
Article

Root-to-shoot signalling for the coding of support thickness in pea plants

Silvia Guerra¹, Bianca Bonato¹, Qiuran Wang¹, Alessandro Peressotti², Francesca Peressotti³, Walter Baccinelli⁴, Maria Bulgheroni⁴ and Umberto Castiello^{1*}

¹ Department of General Psychology, University of Padova, Padova, Italy; silvia.guerra.5@phd.unipd.it; bianca.bonato.1@phd.unipd.it; qiuran.wang@phd.unipd.it; umberto.castiello@unipd.it

² Department of Agricultural, Food, Environmental and Animal Sciences, University of Udine, Udine, Italy; alessandro.peressotti@uniud.it

³ Department of Developmental Psychology and Socialisation, University of Padova, Padova, Italy; Francesca.peressotti@unipd.it

⁴ Ab.Acus S.r.l., Milan, Italy; walterbaccinelli@ab-acus.eu; mariabulgheroni@ab-acus.com

* Correspondence: umberto.castiello@unipd.it

Simple Summary: A growing number of evidence has reported the unique ability of climbing plants to locate a support in the environment and process its different features to modulate their searching and attachment behavior accordingly. To date, the mechanism underlying the coding of support thickness are yet to be uncovered. Here, we look at the interaction between the above- (i.e., stem and tendrils) and belowground (i.e., the root system) organs of pea plants (*Pisum sativum* L.) to this endeavor by manipulating the above and belowground thickness of a support. Results suggest that the coding of object thickness is reached via a functional equilibrium subtended by a crosstalk between the grounded and the aerial components of the plant.

Abstract: Plants characterized by a soft or weak stem, such as climbing plants, need to find a potential support (e.g., wooden trunk) to reach greater light exposure. Since Darwin's research on climbing plants, several studies on their searching and attachment behaviors have demonstrated their unique ability to process different support features to modulate their movements accordingly. Nevertheless, the strategies underlying this ability are yet to be uncovered. The present research tries to fill this gap by investigating how the interaction between above- (i.e., stem, tendril, ...) and belowground (i.e., the root system) plant organs influence the kinematics of the approach-to-grasp movement. With three-dimensional (3D) kinematical analysis, we characterized the movement of pea plants (*Pisum sativum* L.) towards a support with different thicknesses above and belowground (i.e., thin below, thick aboveground, or the opposite). As a control condition, the plants were presented to supports with the same thickness below- and aboveground (i.e., either entirely thin or thick). The results suggest an integration between the information from below- and aboveground for driving the reach-to-grasp behavior of the aerial plant organs. Information about the support conveyed by the root system seems particularly important to fulfil the end-goal of the movement.

Keywords: Plant behavior; root-to-shoot signaling; circumnutation; climbing plants; kinematics

1. Introduction

Climbing plants need to attach themselves to an external support to grow vertically in order to enhance light acquisition. The availability of supports influences climber diversity in a variety of environments, and climbers that fail to encounter a support often show reduced growth and/or reproduction compared with those successfully climbing onto an external support [1]. This has been observed in forests [2,3], open habitats [4-6] and controlled environments [7,8]. Support-finding not only involves enhanced fitness, but also triggers changes in growth form, biomass allocation, morphology, and physiology

[7,9-17]. Therefore, the location of a suitable support is a key process in the life history of climbing plants [18].

The study of climbing plants behavior is based on Darwin's observations regarding the oscillatory movements, exploratory in nature, performed by the stem and the tendrils, which he named circumnutation [19]. Since then, a plethora of studies have investigated the underlying mechanisms that support the searching and attachment behaviors of climbing plants at the anatomical [20,21], biomechanical [22,23], physiological [13,14,24-26] and cellular [27,28] levels.

Nevertheless, despite the prolonged attention to climbing plants, we know surprisingly little about how climbers make 'decisions' regarding support searching and attachment behaviors [29]. When Darwin [19] conducted simple experiments indoor, he noticed that vines are not only able to locate their supports and grow towards them, but they can even show aversion to some of them. He first described this effect in *Bignonia capreolata* L. tendrils that initially seized and then let go the sticks that were inappropriate in terms of size [19]. Darwin [19] also observed that when the *Bignonia capreolata* L. tendrils encountered a support (i.e., a stick), they bend and curl around it. If, instead, because of its thickness or excessive smoothness, a support was perceived as 'inadequate', after initially seizing it, the tendrils drop it. A similar phenomenon was observed when herbaceous twining vines encountered a very thick trunk. Instead of winding around the tree trunk, they wound around themselves. Regarding annual vines, Darwin [19] commented that, independently of diameter constraints, it would have been maladaptive for the vines to wrap around thick, hence large, trees, as it would be unlikely that they would 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 can modify their circumnutation patterns to a greater or lesser extent depending on features of the targeted support, when compared with what would be expected by chance movement [12]. Indeed, several host tree attributes may determine the probability of colonization by climbers [18]. For instance, the thickness (i.e., diameter) of supports influences their suitability for twining plants. Specifically, both theoretical and empirical approaches show that when support diameter increases beyond some point, twining plants are unable to maintain tensional forces and therefore lose attachment to the trellis [2,23,30,31]. That these plants have problems to twine around a thick support was already pointed out by Darwin [19], who reported that the shoots of the twining vine *Wisteria sinensis* (Sims) Sweet could not climb onto a support about 15 cm wide. Field studies in tropical, sub-tropical and temperate rainforests confirm that the relative abundance of stem twiners decreases with increasing tree diameter [2,30,32,33]. The support-size biomechanical constraints for twining plants are intermediate compared with tendril climbers, whose upper limit of usable trunk diameter is even lower [2,23,30,33-36].

Evidence from laboratory settings further demonstrates the support-thickness effects by using kinematic analysis to characterize the movements of *Pisum sativum* L. (from now on *P. sativum*) [37-41]. Guerra and colleagues [39], for example, demonstrated that *P. sativum* plants can perceive a support and modulate the kinematics of the tendrils' velocity and aperture depending on the thickness of the support. The average and the maximum velocity of the tendrils were found to be higher for thinner supports compared to 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 support was thinner. Likewise, the maximum distance between the tendrils was significantly greater for the thinner with respect to thicker support [37-39]. This phenomenon was explained in the fact that, for plants, reaching and grasping thicker supports is a more energy-consuming process than grasping thinner supports. Indeed, grasping a

thick support implies that plants must increase the tendrils length to efficiently coil it [42], and to strengthen the tensional forces to resist gravity [12]. Since these processes are characterized by a high adenosine triphosphate (ATP) consumption, coiling thicker supports results in more energy expenditure [23]. Coherently, the reduction of movement velocity during the approaching manoeuvre and a greater aperture may allow climbing plants to preserve energy for the coiling phase to reduce the risk of errors and assure a firm attachment to the support. The reduction of movement velocity may also serve to lengthen the time window within which tendrils establish contact points with the support. Therefore, the extra time needed to reach a thick support may allow climbing plants to correct tendrils trajectories and select more accurately contact points to twin more firmly on the support.

Although both ecological and laboratory findings have provided evidence about the relationship between the behavior of climber plants and support thickness, the mechanisms underlying thickness coding and processing remain obscure [37-39]. A variety of hypotheses based on the perception abilities of plants have been put forward [43]. Some reports have, for example, demonstrated that 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 thickness of the support [44,45]. In addition to proprioception, plants may have at their disposal some kind of 'plant-specific vision system' that could process the proprieties of elements present in the environment [46,47]. Some authors have proposed the possibility of plants using echolocation to acquire information about the surroundings. Recent reports have suggested that plants could get information about their surroundings by emitting sonic clicks (i.e., clicking) and perceiving the returning echoes [48]. Finally, plants may acquire information about the external stimuli 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 [43,49,50].

While 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 [51-59]. A great deal of plant decision-making can be ascribed to the root cap system [60-63]. Consider the highly sophisticated responses of roots, such as gravitropism and thigmotropism [61,64-66]. Roots stop developing downwards when they encounter a physical obstacle and instead begin to grow horizontally [67]. The touch sensor might be the most likely candidate in obstacle perception given its immediate physical interaction with the obstacle. But there is also evidence that obstacle avoidance may rely on root exudates, the cocktail of compounds secreted by roots, which allow plants to explore the soil environment and to gain information from it [54,68,69]. In fact, root recognition and navigation around physical obstacles is prevented when activated charcoal, which absorbs many compounds, is mixed to the substrate [70,71].

The pivotal importance of the root system for the coding of support thickness has been decisively revealed in a recent study with *P. sativum* plants [40]. In one experiment, the movement of the tendrils directed to a support inserted into the substrate was investigated. In another experiment, the very same support was lifted from the ground to prevent the root system from sensing it. The results confirmed that tendrils' kinematics depend on the support thickness when it was available to the root system but not when it was unavailable to the roots. When the support was lifted from the ground, the plants continued to circumnutate but they were unable to localize it and therefore they fell down. These findings suggest that the root system is involved in sensing the presence and the thickness of a support and that the information perceived affects the planning and the execution of the approach-to-grasp movements of the climbing plants. At mini-

mum, they suggest that the plant's aboveground organs are unable to code for the thickness of the support without the sensory input from the roots. This is an intriguing and puzzling conclusion that inevitably calls for a question: why does *P. sativum* plants rely on underground stimuli to drive aboveground behavior? This is a challenging question because what the root system finds in the soil is not a reliable proxy for what is happening above it.

In the light of all these considerations, the research question addressed by the current study is to further investigate the contribution of the root system to the coding of support thickness by exploring the interactivity between the root system and the shoot growth [76]. To test this, the movement of *P. sativum* plants towards a support that differed in thickness with respect to the above- and belowground parts was assessed (i.e., perturbed conditions). A group of plants was tested with a support in which the belowground part was thin, and the aboveground part was thick ('Thin-Below' condition; see Figure 1a); and another group was tested with the inversed conditions: the support was thick belowground and thin aboveground ('Thick-Below' condition; see Figure 1b). Movements during perturbed trials were compared with one-thickness supports that could be either thin or thick (i.e., control conditions). Specifically, trials for the 'Thin-Below' perturbed condition were compared with trials for the 'Control-Thick' condition (Figure 1a,d), and movements for the 'Thick-Below' condition were compared with movements for the 'Control-Thin' condition (Figure 1b,c).

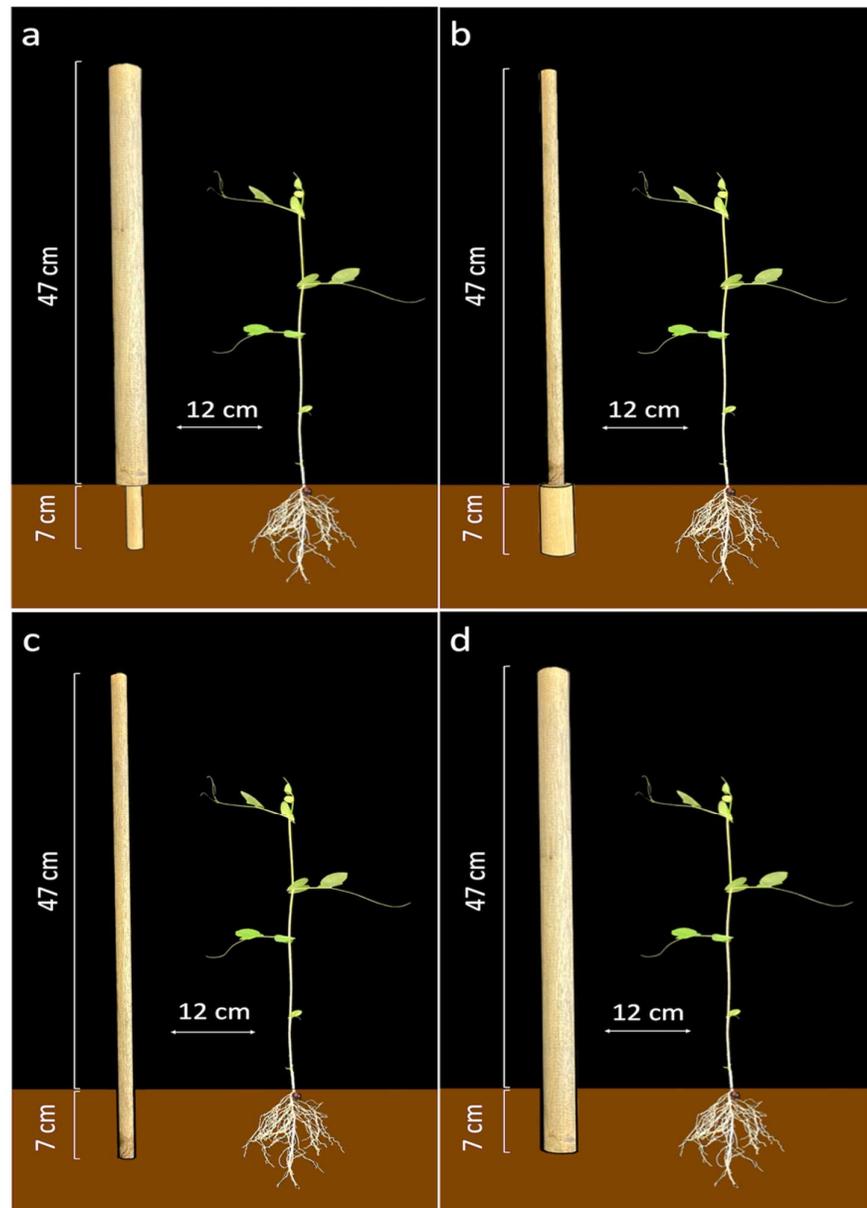


Figure 1. Support for the 'Thin-Below' condition. (a) The 'Thick-Below' condition (b), the 'Control-Thin' condition (c) and the 'Control-Thick' condition (d). The support was positioned in front of the first plant's leaf at a distance of 12 cm.

We hypothesized that if the roots play a pivotal role in sensing support thickness, then kinematical parameterization would be driven by the thickness of the belowground part of the support. In such circumstances, we expect differences between the perturbed and the control conditions because the thickness for the belowground part of the support used for the perturbed conditions differ from the thickness of the support used for the control conditions. Remember that the movement of *P. sativum* plants towards supports of different thicknesses are characterized by specific kinematical signatures [37-40].

On the other hand, if the aerial part of the plant has some involvement in sensing support thickness, then no significant differences between the perturbed and control conditions should be observed given that the thickness for the upper part of the supports used for the perturbed conditions is similar to the supports used for the control conditions.

A third hypothesis implies a crosstalk between the roots and the aerial part of the plant that inevitably will be affected by the mismatch between the below- and aboveground part of the supports. If the belowground information is incongruent with the end-goal of the movement, an adjustment by the above-ground organs (i.e., stem, tendrils, ...) should occur and the movement reprogrammed accordingly.

2. Materials and Methods

2.1. Subjects.

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

Table 1. Sample description

| Control-Thick vs Thin-Below | | |
|-----------------------------|----------------------------------|------------------------------------|
| | Control-Thick | Thin-Below |
| N° | 10 | 10 |
| Distance | 12 cm | 12 cm |
| Germination period | 6 d (\pm 0.5; Range 4 - 10) | 5 d (\pm 1.22; Range 5 - 12) |
| Age | 21 d (\pm 3.1; Range 14 - 26) | 16.5 d (\pm 1.7; Range 14 - 19) |
| Control-Thin vs Thick-Below | | |
| | Control-Thin | Thick-Below |
| N° | 10 | 10 |
| Distance | 12 cm | 12 cm |
| Germination period | 5.5 d (\pm 0.6; Range 4 - 7) | 5 d (\pm 1.5; Range 3 - 10) |
| Age | 14 d (\pm 2; Range 10 - 20) | 21.5 d (\pm 5.6; Range 9 - 26) |

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

2.2. Supports.

The supports were 54 cm height wooden poles (i.e., the belowground part of the support was 7 cm long, while the aboveground part of the support was 47 cm height) positioned at 12 cm from the plant's first unifoliate leaf (Figure 2). The support varied in diameter depending on experimental conditions (see Figure 1). For the (i) Thin-below' perturbation (Figure 1a) the belowground part of the support was 1.2 cm in diameter, whereas the aboveground part of the support was 3 cm in diameter; (ii) 'Thick-below' perturbation (Figure 1b), the belowground part of the support was 3 cm in diameter, whereas the aboveground of the support was 1.2 cm; (iii) 'Control-Thin' condition (Figure 1c) the diameter was 1.2 cm; (iv) 'Control-Thick' condition (Figure 1d) the diameter was 3 cm in diameter.

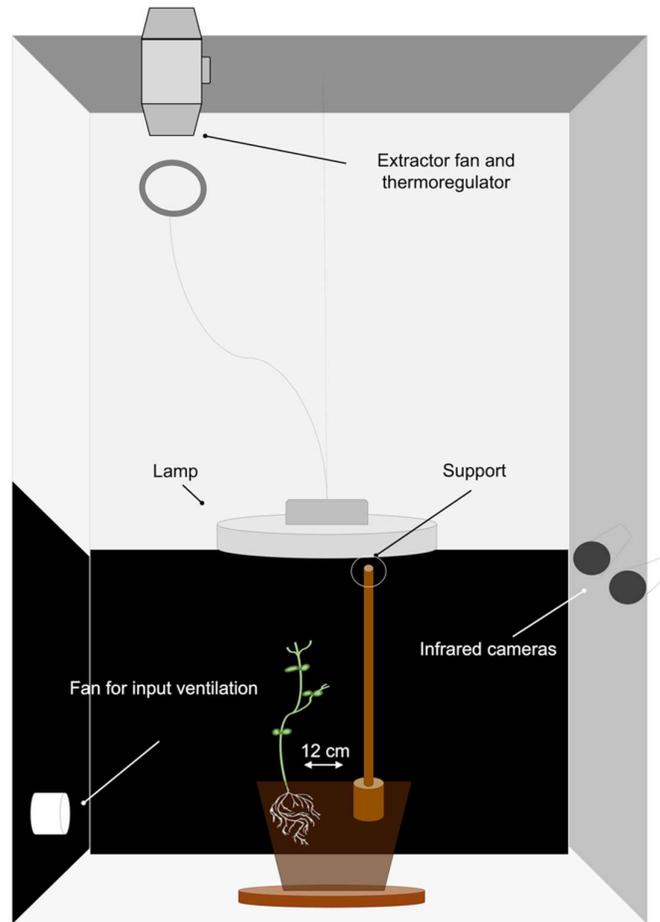


Figure 2. Graphical representation of the experimental set up. The represented example is for the 'Thick-Below' condition.

2.3. Germination and growth conditions.

Cylindrical pots (diameter 20 cm; height 20 cm) were filled with silica sand (type 16SS, dimension 0.8/1.2 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; 10x, liquid, plant cell culture tested; SIGMA Life Science). The pots were then watered with tap water as needed three times a week. One seed per pot was placed at 6 cm from the pot's border and sowed at a depth of 2.5 cm. Each pot was then enclosed in a growth chamber (Cultibox SG combi 80x80x160 cm; Figure 2) 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 - 102m³/h). The two-fan combination allowed for a steady air flow rate into the growth chamber with a mean air residence time of 60 seconds. The fan was placed so that air movement did not affect the plants' movements. Plants were grown with an 11.25- hour photoperiod (5.45 am to 5 pm) under a cool white LED lamp (V-TAC innovative LED lighting, VT-911-100W, Des Moines, IA, USA or 100W Samsung UFO 145lm/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 $\mu\text{mol}_{\text{ph}}/(\text{m}^2\text{s})$ (quantum sensor LI-190R, Lincoln, Nebraska USA). Reflective

Mylar® film of chamber walls allowed for a better uniformity in light distribution. The experimental methodology was applied to the single plants that were grown individually in a growing chamber.

2.4. 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 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 anatomical landmarks of the *P. sativum* plants (e.g., the tendrils) and the background, black felt velvet was fixed on some sectors of the walls of the boxes and the wooden supports 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 with 18 mm of side, 10 columns, 7 rows) from multiple angles and distances in natural non-direct 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 minutes (frequency 0.0056 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 3D trajectory of each marker.

In the cases where the plant grasped the support, the coiled leaf was analyzed. 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 started to coil around the support. The markers on the anatomical landmarks of interest, namely the tips of the tendrils were inserted post-hoc (Figure 3a). The markers were also positioned on the support (i.e., on both the lowest and the highest point of the support) as reference points.

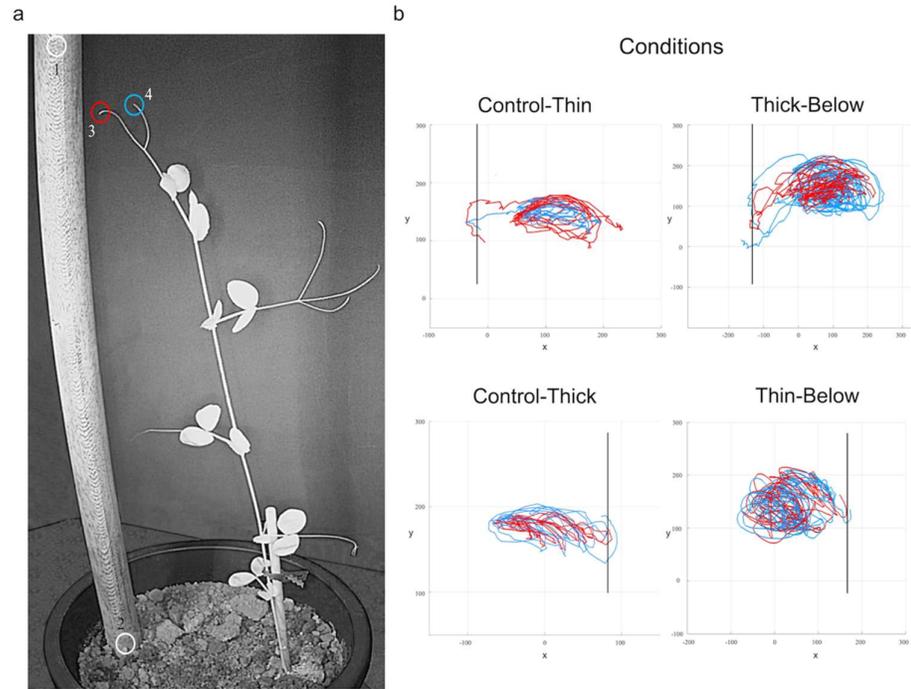


Figure 3. The landmarks considered and examples of the spatial trajectories. (a) The landmarks considered were the support (1, 2) and the tip of the tendrils (3, 4). The colors of the circles correspond to the colors of the trajectories shown in the right-side panel. Panel (b) represents the trajectories for the tip of the tendrils for the ‘Control-Thin’, ‘Thin-Below’, ‘Control-Thick’ and ‘Thick-Below’ support conditions. The support is represented by the solid vertical line. The axis x and y refer to the sagittal and vertical axis in mm, respectively.

The tracking procedures were at first performed automatically throughout the time course of the movement sequence using the Kanade-Lucas-Tomasi (KLT) 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 3D trajectory of each tracked marker was computed by triangulating the 2D trajectories obtained from the two cameras (Figure 3b). The dependent variables specifically tailored to test our experimental hypothesis on the basis of previous evidence [39,40] were: (i) the movement time; (ii) the spatial trajectories of the landmarks considered; (iii) the maximum velocity of the tendrils during circumnutation; (iv) the time it took for maximum tendril velocity to be reached as a percentage of movement duration; (v) the maximum aperture of the tendrils corresponding to the maximum distance reached by the tip of the tendrils during the approach phase; and (vi) the time it took for the maximum aperture of the tendrils to be reached as a percentage of movement duration.

Statistical tests were carried out to compare the median values for each of the dependent measures considered across all 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 [72]. All statistical analyses were carried out using the computing environment R [73] software and the function `wilcox.test`.

3. Results

3.1. Qualitative results

For all the experimental conditions, the tip of the tendrils showed a growing movement pattern characterized as circumnutation (Figure 3a,b), which aims to find a potential support in the environment. Once the plant detected and perceived the support, strategically modified the trajectory of its tendrils that started to bend toward the support to approach and clasp it. Importantly, plants directed their movement toward the support and shaped the choreography of the tendrils depending on support thickness before any physical contact with it [37-40] (see Supplementary Materials Video S1 and S2).

3.2. Kinematical results

Control conditions

The pattern of results obtained for the control conditions mirror those reported in previous studies in which one-sized 'thick' and 'thin' supports were compared (see Table 2) [37-40]. Movement time was longer for the 'Control-Thick' than the 'Control-Thin' condition (Figure 4). The maximum tendrils velocity was lower, and the peak of maximum tendrils velocity occurred earlier for the thicker than the thinner support (Table 2). The maximum tendrils aperture was wider and the time at which it occurred was later for the thinner than the thicker support (Table 2). This aspect is important because it provides a confirmation that *P. sativum* plants exhibit a different kinematical pattern for thick and thin supports [37,39,40]. And therefore, they provide the ideal comparison for investigating the effects determined by the perturbed conditions.

Table 2. Kinematical values

| Control-Thick vs Control-Thin | Median | |
|---------------------------------------|---------------|--------------|
| | Control-Thick | Control-Thin |
| Maximum tendrils velocity (mm/min) | 11.86 | 13.04 |
| Time of maximum tendrils velocity (%) | 76.78 | 79.93 |
| Maximum tendrils aperture (mm) | 30.80 | 38.52 |
| Time of maximum tendrils aperture (%) | 81.9 | 87.22 |
| Control-Thick vs Thin-Below | Median | |
| | Control-Thick | Thin-Below |
| Maximum tendrils velocity (mm/min) | 11.86 | 15.05 |
| Time of maximum tendrils velocity (%) | 76.78 | 46.09 |
| Maximum tendrils aperture (mm) | 30.80 | 53.40 |
| Time of maximum tendrils aperture (%) | 81.9 | 68.72 |
| Control-Thin vs Thick-Below | Median | |
| | Control-Thin | Thick-Below |
| Maximum tendrils velocity (mm/min) | 13.04 | 14.36 |
| Time of maximum tendrils velocity (%) | 79.93 | 55.37 |
| Maximum tendrils aperture (mm) | 38.52 | 42.66 |
| Time of maximum tendrils aperture (%) | 87.22 | 84.56 |

mm = millimeters; min = minutes; % = percentage of movement duration.

Note.

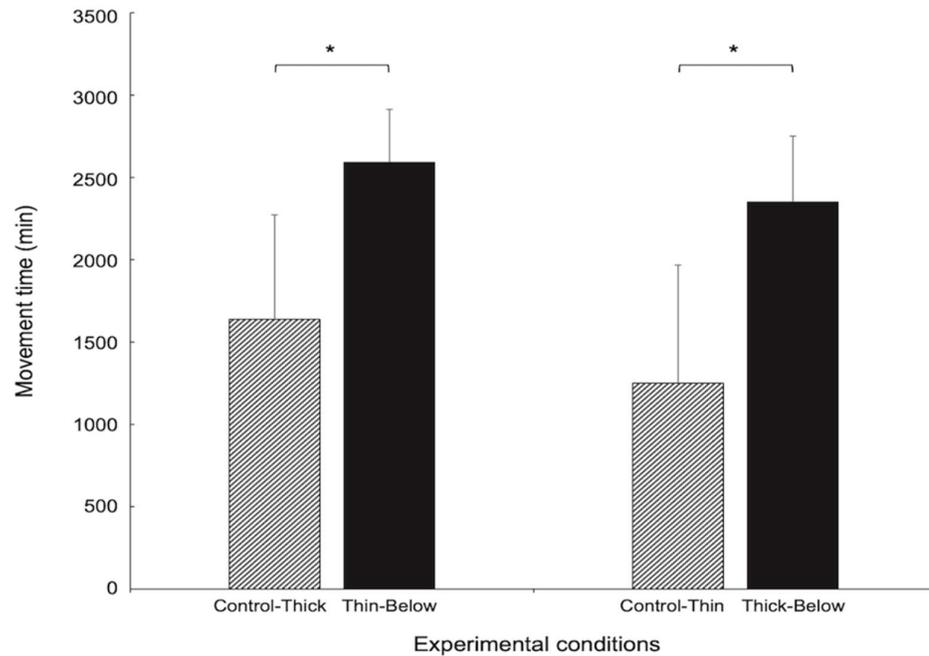


Figure 4. Bar plots representing the kinematical values for the comparisons between the Control-Thick and Thin-Below support conditions and between the Control-Thin and Thick-Below support conditions for the Movement time. Bars refer to the median, while error bars refer to the absolute deviation (MAD). Asterisks indicate that the difference between the perturbed and the control conditions was significant.

‘Thin-Below’ vs ‘Control-Thick’

Movement time was longer for the perturbed than for the control condition ($W=297$; $p=.024$; $r=.29$; Figure 4). The maximum tendrils velocity was higher for the perturbed than for the control condition ($W= 192$; $p=.001$; $r= .41$; Table 2). The time at which the maximum velocity of the tendrils occurred was earlier for the perturbed than for the control conditions ($W= 540$; $p=.006$; $r= .35$; Table 2). The maximum aperture of the tendrils was greater for the perturbed than for the control condition ($W= 134$; $p<.001$; $r= .46$; Table 2). Further, the time at which the maximum aperture of the tendrils occurred was earlier for the perturbed than for the control trials ($W= 460$; $p=.004$; $r= .37$; Table 2).

‘Thick-Below’ vs ‘Control-Thin’

Movement time was longer for the perturbed than for the control condition ($W=238.5$; $p=.001$; $r=.40$; Figure 4). Similarly, the peak of maximum velocity of the tendrils occurred earlier for the perturbed than for the control trials ($W= 483$; $p=.037$; $r= .27$; Table 2).

4. Discussion

We explored the interplay between the below- and aboveground parts of *P. sativum* plants for the coding of support thickness. The results show differences in kinematical patterning when comparing perturbed and control trials. First and foremost, for both the perturbed conditions movement duration is longer than for the control trials, suggesting

that the thickness mismatch characterizing the perturbation reflects on the duration of the movement. It might well be that the more information is needed to complete a task, the higher the time to perform it. Indeed, the perturbed support requires more information than the unperturbed support given that the evaluation for the two thicknesses needs to be performed.

When comparing the 'Thin-Below' with the 'Control-Thick' conditions, it is observed a differential pattern of results depending on the considered kinematical measures. The amplitude of maximum velocity and aperture of the tendrils suggest that *P. sativum* plants adjust the kinematical pattern of the movement on the basis of the belowground (i.e., thin) part of the support. That is, the maximum tendrils velocity was higher, and the maximum tendrils aperture was wider for the perturbed than for the control thick condition. Remember that this is the pattern previously observed for one-sized thinner supports [37,39,40]. Therefore, it seems that the pattern of the movement in terms of amplitudes is based on the information provided by the root system. However, when considering the temporal parameters, the time at which the maximum peak velocity and grip aperture occur, *P. sativum* plants adjust the kinematical pattern of the movement on the basis of the aboveground (i.e., thick) part of the support. That is, the time at which the peaks of maximum velocity and maximum aperture of the tendrils occurred earlier for the perturbed than for the control condition. Remember that this is the pattern previously observed for one-sized thicker supports [37,39,40]. Consequently, it seems that the pattern of the movement in terms of time is based on the information gained by the aerial part of the support.

Altogether these observations suggest a crosstalk between the roots and the aerial components of the plant. The higher velocities determined by the processing of the 'thin' part of the support need to be compensated by an earlier occurrence of key kinematical parameters in order to establish a functional equilibrium between the roots and the shoot. To explain, the time of maximum tendrils velocity and aperture are crucial landmarks because they reflect, respectively, the time at which the tendrils start to slow down and close upon the support during the approaching phase. Uncertainty regarding that time might compromise the clasping of the pole. Therefore, if the information coming from the belowground part of the support is inappropriate to maximize the chance of attachment, then modifications at the level of the aboveground organs of the plant are needed.

Turning to the comparison between the 'Thick-Below' and the 'Control-Thin' conditions we found no evidence for such crosstalk and no kinematical effects dictated by the perturbation occurred. It seems that what has been programmed on the basis of the below part of the support (i.e., thick) well fits the requirements for grasping the above part of it (i.e., thin). Our preferred interpretation of these findings relies on the demonstration that for *P. sativum* plants [37,39,40] and climbing plants in general [23,29] grasping a thicker support is much more demanding than grasping a thinner support. Therefore, it might be easier to adapt a pattern of movement related to a thicker more demanding support for grasping a less demanding thinner support. In such circumstances, the effects of the perturbation are minimized and no difference with the control condition is found.

Altogether, these results indicate that the roots convey 'information' to shoot that in turn can regulate growth and behavior accordingly. This is suggestive of a sort of functional equilibrium between the roots and shoot organs based on a signalling interactive process [74-76]. It is well-known that these kinds of signals can determine an indirect root system effect on shoot attributes including leaf size and the capacity to orient leaves [74] and, possibly, the dynamics of the tendrils for adapting to thickness [37-40].

At this stage, the natural question is: how do plants integrate the information from the above- and belowground organs in order to meet functional requirements? We are aware

that our data say very little regarding possible physiological mechanisms underlying such effects, nevertheless some speculative thoughts can be advanced. A possibility may rely on the propagation of electrical signals between the root system and the shoot [77-80]. Both the root system and the aerial part of the plant (i.e., stem, leaves, ...) can generate electrical signals that can be propagated from the root to the shoot (and vice versa) leading the coordination of the physiological functioning of the whole body of the plant. To date, four different types of transmission of electrical signals in plants are reported: (i) the wound potentials [81]; (ii) the action potentials (AP) [82]; (iii) the slow wave potentials (SWP) [83-85]; and (iv) the systemic potentials (SP) [86,87]. The first operates at a short distance, while the AP, SWP and the SP play a fundamental role in the root-to-shoot signalling providing a two-way communication between roots and shoots.

Another, not mutually exclusive possibility is the propagation of chemical signals such as the growth hormones (i.e., auxin, cytokinin - CK, brassinosteroids - BRs, gibberellins - GA and strigolactones - SLs) which play a role in the development and growth of the new organs in the above- and belowground parts of the plant [88-92]. It has been reported that the hormones can move rapidly from the root to shoot and vice versa through the xylem and the phloem, respectively [93,94]. For instance, the cytokinins like trans-zeatin synthesized in the root have been detected in the xylem sap and they play a role in the shoot growth [95,96]. The shoot controls the export of cytokinin from the root to the shoot and this is dependent on the feedback signal generated from the branching regulator RMS4 (RAMOSUS4) acting in the shoot in *P. sativum* plants [97]. In addition, cytokinin export to the shoot is sensitive to nitrogen, which lead to changes in root and shoot architecture (e.g., leaf expansion) [98-100]. Both miRNAs and auxins are possible candidates for the shoot-to-root signals mediating systemic nitrogen responses [101]. For example, the nitrate supply to roots is linked to lateral root responses through the modulation of shoot-to-root auxin transport in *Arabidopsis thaliana* L. [102].

5. Conclusions

The present results suggest a possible crosstalk between the above- and the belowground parts of *P. sativum* plants for the processing of the thickness characterizing a potential support. The integration of the information from both above- and belowground plant organs might provide the plant a full reconstruction of the surroundings, leading to a flexible adaptation of their behavior to ever-changing situations [41,56-58,61,62,103].

Future studies aimed at investigating both kinematics and physiological measures are needed to further explore the functional equilibrium and interactivity between the above- and belowground plants organs. The integrated analysis of plant growth responses at kinematical and physiological level might provide a new suite of investigative tools that may expand our understanding on plant behavior and ecophysiology.

Supplementary Materials: The following are available online at www.mdpi.com/xxx/s1, Video S1: Thick-Below stimulus condition; Video S2: Thin-Below stimulus conditions.

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