

TOPICAL REVIEW • OPEN ACCESS

## Taking inspiration from climbing plants: methodologies and benchmarks—a review

To cite this article: Isabella Fiorello *et al* 2020 *Bioinspir. Biomim.* **15** 031001

View the [article online](#) for updates and enhancements.



**IOP | ebooks™**

Bringing you innovative digital publishing with leading voices to create your essential collection of books in STEM research.

Start exploring the collection - download the first chapter of every title for free.

# Bioinspiration & Biomimetics

**OPEN ACCESS****TOPICAL REVIEW**

## Taking inspiration from climbing plants: methodologies and benchmarks—a review

**RECEIVED**

16 October 2019

**REVISED**

10 January 2020

**ACCEPTED FOR PUBLICATION**

7 February 2020

**PUBLISHED**

18 March 2020

Original content from this work may be used under the terms of the [Creative Commons Attribution 3.0 licence](https://creativecommons.org/licenses/by/4.0/).

Any further distribution of this work must maintain attribution to the author(s) and the title of the work, journal citation and DOI.

Isabella Fiorello<sup>1,2</sup>, Emanuela Del Dottore<sup>2</sup>, Francesca Tramacere<sup>2</sup> and Barbara Mazzolai<sup>2</sup><sup>1</sup> The Biorobotics Institute, Scuola Superiore Sant'Anna, Pisa, Italy<sup>2</sup> Center for Micro-Biorobotics, Istituto Italiano di Tecnologia, Pontedera, ItalyE-mail: [barbara.mazzolai@iit.it](mailto:barbara.mazzolai@iit.it)**Keywords:** biomimetics, climbing plants, methodology and benchmarks, robotics, adaptation, movements, behaviour

### Abstract

One of the major challenges in robotics and engineering is to develop efficient technological solutions that are able to cope with complex environments and unpredictable constraints. Taking inspiration from natural organisms is a well-known approach to tackling these issues. Climbing plants are an important, yet innovative, source of inspiration due to their ability to adapt to diverse habitats, and can be used as a model for developing robots and smart devices for exploration and monitoring, as well as for search and rescue operations. This review reports the main methodologies and approaches used by scientists to investigate and extract the features of climbing plants that are relevant to the artificial world in terms of adaptation, movement, and behaviour, and it summarizes the current available climbing plant-inspired engineering solutions.

### 1. Introduction

Natural systems provide ingenious and efficient solutions to complex problems. Charles Darwin wrote: *'The more I study nature, the more I become impressed with ever-increasing force that the contrivances and beautiful adaptations slowly acquired through each part [...] transcend in an incomparable manner the contrivances and adaptations which the most fertile imagination of man could invent.'* [1]. The beauty and efficiency of nature have also long inspired engineers [2], aimed at transferring ideas from biology to technology. The specific term *biomimetics* was coined in 1969 by the famous bio-engineer Otto Schmitt [3].

Many other scientists have since used *biomimetics* to refer to the mimicking of natural systems in artefacts [4–8]. Roboticians have more recently developed several solutions inspired by natural systems, giving rise to the branch of science known as 'Bioinspired Robotics'. The bioinspired approach in robotics has made impressive scientific achievements, typically by looking at the animal kingdom, e.g. among many, the octopus [9–12], the caterpillar [13, 14], worms [15, 16], geckos [17–22], and insects [23–25].

More recently, plants have been considered as a model to develop self-adaptable growing robots [26–28]. Plants have the ability to grow and continuously adapt their body to the surroundings, showing high plasticity and adaptability to changing environ-

ments, thus they have colonized almost all habitats on earth [29, 30]. The indeterminate growth and high adaptability are also relevant in robotics for developing new machines that can exploit their material properties and interaction with the environment to efficiently move and act. To this aim, climbing plants among all show many interesting and peculiar features [31, 32]. Firstly, they need to grow vertically and rapidly at the apical level of shoots to find a suitable support and to enhance light acquisition (or they perish), for which they minimize their energy consumption [33]. Secondly, vines and lianas develop flexibility and toughness in their stem because they need to survive extreme mechanical stresses in their habitat (e.g. movement or falls of trees and branch) [34]. Thirdly, many climbing plants have a sophisticated fibre arrangement which can affect the mechanical properties of the plant stem, leaf or attachment organ [35]. Fourthly, climbing plants can perform several kinds of movements (e.g. circumnutation is particularly evident in twining stems and used to find a support) [36]. Fifthly, their sensory capacity (e.g. tactile perception) enables them to perceive the environment [37–41], and their adhesive properties (e.g. tendrils, adhesive pads, adventitious roots and hook-like structures) enable them to climb and adhere [32, 42]. Finally, some climbing plants have the capacity to morphologically change their leaf form and shape, for example for camouflage in possible hostile environments [43] or during different growth

stages [44]. Understanding the key biological principles behind these, and other features of climbing plants is important for developing smart materials, adhesive devices, and autonomous robots for exploration, monitoring, search and rescue applications [30]. However, clear and useful biological investigations require a methodological approach to really understand the possible reasons for a particular phenomenon in order to facilitate and correctly translate the working principles from nature to the artificial world.

Reviews have typically focused on the adhesive mechanisms of climbing plants and their biomimetic potential [45] or on analysing the biomechanics of specific species [32, 42]. The aim of this review is to provide an overview of the methodological approaches and tools exploited by researchers for extracting the relevant biological features of climbing plants that might be adopted to design their artificial counterparts.

The review is divided into three main themes: (i) adaptation, (ii) movements, and (iii) behaviour. Section 2 deals with adaptation and details the current morphological and biomechanical tools and methods used to investigate the material structure-properties in climbing plants, as well as their tissue architecture and variation in material properties from macro to micro-scale. Section 3 explores the recent studies on movements with an overview of the tracking methods and ad hoc software for the analysis of kinematics. Section 4 analyses the approaches used to explore the theories behind the behaviour in climbing plants, gaining insights into the localization of the support, the perception and the differentiation of external stimuli. Section 5 then describes the relative artificial systems for the three main themes presented in sections 2–4. Directions for future research are suggested in section 6. For greater clarity, the structure of the review is presented in an organizational chart (figure 1).

## 2. Adaptation

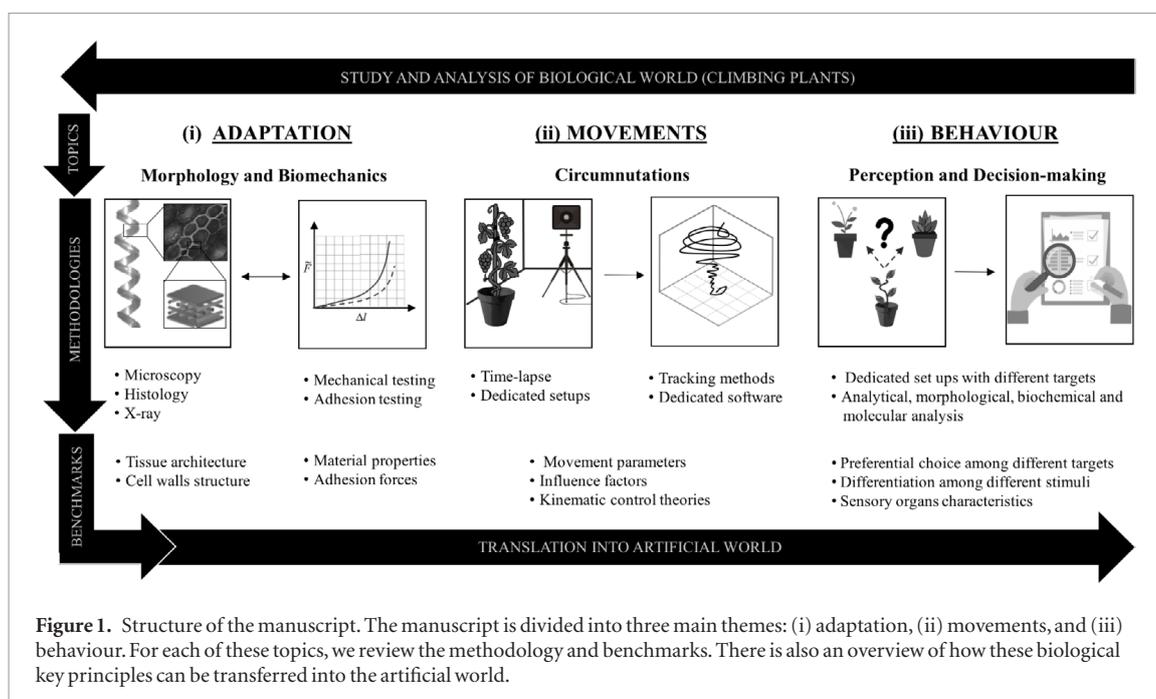
### 2.1. Overview

Climbing plants are able to adapt their growth to a wide range of environmental contexts, from forests to grasslands and riverbanks. They move continuously by growing to compete for sunlight, optimizing their resources and minimizing costs [32, 33]. Plant motion is strongly related to material properties and anatomical features. Morphological and biomechanical investigations provide a deeper understanding of the adaptive response of plants to mechanical stress, extracting fundamental information on the architecture of the plant tissue and cell wall material and mechanics. Table 1 provides a general overview of the main methodologies used to extract the morphological and biomechanical features in climbing plants, which are relevant for investigating their adaptive behaviour.

### 2.2. Methodologies and benchmarks for morphological studies

Morphological investigations analyze a plant's architecture through different scales, thus adopting different tools and methodologies. At the microscale level, several microscopic techniques have been widely used for the anatomical study of climbing plants [12, 33, 43–47]. Light microscopy combined with histological techniques provides an in-depth analysis of different types of tissues and cells. Conventionally, the plant tissue is chemically fixed to preserve and make visible the microscopic structure, sectioned using a microtome, and stained to detect specimen features by enhancing tissue contrast [66]. This approach has revealed the cellular basis for circumnutation and coiling, highlighting the involvement of specialized fibers, known as gelatinous fibers (*g*-fibers), in the actuation of the motion [50]. Darkfield and UV-light microscopy observations of coiled cucumber tendrils have been demonstrated to have a *g*-fiber ribbon, consisting of two cell layers with different reinforcements, suggesting that coiling takes place via an asymmetric contraction of *g*-fibers (figure 2(A)) [51]. An overview of *g*-fiber distributions in different species of tendrils and twining vines is reported in figure 2. Tendrils can be divided into three groups with respect to their internal anatomy, including (1) tendrils with adhesive properties (e.g. *g*-fibers at the center of the tendril, figure 2(B)); (2) those that coil in many directions (*g*-fibers are distributed as bilayer cells along the inner surface of the coil, figure 2(C)); or (3) towards a single direction (e.g. *g*-fibers are distributed in a cylindrical configuration, figure 2(A)). On the other hand, in twining vines, *g*-fibers occur as isolated cells in the cortex (figure 2(D)) [50, 51]. The diversity of climbing plant species is highlighted by such variations of *g*-fiber arrangements which suggests the underlying mechanism for circumnutation or coiling movements in one species or the other, as well as characterizing the diversity in their constitutive materials. Microscopy analyses on climbing plant's stems have been used to identify the correlation between the evolution of specialized biomechanical climbing architectures and the anatomical organization of internal stem's structures [49]. For the adaptation of climbing plants, one fundamental aspect is the presence/absence of primary/secondary growth [49]. Stained red sections of *Lycopodiella cernua*'s stems with primary growth have shown a different organization of lignified mechanical hypodermal tissues during ontogeny (with an increase of hypoderm's thickness from basal to median stem, and a decrease from median to apical level) [49]. Instead, microscopy analyses on the *C. guianense*'s stems with secondary growth have shown a timely development of large diameter vessels during ontogeny, which is strictly correlated to a reduction of the stem stiffness [67].

Scanning electron microscopy (SEM) has been used for high resolution investigations of climbing



plant surfaces and internal structures [35, 47, 54]. A typical procedure for the preparation of plant tissue and observation by SEM includes: fixation (e.g. usually using fixative chemicals, such as glutaraldehyde), dehydration (e.g. air drying or critical point drying), and coating with metal [68, 69]. Several surfaces of climbing plants have been examined in detail using this technique, such as the adhesive pads with papillae cells in *Passiflora discophora* [55], the aerial root hairs in *Syngonium podophyllum* [47], adaxial and abaxial hooks in *Galium aparine* [54], and root clusters and hairs of the attachment system of *Hedera helix* [56].

The authors in [35] investigated the formation and evolution of the tendril helical morphology of *Luffa cylindrica*, by characterizing the biological material across different scales (from nm to cm). Using SEM, the microstructures of tendril filaments were characterized in terms of size, organization and hierarchy of the internal structures. The authors thus identified the role of each hierarchical component and the relation among them, in terms of chirality transfer, also by comparing experimental results with theoretical model predictions. The results suggested that cellulose fibrils play a key role in the chirality transfer of tendrils from the subcellular to macroscale level, thus affecting the mechanical properties and architecture of tendrils, which were controlled by hydraulic forces. In addition, *L. cylindrica* tendrils show a rubber-like behaviour (due to the hyper-elasticity of cellulose fibril helix) which provides large elongation and flexibility for climbing on given supports [70].

Polarized light microscopy and x-ray analyses are widely used to investigate the cell-wall structure and cellulose microfibril angle (MFA) in climbing plants. Such studies have been carried out, for example, on the woody structure of lianas [57, 71], in tendrils [52], and

in cleavers [53]. X-ray analyses have been performed on stiff and flexible dried wood samples, produced during the self-supporting and non-self-supporting growth phase, respectively, of *Bauhinia guianensis* and *Condylocarpon guianense* tropical lianas [57, 67]. With the exception of the flexible wood in *Condylocarpon*, the comparison of the MFA in lianas wood, during different ontogenetic stages, showed MFA values (from 0 to 35°) within the same range as self-supporting plants, such as trees [57, 72]. This thus showed the analogy of mechanical properties in the biological material across different species which enable similar functionalities (self-supporting structures).

The staining protocol using permanganate stain for lignin used in polarized light microscopy investigations, in the twisted tendrils of *Brunnichia ovata*, enabled the observation of the cellulose microfibril orientation among adjacent cells, which seems to be oriented perpendicularly to each other [52]. Polarized light microscopy investigations have also led to the examination of the MFA between the fibers of cell walls and the tracheary elements of basal stems in the cleaver of *Galium aparine*. Interestingly, this angle was found to be 8° [53], which is similar to the MFA value of self-supporting trees and *Bauhinia* lianas [57, 72], highlighting the similarity of the behaviour and fibril functioning in these species.

Further analyses on g-fibers or the microfibril organization, combined with a better understanding of where and how lignification occurs among different species of climbing plants, will provide an in-depth knowledge regarding the morphology and circumnutation mechanics in climbing plants. This research will also contribute to methods for fabricating advanced bio-inspired materials for use, for instance into the mechanical actuation of circumnutation in robotic grippers and manipulators.

**Table 1.** The main methodologies used to extract the relevant morphological and biomechanical features in climbing plants for investigating their adaptive behaviour.

Features	Methodology	Objective	Extracted features	References
Morphology	Light microscopy in combination with histology	To investigate plant structures.	Tissue organization in stem and tendrils	[46–49]
		Histology characterizes tissue morphology and anatomy and ensures precise sample sectioning. The use of an antibody enables a specific target to be recognized	G-fiber role and distribution in tendrils and twining vines	[50, 51]
	Scanning electron microscope	To extensively investigate plant micro/nano structures (higher resolution respect to light microscope)	Microfibril orientation in cell walls (polarized light)	[52, 53]
Biomechanics	X-ray analysis	To characterize plant cell wall structure at the nanoscale	Surface characterization	[47, 54–56]
			Internal structure characterization	[35]
	Tensile test	To evaluate the mechanical behaviour of material under tension and compression conditions	Microfibril orientation in cell walls	[57]
			Young's modulus ( $E$ ) values	[46, 51, 53, 58, 59]
			Bending modulus ( $E_{\text{bending}}$ ) values	[46, 48]
			Shear modulus ( $G$ ) values	[46]
			Torsional modulus ( $G_{\text{torsion}}$ ) values	[48]
			Pull-off force ( $F_{\text{pull-off}}$ ) of hooks, adventitious roots, adhesive pads, etc.	[56, 60–62]
			Friction force ( $F_{\text{friction}}$ ) of leaf covered with hooks	[54]
<i>In vivo</i> attachment test	To measure the <i>in vivo</i> squeezing force of plants stems around a sensorized mechanical pole (TWIFOR)	Squeezing force ( $F_{\text{in vivo}}$ ) of twining vines	[46, 63, 64]	
		Micro-contact test	To measure the contact separation force between a hooked microstructure and a loop using a micromanipulator	Pull-off force ( $F_{\text{pull-off}}$ ) of a single hook
Nanoindentation	To evaluate the mechanical response of small plant material volumes under load, using a diamond tip	Young's modulus ( $E$ ) (e.g. cellulose fibrils in cell wall)	[29]	

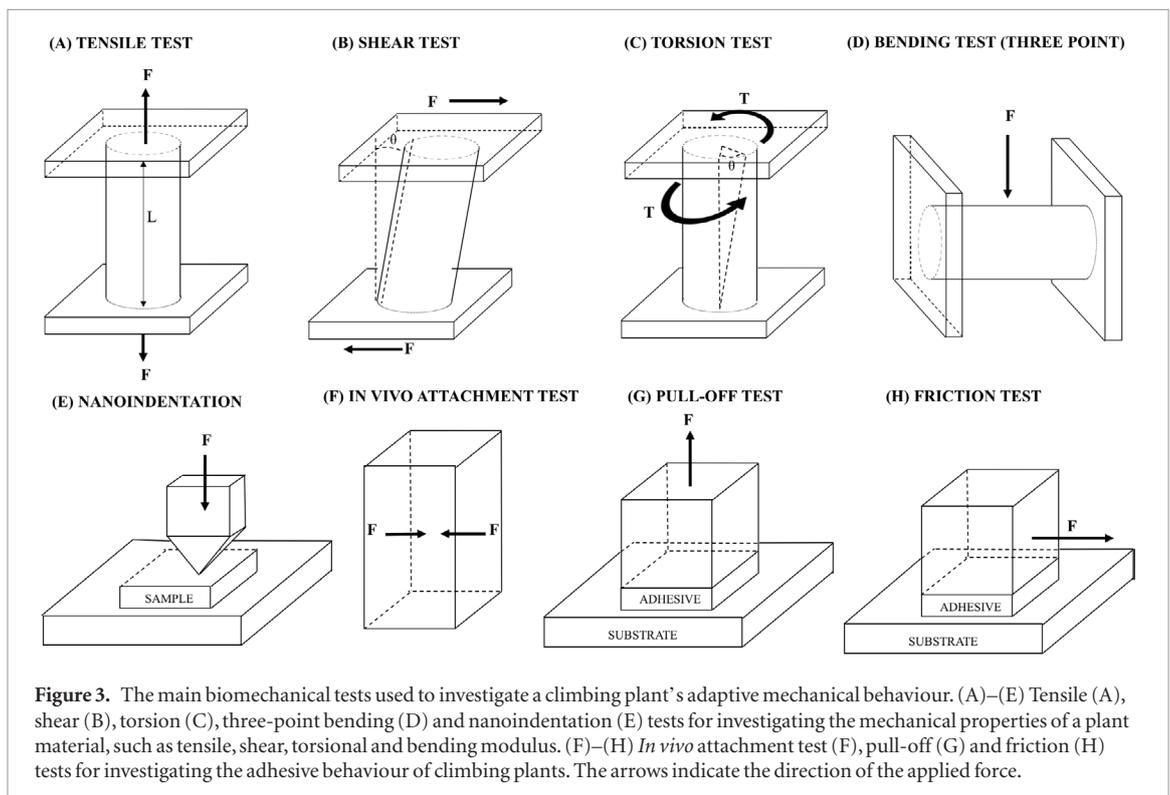
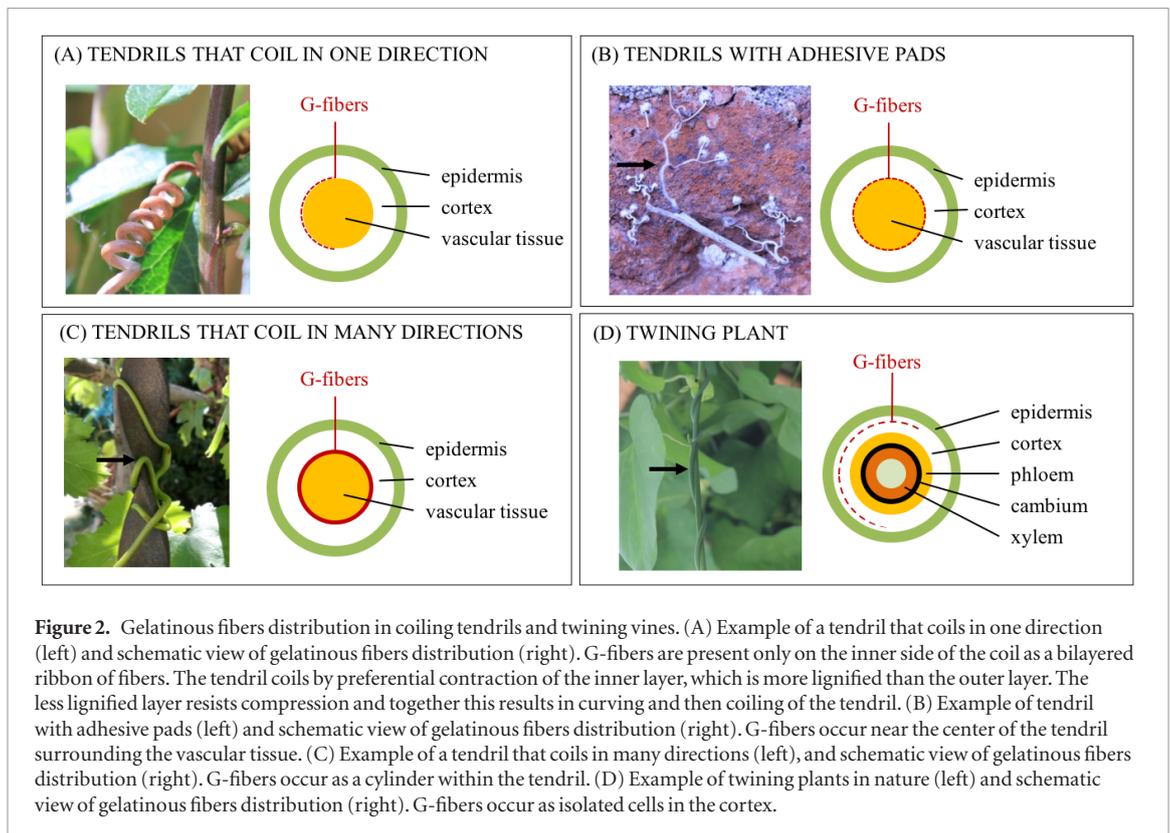
### 2.3. Methodologies and benchmarks for biomechanics

Biomechanical investigations study the mechanical properties and deformation behaviour of materials from the macro to microscale, which are relevant for underlining the correlation between the structure, functioning and movements in climbing plants [42, 49, 73]. Biomechanical features are strictly correlated to the climbing modes and developmental stages during growth [49]. Figure 3 shows the main biomechanical tests used to investigate these properties of climbing plants.

At the macroscale level, there are several biomechanical methods for extracting many material parameters, such as the elastic modulus in tension,

bending, shear and torsion phases [42]. These values can be measured using uniaxial or biaxial/multi-axial load cells, in tensile, flexural, shear and torsion tests. Such tests are often performed using commercial universal testing machines or customized set-ups [29]. Notably, biological materials, including plant stems, are not homogeneous but often have multi-compound complex structures [74]. This implies that the measurements are strongly affected by the length of the samples, the specific section from which they are extracted, and the age of the plant.

The elastic modulus in tension, also known as Young's modulus, is a measure of the mechanical stress required to axially elongate a material [29]. In general, in tensile tests, two extremities of the sam-



ple are fixed with clamps or chucks, a load is applied perpendicularly to the cross-sectional area, and the tensile force is recorded as a function of the displacement [29]. On the other hand, the elastic modulus in shear, also known as shear modulus, is a measure of the stress required to transversely deform the material [29]. Unlike the tensile test, in a shear test, a parallel load is applied to a cross-sectional area of the sample.

Several works have focused on measuring Young's modulus (e.g.  $E_{\text{bending}}$  is the more appropriate value to compare different stem's properties) of a climbing plant's stem and tendrils, at various development stages [46, 53, 70].

Young's modulus of the woody lianas, such as *M. scandens* and *C. guianense*, have been, for example, characterized by finding a decreasing value during ontog-

eny, which is different from trees [49, 67, 73, 75]. This finding is explained by the fact that young stems with narrow diameter need to search for a support to grasp onto, and to do that they rapidly develop high rigidity or stiffness: consequently, young stems have a higher Young's modulus ( $E = 3000\text{--}5000\text{ N mm}^{-2}$ ) compared to the older stems ( $E = 2000\text{--}500\text{ N mm}^{-2}$ ). In fact, when the older stems are already firmly attached to a supporting structure, they require less or almost no reinforcement from the basal part of the stem, which could hang on the support, becoming more flexible [75, 76]. However, some climbing plants attach less strongly to the support and may still depend from basal stem's rigidity supplied, retaining higher stiffness [77].

Unlike the previously mentioned woody lianas, the stems of twining plants of the air potato (*Dioscorea bulbifera*) have a smaller Young's modulus ( $E = 690 \pm 100\text{ N mm}^{-2}$ , which however are higher than the shear modulus values ( $G = 248 \pm 33\text{ N mm}^{-2}$  in the primary growth zone of *D. bulbifera*) [46]. The extraction of these two parameters in twiners contributed to an understanding of the generation of the squeezing force that enables these plants to ascend their supports without the use of adhesive or hook-like structures.

The results of tensile tests, up to failure, on the basal stems of the cleavers *Galium aparine* have highlighted the impressively high extensibility of this plant [53, 78], which obtained a breaking strains of  $24\% \pm 7\%$  and a Young modulus of  $235 \pm 16\text{ MPa}$  [53]. To date, the mechanism behind this high breaking strain is not yet clearly understood. Nevertheless, ontogenetic factors seem to play a relevant role in the adaptation of such mechanical properties, as demonstrated by the lower stiffness reached by domesticated Manioc with respect to its wild counterpart, where the internal wood and wall structure produce a stiffer stem, less prone to brittle fracture, with failure occurring at higher bending stresses compared with shrub and liana phenotypes of the domesticate [71]. Such adaptation seems to be dictated by the needs emerging from different environmental habitats, e.g. in agricultural environments, a flexible stem can be more easily maneuverable, while wild habitats require stiff stems to ensure the survival of the plant.

At the microscale level, customized micro-tensile testing machines are usually developed to extract the Young's modulus on very fine structures, e.g. in aerial roots of *Hedera helix* ( $E = 109\text{ N mm}^{-2}$ ) [56] and in microhooks of *G. aparine* fruits ( $E = 2020 \pm 1500\text{ N mm}^{-2}$ ) [65, 79].

Other biomechanical studies have evaluated the stiffness during bending and torsion of climbing plant structures [34, 42, 48, 49, 77, 80]. One of the most interesting works regards the leaf-climbing semi-woody monocot *Flagellaria indica* [48]. This species attaches itself to the surrounding vegetation using tendril-like leaves. The authors detailed the different mechanical properties of this leaf-climber along the stem at dif-

ferent stages of growth, demonstrating an anomalous behaviour. The bending ( $E_{\text{bending}}$ ) and torsional ( $G_{\text{torsion}}$ ) modulus were evaluated along the stem at different developmental stages.  $E_{\text{bending}}$  and  $G_{\text{torsion}}$  measure the ability of a material to resist bending or twisting when a force or torque is applied, respectively. To evaluate the  $E_{\text{bending}}$ , the authors performed a three-point bending test by selecting three different points along the stem. On the other hand, to evaluate the  $G_{\text{torsion}}$ , they used a testing machine with a set up consisting of a fixed and a rotatable chuck; the sample was fixed to the chucks and twisted due to the applied force [48]. The results show different biomechanical properties for each developmental stage. The  $E_{\text{bending}}$  values were generally higher than the  $G_{\text{torsion}}$  values, with an increase in  $E_{\text{bending}}$  when  $G_{\text{torsion}}$  increased, and a decrease in both values when the distance from the base increased. Thus, in *F. indica* the bending and torsion abilities dramatically reduce with the age and distance from the apical regions, however they are very affective up to about 1 m from the apex providing high flexibility and, at the same time, resistance to structure deformation. Such behaviour is the opposite of other climbers, in which the increase in stiffness from the basal to apical stem regions is expected (as also reported above in *M. scandens* and *C. guianense*) [75, 76]. Furthermore, some woody climbers, such as *Croton pullei*, show a shift from free-standing growth phase (constant Young's modulus) to supported growth phase (decrease of Young's modulus) during ontogeny, thus moving from a typical semi-self-supporting plants patterns to non-self-supporting behaviour [76, 80].

An evaluation of such biomechanical properties, across different species and regions, is fundamental for it to be transferred to the field of bioinspired robotics, since it guides the selection of the most appropriate biological model for the specific task required.

To evaluate the mechanical response of small volumes of plant materials under load, nanoindentation can be used [83, 84], as it is able to reach the cell wall scale [29, 85]. In a nanoindentation test, an indenter with a fine tip at a certain load is driven into the specimen [29]. This kind of instrument can also test the mechanical properties of a structure in different regions (e.g. outer and inner parts). However, to the best of our knowledge, there are currently no studies using nanoindentation on climbing plant tissues. This method has however been used to investigate the mechanical properties of *Zea mays* primary roots [86]. Similar investigations on climbing plants would lead to new knowledge regarding the properties of biological materials for a more effective technology transfer to robot body materials and actuators [87, 88].

In terms of the biomechanics of climbing plants, the adhesive mechanisms have been studied the most [32, 42, 45]. Based on the attachment mechanism used to cling to their host, Charles Darwin categorized climbing plants into five classes: twining plants, tendril-bearers, leaf-climbers, hook-climbers, and root-climbers [31].

Pull-off and friction tests are commonly used to investigate the adhesion and friction forces in climbing plants [42]. TWIFOR is an electronic device used to measure *in vivo* the squeezing force during the growth of twining vines [46, 63, 64]. Custom-made and portable tensile testing machines have been developed to test *in situ* the attachment behaviour of adhesive pads in tendrils and roots in root climbers, under natural conditions [61]. Some examples include friction experiments performed on hook-climbers (hooked leaves of *G. aparine*) with a dedicated set-up [53, 54]. The separation force between a hooked microstructure and a loop was investigated using a micro-contact tensile test, equipped with a micromanipulator [54].

In leaf-climbers, the attachment forces of the tendril-like leaf of *F. indica* were obtained using a dedicated set-up for tension testing [82]. In general, the values of the attachment force obtained from climbing plants, while ascending to light and adapting to their habitats, range from a minimum of 5 mN (measured on a single hook of *G. aparine*) [54] to a maximum of 38 N (measured on a tendril-like leaf of *F. indica*) [82] (table 2).

Climbing plants select specific supports in their habitat particularly on the basis of their diameter and surface characteristics (e.g. smooth or rough surfaces). These plants are thus able to grasp, coil, or adhere to a support, with species-specific behaviour. For example, twining plants are able to grow vertically by squeezing around trees (large structures) in the tropical rainforest (e.g. the woody vines *M. scandens*) [75, 76] or poles and rods (slender structures) in forests or grasslands (e.g. the common twiners *D. purpurea* and *D. bulbifera*) [46, 81].

Experiments on *I. pupurea* using the supports of two different diameters showed a similar twining force of the stems, however a greater normal force was found for the unit stem length on slender poles, due to the difference in their helical geometry, making them unstable with larger poles [81]. In addition, it seems that the stem twists increased with the roughness of the surface texture of the support, although the values were not quantified [46].

A model of the mechanical action of twining stems compared a twining plant to a growing elastic filament in contact with a rigid cylindrical support [89]. Based on this model, the authors extracted the critical support radius ( $R$ ), which can be expressed as a function of plant helix parameters. This represents a key factor behind the ability of a twining plant to coil around a cylindrical support—if the support has a radius greater than  $R$ , the twining plant is not able to coil around it [89].

Leaf-climbers of *F. indica* are monocotyledons and therefore lack wood but can nevertheless grow on the host vegetation and over poles and rods in tropical and subtropical forests. Experiments with this plant show that smaller the diameter of the support, the

higher the attachment forces and the higher number of coils [82]. The texture of the host structure also influences the attachment force: rough surfaces induce a higher friction force than a smooth surface (e.g. the authors in [82] were using bamboo as rough support and aluminum rod as smooth support), due to the interlocking of the papillate cells of apical leaves with the structures of the support surface [82]. Through chemical adhesion, root- and tendril-climbers are able to grow over a wide range of smooth and rough surfaces such as trees, walls and buildings. This strategy enables them to colonize almost all habitats, ranging from mountains to forests and coastal areas [58, 61, 62]. Hook-climbers, such as the cleaver *G. aparine*, are able to climb over micro-rough surfaces by mechanical interlocking in different environments ranging from forests to hedgerows and arable fields [54].

A general overview of the biomechanical benchmarks extracted in climbing plants in correlation with the type of support and habitat is reported in table 2. This overview underlines the wide diversity of strategies adopted by climbing plants in different environments and helps in understanding the most efficient approach possible when exploiting plant features in artificial solutions, taking into account the environment where the robot is designed to move.

### 3. Movements

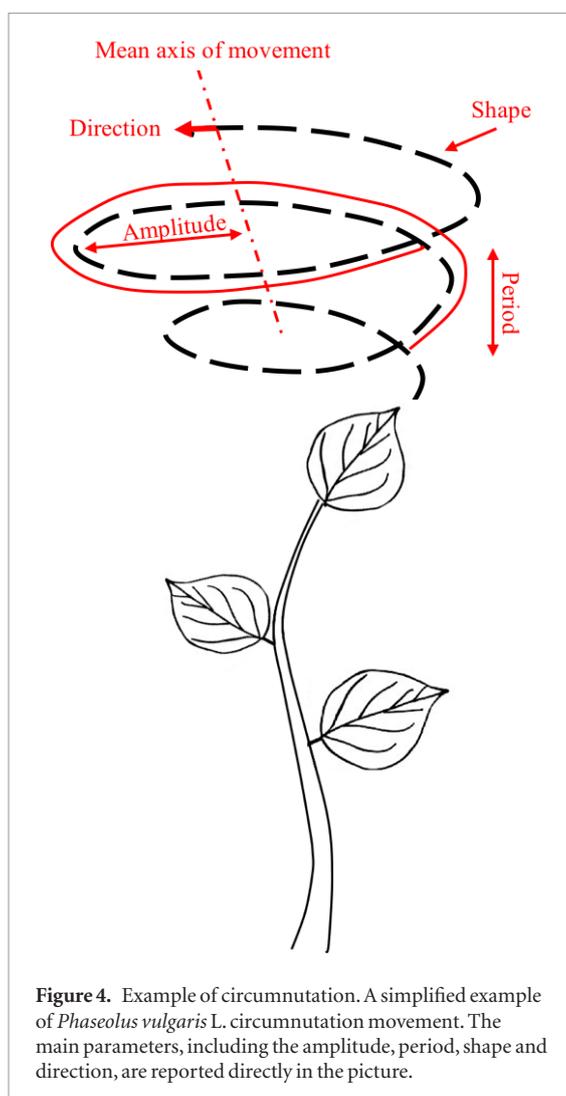
#### 3.1. Overview

The main difference between animals and plants is the sessile, but nevertheless mobile nature of plants. This movement involves many different organs, including stems, roots, flowers and leaves [90]. They can be active (requiring metabolic energy) or passive (not requiring metabolic energy after formation of the structure), reversible or irreversible, nastic (if not dependent on the direction of a stimulus) or tropic (if the movement is a directional response to a stimulus) [91–93].

Climbing plants are also particularly active in circumnutation movements. Circumnutation is defined as ‘a particular class of nutations present in plant organs that are actively growing, which generate elliptical/spiral trajectories’ [93]. They represent a remarkable strategy adopted by plants for navigating towards supports, and they have been characterized in a variety of species among a variety of plant organs [93, 94]. Circumnutations in tendrils and shoots of twining vines are particularly evident [32, 74, 90]. Circumnutation and thigmotropism are strongly connected in twining plants, and the particular circumnutation strategy adopted by a specific plant can define its success or failure in colonizing a certain area [95]. Studying this movement reveals how a plant can adapt in certain environments. Experimental set-ups with cameras for recording plant movements with tracking methods and software can be used to investigate this feature of climbing plants [90, 96].

**Table 2.** The biomechanical benchmarks extracted in climbing plants in correlation with their habitat.

Classes	Species (common name)	Attachment strength, force (mN) (sample and substrate)	Young's or bending modulus, ( $N\ mm^{-2}$ ) (source of material)	Typical support	Native habitat (continent)	References
Twining plants	<i>Dioscorea bulbifera</i> (air potato)	100–300 (squeezing force of shoot on a pole)	$690 \pm 100$ (stem, 600 mm from the apex)	Regular structures for vertical growth	Forests, grasslands, riverbanks and shrublands (Africa and Asia)	[46]
	<i>Ipomea purpurea</i> (morning glory)	$167 \pm 46$ (squeezing force of shoot on slender pole)	Data not available	(e.g. host plants, poles and rods)	Forests, ruderal areas and wasteland (South America)	[81]
	<i>Mariapa scandens</i> (Liana)	$185 \pm 90$ (squeezing force of shoot on thicker pole)	3000–5000 (young stem)	Large structures for vertical growth (e.g. trees and branches)	Tropical rainforests (South America)	[75, 76]
	<i>Condylocarpon guianense</i> (Liana)	Data not available	2000–500 (old stem)			[49, 57, 67]
Leaf-climbers	<i>Flagellaria indica</i> (Whip vine)	2000–3000 (tensile force of tendril-like leaf on thicker aluminum rod)	$1153.4 \pm 991.1$ (young stem, $G_1 = 0-1\ m$ from apex)	Horizontal/vertical structures for coiling	Tropical and sub-tropical forests (Asia, Africa and Australia)	[48, 82]
		$8000-38\ 000$ (tensile force of tendril-like leaf on slender aluminum rod)	$5192.7 \pm 1308.1$ (young stem, $G_2 = 4-13\ m$ distance to base)	(e.g. host plants, poles and rods)		
			$11673.9 \pm 2030.1$ (old stem, $G_3 = 0-1\ m$ distance to base)			
Tendrils bearers	<i>Parthenocissus tricuspidata</i> (Boston ivy)	$7590 \pm 2530$ , $F_{max} = 14\ 000$ (pull-off force of pads on plaster)	Data not available	Smooth and micro-rough objects using irreversible chemical adhesion (e.g. trees, rocks and walls)	Hillsides, mountains and urban areas (Asia and North America)	[61, 62]
Root-climbers	<i>Hedera helix</i> (english ivy)	$3810 \pm 2410$ (pull-off force of clustered roots on tree bark)	109 (individual root)		Forest, riverbanks and coastal areas (Europe, Asia and South America)	[58, 61]
Hook climbers	<i>Galium aparine</i> (Cleaver)	5 (pull-off force of single adaxial hook using a Kevlar loop, $90^\circ$ )	$235 \pm 116$ (basal stem)	Micro-rough objects using reversible mechanical adhesion (e.g. rope, Asia, and North America)	Forests, hedgerows, wasteland, arable fields, grasslands, and roadsides (Europe, Asia, and North America)	[53, 54]
		From $8.8 \pm 1.8$ to $21.9 \pm 13.4$ (Friction force of adaxial leaf surface on plastic mold and foam plastic, respectively)				
		20 (pull-off force of single abaxial hook using Kevlar loop, $-45^\circ$ )	$2020 \pm 1500$ (fruit hook)			
	From $33.3 \pm 15.1$ to $71.4 \pm 24.6$ (Friction force of abaxial leaf surface on foam plastic and VELCRO Vel-Loop, respectively)					
	<i>Lycopodiella cernua</i> (Staghorn clubmoss)	Data not available	$500-11\ 000$ (sclerenchyma stem tissues)	Surrounding vegetation structures (e.g. using lateral branches)	Tropical rainforests (South America)	[49]



### 3.2. Methodologies and benchmarks for circumnutation studies

Since Charles Darwin's time, circumnutation has been widely investigated in the plant kingdom. However, the first methods for tracking and recording plant movements were not reliable, due to a lack of standardization and the poor accuracy of the recording methods (e.g. often plant motion was recorded by periodically monitoring the plant organ position by the human eye or mechanical recording systems) [93]. Digital time-lapse recording systems have since opened up incredible opportunities for investigating circumnutation movements in plants [90]. A plethora of studies on the growth kinematics of plants have been performed to understand their behaviours (e.g. [97–99]). These experiments require autonomous or semi-autonomous methods for image analysis, leading to the recent trend in developing new tools for studying plant kinematics and extracting relevant features. These tools typically follow the path taken over time and space by a recognizable part of the observed plant organ [45, 100–102].

Among climbing plants, the most studied biological models are the twining shoots of the common bean (e.g. *Phaseolus vulgaris* L.), and tendrils in *Pisum*,

*Passiflora* and *Sicyos* [90, 103, 104]. The parameters characterizing circumnutation movements are (1) the amplitude (radius of the helix), (2) the period (time needed to perform one complete cycle of movement), (3) the shape (circular, elliptical, pendulum or irregular) and (4) the direction of motion, which can be clockwise (cw) or counterclockwise (ccw) [90]—see figure 4.

Circumnutation parameters vary among different plant species and organ morphologies. For example, studies on *Phaseolus vulgaris* L. have shown that the amplitude for a shoot movement is generally about 10 cm [105, 106]; the period ranges from 90 to 100 min [105, 106]; the shape is predominantly elliptical or circular [105, 106]; and the direction of the movement is typically counterclockwise [107]. In *Phaseolus multiflorus*, temperature affects the periodicity of nutation, with a decrease in the cycle length if the temperature increases (27 min/15 °C; 12 min/27 °C) [103]. Current automated methods including digitalized recording devices coupled with computer and data analysis systems provide an accurate analysis of the trajectory along the three-dimensional axis of the shoot apex [106]. A typical set-up for investigating circumnutation in twining bean stems consists of a support, such as a pole, used for the plant to climb around, and two cameras, one positioned at the bottom of the pole, the other laterally [104].

Although circumnutation is known to be induced by variations in cell volume, the complete mechanism chain is still not completely understood [90, 94]. A dedicated experimental set-up has been developed for investigating cell elongation and revolving movements in *P. vulgaris* L. shoots [98]. In that study, a picture of the epidermal cells (marked with a dye droplet) in the bending zone was taken every ten minutes using a horizontal inverted microscope (time-lapse microphotography methods); at the same time, the revolving movement of the shoot was recorded using a video-camera placed above the shoot with the images observed on a monitor [98]. Interestingly, the researchers discovered that during growth and at the same time as the revolving movement, some cells in the bending zone of the bean shoot displayed reversible and rhythmic changes in length variations. This behaviour clearly suggests that circumnutation is driven by variations in turgor pressure, due to cell shrinking/swelling phenomena in the bending zone [98].

Several studies have investigated the influence of light, darkness, mechanical stress, temperature and gravity on circumnutation [90]. A simple dedicated device equipped with photoelectric sensors was developed to investigate the effect of external conditions, such as light, temperature and humidity, on *P. vulgaris* L. [108]: temperature, rather than light and humidity, was found to strongly affect the duration of circumnutation [108]. Another study [99], exploiting time-lapse monitoring using infrared imaging, demonstrated a strong influence on the frequency of nutation of dark treatments in *Arabidopsis thaliana* stems. This plant

**Table 3.** Examples of tendril-bearer species. Description of the site of irritability (ventral or dorsal), the sensitivity (minimum weight needed for a response), and the reaction time of a given species. Adapted from [39].

Species (family)	Irritability (dorsal and/or ventral)	Sensitivity (mg)	Reaction time	References
<i>Passiflora gracilis</i> (Passifloraceae)	Ventral	1.0	25 sec	[31, 127]
<i>Cissus discolor</i> (Vitaceae)	Ventral and dorsal	9.3	35 min	[31, 128]
<i>Pisum sativum</i> (Leguminosae)	Ventral	9.3	2 min	[31, 40, 129]
<i>Sycos angulatus</i> (Cucurbitaceae)	Ventral	3.5	30 sec	[127, 128]
<i>Corydalis claviculata</i> (Fumariaceae)	Not available	8.1	18 h	[31, 127]

model has been widely used for investigating and characterizing circumnutation by setting several different ambient conditions, and producing results on a wider spectrum for the movement [94, 109]. Similar experiments on different varieties of climbers could be of interest for a better characterization of this motion, including the vine family.

Mechanical stress can also affect circumnutation in *P. vulgaris* L. [110]. Beans stimulated with 10 rubs showed an increase in circumnutation from 1.4 to 2.0 h. A similar effect was found in plants subjected to thermal stress, including high (45 °C) or low (0 °C) temperatures [110], confirming previous results [108]. An improved version of the same device [108] was developed for the continuous measurements of circumnutation in tendrils [111].

Experiments on earth and in space have shown a relationship between gravity and circumnutation [103, 112]. Although the origin and the role of circumnutation are not completely clear, the most accepted theory proposes that circumnutation is induced by the interaction between an internal oscillator and gravitropism [94].

Software has been developed for plant analysis from images or videos (a collection is available at [www.plant-image-analysis.org](http://www.plant-image-analysis.org)), which captures specific characteristics: leaves (e.g. [113, 114]), roots (e.g. [115–117]), and shoots (e.g. [118]). For example, the Circumnutation Tracker [96] uses time-lapse images as input, obtained by observing the plant from the top, and provides period, length, rate, shape, and direction of movements. The software was tested on *Helianthus annuus* L. seedlings, which, however, have a quite different shoot apparatus from vines, thus the software still needs to be verified on climbing plants.

Once a shoot or tendril tip position is obtained over time, a Fourier analysis can be performed to evaluate circumnutation period and amplitude [98], and the trajectories analyzed with a geometry of three dimensional curves [119–121]. These kinds of investigations may lead to the discovery of new features in the growth mechanism, which can also be exploited for the control of robots. In fact, the growth mechanics of plants has already inspired kinematic models of a plant-inspired robot [122]; while, circumnutation has attracted research into formalizing the kinematics [123], applying such movements for driving the search of a support in tendril-like inspection robots [124], or

for investigating the role of circumnutation in plant roots with a robo-physical approach and analyzing the resulting behaviour by using observable and sensorized artificial roots [125, 126]. However, such work is only possible through a preliminary and accurate data analysis of the biological model.

## 4. Behaviour

### 4.1. Overview

Plants act constantly in a dynamic environment, which subject the plant to a multitude of different stimuli. In order to survive, plants need to perceive, to propagate the external signals and to process the incoming data. These abilities are known as plant cognition [121], which define their phenotype and survival without a central brain control system. Studying climbing plants would be particularly interesting in terms of two main features: (i) the ability to differentiate and process different stimuli, and (ii) the ability to localize the surrounding items and different external supports. Investigations on the strategies used by climbing plants to localize and perceive a support require dedicated sets of experiments, appropriate touch testing set-ups, and a multidisciplinary approach.

### 4.2. Methodologies and benchmarks for perception studies

The adaptive growth of plants is grounded on the ability to perceive, differentiate, and respond to environmental stimuli. Sensitivity to contact stimulation is vital for climbing plants because they need to rapidly find an external support and understand whether or not it will facilitate their growth, otherwise they perish [34, 41]. In many lianas of the tropical rainforest, the apical part act as a ‘searcher’ looking for a suitable support or growing towards light [34]. Investigations into the effects of the mechanical perturbation induced by stimuli, such as touch, gravity, rain or wind, on plants need to be performed at different levels, using anatomical, biomechanical, biochemical and molecular methods [41].

The most common biological model used for investigating plant response and/or mechanical stimuli differentiation is *Arabidopsis thaliana* [37, 130–132]. There are fewer studies on climbing plants, and these mainly use tendril-bearers to analyze their mechano-

**Table 4.** Main approaches and discoveries concerning the recognition of a support in climbing plants.

Selected plant	Stimulus	Target	Methodology	Discovery	References
Monstera gigantea	Darkness	Host trees	Measure of average angle and standard deviation of growth towards the host	Growth toward the target is due to darkness caused by tree's host shadow (skototropism)	[139]
Cuscuta pentagona	Volatile cues	Natural and artificial plants, grasses of different colours and most soil types	Tracking methods in association with a dedicated set up and gas chromatography	Growth toward the target is due to emission of volatile cues (which mediate ecological interaction among plant species)	[140]
Ipomea hederacea	Colour of the support	Black, blue, red, white, green, and yellow stakes/painted structures or corn	Measure of photon densities and frequency (%) of plants that successfully climb over a given object	Growth path is preferentially toward given coloured structure (green, yellow, white) or corn plants	[141]
Boquila trifoliolata	Undiscovered	Host trees	Leaf phenotype analysis of all leaf traits	Leaf morphing by mimicking several hosts for protection against herbivores	[43]

sensing (e.g. *Bryonia dioica* Jacq.) [133–136]. In the early studies, a climbing plant was stimulated by applying a mechanical stress, such as touching, rubbing or flexing using weights [31, 39, 41, 134]. A rough support, applied along the tendril surface, was generally found to elicit a better response than a smooth support [133, 137].

Key features during artificial translation are the shape and the mechanical aspects of a given specialized sensory organ.

The most studied mechanosensory organ in climbing plants is the dome-shaped structure present in the epidermal cells of *B. dioica* Jacq. tendrils, called 'tactile bleps' [136]. SEM investigations showed that they are homogeneously distributed on both the upper and lower side of the tendril, with a basal size of about 4–5  $\mu\text{m}$  [136]. Tactile bleps are composed of heterogeneous materials, including cellulose, callose, cytoplasm and cell walls, and they are more sensitive to shear than normal stimulation [136]. The calcium-related cytological pathway with calmodulin protein is the most common touch-sensitive process in plants [37, 138]. In tactile bleps, the membrane-associated calcium was localized using CTC (chlortetracycline) fluorescence and investigations into the biochemical assay, demonstrating that tactile bleps are the site of calcium accumulation [136].

Similar mechanosensing structures are found in the tendrils of *P. tricuspidata* [59]. Its shoot surface is covered with small hooks showing patterns of protrusions and socket cells at the base of the hook. The authors suggested that the socket cells may trigger contact recognition, while the protrusions act as mechanoreceptors, as in the case of the tactile bleps found in *B. dioica* [59, 136]. Besides tactile bleps, many other types of epidermal cells may act as mechanoreceptors in climbing plants, and these still need to be classified.

Other benchmarks that could be useful for the artificial translation of plant perception include the type of stimulus, reaction time, irritability area (e.g. dorsal or ventral), sensitivity (e.g. the minimum weight

needed for a response) and the type of response. Early studies extracted some of these benchmarks from the tendrils of different species, which were mechanically perturbed [31, 39]. Table 3 summarizes the characteristics of selected examples of tendrils species.

The irritability of tendrils occurs on the ventral and/or dorsal surfaces [39]. Some tendrils of plants such as *P. gracilis* (Passifloraceae), *P. sativum* (Leguminosae) and *S. angulatus* (Cucurbitaceae), are only sensitive on the ventral surface, while others, such as *C. discolor* (Vitaceae) are sensitive on both sides [38]. The sensitivity ranges from 1.0 mg in *P. gracilis* to 9.3 mg in *P. sativum* and *C. discolor* [37].

The minimum weight for promoting coiling is 0.25 mg [134]. The reaction time ranges from a few seconds to many hours in relation to different species [39]. The response to touch in climbing plants is a positive thigmotropism, which means that bending follows the direction of the stimulus [37].

Given that these experiments were performed several decades ago, many parameters still need to be analysed. For example, the kinetics of the stimulus-response in climbing plants could be better investigated using an accurate feedback system for angle determination, as in the studies on *Arabidopsis thaliana* roots [142]. In addition custom-made tools could be used to control the force, area and frequency of the induced mechanical stimuli [143].

Plants are probably also able to differentiate between different mechanical stimuli. For instance, in [144], the authors investigated the effects of wind and an artificially-induced mechanical stress on leaf traits in *Plantago major* plants, and observed different morphological and biomechanical changes (e.g. slender/thicker petioles). They used a rotating table at a fixed speed, on top of which the plant was placed. While rotating, the plants were randomly stimulated by brush or wind, which was measured with an anemometer [144].

We are still far from understanding the perception mechanisms in plants. Identifying which types

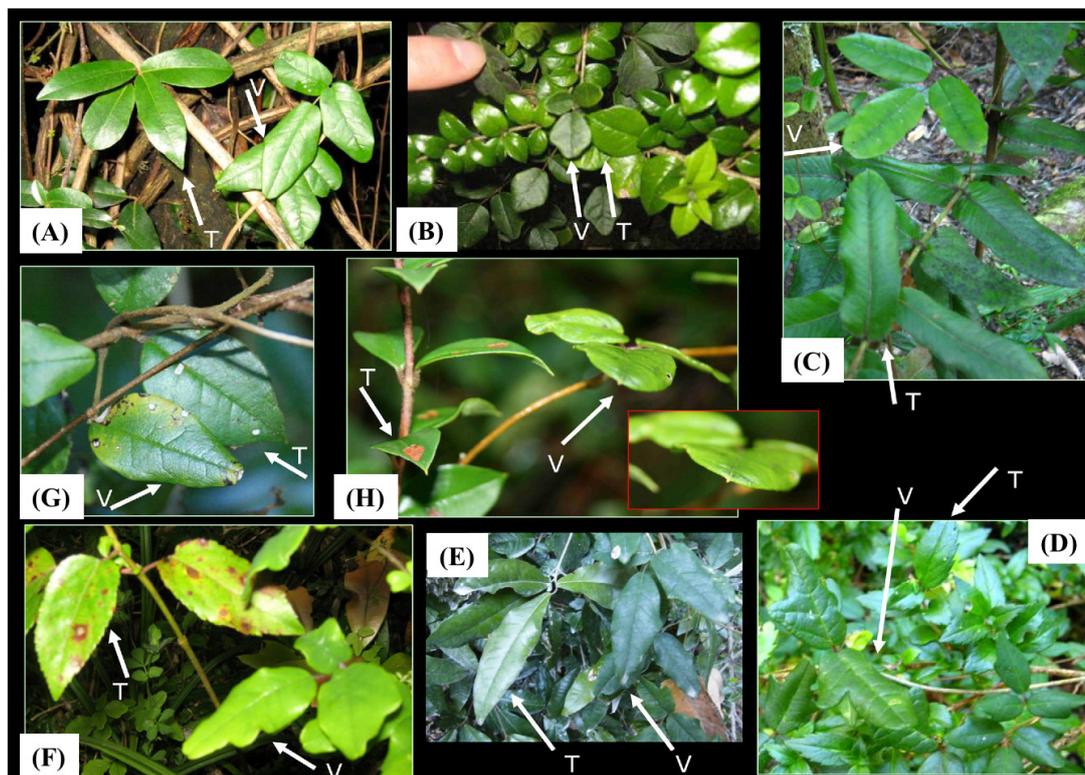


Figure 5. Leaf mimicry in the woody vine *Boquila trifoliolata*. Reprinted from [43].

of sensory organs are involved in the response to touch stimulations, would help to clarify how climbing plants differentiate between useful stimuli from perturbations. Research in this field would open new opportunities for developing new sensors and multifunctional materials for soft robotics.

#### 4.3. Methodologies and benchmarks for decision-making studies

Although a random motion may be involved in the search for a support in some species of climbing plants [33], some studies have also considered decision-making abilities in plants [43, 133, 139–141], as already reported for other organisms lacking a central brain (e.g. [145–147]).

Table 4 summarizes the main approaches and discoveries concerning the recognition of a support in climbing plants. The experimental targets of the selected experiments include natural host trees or plants, artificial plants or different coloured supports. Various studies have used different targets and approaches, and have discovered which type of stimulus is involved in the preferential choice of a support.

One of the oldest works regards the tropical twining vine *Monstera gigantea*, which lives in Caribbean lowland forests [139]. The authors considered two main variables: (i) the average angle of growth, and (ii) the standard deviation in the growth of the elongating stem of *M. gigantea* seedlings towards the host tree. If the angle and the standard deviation were  $0^\circ$ , it meant that the average growth of the selected models was directed towards the target and all the selected seedlings were

growing in the same direction. The authors thus demonstrated that all seedlings, coming from all directions, move by growing towards the shadow sector of the horizon (skototropism), produced by the host trees (or panel supports). This type of attraction was observed to decrease with the distance to the tree, and to increase with an increase in tree diameter [139].

Another very interesting work investigated the ability of the twining vine *Ipomoea hederacea* (Ivyleaf morning glory) to differentiate between objects of various colours and plants [141]. The experiments were conducted in a greenhouse and in the field, evaluating whether and how many morning glory plants exhibited climbing or non-climbing on coloured objects (e.g. black, red, blue, yellow, green and white stake or painted structures), or on corn plants as hosts. A radio spectrometer was used to measure the spectral quality of the reflected solar radiation of each stake/painted structure. The frequency (%) of morning glory plants that successfully climbed over a given object was calculated. In addition, objects were placed at different distances to evaluate whether plants responded to the spatial distribution of the objects. Greenhouse experiments showed that morning glory plants grew preferentially on corn plants (92%), and over green and yellow stakes (75%), while field experiments showed that plants grew preferentially on green (67%) and white (64%) structures, and corn plants (61%). In both environments, only a few vines grew over black stakes (10%–17%). In addition, Ivyleaf morning glory plants seemed to respond to the spatial distribution of the objects and probably used reflectance to preferen-

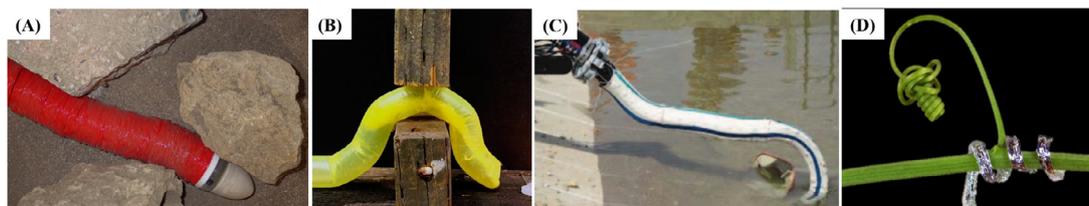
**Table 5.** Main examples of how climbing plant features have been transferred into real-world applications.

Artificial systems	Bioinspiration	Translation	Real-world applications	References
Growing robots	Cell elongation and/or division at the apical tips in plants	Skin eversion for lengthening from the tip. The relative length of opposite sides were controlled by launch/un-launch of pitches  Symmetric deposition of PLA using a miniaturized 3D printer at tip level. Tip is sensorized	Exploration, monitoring, search and rescue	[153, 154, 174]  [27]
	Differential cell distribution at the opposite sides of tips for bending in plants	Asymmetric deposition of PLA using a miniaturized 3D printer at tip level (e.g. printing different thickness layers or variable number of layers). Tip is sensorized		[122, 152]
Continuum robots	Tendrill-like behaviour (e.g. the capacity to go into tight spaces)	Spring-loaded modular bending segments (1)	Minimally invasive inspection in space	[156]
		Improved design of (1), with an increase in the length (increased number of springs in series) and a decrease in spring stiffness		[157–159]
Programmable materials	Reversible plant movements (e.g. circumnutation and coiling in tendrils)	Models, simulations and fabrication making use of SMA  Electrosorption of ions on flexible carbon electrodes driven by low input voltages	Manipulation and grasping	[162]  [166]
	G-fibre asymmetric contraction during tendril coiling (different reinforcement level)	3D printing of an active polymer material on a paper substrate, resulting in a bilayer structure with an active and an inactive part		[165]
Dry adhesives	Biomimetic design of natural prickles of the hook-climber <i>Rosa arvensis</i> Splendens	3D Laser Lithography, molding of PDMS, and casting of PCL@Au NPs for actuation	Mechanical interlocking for attachment with micro-rough surfaces	[167]
	Biomimetic design of natural hooks of the hook-climber <i>Galium aparine</i>	3D prototyping technique and Fe <sub>3</sub> O <sub>4</sub> NPs for actuation		[169]
	Biomimetic replica of natural surfaces of the hook-climber <i>Galium aparine</i>	3D Laser Lithography technique  Resin replica molding technique		[168]
Wet adhesives	Biomimetic of the honey-comb like microstructure of the tendril-bearer <i>Parthenocissus tricuspidata</i>	Hierarchical anodic aluminum oxide template	Adhesive for high water adhesion (e.g. industry)	[170]
Nanoparticles	Arabinogalactan protein-rich nanoparticles obtained from the sticky exudates of the adhesive roots (INPs) of the root-climber <i>Hedera helix</i>	Production, isolation, purification, and characterization of INPs.  Formation of INP-drug conjugates	Biocompatible nanomaterial for medicine (e.g. drug delivery)	[151]
Sensors	Sensory organs for mechanoperception (tactile blep) in tendrils of <i>Bryonia dioica</i>	Tactile blep design used in FEM simulations	Electronic skin (e.g. soft robotics)	[25]
	Distribution and structure of the sensory organs (tactile papillae) in tendrils of <i>Cucumis sativus</i>	Tactile sensors based on fiber optic light modulation	Surgical soft manipulator	[172]

tially direct their growth towards an object for climbing [141]. Future studies could focus on performing similar experiments with other climbing plants species to verify the level of variety among species and to validate the presence of other stimuli and mechanisms involved in support identification.

Experiments on the parasitic climbing plant *Cuscuta pentagona* (dodder) elucidated the role of different stimuli on the preferential growth direction of the

plant apex [140]. The authors monitored the growth of the dodder placed near a piece of filter paper towards a stimulus (e.g. natural tomato, glasses with a different colour, moist soil, volatiles or artificial plants) at the opposite side. The final position of the apexes was marked and the percentage of success in reaching the target was calculated [140]. Comparing the response to natural tomatoes and artificial plants, the dodder was more responsive to natural (73%–80%



**Figure 6.** Selected examples of plant-inspired robots. (A) The first self-adaptable growing robot inspired by plant roots. (B) Soft robots inspired from apical extension in filamentous structures. Adapted from [173]. (C) Vine-inspired continuum robot (OCTARM). Adapted from [161]. (D) Tendril-like soft robot based on reversible osmotic actuation.

of seedlings grown towards the target) with respect to artificial plants (40% of seedlings grown towards the target), demonstrating the role of chemical volatile cues in host localization [140].

One of the most fascinating, yet unclear and still mysterious, findings involves the woody vine climbing plant *Boquila trifoliolata* living in the temperate rainforest of southern Chile [43]. The authors discovered that the leaves of this species can morph and mimic its host. In fact it seems that the leaves of this plant can change colour, as well as shape, orientation, petiole length and/or tip spininess in order to protect itself against herbivorous (figure 5) [43]. The authors observed this phenomenon in the climber's natural habit, and performed a phenotype analysis of plant leaf traits to investigate how this plant finds host trees [43]. They did not identify the stimulus involved but speculated that the host emits volatile cues that can be detected by *B. trifoliolata*, or alternatively that the leaf morphing might entail a horizontal gene transfer between plants. Leaf morphology change is a well-known phenomenon in other climbing plants, such as English ivy, induced by developmental evolution (heterophylly) [44]; however, the morphological change occurring in the *B. trifoliolata* seems to differ in the mimicking ability that this plant appears to show for its host, with an underlying mechanism still unknown (e.g. whether the change is intrinsic to the developmental trajectory or induced by external cues) [43]. Recent insights into how gene activity directs organ shape suggest the existence of a feedback system for the mechanical regulation of morphogenesis in leaves, which means that mechanical heterogeneity within the tissue may be necessary for organ shape morphogenesis [148]. Biological investigations on this specific plant model could provide a deeper understanding of the mechanisms behind plant responses to signals. If a plant is able to mimic its host, it has some undiscovered ways of acquiring and processing information on the shapes and forms of the host plant which might converge into recognition ability behaviour [149]. Furthermore, discovering the mechanisms driving this morphogenesis opens up new opportunities in the artificial world for developing controllable morphing devices and robots that are able to autonomously adapt and/or change their body, if necessary, with respect to any objects and/or context.

## 5. How knowledge of plant can be transferred to the artificial world

The last few years have witnessed an increase in the number of artificial systems inspired by plants [150], particularly by climbing plants [30, 45]. Since this review aims at providing methodological guidance for biological investigations useful for technology and not to review plant-inspired artificial systems, here we provide an overview of the main plant-inspired implementations available to date. Table 5 summarizes such systems, which include innovative growing and continuum robots, programmable materials, dry and wet adhesive surfaces, and nanoparticles and sensors, for applications spanning from space to robotics and medicine [124, 126, 151]. Figure 6 shows a selection of the main climbing plant-inspired robots developed in recent years.

Growth ability is one of the most interesting features for designing innovative artefacts acting in real and unstructured environments. Plant roots have been investigated to develop the first autonomous robot able to move in soil by growing [26, 27]. This robot, named Plantoid, embeds a miniaturized 3D printer in the tip of the root-like robotic system and moves in the environment by adding new thermoplastic material layers [122] (figure 6(A)). The robotic tip integrates sensors to detect environmental stimuli (e.g. humidity, gravity, temperature and touch) and implements a tropic-like behaviour to direct its motion [26, 152]. Other examples of artificial growth include soft robots that elongate by skin eversion in order to lengthen themselves from the tip by pressurizable chambers, and bending by launch/unlaunch of pitches (figure 6(B)) [153, 154]. An overview of artificial systems implementing growth or eversion abilities is reported in [155].

The first continuum robot inspired by the biology of tendrils was developed at NASA's Johnson Space Center for minimally invasive inspection in space [156]. This tendril-like robot is a long slender manipulator, designed with multiple bendable segments containing compression and extension springs [156]. Improved versions of this robot accounted for an increased number of springs and a decreased stiffness of the spring (figure 6(C)) [157–161]. Another work on plant-like systems focused on circumnutation

movements and coiling as strategies for grasping objects [162]. The authors proposed a simplified kinematic model that was implemented on a prototype actuated by shape memory alloys (SMA) to perform coiling [162]. The coiling mechanism in tendrils has been widely mimicked for developing new innovative programmable materials [163–165].

A very interesting example of this type of transference includes a tendril-inspired soft gripper with programmable deformations that can bend, perform spiral and helical motions for grasping [165]. This device was fabricated via a 3D printing approach of a thermal-responsive polymer material on a paper substrate, resulting in a bilayer structure with different patterns with an active and an inactive layer [165]. A variable-stiffness tendril-like soft robot based on osmotic actuation has been developed through the use of the electrosorption of ions on flexible carbon electrodes driven by input voltages (figure 6(D)) [166].

New dry and wet adhesive materials have been inspired by the attachment and anchoring mechanisms of climbing plants [45, 151, 167–170]. Some recent works regard the hook-climber *G. aparine* [167–169]. This plant shows a unique ability to adhere to several micro-rough objects, above all via its leaves, using hooks for mechanical interlocking [54]. *G. aparine* has been used as a model for developing new soft dry adhesive devices based on epoxy resin molding [168]. Artificial arrays of hooks at different scales were designed by extracting the morphological parameters from the abaxial and adaxial hooks in the real plant and fabricated using direct laser lithography (DLL) for the rapid prototyping of 3D microstructures [169].

Novel control devices for the remote release of objects at different scales have been inspired by hook climbers [167, 171]. Specifically, a rose-inspired biomimetic device with micro-prickle-like hooks with variable stiffness was developed using a combination of different techniques, such as DLL, molding of PDMS and casting of polycaprolactone with embedded gold nanoparticles (PCL@Au NPs) [171]. Also, a 3D printed biomimetic surface has been fabricated with tunable frictional anisotropy, containing hooked structures made of rigid PLA embedded in Fe<sub>3</sub>O<sub>4</sub> nanoparticles, capable of supporting layer rigidity variation [167]. Observations of the biological adhesion of *P. tricuspidata* and their microstructure, led to an advanced composite adhesive material for high water adhesion that was made into a polystyrene honeycomb-like microstructure [170]. Nanoparticles composed of arabinogalactan proteins (INPs) were obtained from the sticky exudates of the adhesive roots of *H. helix* in order to develop biocompatible nanomaterial for drug delivery [151].

The sensory organs of tendrils have inspired the innovative sensors for soft robotics and surgical applications [25, 38, 172]. Blandin's work focused on the tactile bleps of *B. dioica* [25], in which the shape and

biomechanical properties were mimicked in a simplified design, and FEM simulations were performed to evaluate the deformations achievable in the natural bleps [25]. Finally, by mimicking the papillae (sensory organs) design of cucumber tendrils, a tactile sensor based on fiber optic light modulation was built [172].

## 6. Concluding remarks and future outlooks

This review has outlined the biological tools and approaches used in biology for extracting benchmarks from climbing plants in order to: (i) improve the basic knowledge of their properties and behaviour, and (ii) develop innovative artefacts. We have highlighted the main methodologies adopted to investigate the morphological and biomechanical adaptive properties of climbing plants, their circumnutation movements, and their perceptive and recognition behaviours.

Several studies have been performed on climbing plants revealing the structural and biomechanical changes in organization for several lianas and vines [49]. Despite all of these, many aspects remain unrevealed. For instance, there is a lack of data about adhesive roots of vines and lianas (except for few examples [47, 56, 58]). Also, it is still unclear how stems of some species can reach high breaking strain (e.g. strain of *G. aparine* stem does not show correlation with microfibril orientation [53]). A broader dynamic investigation of how mechanical properties and structural arrangements vary along climbing plant bodies from the macro- to the nanoscale could open new opportunities for a deeper understanding of these mechanisms and could lead to the development of bio-inspired soft robots with a high strain capacity and new adhesive devices. One of the main limitations for developing soft climbing plant-inspired growing robots is the type of artificial material available to enable growth, which has to be suitable for managing e.g. deposition or inflation, but at the same time it is desirable to embed both sensing and actuation ability. A deep 3D reconstruction of the climbing plant organs can lead to fiber-oriented innovative materials for sensing and actuators in soft robotics.

Further research on circumnutation in twining vines and tendrils could help to improve our knowledge of growth-induced motions in plants. New software is needed to perform accurate analyses of circumnutation in order to obtain kinematic control theories, which would be useful in robotics. Also, only a few sensory organs in climbing plants have been investigated (e.g. tactile bleps in *B. dioica*, [136]). Further research needs to focus on the characterization of sensory organs of various species and on the mechanisms behind the identification and recognition of several stimuli, for developing new multifunctional materials and sensors. Finally, we still have a limited knowledge on how climbing plants direct their growth preference

towards different targets (e.g. through the detection of volatile cues [140]).

The discovery of the morphing abilities of *B. trifoliolata* [43] has opened up new issues, such as whether and how a plant can recognize shape and forms without a brain or vision. This morphing capability is unique among living organisms and it could be correlated to structural and biomechanical internal changes. A recent discovery suggests that simple changes in cell wall stiffness in plants can induce morphogenesis during the shape of organ development [148].

A deeper understanding of these mechanisms will open up new opportunities in the artificial world for developing autonomous intelligent systems that can morph and adapt their body to unpredictable scenarios. Disruptive innovations will come from the pioneering research on climbing plant-inspired soft robots, which could be applied to a wide range of fields, including architecture and urban environment maintenance and development (e.g. self-repairing growing structures), in exploration and inspection applications (e.g. in archaeological sites or other and delicate confined spaces), or for continuous monitoring in unstructured environments.

## Acknowledgments

This work was funded by RoboCom ++, the European Commission under the FLAG-ERA Joint Transnational Call (JTC) 2016, by SMASH-Smart Machines for Agricultural Solutions Hightech (Tuscany-Italy POR FESR 2014-2020), by EOLO, the Regional Tuscany project (no. 12866/2016 e 7148/17) and by GrowBot, the European Union's Horizon 2020 Research and Innovation Programme under Grant Agreement No. 824074.

## ORCID iDs

Isabella Fiorello  <https://orcid.org/0000-0003-2613-9505>

Emanuela Del Dottore  <https://orcid.org/0000-0001-6874-1970>

## References

- [1] Darwin C 1862 *On the Various Contrivances by Which British and Foreign Orchids are Fertilised by Insects: and on the Good Effects of Intercrossing* (London: J. Murray)
- [2] McCurdy E 2013 *The Mind of Leonardo da Vinci* (Mineola, NY: Courier Corporation)
- [3] Schmitt O H 1969 Some interesting and useful biomimetic transforms *3rd Int. Biophysics Congress* vol 1069 p 197
- [4] Bar-Cohen Y 2006 Biomimetics—using nature to inspire human innovation *Bioinspir. Biomim.* **1** P1
- [5] Bhushan B 2009 Introduction: biomimetics: lessons from nature—an overview *Phil. Trans.* **367** 1445–86
- [6] Xia Z 2016 *Biomimetic Principles and Design of Advanced Engineering Materials* (New York: Wiley)
- [7] Vincent J F 2009 Biomimetics—a review *Proc. Inst. Mech. Eng. H* **223** 919–39
- [8] Vincent J F, Bogatyreva O A, Bogatyrev N R, Bowyer A and Pahl A-K 2006 Biomimetics: its practice and theory *J. R. Soc. Interface* **3** 471–82
- [9] Laschi C, Mazzolai B, Mattoli V, Cianchetti M and Dario P 2009 Design of a biomimetic robotic octopus arm *Bioinspir. Biomim.* **4** 015006
- [10] Tramacere F, Follador M, Pugno N and Mazzolai B 2015 Octopus-like suction cups: from natural to artificial solutions *Bioinspir. Biomim.* **10** 035004
- [11] Calisti M 2017 Soft robotics in underwater legged locomotion: from octopus-inspired solutions to running robots *Soft Robotics: Trends, Applications and Challenges* (Berlin: Springer) pp 31–6
- [12] Sareh S et al 2017 Anchoring like octopus: biologically inspired soft artificial sucker *J. R. Soc. Interface* **14** 20170395
- [13] Wang W, Wang K and Zhang H 2009 Crawling gait realization of the mini-modular climbing caterpillar robot *Prog. Natural Sci.* **19** 1821–9
- [14] Hu W, Lum G Z, Mastrangeli M and Sitti M 2018 Small-scale soft-bodied robot with multimodal locomotion *Nature* **554** 81
- [15] Shepherd R F et al 2011 Multigait soft robot *Proc. Natl Acad. Sci.* **108** 20400–3
- [16] Kandhari A, Huang Y, Daltorio K, Chiel H and Quinn R 2018 Body stiffness in orthogonal directions oppositely affects worm-like robot turning and straight-line locomotion *Bioinspir. Biomim.* **13** 026003
- [17] Tricinci O et al 2017 Dry adhesion of artificial gecko setae fabricated via direct laser lithography *Conf. on Biomimetic and Biohybrid Systems* (Berlin: Springer) pp 631–6
- [18] Glick P, Suresh S A, Ruffatto D, Cutkosky M, Tolley M T and Parness A 2018 A soft robotic gripper with gecko-inspired adhesive *IEEE Robot. Autom. Lett.* **3** 903–10
- [19] Autumn K, Dittmore A, Santos D, Spenko M and Cutkosky M 2006 Frictional adhesion: a new angle on gecko attachment *J. Exp. Biol.* **209** 3569–79
- [20] Jiang H et al 2017 A robotic device using gecko-inspired adhesives can grasp and manipulate large objects in microgravity *Sci. Robot* **2** eaan4545
- [21] Wang S, Jiang H and Cutkosky M R 2016 A palm for a rock climbing robot based on dense arrays of micro-spines *2016 IEEE/RSJ Int. Conf. on Intelligent Robots and Systems* (IEEE) pp 52–9
- [22] Chattopadhyay P and Ghoshal S K 2018 Adhesion technologies of bio-inspired climbing robots: a survey *Int. J. Robot. Autom.* **33**
- [23] Ma K Y, Chirarattananon P, Fuller S B and Wood R J 2013 Controlled flight of a biologically inspired, insect-scale robot *Science* **340** 603–7
- [24] Karpelson M, Wei G-Y and Wood R J 2008 A review of actuation and power electronics options for flapping-wing robotic insects *IEEE Int. Conf. on Robotics and Automation, 2008. ICRA 2008* (IEEE) pp 779–86
- [25] Blandin A A, Totaro M, Bernardeschi I and Beccai L 2017 Tunable normal and shear force discrimination by a plant-inspired tactile sensor for soft robotics *Conf. on Biomimetic and Biohybrid Systems* (Berlin: Springer) pp 25–34
- [26] Sadeghi A, Mondini A and Mazzolai B 2017 Toward self-growing soft robots inspired by plant roots and based on additive manufacturing technologies *Soft Robot.* **4** 211–23
- [27] Sadeghi A, Tonazzini A, Popova L and Mazzolai B 2014 A novel growing device inspired by plant root soil penetration behaviors *PLoS One* **9** e90139
- [28] Laschi C, Mazzolai B and Cianchetti M 2016 Soft robotics: Technologies and systems pushing the boundaries of robot abilities *Sci. Robot* **1** eaah3690
- [29] Niklas K J and Spatz H-C 2012 *Plant Physics* (Chicago, IL: University of Chicago Press)
- [30] Mazzolai B, Beccai L and Mattoli V 2014 Plants as model in biomimetics and biorobotics: new perspectives *Frontiers Bioeng. Biotechnol.* **2** 2
- [31] Darwin C 1865 On the movements and habits of climbing plants *Bot. J. Linnæan Soc.* **9** 1–118

- [32] Isnard S and Silk W K 2009 Moving with climbing plants from Charles Darwin's time into the 21st century *Am. J. Bot.* **96** 1205–21
- [33] Gianoli E 2015 The behavioural ecology of climbing plants *AoB Plants* **7** plw013
- [34] Rowe N and Speck T 2005 Plant growth forms: an ecological and evolutionary perspective *New Phytol.* **166** 61–72
- [35] Wang J-S et al 2013 Hierarchical chirality transfer in the growth of towel gourd tendrils *Sci. Rep.* **3** 3102
- [36] Smyth D R 2016 Helical growth in plant organs: mechanisms and significance (in eng) *Development* **143** 3272–82
- [37] Braam J 2005 In touch: plant responses to mechanical stimuli *New Phytol.* **165** 373–89
- [38] Astreimidi Blandin A, Bernardeschi I and Beccai L 2018 Biomechanics in soft mechanical sensing: from natural case studies to the artificial world *Biomimetics* **3** 32
- [39] Jaffe M and Galston A 1968 The physiology of tendrils *Ann. Rev. Plant Physiol.* **19** 417–34
- [40] Jaffe M and Galston A 1966 Physiological studies on pea tendrils. I. Growth and coiling following mechanical stimulation *Plant Physiol.* **41** 1014–25
- [41] Jaffe M and Forbes S 1996 Thigmomorphogenesis: the effect of mechanical perturbation on plants *Plant Growth Regul.* **12** 313–24
- [42] Rowe N P and Speck T 2014 Stem biomechanics, strength of attachment, and developmental plasticity of vines and lianas *Ecology of Lianas* (Hoboken, NJ: Wiley) pp 323–41
- [43] Gianoli E and Carrasco-Urra F 2014 Leaf mimicry in a climbing plant protects against herbivory *Curr. Biol.* **24** 984–7
- [44] Chitwood D H and Sinha N R 2016 Evolutionary and environmental forces sculpting leaf development *Curr. Biol.* **26** R297–306
- [45] Burris J N, Lenaghan S C and Stewart C N 2017 Climbing plants: attachment adaptations and bioinspired innovations *Plant Cell Rep.* **37** 565–74
- [46] Isnard S, Cobb A R, Holbrook N M, Zwieniecki M and Dumais J 2009 Tensioning the helix: A mechanism for force generation in twining plants *Proc. R. Soc. B* **726**
- [47] Yang X and Deng W 2017 Morphological and structural characterization of the attachment system in aerial roots of syngonium podophyllum *Planta* **245** 507–21
- [48] Hesse L, Wagner S T and Neinhuis C 2016 Biomechanics and functional morphology of a climbing monocot *AoB Plants* **8** plw005
- [49] Rowe N, Isnard S and Speck T 2004 Diversity of mechanical architectures in climbing plants: an evolutionary perspective *J. Plant Growth Regul.* **23** 108–28
- [50] Bowling A J and Vaughn K C 2009 Gelatinous fibers are widespread in coiling tendrils and twining vines *Am. J. Bot.* **96** 719–27
- [51] Gerbode S J, Puzey J R, McCormick A G and Mahadevan L 2012 How the cucumber tendril coils and overwinds *Science* **337** 1087–91
- [52] Meloche C G, Knox J P and Vaughn K C 2007 A cortical band of gelatinous fibers causes the coiling of redvine tendrils: a model based upon cytochemical and immunocytochemical studies *Planta* **225** 485–98
- [53] Goodman A M 2004 Mechanical adaptations of cleavers (*Galium aparine*) *Ann. Bot.* **95** 475–80
- [54] Bauer G, Klein M C, Gorb S N, Speck T, Voigt D and Gallenmüller F 2011 Always on the bright side: the climbing mechanism of *Galium aparine* *Proc. Biol. Sci.* **278** 2233–9
- [55] Bohn H F, Günther F, Fink S and Speck T 2015 A passionate free climber: structural development and functional morphology of the adhesive tendrils in *Passiflora discophora* *Int. J. Plant Sci.* **176** 294–305
- [56] Melzer B, Steinbrecher T, Seidel R, Kraft O, Schwaiger R and Speck T 2010 The attachment strategy of English ivy: a complex mechanism acting on several hierarchical levels *J. R. Soc. Interface* **7** 1383–9
- [57] Hoffmann B, Chabbert B, Monties B and Speck T 2003 Mechanical, chemical and x-ray analysis of wood in the two tropical lianas *Bauhinia guianensis* and *Condylocarpon guianense*: variations during ontogeny *Planta* **217** 32–40
- [58] Melzer B, Seidel R, Steinbrecher T and Speck T 2011 Structure, attachment properties, and ecological importance of the attachment system of English ivy (*Hedera helix*) *J. Exp. Bot.* **63** 191–201
- [59] Steinbrecher T, Beuchle G, Melzer B, Speck T, Kraft O and Schwaiger R 2011 Structural development and morphology of the attachment system of *Parthenocissus tricuspidata* *Int. J. Plant Sci.* **172** 1120–9
- [60] Isnard S and Rowe N 2008 Mechanical role of the leaf sheath in rattans *New Phytol.* **177** 643–52
- [61] Steinbrecher T, Danninger E, Harder D, Speck T, Kraft O and Schwaiger R 2010 Quantifying the attachment strength of climbing plants: a new approach *Acta Biomater.* **6** 1497–504
- [62] Yang X 2014 Review on the adhesive tendrils of *Parthenocissus Chin. Sci. Bull.* **59** 113–24
- [63] Matista A and Silk W 1997 An electronic device for continuous, *in vivo* measurement of forces exerted by twining vines *Am. J. Bot.* **84** 1164–4
- [64] Silk W K and Holbrook N M 2005 The importance of frictional interactions in maintaining the stability of the twining habit *Am. J. Bot.* **92** 1820–6
- [65] Gorb E, Popov V and Gorb S 2002 Natural hook-and-loop fasteners: anatomy, mechanical properties, and attachment force of the jointed hooks of the *Galium aparine* fruit *WIT Trans. Ecol. Environ.* **57**
- [66] Mauseth J D 1988 *Plant Anatomy (no. 04; QK641, M3.)* (California: Benjamin/Cummings Publishing Company)
- [67] Rowe N P and Speck T 1996 Biomechanical characteristics of the ontogeny and growth habit of the tropical liana *Condylocarpon guianense* (apocynaceae) *Int. J. Plant Sci.* **157** 406–17
- [68] Crang R F 1988 Artifacts in specimen preparation for scanning electron microscopy *Artifacts in Biological Electron Microscopy* (New York: Plenum) pp 107–29
- [69] Pathan A, Bond J and Gaskin R 2008 Sample preparation for scanning electron microscopy of plant surfaces—horses for courses *Micron* **39** 1049–61
- [70] Guo Q, Dong J, Liu Y, Xu X, Qin Q and Wang J 2010 Macroscopic and microscopic mechanical behaviors of climbing tendrils *Acta Mech. Sin.* **35** 702–10
- [71] Ménard L, McKey D, Mühlen G S, Clair B and Rowe N P 2013 The evolutionary fate of phenotypic plasticity and functional traits under domestication in manioc: Changes in stem biomechanics and the appearance of stem brittleness *PLoS One* **8** e74727
- [72] Lichtenegger H, Müller M, Paris O, Riekel C and Fratzl P 1999 Imaging of the helical arrangement of cellulose fibrils in wood by synchrotron x-ray microdiffraction *J. Appl. Crystallog.* **32** 1127–33
- [73] Herrel A, Speck T and Rowe N P 2006 *Ecology and Biomechanics: a Mechanical Approach to the Ecology of Animals and Plants* (Boca Raton, FL: CRC Press)
- [74] Wagner S T, Isnard S, Rowe N P, Samain M S, Neinhuis C and Wanke S 2012 Escaping the lianoid habit: evolution of shrub-like growth forms in *Aristolochia subgenus Isotrema* (Aristolochiaceae) *Am. J. Bot.* **99** 1609–29
- [75] Speck T, Rowe N, Civyrel L, Classen Bockhoff R, Neinhuis C and Spatz H C 2003 The potential of plant biomechanics in functional biology and systematics *Deep Morphology: Toward a Renaissance of Morphology in Plant Systematics* ed T F Stuessy et al (Ruggell, Lichtenstein: ARG Gantner Verlag) pp 241–71
- [76] Speck T and Burgert I 2011 Plant stems: functional design and mechanics *Ann. Rev. Mater. Res.* **41** 169–93
- [77] Gallenmüller F, Rowe N and Speck T 2004 Development and growth form of the neotropical liana *Croton nuntians*: the effect of light and mode of attachment on the biomechanics of the stem *J. Plant Growth Regul.* **23** 83–97
- [78] Koehl M and Wainwright S 1977 Mechanical adaptations of a giant kelp *Limnol. Oceanogr.* **22** 1067–71
- [79] Chen Q, Gorb S N, Gorb E and Pugno N 2013 Mechanics of plant fruit hooks *J. R. Soc. Interface* **10** 20120913
- [80] Gallenmüller F, Müller U, Rowe N and Speck T 2001 The growth form of *Croton pullei* (Euphorbiaceae)-functional

- morphology and biomechanics of a neotropical liana *Plant Biol.* **3** 50–61
- [81] Scher J L, Holbrook N M and Silk W K 2001 Temporal and spatial patterns of twining force and lignification in stems of *Ipomoea purpurea* *Planta* **213** 192–8
- [82] Rjosk A, Neinhuis C and Wagner S T 2018 A rare climbing habit: functional properties of the leaf-climbing monocot *Flagellaria indica* (Flagellariaceae) *Flora* **239** 71–86
- [83] Gindl W, Gupta H, Schöberl T, Lichtenegger H and Fratzl P 2004 Mechanical properties of spruce wood cell walls by nanoindentation *Appl. Phys. A* **79** 2069–73
- [84] Geitmann A 2006 Experimental approaches used to quantify physical parameters at cellular and subcellular levels *Am. J. Bot.* **93** 1380–90
- [85] Burgert I 2006 Exploring the micromechanical design of plant cell walls *Am. J. Bot.* **93** 1391–401
- [86] Calusi B, Tramacere F, Filippeschi C, Pugno N M and Mazzolai B 2017 A biomechanical characterization of plant root tissues by dynamic nanoindentation technique for biomimetic technologies *Conf. on Biomimetic and Biohybrid Systems* (Berlin: Springer) pp 532–6
- [87] Wolf S et al 2016 Variable stiffness actuators: review on design and components *IEEE/ASME Trans. Mech.* **21** 2418–30
- [88] Kim S, Laschi C and Trimmer B 2013 Soft robotics: a bioinspired evolution in robotics *Trends Biotechnol.* **31** 287–94
- [89] Neukirch S and Goriely A 2006 Twining plants: how thick should their supports be? *Proc. 5th Plant Biomechanics Conf. (Stockholm)*
- [90] Stolarz M 2009 Circumnutation as a visible plant action and reaction: physiological, cellular and molecular basis for circumnutations *Plant Signal. Behav.* **4** 380–7
- [91] Brauner L 1954 Tropisms and nastic movements *Ann. Rev. Plant Physiol.* **5** 163–82
- [92] Skotheim J M and Mahadevan L 2005 Physical limits and design principles for plant and fungal movements *Science* **308** 1308–10
- [93] Darwin G H 1880 XX. On the secular changes in the elements of the orbit of a satellite revolving about a tidally distorted planet *Phil. Trans. R. Soc.* **171** 713–891
- [94] Migliaccio F, Tassone P and Fortunati A 2013 Circumnutation as an autonomous root movement in plants *Am. J. Bot.* **100** 4–13
- [95] Larson K C 2000 Circumnutation behavior of an exotic honeysuckle vine and its native congener: influence on clonal mobility *Am. J. Bot.* **87** 533–8
- [96] Stolarz M, Zuk M, Król E and Dziubinska H 2014 Circumnutation tracker: novel software for investigation of circumnutation *Plant Methods* **10** 24
- [97] Popova L, Russino A, Ascrizzi A and Mazzolai B 2012 Analysis of movement in primary maize roots *Biologia* **67** 517–24
- [98] Caré A-F, Nefed'ev L, Bonnet B, Millet B and Badot P-M 1998 Cell elongation and revolving movement in *Phaseolus vulgaris* L. twining shoots *Plant Cell Physiol.* **39** 914–21
- [99] Someya T 2006 The world's first sheet-type wireless power transmission system Press Interview Handout, University of Tokyo
- [100] Yang W et al 2011 High-throughput measurement of rice tillers using a conveyor equipped with x-ray computed tomography *Rev. Sci. Instrum.* **82** 025102
- [101] Basu P, Pal A, Lynch J P and Brown K M 2007 A novel image-analysis technique for kinematic study of growth and curvature *Plant Physiol.* **145** 305–16
- [102] Garcia B, Campilho A, Scheres B and Campilho A 2004 Automatic tracking of *Arabidopsis thaliana* root meristem in confocal microscopy *Int. Conf. Image Analysis and Recognition* (Berlin: Springer) pp 166–74
- [103] Johnsson A and Heathcote D 1973 Experimental evidence and models on circumnutations *Z. Pflanzenphysiol.* **70** 371–405
- [104] Calvo P, Raja V and Lee D N 2017 Guidance of circumnutation of climbing bean stems: An ecological exploration *bioRxiv* **122358**
- [105] Millet B, Melin D, Bonnet B, Ibrahim C and Mercier J 1984 Rhythmic circumnutation movement of the shoots in *Phaseolus vulgaris* L *Chronobiol. Int.* **1** 11–9
- [106] Millet B and Badot P-M 1996 The revolving movement mechanism in phaseolus; new approaches to old questions *Vis. Biorhythm.* **77** 98
- [107] Baillaud L 1962 Les mouvements d'exploration et d'enroulement des plantes volubiles *Physiology of Movements/ Physiologie der Bewegungen* (Berlin: Springer) pp 635–715
- [108] Agosti R D and Millet B 1991 Influence of environmental factors on the ultradian rhythm of shoot movement in *Phaseolus vulgaris* L *Biol. Rhythm Res.* **22** 325–32
- [109] Schuster J and Engelmann W 1997 Circumnutations of *Arabidopsis thaliana* seedlings *Biol. Rhythm Res.* **28** 422–40
- [110] Anderson-Bernadas C, Cornelissen G, Turner C M and Koukkari W L 1997 Rhythmic nature of thigmomorphogenesis and thermal stress of *Phaseolus vulgaris* L. shoots *J. Plant Physiol.* **151** 575–80
- [111] Kayali S, Montavon M, Simon P and Greppin H 1994 A device for the continuous measurement of the circumnutation of tendrils *Plant Physiol. Biochem.* **32** 577–81
- [112] Johnsson A 1997 Circumnutations: results from recent experiments on Earth and in space *Planta* **203** S147–58
- [113] Biot E et al 2016 Multiscale quantification of morphodynamics: MorphoLeaf software for 2D shape analysis *Development* **143** 3417–28
- [114] Remmler L and Rolland-Lagan A-G 2012 Computational method for quantifying growth patterns at the adaxial leaf surface in three dimensions *Plant Physiol.* **159** 27–39
- [115] Clark R et al 2011 Three-dimensional root phenotyping with a novel imaging and software platform *Plant Physiol.* **156** 455–65
- [116] Lobet G, Pagès L and Draye X 2011 A novel image analysis toolbox enabling quantitative analysis of root system architecture *Plant Physiol.* **157** 29–39
- [117] Russino A, Ascrizzi A, Popova L, Tonazzini A, Mancuso S and Mazzolai B 2013 A novel tracking tool for the analysis of plant-root tip movements *Bioinspir. Biomim.* **8** 025004
- [118] Wang L, Uilecan I V, Assadi A H, Kozmik C A and Spalding E P 2009 HYPOTrace: image analysis software for measuring hypocotyl growth and shape demonstrated on *Arabidopsis* seedlings undergoing photomorphogenesis *Plant Physiol.* **149** 1632–7
- [119] Crenshaw H C, Ciampaglio C N and McHenry M 2000 Analysis of the three-dimensional trajectories of organisms: estimates of velocity, curvature and torsion from positional information *J. Exp. Biol.* **203** 961–82
- [120] Bullitt E, Gerig G, Pizer S M, Lin W and Aylward S R 2003 Measuring tortuosity of the intracerebral vasculature from MRA images *IEEE Trans. Med. Imaging* **22** 1163–71
- [121] Popova L, van Dusschoten D, Nagel K A, Fiorani F and Mazzolai B 2016 Plant root tortuosity: an indicator of root path formation in soil with different composition and density *Ann. Bot.* **118** 685–98
- [122] Del Dottore E, Mondini A, Sadeghi A and Mazzolai B 2018 A plant-inspired kinematic model for growing robots *2018 IEEE Int. Conf. on Soft Robotics* (IEEE) pp 20–4
- [123] Bastien R and Meroz Y 2016 The kinematics of plant nutation reveals a simple relation between curvature and the orientation of differential growth *PLoS Comput. Biol.* **12** e1005238
- [124] Wooten M, Frazelle C, Walker I D, Kapadia A and Lee J H 2018 Exploration and inspection with vine-inspired continuum robots *2018 IEEE Int. Conf. on Robotics and Automation* (IEEE) pp 1–5
- [125] Del Dottore E, Mondini A, Sadeghi A, Mattoli V and Mazzolai B 2016 Circumnutations as a penetration strategy in a plant-root-inspired robot *2016 IEEE Int. Conf. on Robotics and Automation* (IEEE) pp 4722–8
- [126] Del Dottore E, Mondini A, Sadeghi A, Mattoli V and Mazzolai B 2017 An efficient soil penetration strategy for explorative robots inspired by plant root circumnutation movements *Bioinspir. Biomim.* **13** 015003

- [127] Sachs J 1887 *Lectures on the Physiology of Plants* (Oxford: Clarendon)
- [128] Fitting H 1936 Untersuchungen über den Haptotropismus der Ranken *Planta* **25** 206–39
- [129] Jacquiot C 1949 Comptes rendus hebdomadaires des séances de l'Académie des sciences **229** 241–3
- [130] Pigliucci M 2002 Touchy and bushy: phenotypic plasticity and integration in response to wind stimulation in *Arabidopsis thaliana* *Int. J. Plant Sci.* **163** 399–408
- [131] Braam J and Davis R W 1990 Rain-, wind-, and touch-induced expression of calmodulin and calmodulin-related genes in *Arabidopsis* *Cell* **60** 357–64
- [132] Biddington N L 1986 The effects of mechanically-induced stress in plants—a review *Plant Growth Regul.* **4** 103–23
- [133] Vaughn K C and Bowling A J 2011 1 biology and physiology of vines *Horticult. Rev.* **38** 1
- [134] Simons P 1992 *The Action Plant: Movement and Nervous Behaviour in Plants* (Oxford: Blackwell)
- [135] Engelberth J 2003 Mechanosensing and signaltransduction in tendrils *Adv. Space Res.* **32** 1611–9
- [136] Engelberth J, Wanner G, Groth B and Weiler E W 1995 Functional anatomy of the mechanoreceptor cells in tendrils of *Bryonia dioica* Jacq *Planta* **196** 539–50
- [137] MacDougal D 1893 Frost plants: a resume *Science* **569** 351–2
- [138] Trewavas A and Knight M 1994 Mechanical signalling, calcium and plant form *Signals and Signal Transduction Pathways in Plants* (Berlin: Springer) pp 93–105
- [139] Strong D R Jr and Ray T S Jr 1975 Host Tree Location Behavior of a Tropical Vine (*Monstera gigantea*) by Skototropism *Science* **190** 804–6
- [140] Runyon J B, Mescher M C and De Moraes C M 2006 Volatile chemical cues guide host location and host selection by parasitic plants *Science* **313** 1964–7
- [141] Price A J and Wilcut J W 2007 Response of ivy leaf morning glory (*Ipomoea hederacea*) to neighboring plants and objects *Weed Technol.* **21** 922–7
- [142] Mullen J L, Wolverton C, Ishikawa H and Evans M L 2000 Kinetics of constant gravitropic stimulus responses in *Arabidopsis* roots using a feedback system *Plant Physiol.* **123** 665–70
- [143] Meder F et al 2018 Energy conversion at the cuticle of living plants *Adv. Funct. Mater.* **xx** 1806689
- [144] Anten N P, Alcalá-Herrera R, Schieving F and Onoda Y 2010 Wind and mechanical stimuli differentially affect leaf traits in *Plantago major* *New Phytol.* **188** 554–64
- [145] Reid C R, MacDonald H, Mann R P, Marshall J A, Latty T and Garnier S 2016 Decision-making without a brain: how an amoeboid organism solves the two-armed bandit *J. R. Soc. Interface* **13** 20160030
- [146] Dussutour A, Ma Q and Sumpter D 2019 Phenotypic variability predicts decision accuracy in unicellular organisms *Proc. R. Soc. B* **286** 20182825
- [147] Reid C R, Garnier S, Beekman M and Latty T 2015 Information integration and multiattribute decision making in non-neuronal organisms *Anim. Behav.* **100** 44–50
- [148] Qi J et al 2017 Mechanical regulation of organ asymmetry in leaves *Nat. Plants* **3** 724
- [149] Gianoli E 2017 Eyes in the chameleon vine? *Trends Plant Sci.* **22** 4–5
- [150] Mazzolai B, Mattoli V, Beccai L and Sinibaldi E 2014 Emerging technologies inspired by plants *Bioinspired Approaches for Human-Centric Technologies* (Berlin: Springer) pp 111–32
- [151] Huang Y et al 2015 Exploring naturally occurring ivy nanoparticles as an alternative biomaterial *Acta Biomater.* **25** 268–83
- [152] Sadeghi A et al 2016 A plant-inspired robot with soft differential bending capabilities *Bioinspir. Biomim.* **12** 015001
- [153] Tsukagoshi H, Arai N, Kiryu I and Kitagawa A 2011 Tip growing actuator with the hose-like structure aiming for inspection on narrow terrain *Int. J. Autom. Technol.* **5** 516–22
- [154] Hawkes E W, Blumenschein L H, Greer J D and Okamura A M 2017 A soft robot that navigates its environment through growth *Sci. Robot.* **2** eaan3028
- [155] Del Dottore E, Sadeghi A, Mondini A, Mattoli V and Mazzolai B 2018 Toward growing robots: a historical evolution from cellular to plant-inspired robotics *Frontiers Robot. AI* **5** 16
- [156] Mehling J S, Diftler M A, Chu M and Valvo M 2006 A minimally invasive tendril robot for in-space inspection *The 1st IEEE/RAS-EMBS Int. Conf. on Biomedical Robotics and Biomechatronics, 2006. BioRob 2006* (IEEE) pp 690–5
- [157] Tonapi M M, Godage I S and Walker I D 2014 Next generation rope-like robot for in-space inspection *2014 IEEE Aerospace Conf.* (IEEE) pp 1–13
- [158] Wooten M B and Walker I D 2015 A novel vine-like robot for in-orbit inspection *45th Int. Conf. on Environmental Systems*
- [159] Nahar D, Yanik P M and Walker I D 2017 Robot tendrils: long, thin continuum robots for inspection in space operations *2017 IEEE Aerospace Conf.* (IEEE) pp 1–8
- [160] Wooten M and Walker I 2018 Vine-inspired continuum tendril robots and circumnutations *Robotics* **7** 58
- [161] Walker I D 2015 Biologically inspired vine-like and tendril-like robots *2015 Science and Information Conf.* (IEEE) pp 714–20
- [162] Vidoni R, Mimmo T and Pandolfi C 2015 Tendril-based climbing plants to model, simulate and create bio-inspired robotic systems *J. Bionic Eng.* **12** 250–62
- [163] Deng J et al 2017 Preparation of biomimetic hierarchically helical fiber actuators from carbon nanotubes *Nat. Prot.* **12** 1349–58
- [164] Wang M, Lin B-P and Yang H 2016 A plant tendril mimic soft actuator with phototunable bending and chiral twisting motion modes *Nat. Commun.* **7** 13981
- [165] Wang W, Li C, Cho M and Ahn S-H 2018 Soft tendril-inspired grippers: shape morphing of programmable polymer–paper bilayer composites *ACS Appl. Mater. Interfaces* **10** 10419–27
- [166] Must I, Sinibaldi E and Mazzolai B 2019 A variable-stiffness tendril-like soft robot based on reversible osmotic actuation *Nat. Commun.* **10** 344
- [167] Ji Z et al 2018 Biomimetic surface with tunable frictional anisotropy enabled by photothermogenesis-induced supporting layer rigidity variation *Adv. Mater. Interfaces* **6** 1801460
- [168] Andrews H G and Badyal J P S 2014 Bioinspired hook surfaces based upon a ubiquitous weed (*Galium aparine*) for dry adhesion *J. Adhes. Sci. Technol.* **28** 1243–55
- [169] Fiorello I, Tricinci O, Mishra A K, Tramacere F, Filippeschi C and Mazzolai B 2018 Artificial system inspired by climbing mechanism of *Galium aparine* fabricated via 3D laser lithography *Conf. on Biomimetic and Biohybrid Systems* (Berlin: Springer) pp 168–78
- [170] He T, Zhang L and Deng W 2011 Designing polystyrene honeycomb-like microstructure with high water adhesion *Mater. Chem. Phys.* **131** 23–6
- [171] Fiorello I, Meder F, Tricinci O, Filippeschi C and Mazzolai B 2019 Rose-inspired micro-device with variable stiffness for remotely controlled release of objects in robotics *Conf. on Biomimetic and Biohybrid Systems* (Berlin: Springer) pp 122–33
- [172] Sareh S et al 2014 Bio-inspired tactile sensor sleeve for surgical soft manipulators *2014 IEEE Int. Conf. on Robotics and Automation* (IEEE) pp 1454–9
- [173] Coad M M et al 2019 Vine robots: design, teleoperation, and deployment for navigation and exploration *IEEE Robotics & Automation Magazine* (in preparation) (<https://doi.org/10.1109/MRA.2019.2947538>)
- [174] Greer J D, Blumenschein L H, Okamura A M and Hawkes E W 2018 Obstacle-aided navigation of a soft growing robot *2018 IEEE Int. Conf. on Robotics and Automation* (IEEE) pp 1–8