signaling F-box protein auxin signaling pathway (Lee et al., 2020;



Zhang & Friml, 2020). Other findings have confirmed that physical obstruction induces changes in the placement of root mass such as fewer and lower lateral roots not noted in areas without obstacles (Hodge, 2009; Semchenko et al., 2008).

Whether roots are also able to process the intrinsic features of the objects they encounter has received little attention in ecological and physiological literature. In this respect, the results outlined here not only confirm that the roots of pea plants (*P. sativum* L.) are sensitive to inanimate objects (Takahashi & Suge, 1991) but also that such ability extends to the coding of structural characteristics (i.e., thickness).

It has already been demonstrated that pea plants are able to detect and avoid inanimate objects in the soil (*P. sativum* L.; Falik et al., 2005). This effect appeared to be mediated by the diffusion and accumulation of root exudates in the vicinity of the objects, causing inhibited root growth in the direction of the accumulated exudates (Falik et al., 2005). It has been experimentally proven that plants do not perceive objects and even grow toward them if exudates have been removed from the substrate (Falik et al., 2005). This mechanism might also explain our results. The diffusion and accumulation of root exudates serve not only to avoid growth in the vicinity of inanimate objects (Darwin & Darwin, 1880; Falik et al., 2005; Leyser & Day, 2003) but also to process the features of the objects encountered. In other words, diffusion properties, accumulation and effectiveness of exudates may signal the physical properties of a potential stimulus. Although study findings have not identified the substances that are responsible for the ability to process object thickness, they suggest that chemical compounds might be involved to this endeavor.

### Conclusions

The present study has provided evidence that the root system of pea plants (*P. sativum* L.) plays a pivotal role in sensing the presence and the thickness of a stimulus. Studies in a natural setting are of course warranted to verify the relevance of these findings in an ecological context (Calvo & Trewavas, 2021). The fact that a plant responds in a particular way in an unnatural environment does not necessarily mean it will do so in the natural one. Integrating these results with ecological observations may lead to identifying specific behavioral cues during stimulus sensing processes in plants, enhancing our knowledge about plant behavior.

Thus, although studies have demonstrated that roots display a wide range of sophisticated responses (that is, the ability to: [a] avoid obstacles [Falik et al., 2005], [b] recognize kin from nonkin [Dudley & File, 2007], and [c] detect nutrient patches and modify root system growth [Hodge, 2009; Hodge et al., 2009] and so forth), it should be remembered that in a natural environment, the plant and its root system are subject to a wide range of signals and stimuli. It is possible that if many things are going on, the plant ultimately responds to the strongest environmental stimulus (e.g., the availability of a nutrient or the presence of other plant roots, etc.) rather than be overwhelmed. In other words, the context in which the response is observed may ultimately be as important as the response itself. These findings nevertheless strongly support the idea that the root tip functions as a “command center” (Baluška et al., 2004) or, as recently pointed out, as a “cognitive center” (Baluška et al., 2009; Segundo-Ortín & Calvo, 2019; Castiello, 2021; Parise et al., 2020; Trewavas, 2009, 2016, 2017) implying

that it is capable of processing multiple environmental cues providing information about the underground environment and leading to adaptive behavior. The idea is in line with the “root-brain hypothesis” of Charles and Francis Darwin (Darwin & Darwin, 1880) according to which each root apex acts as both a sensory organ and a “brain-like” command center generating specific cognition and behavior (Baluška et al., 2004, 2010). Roots thus may be able to solve cognitive problems such as where, how or whether to grow at all and to field the interaction between effectors and objects (Castiello, 2021; Hodge et al., 2009; Trewavas, 2009).

### References

- Baluška, F., & Mancuso, S. (2016). Vision in plants via plant-specific ocelli? *Trends in Plant Science*, 21(9), 727–730. <https://doi.org/10.1016/j.tplants.2016.07.008>
- Baluška, F., Barlow, P. W., Volkmann, D., & Mancuso, S. (2007). Gravity-related paradoxes in plants: Plant neurobiology provides the means for their resolution. In G. Witzany (Ed.), *Biosemiotics in transdisciplinary context: Proceedings of the gathering in biosemiotics* (Vol. 6, pp. 9–35). Umweb.
- Baluška, F., Lev-Yadun, S., & Mancuso, S. (2010). Swarm intelligence in plant roots. *Trends in Ecology and Evolution*, 25(12), 682–683. <https://doi.org/10.1016/j.tree.2010.09.003>
- Baluška, F., Mancuso, S., Volkmann, D., & Barlow, P. (2004). Root apices as plant command centres: The unique ‘brain-like’ status of the root apex transition zone. *Biologia*, 59(13), 7–19.
- Baluška, F., Mancuso, S., Volkmann, D., & Barlow, P. W. (2009). The ‘root-brain’ hypothesis of Charles and Francis Darwin: Revival after more than 125 years. *Plant Signaling and Behavior*, 4(12), 1121–1127. <https://doi.org/10.4161/psb.4.12.10574>
- Barlow, P. W. (2010). Plant roots: Autopoietic and cognitive constructions. *Plant Root*, 4, 40–52. <https://doi.org/10.3117/plantroot.4.40>
- Barlow, P. W. (2006). Charles Darwin and the plant root apex: Closing a gap in living systems theory as applied to plants. In F. Baluška, S. Mancuso, & D. Volkmann (Eds.), *Communication in plants* (pp. 37–51). Springer. [https://doi.org/10.1007/978-3-540-28516-8\\_3](https://doi.org/10.1007/978-3-540-28516-8_3)
- Bauer, G., Klein, M.-C., Gorb, S. N., Speck, T., Voigt, D., & Gallenmüller, F. (2011). Always on the bright side: The climbing mechanism of *Galium aparine*. *Proceeding of the Royal Society Biological Sciences*, 278(1715), 2233–2239. <https://doi.org/10.1098/rspb.2010.2038>
- Bowling, A. J., & Vaughn, K. C. (2009). Gelatinous fibers are widespread in coiling tendrils and twining vines. *American Journal of Botany*, 96(4), 719–727. <https://doi.org/10.3732/ajb.0800373>
- Braam, J. (2005). In touch: Plant responses to mechanical stimuli. *The New Phytologist*, 165(2), 373–389. <https://doi.org/10.1111/j.1469-8137.2004.01263.x>
- Cahill, J. F., Jr., & McNickle, G. G. (2011). The behavioral ecology of nutrient foraging by plants. *Annual Review of Ecology, Evolution, and Systematics*, 42(1), 289–311. <https://doi.org/10.1146/annurev-ecolsys-102710-145006>
- Calvo, P., & Friston, K. (2017). Predicting green: Really radical (plant) predictive processing. *Journal of the Royal Society, Interface*, 14(131), Article 20170096. <https://doi.org/10.1098/rsif.2017.0096>
- Calvo, P., & Trewavas, A. (2021). Cognition and intelligence of green plants. Information for animal scientists. *Biochemical and Biophysical Research Communications*, 564, 78–85. <https://doi.org/10.1016/j.bbrc.2020.07.139>
- Carrasco-Urra, F., & Gianoli, E. (2009). Abundance of climbing plants in a southern temperate rain forest: Host tree characteristics or light availability? *Journal of Vegetation Science*, 20(6), 1155–1162. <https://doi.org/10.1111/j.1654-1103.2009.01115.x>

- Castiello, U. (2021). (Re)claiming plants in comparative psychology. *Journal of Comparative Psychology*, 135(1), 127–141. <https://doi.org/10.1037/com0000239>
- Ceccarini, F., Guerra, S., Peressotti, A., Peressotti, F., Bulgheroni, M., Baccinelli, W., Bonato, B., & Castiello, U. (2020). Speed-accuracy trade-off in plants. *Psychonomic Bulletin and Review*, 27(5), 966–973. <https://doi.org/10.3758/s13423-020-01753-4>
- Ceccarini, F., Guerra, S., Peressotti, A., Peressotti, F., Bulgheroni, M., Baccinelli, W., Bonato, B., & Castiello, U. (2021). On-line control of movement in plants. *Biochemical and Biophysical Research Communications*, 564, 86–91. <https://doi.org/10.1016/j.bbrc.2020.06.160>
- Chittka, L., Skorupski, P., & Raine, N. E. (2009). Speed-accuracy tradeoffs in animal decision making. *Trends in Ecology and Evolution*, 24(7), 400–407. <https://doi.org/10.1016/j.tree.2009.02.010>
- Clark, L. J., Whalley, W. R., & Barraclough, P. B. (2003). How do roots penetrate strong soil? *Plant and Soil*, 255(1), 93–104. <https://doi.org/10.1023/A:1026140122848>
- Crepy, M. A., & Casal, J. J. (2015). Photoreceptor-mediated kin recognition in plants. *The New Phytologist*, 205(1), 329–338. <https://doi.org/10.1111/nph.13040>
- Darwin, C. (1875). *The movements and habits of climbing plants*. John Murray.
- Darwin, C., & Darwin, F. (1880). *The power of movement in plants*. John Murray.
- Dudley, S. A., & File, A. L. (2007). Kin recognition in an annual plant. *Biology Letters*, 3(4), 435–438. <https://doi.org/10.1098/rsbl.2007.0232>
- Edelmann, H. G., & Roth, U. (2006). Gravitropic plant growth regulation and ethylene: An unsought cardinal coordinate for a disused model. *Protoplasma*, 229(2–4), 183–191. <https://doi.org/10.1007/s00709-006-0205-z>
- Falik, O., Reides, P., Gersani, M., & Novoplansky, A. (2005). Root navigation by self-inhibition. *Plant, Cell and Environment*, 28(4), 562–569. <https://doi.org/10.1111/j.1365-3040.2005.01304.x>
- Gagliano, M., Mancuso, S., & Robert, D. (2012). Towards understanding plant bioacoustics. *Trends in Plant Science*, 17(6), 323–325. <https://doi.org/10.1016/j.tplants.2012.03.002>
- Gandar, P. W. (1983). Growth in root apices. I. The kinematic description of growth. *Botanical Gazette*, 144(1), 1–10. <https://doi.org/10.1086/337337>
- Gerbode, S. J., Puzey, J. R., McCormick, A. G., & Mahadevan, L. (2012). How the cucumber tendril coils and overwinds. *Science*, 337(6098), 1087–1091. <https://doi.org/10.1126/science.1223304>
- Gianoli, E. (2015). The behavioural ecology of climbing plants. *AoB Plants*, 7, plv013. <https://doi.org/10.1093/aobpla/plv013>
- Goriely, A., & Neukirch, S. (2006). Mechanics of climbing and attachment in twining plants. *Physical Review Letters*, 97(18), Article 184302. <https://doi.org/10.1103/PhysRevLett.97.184302>
- Guerra, S., Peressotti, A., Peressotti, F., Bulgheroni, M., Baccinelli, W., D'Amico, E., Gómez, A., Massaccesi, S., Ceccarini, F., & Castiello, U. (2019). Flexible control of movement in plants. *Scientific Reports*, 9(1), Article 16570. <https://doi.org/10.1038/s41598-019-53118-0>
- Hamant, O., & Mouliat, B. (2016). How do plants read their own shapes? *The New Phytologist*, 212(2), 333–337. <https://doi.org/10.1111/nph.14143>
- Hammond, J. P., & White, P. J. (2011). Sugar signaling in root responses to low phosphorus availability. *Plant Physiology*, 156(3), 1033–1040. <https://doi.org/10.1104/pp.111.175380>
- Hodge, A. (2004). The plastic plant: Root responses to heterogeneous supplies of nutrients. *The New Phytologist*, 162(1), 9–24. <https://doi.org/10.1111/j.1469-8137.2004.01015.x>
- Hodge, A. (2009). Root decisions. *Plant, Cell and Environment*, 32(6), 628–640. <https://doi.org/10.1111/j.1365-3040.2008.01891.x>
- Hodge, A., Berta, G., Doussan, C., Merchan, F., & Crespi, M. (2009). Plant root growth, architecture and function. *Plant and Soil*, 321(1–2), 153–187. <https://doi.org/10.1007/s1104-009-9929-9>
- Jaffe, M. J. (1979). On the mechanism of contact coiling of tendrils. In F. Skoog (Ed.), *Plant growth substances 1979: Proceedings in Life Sciences*. Springer. [https://doi.org/10.1007/978-3-642-67720-5\\_49](https://doi.org/10.1007/978-3-642-67720-5_49)
- Jaffe, M. J., & Galston, A. W. (1968). The physiology of tendrils. *Annual Review of Plant Physiology*, 19(1), 417–434. <https://doi.org/10.1146/annurev.pp.19.060168.002221>
- Karban, R. (2015). *Plant sensing and communication*. University of Chicago Press. <https://doi.org/10.7208/chicago/9780226264844.001.0001>
- Kozłowski, T. T. (1999). Soil compaction and growth of woody plants. *Scandinavian Journal of Forest Research*, 14(6), 596–619. <https://doi.org/10.1080/02827589908540825>
- Kutschera, U., & Niklas, K. J. (2009). Evolutionary plant physiology: Charles Darwin's forgotten synthesis. *Naturwissenschaften*, 96(11), 1339–1354. <https://doi.org/10.1007/s00114-009-0604-z>
- Lee, H.-J., Kim, H.-S., Park, J. M., Cho, H. S., & Jeon, J. H. (2020). PIN-mediated polar auxin transport facilitates root-obstacle avoidance. *The New Phytologist*, 225(3), 1285–1296. <https://doi.org/10.1111/nph.16076>
- Leyser, O., & Day, S. (2003). *Mechanisms in plant development*. Blackwell Science.
- Li, X., & Zhang, W. (2008). Salt-avoidance tropism in *Arabidopsis thaliana*. *Plant Signaling and Behavior*, 3(5), 351–353. <https://doi.org/10.4161/psb.3.5.5371>
- Mahall, B. E., & Callaway, R. M. (1992). Root communication mechanisms and intra-community distributions of two Mojave Desert shrubs. *Ecology*, 73(6), 2145–2151. <https://doi.org/10.2307/1941462>
- Massa, G. D., & Gilroy, S. (2003). Touch modulates gravity sensing to regulate the growth of primary roots of *Arabidopsis thaliana*. *The Plant Journal*, 33(3), 435–445. <https://doi.org/10.1046/j.1365-313x.2003.01637.x>
- Meyer, D. E., Abrams, R. A., Kornblum, S., Wright, C. E., & Smith, J. E. (1988). Optimality in human motor performance: Ideal control of rapid aimed movements. *Psychological Review*, 95(3), 340–370. <https://doi.org/10.1037/0033-295x.95.3.340>
- Montagu, K. D., Conroy, J. P., & Francis, G. S. (1998). Root and shoot response of field-grown lettuce and broccoli to a compact subsoil. *Australian Journal of Agricultural Research*, 49(1), 89–97. <https://doi.org/10.1071/A97051>
- Niklas, K. J. (2011). Climbing plants: Attachment and the ascent for light. *Current Biology*, 21(5), R199–R201. <https://doi.org/10.1016/j.cub.2011.01.034>
- Novak, K. E., Miller, L. E., & Houk, J. C. (2002). The use of overlapping submovements in the control of rapid hand movements. *Experimental Brain Research*, 144(3), 351–364. <https://doi.org/10.1007/s00221-002-1060-6>
- Okada, K., & Shimura, Y. (1990). Reversible root tip rotation in *Arabidopsis* seedlings induced by obstacle-touching stimulus. *Science*, 250(4978), 274–276. <https://doi.org/10.1126/science.250.4978.274>
- Okamoto, K., Ueda, H., Shimada, T., Tamura, K., Kato, T., Tasaka, M., Morita, M. T., & Hara-Nishimura, I. (2015). Regulation of organ straightening and plant posture by an actin-myosin XI cytoskeleton. *Nature Plants*, 1(4), Article 15031. <https://doi.org/10.1038/nplants.2015.31>
- Parise, A. G., Gagliano, M., & Souza, G. M. (2020). Extended cognition in plants: Is it possible? *Plant Signaling & Behavior*, 15(2), Article 1710661. <https://doi.org/10.1080/15592324.2019.1710661>
- Putz, F. E., & Holbrook, N. M. (1992). Biomechanical studies of vines. In F. E. Putz & H. A. Mooney (Eds.), *The biology of vines* (pp. 73–98). Cambridge University Press. <https://doi.org/10.1017/CBO9780511897658.005>
- Rowe, N. P., Isnard, S., Gallenmüller, F., & Speck, T. (2006). Diversity of mechanical architectures in climbing plants: An ecological perspective. In A. Herrel, T. Speck, & N. P. Rowe (Eds.), *Ecology and biomechanics: A mechanical approach to the ecology of animals and plants* (pp. 35–59). CRC Press. <https://doi.org/10.1201/9781420001594.ch2>

- Segundo-Ortin, M., & Calvo, P. (2019). Are plants cognitive? A reply to Adams. *Studies in History and Philosophy of Science*, 73, 64–71. <https://doi.org/10.1016/j.shpsa.2018.12.001>
- Sousa-Baena, M. S., Hernandez-Lopes, J., & Van Sluys, M. A. (2021). Reaching the top through a tortuous path: Helical growth in climbing plants. *Current Opinion in Plant Biology*, 59, Article 101982. <https://doi.org/10.1016/j.pbi.2020.101982>
- Pfeffer, S. E., Bolek, S., Wolf, H., & Wittlinger, M. (2015). Nest and food search behaviour in desert ants, *Cataglyphis*: A critical comparison. *Animal Cognition*, 18(4), 885–894. <https://doi.org/10.1007/s10071-015-0858-0>
- R Core Team. (2013). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Raja, V., Silva, P. L., Holghoomi, R., & Calvo, P. (2020). The dynamics of plant nutation. *Scientific Reports*, 10(1), Article 19465. <https://doi.org/10.1038/s41598-020-76588-z>
- Rosenthal, R. (1991). *Meta-analytic procedures for social research* (2nd ed.). Sage. <https://doi.org/10.4135/9781412984997>
- Runyon, J. B., Mescher, M. C., & De Moraes, C. M. (2006). Volatile chemical cues guide host location and host selection by parasitic plants. *Science*, 313(5795), 1964–1967. <https://doi.org/10.1126/science.1131371>
- Semchenko, M., Zobel, K., Heinemeyer, A., & Hutchings, M. J. (2008). Foraging for space and avoidance of physical obstructions by plant roots: A comparative study of grasses from contrasting habitats. *The New Phytologist*, 179(4), 1162–1170. <https://doi.org/10.1111/j.1469-8137.2008.02543.x>
- Simojoki, A. (2001). Morphological responses of barley roots to soil compaction and modified supply of oxygen. *Agricultural and Food Science in Finland*, 10(1), 45–52. <https://doi.org/10.23986/afsci.5678>
- Stolarz, M. (2009). Circumnutation as a visible plant action and reaction: Physiological, cellular and molecular basis for circumnutations. *Plant Signaling and Behavior*, 4(5), 380–387. <https://doi.org/10.4161/psb.4.5.8293>
- Takahashi, H., & Suge, H. (1991). Root hydrotropism of an agravitropic pea mutant, ageotropum. *Physiologia Plantarum*, 82(1), 24–31. <https://doi.org/10.1111/j.1399-3054.1991.tb02898.x>
- Trewavas, A. (2005). Plant intelligence. *Naturwissenschaften*, 92(9), 401–413. <https://doi.org/10.1007/s00114-005-0014-9>
- Trewavas, A. (2009). What is plant behaviour? *Plant, Cell and Environment*, 32(6), 606–616. <https://doi.org/10.1111/j.1365-3040.2009.01929.x>
- Trewavas, A. (2016). Intelligence, cognition, and language of green plants. *Frontiers in Psychology*, 7, 588. <https://doi.org/10.3389/fpsyg.2016.00588>
- Trewavas, A. (2017). The foundations of plant intelligence. *Interface Focus*, 7(3), Article 20160098. <https://doi.org/10.1098/rsfs.2016.0098>
- Tronchet, A. (1945). Le comportement des vrilles en présence de tuteurs. *Bulletin de la SBF*, 92(7–8), 147–152. <https://doi.org/10.1080/00378941.1945.10834428>
- Tronchet, A. (1946). Suite de nos observations sur le comportement des vrilles en présence de tuteurs. *Bulletin de la SBF*, 93(1–2), 13–18. <https://doi.org/10.1080/00378941.1946.10834469>
- Tronchet, A. (1977). *La sensibilité des plantes*. Masson.
- Weidenhamer, J. D. (2016). Plant olfaction: Using analytical chemistry to elucidate mechanisms of plant growth and interaction. *Plant and Soil*, 407(1–2), 275–278. <https://doi.org/10.1007/s11104-016-2998-7>
- Weiler, E. W., Albrecht, T., Groth, B., Xia, Z.-Q., Luxem, M., Liß, H., Andert, L., & Spengler, P. (1993). Evidence for the involvement of jasmonates and their octadecanoid precursors in the tendril coiling response of *Bryonia dioica*. *Phytochemistry*, 32(3), 591–600. [https://doi.org/10.1016/S0031-9422\(00\)95142-2](https://doi.org/10.1016/S0031-9422(00)95142-2)
- Wilson, B. F. (1967). Root growth around barriers. *Botanical Gazette*, 128(2), 79–82. <https://doi.org/10.1086/336383>
- Woodworth, R. S. (1899). Accuracy of voluntary movement. *The Psychological Review: Monograph Supplements*, 3(3), Article 114. <https://doi.org/10.1037/h0092992>
- Zhang, Y., & Friml, J. (2020). Auxin guides roots to avoid obstacles during gravitropic growth. *The New Phytologist*, 225(3), 1049–1052. <https://doi.org/10.1111/nph.16203>

Received November 10, 2020

Revision received May 11, 2021

Accepted May 23, 2021 ■