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

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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]. Roboticists 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 environments, 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 branches) [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. tendrilis, 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 are 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 *Condylacarpus guianense* tropical lianas [57, 67]. With the exception of the flexible wood in *Condylacarpus*, 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 circumnutations 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.
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/multiaxial 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-

| Features       | Methodology                          | Objective                                                                 | Extracted features                                                                 | References |
|----------------|--------------------------------------|---------------------------------------------------------------------------|-----------------------------------------------------------------------------------|------------|
| Morphology     | Light microscopy in combination with  | To investigate plant structures, histology characterizes tissue morphology | Tissue organization in stem and tendrils, G-fiber role and distribution in tendrils | [46–49]   |
|                | histology                            | and anatomy and ensures precise sample sectioning, The use of an antibody   | and twining vines, Microfibril orientation in cell walls (polarized light)         |            |
|                |                                      | enables a specific target to be recognized                                  |                                                                                   | [50, 51]  |
| Scanning       | micro-electron microscope             | To extensively investigate plant micro/nano structures (higher resolution    | Surface characterization, Internal structure characterization                       | [47, 54–56]|
|                |                                      | respect to light microscope)                                               |                                                                                   | [35]      |
| X-ray analysis |                                      | To characterize plant cell wall structure at the nanoscale                  | Microfibril orientation in cell walls                                           | [57]      |
| Biomechanics   | Tensile test                          | To evaluate the mechanical behaviour of material under tension and          | Young’s modulus (E) values                                                        | [46, 51, 53, 58, 59]|
|                |                                      | compression conditions                                                      |                                                                                   |            |
|                | Flexure test                          | To evaluate the mechanical behaviour of material under bending conditions   | Bending modulus (E_{bending}) values                                              | [46, 48]  |
|                |                                      | (e.g. three-point bending test)                                             |                                                                                   |            |
|                | Shear test                            | To evaluate the mechanical behaviour of material under shear load conditions,| Shear modulus (G) values                                                          | [46]      |
|                |                                      | when two planes of the same object try to slide past one another            |                                                                                   |            |
|                | Torsion test                          | To evaluate the mechanical behaviour of material under the application of   | Torsional modulus (G_{torsion}) values                                            | [48]      |
|                |                                      | an external torque                                                          |                                                                                   |            |
|                | Pull-off test                         | To measure the resistance to detachment of a sample from a substrate under  | Pull-off force (F_{pull-off}) of hooks, adventitious roots, adhesive pads, etc.   | [56, 60–62]|
|                |                                      | the application of a perpendicular tensile force                            |                                                                                   |            |
|                | Friction test                         | To measure the resistance between two surfaces in contact sliding against   | Friction force (F_{friction}) of leaf covered with hooks                          | [54]      |
|                |                                      | each other under the application of a horizontal force                      |                                                                                   |            |
| In vivo        | attachment test                       | To measure the in vivo squeezing force of plans stems around a sensorized    | Squeezing force (F_{squeezing}) of twining vines                                  | [46, 63, 64]|
|                |                                      | mechanical pole (TWIFOR)                                                    |                                                                                   |            |
| Micro-contact  | test                                 | To measure the contact separation force between a hooked microstructure and  | Pull-off force (F_{pull-off}) of a single hook                                    | [54, 65]  |
| Nanoindentation|                                      | a loop using a micromanipulator                                              |                                                                                   |            |
|                |                                      | To evaluate the mechanical response of small plant material volumes under   | Young’s modulus (E) (e.g. cellulose fibrils in cell wall)                         | [29]      |
|                |                                      | load, using a diamond tip                                                    |                                                                                   |            |
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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 $M. \text{scadens}$ and $C. \text{guianense}$, 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 \( (E = 3000–5000 \text{ N mm}^{-2}) \) compared to the older stems \( (E = 2000–500 \text{ N mm}^{-2}) \). 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% ± 7% and a Young modulus of 235 ± 16 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 different 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. scadens 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. scadens* [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].
| Classes                  | Species (common name)                      | Attachment strength, force (mN) | Typical support                                                                 | Native habitat (continent)                              | References |
|-------------------------|--------------------------------------------|--------------------------------|--------------------------------------------------------------------------------|---------------------------------------------------------|------------|
| Twining plants          | Dioscorea bulbifera (air potato)           | 100–300                        | Regular structures for vertical growth in forests, palms, and shrubs             | Africa and Asia                                         | [48]       |
|                         | Ipomea purpurea (morning glory)            | 167                            | Large structures for vertical growth in forests, palms, and shrubs               | South America                                           | [81]       |
|                         | Marupa scabra (Liana)                      | Data not available             |                                                                                   |                                                        |            |
|                         | Convolvulus quatemose (Liana)              | Data not available             |                                                                                   |                                                        |            |
| Leaf-climbers           | Flagellaria indica (Whip vine)             | 2000–3000                      | Vertical structures for coiling in forests, palms, and shrubs                    | Asia, Africa and Australia                               | [48, 82]  |
|                         | Parthenocissus tricuspidata (Boston ivy)   | 7590 ± 2530                    |                                                                                   | Asia and North America                                   | [61, 62]  |
| Root-climbers           | Hedera helix (english ivy)                 | 3810 ± 2410                    |                                                                                   | Europe, Asia and South America                           | [58, 61]  |
| Hook climbers           | Galium aparine (Cleaver)                   | 5                              |                                                                                   | Europe, Asia and North America                           | [53, 54]  |
| Hook bearers            | Lycopodiella cernua (Staghorn clubmoss)    | Data not available             |                                                                                   | South America                                           | [49]       |

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

![Figure 4. Example of circumnutation. A simplified example of Phaseolus vulgaris L. circumnutation movement. The main parameters, including the amplitude, period, shape and direction, are reported directly in the picture.](image-url)
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), 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-bearing to analyze their mechano-

### 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 |
|------------------|------------------------------------|-----------------|--------------|------------|
| *Passiflora gracilis* (Passifloraceae) | Ventral | 1.0 | 25 sec | [31, 127] |
| *Cissus discolor* (Vitaceae) | Ventral and dorsal | 9.3 | 35 min | [31, 128] |
| *Pisum sativum* (Leguminosae) | Ventral | 9.3 | 2 min | [31, 40, 129] |
| *Sycos angulatus* (Cucurbitaceae) | Ventral | 3.5 | 30 sec | [127, 128] |
| *Corydalis claviculata* (Fumariaceae) | Not available | 8.1 | 18 h | [31, 127] |
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 µm [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

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**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 setup and gas chromatography | Growth toward the target is due to emission of volatile cues (which mediate ecological interaction among plant species) | [140] |
| Ipomoea 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] |
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, 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°, 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-
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Future studies could focus on performing similar experiments with other climbing plant 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% 

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**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 | Exploration, monitoring, search and rescue | [153, 154, 174] |
|                    |                 | Symmetric deposition of PLA using a miniaturized 3D printer at tip level. Tip is sensorized |              | [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   | Tendril-like behaviour (e.g. the capacity to go into tight spaces) | Spring-loaded modular bending segments (1) Improved design of (1), with an increase in the length (increased number of springs in series) and a decrease in spring stiffness | Minimally invasive inspection in space | [156] |
| Programmable      | 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] |
| materials          | 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] |
|                    | Biomimetic design of natural prickles of the hook-climber *Rosa arvensis* Splendens | 3D Laser Lithography, molding of PDMS, and casting of PCL@Au NPs for actuation | Remote control device (e.g. to release objects) | [167] |
|                    | Biomimetic design of natural hooks of the hook-climber *Galium aparine* | 3D prototyping technique and Fe$_3$O$_4$ NPs for actuation |              | [169] |
| Dry adhesives      | Biomimetic replica of natural surfaces of the hook-climber *Galium aparine* | 3D Laser Lithography technique Resin replica molding technique | Mechanical interlocking for attachment with micro-rough surfaces | [168] |
| Wet adhesives      | Biomimetic of the honey-comb like microstructure of the tendril-bearer *Parthenocissus tricuspidata* | 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 *Hedera helix* | 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 *Bryonia dioica* | Tactile blep design used in FEM simulations Electronic skin (e.g. soft robotics) | Surgical soft manipulator | [25] |
|                    | Distribution and structure of the sensory organs (tactile papillae) in tendrils of *Cucumis sativus* | Tactile sensors based on fiber optic light modulation |              | [172] |
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 the phenomenon in the climber’s natural habitat, 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 Fe3O4 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 arabinoogalactan 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.

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