Student report TU Delft

Compliant Shell Deformation in Plants: A Designer's Toolbox

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Abstract

The mechanisms that move plants can serve as biological role models for engineers, designers and architects. This practice is slowly being implemented in various engineering fields, with architects often being pioneers. Various methodologies have been written about the subject, but often only from an architectural point of view.

The classification presented in this paper provides a different perspective on the subject. It is structured like a toolbox, containing a clear classification of the technical working principles that plants use to generate motion. With the working principles abstracted, it is no longer necessary to dive deep into the inner workings of plants.

The Scopus and Web of Science databases have been systematically searched for compliant plant movements. Plants mainly move by reallocating water, either actively via osmosis or passively via hygroscopic tissue. In compliant plant mechanisms, these basic movement initiators bring about deformations of plant parts. These movements are classified according to their goal: does the plant move quasi-static or dynamic? And does the plant only use a mechanism or does it rely on the gradual storage and fast release of elastic energy as well? Quasi-static movements are often only mechanical and reversible, while dynamic movements rely on energy storage and are often irreversible due to their failure-based release. A bilayer structure in one form or another is present in almost all mechanisms, proving its large adaptability to various circumstances. This adaptability is achieved by the various configurations of the two layers, including fibre-orientation and cellular set-up.

Existing bio-inspired devices are classified according to the same system. This enables identification of plant mechanisms that are already suited for implementation and exposes plant movements that are not yet used in the human world. Additionally, a lot could be gained from copying mechanisms on a cellular level rather than on a macroscopic level. Most importantly, a change in mindset needs to happen in order to fully benefit the intricate mechanisms that the plant world has to offer.

Contents

1	Introduction			
2	Literature Search Method			
3	Basic Mechanics of Plant Movements and Classification 4			
3.1	Sequence of events leading to plant movements			
3.2	Basic movement initiators			
	3.2.1 Internal factors: active water transport and growth			
	3.2.2 External factors: environmental changes and interaction with other			
	organisms			
3.3	Amplification mechanisms and storage of elastic energy			
3.4	Classification: Goal of Movement versus Amplification Method 7			
3.5	Classification scheme			
4	Plant Movements 9			
4.1	Moving quasi-static with amplification			
	4.1.1 Antagonistic lever mechanism			
	4.1.2 Bilayer movement			
	4.1.3 Folding and unfolding 13			
	4.1.4 Passive lever mechanism and mid-rib bending			
4.2	Moving quasi-static with amplification and elastic energy storage 16			
	4.2.1 Bilayer movement due to failure			
	4.2.2 Snap-through buckling due to edge-growth 17			
4.3	Moving dynamic with amplification			
	4.3.1 Bilayer swelling velocity catapult			
	4.3.2 Midrib bending induced curved-line folding 18			
4.4	Moving dynamic with amplification and elastic energy storage 19			
	4.4.1 Snap-through buckling due to bilayer actuation			
	4.4.2 Impulse due to failure 20			
	4.4.3 Pressure difference			
5	Existing Bio-inspired Devices			
6	Discussion			
6.1	Comparing plant mechanisms			
6.2	Relation between degree of biomimicry, scale and Technology Readiness			
	Level			
6.3	Potential Applications and Future Research			
6.4	Limitations of This Study 28			
7	Conclusion			

1 Introduction

Since their conception, human-made mechanisms rely largely on rigid parts connected by various types of hinges, actuated by, for instance, gears or hydraulics. While these types of mechanisms have served us well for centuries, they pose some disadvantages due to their lack of flexibility and multi-purpose functionality, and their need for maintenance [1].

In nature however, movement often happens quite differently. Especially in the plant kingdom, movement is based on compliance. Actuator and mechanism are often the same thing. Flowers open and close [2], ferns use a catapult to disperse their spores [3], pine-cones and wheat awns passively open and close [4], [5], carnivorous plants catch their prey [6]; all these movements are based on elastic deformations, often distributed over a larger surface. This phenomena is often referred to as 'compliant shell mechanics'. Additionally, plant movements are often based on mechanisms like buckling or fracture; things that engineers usually consider failure modes. Translating these plant-mechanics to engineering working principles could inspire all kinds of new and innovative designs.

Various design and engineering fields are calling for less conventional ways of movement. Within the discipline of architecture there is a growing interest in the smart and flexible design of buildings, spaces and environments [7], [8]. Due to the continuing growth of the world population, humans have to deal with a decreasing amount of room per individual. This is reflected in many trends, ranging from the Tiny House movement to various examples of reconfigurable apartments. Current living environments are build out of stiff and heavy components; think of walls, tables, chairs. If a more adaptive approach is taken, this could save building space and thus material [9]. However, innovative solutions are needed to facilitate this. Environments and the objects contained within them need to become dynamic rather than static; they need to adapt to the needs of people that enter them. Implementing plant mechanics in everyday engineering, even the mechanisms that are normally considered a failure, asks for a paradigm shift amongst engineers [10].

Compliant shell mechanisms are already being implemented in some engineering fields. Early designs include a collapsing sound-wall near train tracks [11], a reconfigurable apartment [12], and the design of a novel shading system [13]. There are some reviews about plant-mechanics and their use as concept generators for design and engineering [14], [15], [16], [17]. However, no systematic overview and characterization of compliant shell mechanics in plants exists.

This review is intended to be a toolbox for engineers, architects and designers. It identifies various types of compliant shell mechanisms in the plant kingdom and abstracts technical working principles out of them. It classifies compliant plant movement mechanics according to 1) the goal for the plant that the movement achieves and 2) the way the mechanism achieves this goal. Different classes of movements emerge and each of them is described in detail. Finally, it will classify existing plant-inspired mechanisms according to the same classification, thereby exposing plant-movements that have not yet been used in bio-inspired mechanisms.

2 Literature Search Method

Both Scopus and Web of Science were systematically searched using the same query, as can be seen in appendix A1. The query yielded 974 and 890 results for Scopus and Web of Science, respectively (last check: march 2019). After removal of duplicates, the papers were manually screened for relevance. The choice to scan this relatively large amount of papers manually, is due to the multi-disciplinary nature of the search and due to the ambiguous nature of the term 'shell'. Only a manual screening would suffice in selecting the right papers. Papers were excluded on the following bases:

- 1. Papers written in a language other than English
- 2. Papers dealing with plant movements that only consisted of growth (for instance the way vines grow and latch themselves on their surroundings [18]). However, some movements that include growth as a movement initiator are treated.
- 3. Papers dealing with the resistance to movement or deformation (for instance the way bark on trees aids in the resistance and deflection of wind loads [19], [20]).
- 4. Papers dealing with movements only based on deformations on cellular level, i.e. individual cells moving (although this is discussed briefly in section 3).
- 5. Papers dealing with movements that do not contain any compliant shell components (for instance the fluid pressure catapult in dwarf mistletoes (*Arceuthobium*) that shoots spores based on liquid pressure [21]).

The complete search-strategy can be seen in figure 22 in appendix A1. Figure 23 displays the overlap of the two databases. The resulting core database consists of a selection of 76 papers. Additionally, 11 papers were taken from the reference lists of these papers, resulting in a final database containing 87 papers. An alphabetic list can be found in appendix A2. These papers form the core of this review; all plant movements and bio-inspired devices are derived from this database.

3 Basic Mechanics of Plant Movements and Classification

In order to properly understand the concepts discussed in this paper, it is necessary to understand some basic principles that plants use for motion. Some excellent long reviews about all different types of plant-motion have been written by Dumais et al [22], Forterre [23], Geitmann [24] and Lenau et al [25]. In this section, a short summary of the relevant basics will be given.

3.1 Sequence of events leading to plant movements

Generally speaking, plant movements occur after a sequence of events, schematically depicted in figure 1. First, the signal (internal) or trigger (external [26]) that signals certain parts to move gets dispatched. Alternatively, environmental factors such as other organisms [27] or temperature changes [28] initiate the movement. Second, a small motion in a small part of the plant, usually a few cells, occurs. Depending on the goal of the movement that the plant has, this small motion is amplified by one or more mechanisms [14]. Finally, again depending on the goal that the plant wants to achieve, this amplification can store elastic energy that is released at a later stage. This enables extra amplification and is often used when a fast motion is required.



Fig. 1. Sequence of events leading up to a plant movement. After the trigger event, one of three things happens. 1) A basic movement is initiated. This is either the swelling or shrinking of cells, or growth of the plant. 2) The basic movement gets amplified by a mechanism. 3) The amplification mechanism, after being actuated by the basic movement, stores elastic energy and releases it.

3.2 Basic movement initiators

3.2.1 Internal factors: active water transport and growth

The most common way of plants to initiate their movement, is by pumping water in and out of cells. While cells of humans and animals only contain a thin membrane, cells of plants are strengthened by a strong cell wall. This wall consists of cellulose microfibrils and hence it resists deformation [29], [30]. Figure 2a depicts the three states a plant cell can be in. If the plant pumps in water via osmosis, the cell membrane deflects against the cell wall. This construction makes the cell capable of enduring a large hydrostatic pressure, a process known as turgor. When pumping water around in this way, the cell maintains or regulates its pressure and to some extent its volume [23]. This mechanism regulates a lot of mechanical properties of plants, among which are posture control [22] and directional growth [25]. In some cases it is even capable of completely folding the plant to a small, protective state, as can be seen with resurrection plants (*Gesneriaceae*) [31]. The active swelling and shrinking of cells is one of the main causes of movements dealt with in this paper.

A special kind of active movement is growth. Although considered by some as just a rearrangement of internal matter [32], normal growth movement is not treated in this paper. An essential part of growing is adding material and that would be impractical when implemented in engineering mechanisms, although there are examples of engineered 'growing' structures that move by depositing new material onto themselves [33]. Apart from just growing in a certain direction, growth sometimes enables additional mechanisms, like unfolding and even snap-through buckling of flowers [2], [34]. These rare cases do get treated in this paper.



(a) Schematic of the swelling and shrinking of a cell due to the active regulation of its water content, also called osmosis. On the left a plasmolyzed cell is depicted. All the water is pumped out and the cell membrane detaches from the cell wall. The stiffness of the cell is drastically reduced. In the middle there is an equilibrium: water is pumped out as fast as it is pumped in, and the cell membrane loosely touches the cell wall. On the right, more water enters the cell and the cell becomes turgent: the cell membrane presses against the cell wall. The whole structure expands and its stiffness is increased.



- (b) Schematic of the shrinking of tissue as it loses water to the environment (left) and the swelling of tissue as it gains water from the environment (right).
- Fig. 2. Comparing turgor in cells due to the active displacement of water via osmosis (a) and due to the passive displacement of water via hygroscopic suction (b).

3.2.2 External factors: environmental changes and interaction with other organisms

Plants also move based on external stimuli. This usually costs the plant no energy, it is a passive movement. Two main groups can be distinguished: expanding or contracting of structures based on changes in the environment, like humidity and temperature; and interaction with other organisms, usually pollinators.

Moving depending on changes in the environment is a clever way to let events happen only when your surroundings are in optimal condition. A good example is the humidity of the surrounding air, which induces hygroscopic swelling and shrinking of cells and tissues (see image 2b). Some tissues of the plant suck up or cast out water to try to level the water content between its cells and the environment. By doing so, they swell or shrink and make the plant move. This movement cost no energy, but is generally slower than movements initiated by the active pumping of water. Examples include the opening of various seed containers [5], [4], [35].

Finally, other organisms can actuate plants themselves. The most common example are flowers that protect their pollen with sheaths or sacks until they open up when a pollinator visits them, like the stamen-bending-mechanism of *Salvia lamiaceae* [27].

3.3 Amplification mechanisms and storage of elastic energy

The movements described above are often limited in their range, speed and strength. To make up for this, plants have developed all kinds of interesting amplification mechanisms [14]. Some of them amplify the basic initial movements directly, others first

use them to store elastic energy in order to later move with more speed or more force. The classification system that is proposed in this paper, is largely based on these amplification mechanisms and their capability to store energy, since it is these mechanisms that are most interesting to designers and engineers. They have to however be treated in conjunction with the basic movements that initiate them. As stated before, actuator and mechanism are often the same thing in plants.

3.4 Classification: Goal of Movement versus Amplification Method

When looking at the sequence of events that constitute a plant movement shown in figure 1, the two most interesting aspects seem to be the goal the plant has to move and what kind of amplification it uses to achieve this goal. One can distinguish two goals a plant might have to move.

- Quasi-static movement: Some (parts of) plants move just to travel a distance, without being concerned about the speed. Virtually all seed-capsule openings that do not actively disperse their seeds fall under this category, for instance the scales of pine-cones [4]. Another example are the seeds of wheat awns that bury themselves in the ground [5].
- **Dynamic movement:** Some (parts of) plants need to move fast in order to achieve their goal. This group mainly consists of carnivorous plants that rely on fast prey capture for gathering of nutrients [36], [37], although there are also carnivorous plants that do not move at all [38]. Other note-worthy examples include the violent attachment of pollen to its pollinators by *Stylidium Turbinatum* [39].

Similarly, three trends can be distinguished when looking at different amplification methods.

- No amplification: Normal growth as described in section 3.2.1 can be considered as a movement without amplification. As stated before, this will not be treated in this paper.
- Amplification by mechanism: The majority of plants amplify their movement in order to get the most out of their limited motor systems. Examples range from simple lever mechanisms (both active, like the moving leaves of the 'sensitive plant' (*Mimosa pudica*) [40]; and passive, like the aforementioned scales of pine-cones [4]), to complex snap-buckling systems in the Venus fly-trap [37].
- Amplification by mechanism and elastic energy storage: When a faster or more powerful movement is required, plants often resort to slow storage and fast release of elastic energy. This can be seen in most seed-capsules that actively disperse their seeds, for instance *Cardamine parviflora* ([41], [42]) or the suction trap of the bladderwort (*Utricularia*, [43]).

This whole classification is meant as a toolbox for designers and engineers. If someone has a design-challenge and would like to be inspired by the solutions nature offers, they have to think: 'What is the goal that I try to achieve?' (or formulated differently: 'What is the problem I need to solve and how do I want to solve it?'). They then have to decide what kind of amplification they want to use, something that is often determined by design-constraints and sometimes determined by personal preference. These two decisions will automatically land them at a certain category, in which they can find various examples of working principles to use.

While a lot of research classifies plant movement based on the whole movement, this paper classifies the working principles distilled from the movements. It might occur that a plant that displays one movement with one purpose is classified in multiple classes due to the fact that multiple working principles work together to accomplish the observed behaviour.

3.5 Classification scheme

During the literature search, 31 plant-movements have been identified. In some cases these are movements occurring in entire genus of plants, while other movements occur in individual species only. When all the plant-movements get classified according to the proposed system, the scheme from 3 is obtained, where the number inside each circle represents the amount of different mechanisms found in the corresponding class.



Fig. 3. Classification scheme. The mechanics behind the plant movements found in literature are all assigned to a category based on the type of movement (x-axis) and their amplification strategy (y-axis).



Fig. 4. Graphs displaying the correlation between reversibility and goal of movement or amplification method.

Some clear trends can be seen when looking at the graph in figure 3. Firstly, the majority of the movements are quasi-static. Secondly, while plants that need to move quasi-static have a tendency to only use a mechanism to amplify their basic movements, plants that move dynamically additionally rely on storage and release of elastic energy.

To get some more insight in why this might be, the reversibility of the movements is plotted against the movement and the amplification in figure 4. From figure 4b it can be deduced that most mechanisms are reversible, while elastic energy storage has a slight tendency to be irreversible. This has to do with the fact that the release is often failure-based, making it impossible for the movement to be repeated. The reversibility is also linked to the goal of the movement. From figure 4a it can be observed that most quasi-static movements are reversible, while there is not really a preferred method when looking at dynamic movements.

4 Plant Movements

With the four classes determined, the different plant mechanisms will now be classified and described in more detail in the coming chapters. Additional characteristics of each mechanism will be provided, including the reversibility (reversible/irreversible), the dimensionality (1D/2D/3D) and the basic movement initiator mentioned in section 3.2. Each class also gets assigned an abbreviation for easy reference in this paper. A list of all abbreviations can be found in appendix A3. Additionally, appendix A4 displays frequently used elements of the figures used to describe the mechanisms.

4.1 Moving quasi-static with amplification

The following mechanisms are used to move quasi-static with an amplification mechanism (QS-A).

- 1. Antagonistic lever mechanism (ALM): reversible, both 2D and 3D, initiated by internal factors
- 2. Bilayer movement (BM): reversible, both 2D and 3D, initiated by both internal and external factors

- 3. Folding and unfolding (FU): reversible and irreversible, 3D, initiated by internal factors
- 4. Passive lever mechanism and mid-rib bending (PLMMB): reversible, both 2D and 3D, initiated by external factors

4.1.1 Antagonistic lever mechanism

One of the simplest amplification mechanisms bears a lot of resemblance with the antagonistic set of muscles found in for instance a human elbow. Depending on the desired direction of the motion, one muscle contracts and the other extends. This antagonistic actuation mechanism is also prevalent in the plant world. It is most often found in the connection between leaves and stems. This region, called the pulvinus, consists of motor-cells that actively regulate their turgor pressure via osmosis [44]. By doing so, they shrink or swell with respect to one-another. This process is sometimes referred to as asymmetric turgor pressure, and it is able to move the leave with respect to the stem (see figure 5a). Examples include plants that track the sun to maximize their exposed surface area for photosynthesis [25]. Another well-know example of this mechanism is seen with the sensitive plant (Mimosa pudica). The leaves of this plant respond to various stimuli, such as touch, diminishing light and heat, by rapidly folding towards their stem [40]. The plant does this to protect its leaves from predators and other harmful factors. The same mechanism is present with the petals of the dandelion (Taraxacum officinale), which follow a circadian, i.e. daily, opening and closing rhythm [45].



(a) Schematic representation of the movement of a leaf with pulvinus. The antagonistic motor cells in the pulvinus change their water content via osmosis. The upper cells swell and the lower ones shrink, making the leaves move towards the stem.



- (b) The leaves of *Mimosa pudica*. The lower left branch has just been touched, so the leaves are in the process of folding inwards.
- Fig. 5. Antagonistic lever mechanism (a) as displayed by for instance *Mimosa Pudica* (b).

A more complex variation of this mechanism is present in the passionflower (*Passiflora decaloba*). This species of flowers is capable of moving its androgynophore, a large stalk onto which both stamen and pistils are attached, in the direction of any stimulus in the horizontal plane. At the base of the androgynophore, a ring of motor-cells is located. When the flower is stimulated by a pollinator, cells at the side of

the stimulus lose their water content and become vacuolized. At the same time, cells on the opposite side become more turgid and swell [46]. This tilts the androgynophore towards the pollinator, thereby depositing pollen with its stamen and/or taking up pollen with their pistils. Movement speeds depend on the species, but generally range between 1.5 to 4.5 degrees per second, with a total movement time of 1.5 to 2 seconds [47].



Fig. 6. Schematic of stamen-bending in *Passiflora* species. The top row depicts a sectioned side view of the total flower, the bottom row depicts a top view of the water content in the ring at the base of the androgynophore. Depending on the location of the pollinator, a few cells in the ring at the base of the flower pump ou part of their water content, while the cells on the opposite side pump in water. This causes the androgynophore to move in the direction of the pollinator, pressing the pollen against their body. Drawing based on the figures from [47].

4.1.2 Bilayer movement

The bilayer mechanism in its different forms is very common amongst plant movement mechanisms. This mechanism uses a structure of two or more layers of material. By actively or passively changing the dimensions of one layer with respect to the other, movement is generated. The basic principle for both the active and passive form is depicted in figure 7.



(b) assive brayer mechanism. Moves the toren environmental changes in humidity or temperature. The microfibrils in the active layer shrink or swell due to the (de)hydration or temperature changes. The passive layer resists the change in dimension, and the whole structure bends.



Fig. 7. Schematic visualization of the passive (a) and active (b) bilayer mechanism.

In its passive form, a so called active layer is paired with a resistive layer ([4], [10]), as seen in figure 7a. In the case of hygroscopic actuated bilayers, the active layer consists of micro-fibrils that elongate when taking up water [4] and abbreviate when drying. This elongation or contraction is then resisted by the resistive layer, so the whole stucture curves to facilitate the desired swelling or shrinking of the active layer.

A well known example of this mechanism is the pine cone, displayed in figure 8a The scales of the cone perform a reversible movement in 2D. Since the seeds the scales protect spread more easily when the environment is dry, its scales close up as the humidity increases by taking up water in their micro-fibril active layer [4]. They open when the air is dry again. Other plants that use a hygroscopic bilayer to time the release of their seeds are some succulents (for instance *Bergeranthus scapigerus*) [48] and the ice plant (*Aizoaceae*) [49].

A more dramatic movement is seen in the stamen of the flower of a lily (*Arabidopsis*), an irreversible movement in 3D. When the flower matures and its pollen are fully grown, the outside surface of the cylinder attached to the anther dries out and shrinks. This forces the cylinder to open up and expose its pollen, ready for dispersal [50], see figure 8b.

The same passive mechanism, but with a different goal, can be found in the seeds of wheat plants. When dispersed from the plant, these seeds use their long awns to ride the winds in the environment, allowing the seed to travel further from the mother plant [4]. When they hit the ground, the bilayer at the base of each awn curls and uncurls repeatedly due to the circadian humidity cycle [5]. This movement wiggles the seed deeper in the ground, where it has a better chance to sprout and grow into a full plant.

The same mechanism occurs in the seeds of Filaree (*Erodium cicutarium*), albeit a more special movement. The awns of these seeds curl into a 3D spiral when drying and straighten out again when the humidity increases. With a drilling motion, this passive cyclic movement buries the seed deeper in the ground [51].



(a) The scales of the pine cone in wet and closed state (bottom left cone) and dry and open state (top cones).Image author: Susan Gerbic. Image used under CC BY-SA 4.0 I license



(b) The stamen of a lily opening up when drying, exposing the pollen.

Fig. 8. Examples of plants that use the passive bilayer mechanism to move.

The active variation of the bilayer has a wider range of applications and is even capable of large curvature reversals. It bears some resemblance with the antagonistic lever mechanism described in section 4.1.1, as it also uses asymmetric turgor pressure as its driving force. The antagonistic lever however only deforms locally, while the deformation of the bilayer is distributed over a larger surface. Brought back to its basic form, this mechanism consists of two layers of cells. Active water transport in and out of cells lets one layer shrink or swell with respect to the other. This results in one side of the surface changing its dimensions with respect to the other, thereby warping the surface (see image 7b). The shrinking can happen in one direction, resulting in a motion that can be considered two-dimensional. When the shrinking of one layer of the surface happens in multiple directions, or when one of both layers shrink in a different direction, motion happens in 3D, resulting in double-curved surfaces.

The active bilayer movement occurs for instance with certain species of *Rhododendron (maximum* and *catawbiense)* [52]. In order to protect critical structures and processes during the cold temperatures occuring during winter, the leaves of these species roll up during low temperatures. When the plant senses low temperatures, it reduces turgor pressure in the abaxial layer of its leaves. This makes it shrink with respect to the adaxial layer. This shrinking is isotropical, but it is guided by the veins and stiff midrib in the leaves, resulting in an anisotropial movement; the leave rolls itself into a cylinder shape (see figure 9). The temperature and amount of roll-up differs per species, with for instance a 50% roll-up at 2° C and 4° C respectively, for *R. catawbiense* and *R. maximum*



Fig. 9. The leaves of Rhododendron in their rolled-up state. Image author: Nicholas A. Tonelli. Image used under Image used under CC BY 2.0 I license

4.1.3 Folding and unfolding

Clever ways of folding and unfolding exist in the plant world. Both leaves and a flowers' petals are essentially very large but thin surfaces being deployed from a small contained origin, so unfolding is necessary. Furthermore, folding back is utilized to protect vital plant organs during for instance cold temperatures. These movements can be either reversible or irreversible, depending on their actuating mechanism.

Generally speaking, two actuating mechanisms can be present that fold or unfold leaves or petals. The first possibility is the deformation of the midrib of the leave or petal either by elongation, abbreviation, or by the bilayer/antagonistic lever mechanism mentioned in sections 4.1.2 and 4.1.1. Alternatively, its outer edge grows (treated in section 4.2.2). As one might suspect, bilayer actuation of the midrib is reversible, while edge growth is not. Elongation or abbreviation of the midrib might be reversible if caused by osmosis-based cell deformation, or irreversible if caused by growth [53].

Elongation of the midrib or middle vein is the cause of irreversible unfolding of tree

leaves. The leaves of the common beech (*Fagus sylvatica*) grow inside a bud, where they are protected by scales. They grow in a compressed state, folded along creases. When fully matured, the bud opens and the unfolding begins [54]. The leave consists of a central vein acting as midrib, from which smaller veins originate. The pattern they make resembles a classical 'Miura-Ori' pattern found in origami [55]. This fold has the property of unfolding simultaneously in orthogonal directions. For the beech leave this means that, when the middle vein grows after opening, it elongates the middle of the leave in one direction and thereby deploys the sides of the leave in the direction perpendicular to it. For an example of this mechanism, see figure 10.

Also caused by movement of the midrib, but in this instance based on the bilayer principle, is the unfolding of the moonflower (*Ipomoea alba*). This flower is known for its extremely wide corolla (8-15 centimetre when blooming, [34]) that is divided in 5 segments by stiff midribs. These midribs form the outer protective encapsulation of the flower before opening, when they are curled up around the vulnerable petals and reproductive organs. The longitudinal edges of the midribs consist of cells that actively regulate their water content, bringing about a gradient in turgor-pressure between the inside and outside of the band. This makes the bud unwind, so the corolla unfolds, although it is argued that this is not the only mechanism that contributes to the unfolding [34].

In addition to this irreversible opening of the corolla, the moonflower also exhibits a 3D, cyclic and thus reversible opening and closing in order to protect its reproductive organs at night. Due to asymmetric turgor pressure mentioned in section 4.1.1, the midribs roll up inwards and cover the fragile flower petals and stamens [34].



Fig. 10. Model depicting the unfolding of leaves.

4.1.4 Passive lever mechanism and mid-rib bending

Some plants need other organisms to actuate their movement. Most prominent in this group are flowers that use the weight and/or force of animals to open up, either to attach their pollen to the animal (*Salvia Lameaceae*) or to expose their pollen and nectar so that the animal can reach them (*Strelitzia Regina*). These movements are 3D and reversible. They could serve as good inspiration to mechanisms that interact with users.

Salvia Lameaceae is mainly pollinated by insects like bees and bumblebees, as can be seen in figure 13a. Its nectar is buried deep inside the flower, near the attachment point of the stalk. Insects are drawn to this nectar, but when they try to reach it they have to push away a small hatch. This hatch is connected to a longer beam containing the pollen at its tip, together they form an L-shaped stamen. The corner of this L-shaped structure is attached to the flower via a flexible tissue, allowing the structure to rotate about its corner.

As can be seen in figure 11, when the hatch is pushed away, the tip of the lever deposits pollen on the back of the pollinator. This pollinator then flies off. Matured

flowers have their style on the same place as young flowers have their pollen, so when a pollinator reaches another flower, it is able to transfer the pollen on its back to the stigma, thereby fertilizing the flower [27].



Fig. 11. Schematic of the lever mechanism in *Salvia lameaceae* as seen from the side. When a pollinator visits, it will try to reach the nectar at the base of the flower. To get there it needs to push the lever with its body. The lever rotates around a flexible structure that serves as a revolute joint, making the stamen rotate downwards to press its pollen against the back of the pollinator. Drawing based on images from [27].

The flower of *Strelitzia Regina* displays a more complicated movement. It is mainly pollinated by bird-of-paradise [16]. These birds land on the long extension, protruding almost horizontally from the centre of the flower. Inside this extension the stamen and style are located, covered by two flaps. These flaps are connected to the extension by vertical sheets. When the weight of the bird causes the extension to bend downwards, these sheets are forced to follow the bending curve. Since they cannot deform in-plane, they bend sideways and open up the flaps [15]. This movement exposes the stamens and style. See also figures 12 and 13b.



Fig. 12. Model depicting the midrib bending mechanism that exposes the stamen and style of Strelitzia.



(a) Flower of Salvia being pollinated by a bumblebee. The stamen-lever of the flower is in actuated position and deposits pollen on the back of the insect. Image author: Gideon Pisanty. Image used under CC BY-SA 3.0 license



- (b) Flower of *Strelitzia*. The blue spike-like structure is the lever that contains the pollen.
 Image author: Brocken Inaglory.
 Image used under CC BY-SA 3.0 license
- Fig. 13. Flowers of *Salvia* (a) and *Strelitzia* (b).

4.2 Moving quasi-static with amplification and elastic energy storage

The following mechanisms are used to move quasi-static with an amplification mechanism and stored elastic energy (QS-A-E).

- 1. Bilayer movement due to failure (BMF): irreversible, 3D, initiated by both internal and external factors
- 2. Snap-through buckling due to edge growth (SBEG): irreversible, 3D, initiated by internal factors

4.2.1 Bilayer movement due to failure

Some seed containers use the deformation of the bilayer from section 4.1.2 to build up energy for movement at a later time. Their seed pods contain valves that protect the seeds until they are mature. These valves consist of hygroscopic bilayers. Due to dehydration, the bilayers want to deform. They are however still attached at their edges to the structure of the seed capsule. This causes a strain on the attachment. If this strain reaches a certain threshold, failure occurs. The connection breaks and the bilayer deforms [35]. Besides moving away to expose the seeds, the bilayer-mechanisms in this case also physically opens the seed container. A generalization of this mechanism is presented in figure 14.



Fig. 14. Schematic representation of the mechanism in a bilayer seed container. Displayed here is a cross-section of a seed pod containing two valves. Upon dehydration, the outer layers lose their water-content and shrink. The deformation this brings about is resisted by the connective tissue, displayed in light green. When the stress exceeds a certain threshold the connective tissue breaks and the valves open.

Seed containers that incorporate this mechanism, are the fruits of the sesame-plant (Sesamum indicum L.). These seed containers are composed of two or more bilayer shells, connected to their neighbours by a thin tissue that ruptures when the stress build-up due to the deforming bilayer is enough. The shells also show an interesting morphology of their bilayers. They do contain an active and passive layer as described in section 4.1.2, but the active layer gradually changes in thickness along the circumference of the seed pod [56]. This causes a varying deformation across the surface of the bilayer, resulting in a double-curved surface.

A slightly different form of the bilayer movement due to failure can be seen in the seed-pods of *Banksia attenuata*. This plant grows in environments that are prone to fire. The openings of its seed pods are sealed by a normal bilayer-surface. Just as with sesame-plant, the bilayer creates tension as it dries out. The passive layer of this bilayer-set however, is much stiffer than with sesame, so it does not deform. When environmental temperatures rise due to a wild fire and the temperature of the seed-pod reach 60-80 degrees Celsius, the elastic modulus of this inner passive layer changes, allowing the bilayer to deform and the seed pod to open to release its seeds [28].

4.2.2 Snap-through buckling due to edge-growth

Besides movement of structural midribs described in section 4.1.3, irreversible flower opening can also be regulated by edge-growth. The petals of the Asiatic lily (*Lilium casablanca*), display an impressive curvature reversal during flower opening. This movement is most likely caused by the elongation of the edges with respect to the centre of the petals, although the aforementioned midrib-growth may also play a role [2]. The growth of the edge creates tension in the petal, which is released when the petal rapidly changes curvature and snaps to its final shape. See also image 15.



Fig. 15. Simplified representation of the edge-growth and consequent snap-through curvature reversal of the petals of a lily. Drawing based on images from [2].

4.3 Moving dynamic with amplification

The following mechanisms are used to move dynamic with an amplification mechanism (D-A).

- 1. Bilayer swelling velocity catapult (BSVC): reversible, 2D, initiated by external factors
- 2. Midrib bending induced curved-line folding (MBCLF): reversible, 2D, initiated by internal factors

4.3.1 Bilayer swelling velocity catapult

The family of mosses *Brachythecium populeum* uses a slight variation of the bilayer principle to disperse its spores. The spores are contained in a capsule, attached to a stalk to raise it just above the plant. The capsule consists of a sack with an opening at the top. At the edges of the opening, small teeth are located. These teeth are build up out of two layers of hygroscopic tissue, so they move depending on the relative humidity of the surrounding air.

Just like the scales of pine-cones, the teeth are closed when air is humid in order to protect their seeds. Where this mechanism differs however, is in the structure of the hygroscopic tissue of the teeth. Not only do the two layers swell and shrink in a different amount, they do so with a different velocity [57]. This causes a fast dipping and flicking motion of the teeth during dessication, resulting in scooping up and releasing some of the spores. Although a clear difference in composition can be observed in the bilayers of the teeth, both when comparing them to each other and when comparing their bases to their tips, it is still not entirely understood how this difference in composition brings about the observed flicking motion [57].

4.3.2 Midrib bending induced curved-line folding

The aquatic carnivorous waterwheel plant (*Aldrovanda vesiculosa*) uses a mechanism related to the one in the flowers of Strelitzia (section 4.1.4). It consists of a wide midrib with two hollow lobes attached to it. When it senses a prey is inside its lobes, changes in turgor pressure in regions on and parallel to the midrib make the midrib bend [58]. Due to the kinematic coupling between the midrib and the lobes, the trap closes. As can be seen in figure 16, this coupling is realized by the curved connection between midrib and the lobes. When the rib bends, the minimum energy position of the lobes is only achieved when they move towards each other. This kinematic amplification ensures

that only a small bending motion is needed for full trap closure [6], [39]. This makes this mechanism capable of moving extremely fast, even in a dense medium such as water. Full trap closure takes 100 - 300 ms [36].



Fig. 16. Simplified representation of the curved-line folding due to midrib bending found in Aldrovanda. Depicted left is the flat position. When the midrib bends downward, as seen on the right, the lobes are forced to move upwards due to the curved folding line.

4.4 Moving dynamic with amplification and elastic energy storage

The following mechanisms are used to move dynamic with an amplification mechanism and stored elastic energy (D-A-E).

- 1. Snap-through buckling due to bilayer actuation (SBBA): reversible, 3D, initiated by both internal factors
- 2. Impulse due to failure (IF): irreversible, both 2D and 3D, initiated by internal factors
- 3. Pressure difference (PD): reversible, 3D, initiated internal factors

4.4.1 Snap-through buckling due to bilayer actuation

Closely related to the waterwheel plant, but incorporating a very different mechanism, is the trap of the terrestrial carnivorous venus plant (*Dionaea muscipula*). It's morphology is similar to the waterwheel plant, with the trap consisting of two lobes connected at the bottom by a midrib. This midrib, however, does not bent when the trap closes [39]. Instead, both lobes consist of two distinctive cell layers that form a bilayer. When prey triggers the trap to close, water is pumped from the layers at the inside of the trap to the layers outside the trap. In mature plants [59] this builds up elastic energy, which is released when the trap rapidly changes curvature from convex to concave, thereby closing the trap [60], [6] (see figure 17). The plant does this in less than 100 ms [60].

See [61] and [37] for a hydro-elastic curvature model of the trap closing. Different trigger stages and their result on the non-linear movement of the lobes are described in [62].



Fig. 17. Schematic of the snap-through buckling of a Venus fly-trap. When the trap is triggered, cells on the inner surface of each of the lobes pump out their water to the outer surface of each of the lobes. This makes the inside shorter and the outside longer, initially straightening the concave lobes. This movement stores elastic energy, which is suddenly released when the lobes rapidly snap to a convex shape, thereby closing the trap.

A similar movement to the snap-buckling of *Donaea* can be observed when looking at the column of *Stylidium*. The flowers of this plant have their pollen on a wide column that is fold backwards. When a pollinator visits the flower, it triggers a rapid flip of the column from the posterior to the anterior petals. During this movement it hits the pollinator and exchanges pollen with it. Althoug this movement is also initiated by loss of turgor of a few cells, its precise mechanics are still unknown [39].

4.4.2 Impulse due to failure

The most common way for plants to use stored elastic energy for fast movement, is by building it up gradually over time before a fast fracture-based release. Due to obstructed, mostly bilayer based deformations of parts of the plant, tension is built up. This tension eventually becomes large enough to break connective tissue, enabling a fast 'snap-back' of the plant to its desired deformed state. The vast majority of movements that incorporate this principle, are movements that propel seeds, spores or pollen. Since most of these movements are enabled by the drying of parts of the plant and they tend to open in a quick fashion, these movements are often referred to as 'explosive dehiscence'.

Various seed-dispersal-mechanisms use the bilayer principle to open and catapult their seeds. The seed pods of *Bauhinia variegate* and the *Cardamine* family consist of two valves that cover the seeds. These valves are connected together at the edges with a thin tissue [63]. Instead of a resistive non-swelling and active swelling layer, however, the valves are build up out of a more sophisticated bilayer.

Bauhinia variegate's bilayer mechanism moves based on the humidity of the surrounding air and is therefore a passive movement. As can be observed in figure 18, both layers deform when drying. Bauhinia's bilayer does not have the active/passive layer configuration as described in section 4.1.2, but has two active layers with a fibre-orientation perpendicular to each other. Both layers shrink perpendicular to each other upon dessication, thereby enabling bilayer deformation to a double curved surface [35], [64]. However, since the valves are still connected to each other at their edges, they can not move. When a certain threshold is reached, the thin connection between the valves breaks and the valves rapidly deform to their desired curled up state, catapulting the spores [52].

The seed dispersal of *Cardamine* (*hirsuta* and *parviflora*) happens in the same manner [21], although here the seeds travel much further. It is argued that this is because of the presence of a turgid cellular tissue that increases the stiffness of the

valves, making it an active movement [65].

These seed-pods also possess a thin wall between the valves that holds the seeds. Sometimes this wall is unsuccessful in letting go of the seeds, making the catapult somewhat unreliable [42].



Fig. 18. Schematic of the movement of the valves of seedpods found in *Bauhinia* variegate and *Cardamine hirsuta* and *parviflora*.

Also based on valves building up tension for a quick release, is the seed dispersal mechanism of jewelweed, otherwise known as the 'touch-me-not' (*Impatiens capensis*). Here, five valves are connected together at their edges as they encapsulate the seeds around a middle stalk, the columella. As in the previous cases, the valves are bi-layers. The inner cells lose water and want to shorten, while the outer cells absorb water and want to stretch. This deformation is counteracted by the connection of the valves to the columella and to themselves [21], putting the inner cell layer under tension and the outer cell layer under compression. As can be seen in figure 19a, the valves rapidly curl up when the connective tissue fails, shooting away the seeds [41].

The filaments of *Cornus Canadensis* that carry the plant's pollen, move according to the same principle. The filaments grow inside the immature bud. Since they grow faster than the petals, they are forced to bend [21] and protrude through the petals, see figure 19b. They are made of an elastic tissue, and favour a straight configuration, so they excite pressure on the petals [44]. Eventually the petals fold away and the filaments straighten out, catapulting the pollen vertically in order to maximize wind dispersal [66]. This use of growth for tensioning a flexible tissue also happens with the stamen of the Mountain Laurel (Kalmia latifolia), although in this case pollinators trigger the release of the stamen [67].

Coincidentally, the coiling awn of the filaree mentioned in section 4.1.2 serves a double purpose as seed launcher in a similar way as the valves of jewelweed and the filaments of *Cornus canadensis*. Due to obstructed deformation of the awns, tension is build up. As this tension is released when the connection of the awns to the plant breaks, the seed is slung in to the air [51].



(a) Schematic of the swelling coiling catapult of *Impatiens Capensis*. Upon drying, the lobes that hold the seeds to the columella in the middle start to curl (second image). When this deformation puts enough pressure on the connection between the valves and the columnella, the valves break free and rapidly spring in their coiled position (third image). The seeds are catapulted away as a result (fourth image). Drawing based on figures in [41] and [21].



(b) The pollen catapult of *Cornus canadensis*. During growth, the stamen grow faster than the petals. This lets them protrude between the petals (second image) as they store elastic energy. When the petals break apart from each other at the top (third image) the stamen quickly straighten out, catapulting the pollen upwards (fourth image). Drawing based on figures in [66] and [21].

Fig. 19. Swelling catapults in Impatiens Capensis (a) and Cornus canadensis (b).

Spore-distribution from ferns and fungi rely on (de)hydration induced failure on a similar manner. Ferns from the family of *Polypodiaceae* grows its spores inside little spheres at the bottom of its leaves. These spheres consist of a thin membrane, held together with a ring of cells called the annulus. As can be seen in figure 20, the annulus is build up out of two distinctive layers of cells [21]. When matured, exposure to the surrounding air causes water to evaporate out of the outer cells of the annulus. This decreases the volume of the outer cells, so the radial cell walls move closer together. This causes the annulus to want to straighten out, putting pressure on the membrane of the sphere. Eventually the membrane ruptures and forms two cups. The annulus straightens out due to further evaporation of the water-content in its outer cells, but this deformation is resisted by the inner cell layer of the annulus. The catapult stores elastic energy as it slowly opens up. When the elastic forces become larger than the vacuum created by the evaporation, cavitation occurs inside the outer cells of the annulus. This causes the annulus to quickly snap back to its original position, thereby launching the spores like a catapult [3].



Fig. 20. The cavitation catapult found in *Polypodiaceae*. When the ring shaped annulus (depicted in brown) is exposed to air, its outer cells lose their water. Sinche the radial cell walls of the outer cells are stiffer than the circular ones, the latter start to cave in (second image). By doing so they tension the inner stiff layer of cells of the annulus. Eventually, cavitation occurs in the outer cells due to the loss of pressure (third image). This quickly increases their volume, and the annulus springs back to its original shape due to the elastic energy build up in the inner layer of cells (fourth image). This catapults the spores. Drawing based on figures in [3].

4.4.3 Pressure difference

A unique kind of mechanism can be found in the trap of the aquatic carnivorous bladderwort (*Utricularia stellaris*). As can be seen in figure 21, these plants have little sacks attached to their stalks. These sacks are closed by a trap door, forming a watertight seal. Special glands inside the sack pump out water [68]. The volume of the sack is reduced as the originally convex walls cave in to a concave position, but the stiffness of the walls makes them want to move back. This creates a pressure difference between the inside of the sack and the surrounding water [39], [68]. When prey swims close to the opening of the trap, it triggers hairs surrounding the opening. This triggering subsequently releases the threshold that holds the door in place and the door swings back, opening the sack [69]. The walls of the sack quickly revert to their original state, thereby sucking in water and the prey that triggered the trap. After this, the trapdoor swings closed again. This process takes less than 0.5 milliseconds [6], although there are signs that it might be an even faster movement [43].



Fig. 21. Schematic of the movement of the bladderwort suction trap. The plant actively pumps water out of its sack. The walls of the sack cave inward (second image), but they resist this motion due to their stiffnes and thus store elastic energy. When prey touches the trigger hairs, the trapdoor opens and the walls quickly revert back to their original shape, sucking in water and the prey (fourth image). The trapdoor then closes.

5 Existing Bio-inspired Devices

The mechanisms identified and classified in the previous chapter can serve as inspiration for engineers and designers. The best way to transfer the principles of plant-mechanisms to the engineering world proves to be challenging however. Various design methodologies have been proposed over time [70], [16], [71], [72], [73], [74], all with their merits and disadvantages. It depends on the specific case and the preferences of the engineer/designer which methodology is best suited.

These methodologies have already led to the design of some interesting plant-based mechanisms. An overview of existing mechanisms, classified according to the same classification presented in section 3.4, can be seen in table 1. Additionally, this table specifies the Technology Readiness Level (TRL) of each existing mechanism. The TRL is a measure of the state of development of a technology and enables objective comparison between different types of mechanisms [75]. Finally, table 1 gives an estimate of the scale difference with respect to the plant-mechanism it is based on.

Most of the devices in table 1 are classified in the QS-A class. Most notable in this class are the devices inspired by the antagonistic lever and bilayer mechanisms. Some concepts from these subclasses are used in soft-robotics, a branch of robotics that uses antagonistic pressure chambers to actuate artificial limbs [76]. Out of all existing devices, they score quite high on the TRL scale, meaning that they are developed far enough to start implementation in commercial environments.

Some other popular examples of devices that are already being used are the Flectofin and Flectofold. Based on the midrib bending found in *Strelitzia* from class QS-A and the curved-line folding from *Aldrovanda* from class D-A, respectively, these mechanisms consist of large vertical beams placed on the facade of buildings. The beams contain flaps that protrude perpendicular from the facade. When actuated, these flaps bend inward due to the kinematic coupling between beam and flaps. By doing so they cover more and more of the building, shading it from the sun.

Devices that score much lower on the TRL-scale, but mimic nature much closer, can be found in, e.g., molecular or self-shaping bilayers from the QS-A-BM class and the snapping composite shells from the D-A-E-SBBA class. These devices were created by closely looking at the microstructure of their parent-plants. The result is a device that incorporates inhomogeneous materials, containing fibres in different directions. This results in a movement that equals the observed plant movement not only in motion, but also in how that motion is achieved.

tructures / Soft robotics [76], [74], [77], [78]	3-4 [77] & 7 [76] 5	1:10 - 1:100 1.10
tructures / Soft robotics [76], [74], [77], [78]	3-4 [77] & 7 [76] 5	1:10 - 1:100 1·10
	r;	1.10
		7.10
	3-4	1:10
[82], [83], [84]	3-4 [83], [84] & 6 [81], [82]	$1{:}10$
	3-4	10.1
on fibre orientation [86], [83], [64], [87], [88]	3-4	1:1
l on ice plant) $[89]$, $[88]$	3-4	1:10
0]	9	1.5
ins [91], [88]	3-4	1:1 - 1:10
based on $Strelitzia$) [15], [16], [71], [70]	$9 \ [92]$	$1{:}100$ [93]
	I	I
etals of lily) [70]	4-6	1:100
	ı	ı
(based on $Aldrowanda$) [13], [94], [70]	8	1:100
	4	1:1 - 1:5
composite shells [96]	4	1:1
	1	I
	,	
	 [82], [83], [84] on fibre orientation [86], [83], [64], [87], [88] d on ice plant) [89], [88] 0] irns [91], [88] based on <i>Strelitzia</i>) [15], [16], [71], [70] betals of lily) [70] betals of lily) [70] interval (13], [94], [70] composite shells [96] 	

6 Discussion

6.1 Comparing plant mechanisms

The systematic review provided in this paper presents a new classification of compliant plant movements that better suits engineers and designers. Clear trends within the movements of plants have been identified. Interesting working principles were derived in order to serve as inspiration.

The most common initiator of movement in the plant world is water. It is either actively moved around via osmosis, or it moves passively due to hygroscopic suction or dehydration. In both cases, it shrinks or swells cells or tissues. These volume-changes drive other mechanisms. In engineering, this is used extensively in some specialized fields, most notably in soft robotics. Most fields however still need to benefit from this principle.

The most common mechanism in the plant world, is the bilayer. Even more sophisticated mechanisms often rely somewhere on the principle of two layers moving with respect to one another, as is evident in the failure-based mechanisms in the opening of seed pods. The bilayer principle is not uncommon in the engineering world either, but it is not used to drive other, more complicated mechanisms that much.

Storing elastic energy for release at a later stage is one of the mechanisms often driven by the bilayer principle. This release is often failure based and therefore irreversible, although carnivorous plants implement reversible mechanisms like snap-buckling and midrib bending to be able to move repeatedly. Together with some pollen dispensers, these plants are the only ones that rely on repeated fast movement.

All mechanisms that move dynamically and use energy to do so, store this energy gradually before a fast release. For plants that need to act on external triggers, this means that they need to store this energy before triggering occurs. Indeed, all carnivorous plants 'set' their trap and wait for prey to trigger them. Most shooting mechanisms on the other hand, release their energy immediately when the slow build-up reaches a certain threshold and do not have a time-delay between reaching maximum energy storage and consecutive release.

A unique group of mechanisms can be found in the folding and unfolding leaves and petals by midrib or edge actuation. These mechanisms mostly rely on growth for actuation, instead of on the bilayer principle. Plants that only need to unfold once can incorporate more intricate folding patterns. They form a small, densely packed bud, before opening to a leaf or petal that spans a large area. In contrast, repeated folding motions like the circadian opening and closing of the moonflower or the movement of the lobes of carnivorous plants produce simpler folding kinematics and are based again on the bilayer principle.

6.2 Relation between degree of biomimicry, scale and Technology Readiness Level

It is clear from table 1 that most existing bio-inspired devices are from the QS-A class. This is of course due to the fact that this class contains the most plants to draw inspiration from, but has also to do with the relative simplicity of the mechanisms in this class. Furthermore, the other classes have a tendency towards irreversible mechanisms, something that is much less useful in engineered devices than it is in the plant world.

When looking at the examples in table 1 in more detail, it becomes clear that engineers can copy nature in a lot of different ways and on a lot of different levels. Some mechanisms just take the general principle as inspiration, while others copy the underlying structure and mechanics in great detail. This is something that again depends on the specific case and preference of the engineer. It furthermore depends on the scale of the bio-inspired device.

Regarding the estimates of the scale differences, it can be observed that the engineered mechanisms tend to be designed larger than the plants they are based upon. Of course, plant tissue has certain limits [97]. This means that the larger the inspired mechanism is compared to the plant, the bigger the difference, especially in material. A good example of this are the Flectofin and Flectofold shading systems. These devices are used to shade complete façades, so they differ in dimensions of the plants with a factor of at least a hundred. Bio-inspired mechanisms with this big of a scale difference tend to just copy the principle of movement and use conventional materials for their fabrication. Smaller devices are capable of mimicking the plant world much closer, as can be seen with the many examples of molecular bilayers, or bilayers that incorporate fibre structures.

The extend to which nature is copied is also reflected in the TRL. Devices that score high on the TRL-scale usually only mimic nature on a macroscopic level without implementing the same material structures (Flectofin and Flectofold). In contrast, devices that copy nature more closely are almost all still in a conceptual stage with a low TRL.

6.3 Potential Applications and Future Research

As is clear by now, plant movements appear simple on the macroscopic scale, but are very intricate on cellular level. Implementation of plant mechanics in the engineering world can be done anywhere between those scales. One can copy an entire microscopic working principle, like the bilayer actuators, or one can base their design loosely on the observed plant mechanism, like the Flectofin and Flectofold. The latter possibility is at the moment the most successful one; bio-inspired devices loosely based on plant mechanics are already being used in society. However, understanding plant movements on a plant mechanisms. Implementing the hierarchical way in which plant movements originate is worth considering.

The distinction between quasi-static and dynamic movements made in this paper is beneficial for its toolbox-oriented setup. This does not mean, however, that working principles derived from quasi-static mechanisms cannot be used for fast bio-inspired devices, especially since they are mostly reversible. Engineers can use regular fast driving forces to actuate these quasi-static mechanisms.

Additionally, the implementation of irreversible plant mechanisms in the engineering world is worth consideration as well. From table 1 it is clear that these plant mechanisms do not have their engineering counterparts, but this group contains some interesting movements that could benefit engineering. One potential application would be to use them in area's where only a one-time movement is required, such as drug delivery. Alternatively, engineers might alter these mechanisms to make them reversible. Movements that rely on fracture-based release, for instance, could also be achieved with reversible release-mechanisms such as physical thresholds, actuated pins or nipples, magnetic connections, et cetera.

A subject not treated in much detail in this paper, but very important in the movement mechanics of plants, is the structure of the tissue of the moving parts. When discussing the various bilayer mechanisms, it became clear that their movement relies heavily upon the fibre-orientation of the different layers; all kinds of interesting 3D-curvatures could be achieved depending on the type of fibres and their direction with respect to one-another. While there is a lot of available research on the subject, there seems to be a gap between conceptual materials actually mimicking plant tissue structure and available products incorporating plant movement mechanics.

The most important step, however, should be taken in actually implementing the

'bio-inspired' way of thinking into the design process of engineers. This requires bridging a gap between the theoretical and often conceptual work about plant movements and the practical application in real life. Soft robotics in engineering and façade shading in architecture are among the pioneers, but even there a change in mindset needs to happen in order to benefit from the more intricate compliant shell mechanics in plants.

6.4 Limitations of This Study

Although a systematic approach was taken when searching for all the relevant compliant mechanisms in the plant world, it proved difficult to say with absolute certainty that all the different subspecies where identified. The restriction to the English language, the absence of relevant keywords, the used definition of shell-deformation or the restriction to compliant movements only could all be the cause of missing important information. Other mechanisms that might be relevant, but are not included in this review, are bio-inspirations that are not reported as such and non-scientific work dealing with bio-inspired devices. All the relevant working principles are included however, and it can be said with certainty that movements not included in this review can be placed in the existing classification system. The classification provides a clear overview of all the possibilities and gives ample leads if one wants to dive into the plant-world themselves.

Albeit a conscious one, the choice not to focus on the cellular level of the mechanics is also limiting to the usability of this review. All the relevant data regarding this subject, however, is present in the referenced papers found in appendix A2. This should provide a great basis for anyone who wants to be inspired by plant movements on a smaller scale.

7 Conclusion

This review presents a new structured classification of compliant shell mechanisms in plants. With its toolbox-like setup, it becomes easier for engineers and designers to implement these mechanisms in their work.

When placing existing bio-inspired devices in the same classification scheme, it becomes clear that certain classes are favoured by engineers. These 'simpler' classes provide inspiration for interesting devices, but the designs could potentially benefit from working principles on the cellular level. Furthermore, there is a lot of unused potential in especially the mechanisms that bring about irreversible dynamical movements. These mechanisms are capable of very fast and complex motions and could inspire all kinds of novel compliant devices.

Supporting information

A1: Search strategy and query

The following queries were used in Scopus and Web of Science, respectively. They differ only in syntax used by the two database search engines.

Scopus

(TITLE-ABS-KEY

((bend OR bending OR folding OR complian* OR morph OR morphing OR deform OR buckle OR warp OR bi-stable OR move OR movement OR moving OR open OR opening OR dispers* OR touch)

 $\rm W/8$ (plant OR plants OR leaf OR stem OR bark OR petal OR seed OR *spore* OR petiole OR flower* OR anther OR stamen OR tree OR moss* OR grass* OR weed* OR herb OR botanic*))

AND

TITLE-ABS-KEY (biomechani* OR kinematic* OR kinetic OR "biomimetic mechanism*" OR biomimetic OR "morphing structur*" OR "mechanical stimul*" OR "mechanical stimul*" OR "mechanical respons*"))

AND NOT TITLE (cell OR flow OR fluid OR gene OR molecul* OR synthes*) AND NOT TITLE-ABS-KEY (protein OR "gene" OR "genes" OR "genetic")

Web of Science

(TS =

((bend OR bending OR fold OR unfold OR folding OR unfolding OR complian* OR morph OR morphing OR deform OR buckle OR warp OR bi-stable OR move OR movement OR moving OR open OR opening OR dispers* OR touch) NEAR/8

(plant OR plants OR leaf OR stem OR bark OR petal OR seed OR *spore* OR petiole OR flower* OR anther OR stamen OR tree OR moss* OR grass* OR weed* OR herb OR botanic*))

AND

TS=(biomechani* OR kinematic* OR kinetic OR "biomimetic mechanism*" OR biomimetic OR "morphing structur*" OR "mechanical stimul*" OR

"mechano-respons*" OR "mechanical response"))

NOT TI=(cell OR flow OR fluid OR gene OR molecul* OR synthes*)

NOT TS=(protein OR "gene" OR "genes" OR "genetic")



Fig. 22. Flowchart depicting the selection of core papers for this review.



Fig. 23. Schematic showing the origin of the 87 papers in the core library. 53 papers were found in both Scopus and Web of Science databases. 16 were in Scopus only and 7 were in Web of Science only. Additionally, 11 papers were obtained from the reference lists of the found papers.

A2: Core papers

	Title	First author	Year	Citation
1	Geometry and Mechanics in the Opening of Chiral Seed Pods	Armon, S.	2011	[35]
2	Bio-inspired self-shaping ceramics	Bargardi, F. L.	2016	[86]
3	Design and testing of botanical thermotropic actuator mechanisms in thermally adaptive building coverings	Barrett, M.	2017	[79]
4	Design concept of a new bio-inspired tactile sensor based on main pulvinus motor organ cells distribution of Mimosa Pudica plant	Basir, S. N.	2015	[80]
5	Mechanism for rapid passive-dynamic prey cap- ture in a pitcher plant	Bauer, U.	2015	[38]
6	Fiber-reinforced plastics with locally adapted stiffness for bio-inspired hingeless, deployable architectural systems	Born, L.	2017	[94]
7	In Touch: Plant responses to mechanical stim- uli	Braam, J.	2004	[26]
8	Actuation systems in plants as prototypes for bioinspired devices	Burgert, I.	2009	[17]
9	Kinematic Amplification Strategies in Plants and Engineering	Charpentier, V.	2017	[14]
10	Light- and humidity-driven actuators with pro- grammable complex shape-deformations	Chen, L.	2019	[81]
11	Mechanical contribution of secondary phloem to postural control in trees: the bark side of the force	Clair, B.	2019	[19]
12	The staminal lever mechanism in Salvia L. (Lamiaceae): A key innovation for adaptive radiation?	Classen-Bockhoff, R	2003	[27]
13	A plant-inspired kinematic model for growing robots	Del Dottore, E.	2018	[33]
14	Flower opening and closure: A review	Doorn, van, W. G.	2003	[53]
15	Vegetable dynamicks: The role of water in plant movements	Dumais, J.	2011	[22]
16	The role of wheat awns in the seed dispersal unit	Elbaum, R.	2007	[5]
17	Structural Principles in the Design of Hygro- scopically Moving Plant Cells	Elbaum, R.	2018	[4]
18	Self-shaping composites with programmable bioinspired microstructures	Erb, R. M.	2013	[87]
19	The mechanics of explosive dispersal and self- burial in the seeds of the filaree, Erodium ci- cutarium (Geraniaceae)	Evangelista, D.	2011	[51]
20	How the Venus fytrap snaps	Forterre, Y.	2005	[60]
21	Slow, fast and furious: understanding the	Forterre, Y.	2013	[23]
00	physics of plant movements		0017	
22	Spore liberation in mosses revisited	Gallenmuller, F.	2017	[57] [94]
23	Actuators acting without actin	Gentinann, A.	2010	[24]
	Continued on next page			

	Title	First author	Year	Citation
24	Honeycomb actuators inspired by the unfolding of ice plant seed capsules	Guiducci	2016	[89]
25	Fast nastic motion of plants and bioinspired structures	Guo, Q.	2015	[58]
26	Photoinduced multi-directional deformation of azobenzene molecular crystals	Hao, Y.	2019	[85]
27	Origami-like unfolding of hydro-actuated ice plant seed capsules	Harrington, M.	2011	[49]
28	The mechanics of explosive seed dispersal in orange jewelweed (Impatiens capensis)	Hayashi, M.	2009	[41]
29	The Seed Dispersal Catapult of Cardamine Parviflora (Brassicaceae) is Efficient but Unre- liable	Hayashi, M.	2010	[42]
30	Morphomechanical Innovation Drives Explo- sive Seed Dispersal	Hofhuis, H.	2016	[65]
31	Climate-Dependent Heat-Triggered Opening Mechanism of Banksia Seed Pods	Huss, C. J.	2018	[28]
32	At the conjunction of biology, chemistry and physics: The fast movements of Dionaea, Al- drovanda, Utricularia and Stylidium	Joyeux, M.	2011	[39]
33	Kinematical, structural and mechanical adap- tations to desiccation in poikilohydric ramonda myconi (gesneriaceae)	Kampowski, T.	2018	[31]
34	Biomimetic building skins: An adaptive approach	Karam, M. A.	2017	[72]
35	Flytrap-inspired robot using structurally in- tegrated actuation based on bistability and a developable surface	Kim, S	2014	[95]
36	Bio-inspired kinetic facade for the thematic pavilion "One Ocean" EXPO 2012 in Yeosu, Korea	Knippers, J	2013	[92]
37	Folding and unfolding of tree leaves with cor- rugation creases	Kobayashi, H.	2001	[55]
38	Deployable Structures in Plants	Kobayashi, H.	2009	[54]
39	Flectofold-a biomimetic compliant shading de- vice for complex free form facades	Korner, A.	2018	[13]
40	Origami-structures in nature: Lessons in de- signing "smart" materials	Kresling, B.	2012	[91]
41	Self-organisation and motion in plants	Lenau T. A.	2014	[25]
42	Fluidic origami with embedded pressure dependent multi-stability: A plant inspired innovation	Li, S.	2015	[77]
43	Fluidic origami: a plant-inspired adaptive structure with shape morphing and stiffness tuning	Li, S.	2015	[78]
44	Plant-inspired adaptive structures and materials for morphing and actuation: a review	Li, S	2017	[88]
45	Nonlinear Dynamics of the Movement of the Venus Flytrap	Li, Y.	2012	[62]

Table 2 – Continued from previous page

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	Title	First author	Year	Citation
46	Growth, geometry, and mechanics of a bloom- ing lily	Liang, HY	2011	[2]
47	Abstraction of plant movements for deployable structures in architecture	Lienhard, J.	2009	[71]
48	Elastic architecture: nature inspired pliable structures	Lienhard, J.	2010	[93]
49	The fern cavitation catapult: mechanism and design principles	Llorens, C.	2016	[3]
50	How plants inspire facades. From plants to architecture: Biomimetic principles for the de- velopment of adaptive architectural envelopes	Lopez, M.	2017	[73]
51	Mechanics without Muscle: Biomechanical In- spiration from the Plant World	Martone, T. P.	2010	[44]
52	Nature-inspired smart solar concentrators by 4D printing	Momeni, F.	2018	[90]
53	A biomechanical model of anther opening re- veals the roles of dehydration and secondary thickening	Nelson, M. R.	2012	[50]
54	Thermonastic leaf movements in Rhododen- dron during freeze-thaw events: Patterns, func- tional significances, and causes	Nilsen, E. T.	2014	[52]
55	Pressure-actuated cellular structures	Pagitz, M.	2012	[76]
56	A Modular approach to adaptive structures	Pagitz, M.	2014	[74]
57	Biomimetic deployable systems in architecture	Poppinga, S.	2010	[15]
58	Plant movements as concept generators for deployable systems in architecture	Poppinga, S.	2010	[16]
59	Faster than their prey New insights into the rapid movements of active carnivorous plants traps	Poppinga, S.	2013	[6]
60	Fastest predators in the plant kingdom: Func- tional morphology and biomechanics of suction traps found in the largest genus of carnivorous plants	Poppinga, S.	2016	[69]
61	Comparative kinematical analyses of Venus flytrap (Dionaea muscipula) snap traps	Poppinga, S.	2016	[59]
62	Toward a New Generation of Smart Biomimetic Actuators for Architecture	Poppinga, S.	2018	[10]
63	Bark, the neglected postural motor system	Poppinga, S.	2019	[20]
64	Meteorosensitive architecture: Biomimetic building skins based on materially embedded and hygroscopically enabled responsiveness	Reichert, S.	2014	[82]
65	Modeling of snapping composite shells with magnetically aligned bio-inspired reinforce- ments	Riley, S. K.	2018	[96]
66	Motions of leaves and stems, from growth to potential use	Riviere, M.	2017	[32]

Table 2 – Continued from previous page

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	Title	First author	Year	Citation
67	Seed Dispersal from Hygroscopic Mesem- bryanthemumFruits; Bergeranthus scapigerus, Schw., and Doro-theanthus bellidiformis, N.E.Br., with a Note on Carpanthea pomeridi- ana, N.E.Br.	Lockyer, S.	1932	[48]
68	Shooting Mechanisms in Nature: A systematic Review	Sakes, A.	2015	[21]
69	Abstraction of bio-inspired curved-line folding patterns for elastic foils and membranes in architecture	Schleicher, S.	2010	[34]
70	A methodology for transferring principles of plant movements to elastic systems in architec- ture	Schleicher, S.	2015	[70]
71	Rapid touch-stimulated movement in the an- drogynophore of Passiflora flowers (subgen. Decaloba; Sect. Xerogona) An adaptation to enhance cross-pollination?	Scorza, L. C.	2014	[47]
72	Vacuolar remodelling mediates touch-induced androgynophoremovement in Passiflora (Subg. Decaloba, Sect. Xerogona) flowersLivia	Scorza, L. C.	2014	[46]
73	Dynamics of flower head movement in bio- system	Shiono, M.	2010	[45]
74	The Hygroscopic Opening of Sesame Fruits Is Induced by a Functionally Graded Pericarp Architecture	Shtein, I.	2016	[56]
75	The biomechanics of fast prey capture in aquatic bladderworts	Singh, A. K.	2011	[43]
76	Physical Limits and Design Principles for Plant and Fungal Movements	Skotheim, J. M.	2005	[97]
77	Dispensing Pollen via Catapult: Explosive Pollen Release in Mountain Laurel (Kalmia latifolia)	Switzer, M. C.	2018	[67]
78	The mechanism for explosive seed dispersal in Cardamine hirsuta (Brassicaceae)	Vaughn, K.	2011	[63]
79	Ultra-fast underwater suction traps	Vincent, O.	2011	[68]
80	Morphing Structures in the Venus Flytrap	Volkov, A. G.	2012	[98]
81	Morphing structures and signal transduction in Mimosa pudica L. induced by localized thermal stress	Volkov A. G.	2013	[40]
82	Morphing structures of the Dionaea muscipula Ellis during the trap opening and closing	Volkov, A. G.	2014	[37]
83	Helical structures mimicking chiral seedpod opening and tendril coiling	Wan, G.	2018	[64]
84	Sensitive Humidity-Driven Reversible and Bidi- rectional Bending of Nanocellulose Thin Films as Bio-Inspired Actuation	Wang, M	2015	[84]
85	How the carnivorous waterwheel plant (Al- drovanda vesiculosa) snaps	Westermeier, A. S.	2018	[36]
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Table 2 – Continued from previous page

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	Title	First author	Year	Citation
86	The biomechanics of Cornus canadensis sta- mens are ideal for catapulting pollen vertically	Whitaker, D. L.	2007	[66]
87	Directed Motility of Hygroresponsive Biomimetic Actuators	Zhang, L.	2016	[83]

Table 2 – Continued from previous page

Tab. 2. Core papers used in the literature review, sorted alphabetically by title.

A3: List of abbreviations

Acronym	Meaning
Classes	
QS-A	Quasi-Static movement with Amplification
QS-A-E	Quasi-Static movement with Amplification and stored
	elastic Energy
D-A	Dynamic movement with Amplification
D-A-E	Dynamic movement with Amplification and stored
	elastic Energy
Mechanisms	
ALM	Antagonistic Lever Mechanism
BM	Bilayer Movement
BMF	Bilayer Movement due to Failure
BSVC	Bilayer Swelling Velocity Catapult
FU	Folding and Unfolding
IF	Impulse due to Failure
MBCLF	Midrib Bending induced Curved-Line Folding
PD	Pressure Difference
PLMMB	Passive Lever Mechanism and Midrib Bending
SBBA	Snap-through Buckling due to Bilayer Actuation
SBEG	Snap-through Buckling due to Edge Growth
Licences	
CC BY 2.0 I	Creative Commons Attribution 2.0 Generic Interna-
	tional License
CC BY-SA 3.0	Creative Commons Attribution-Share Alike 3.0 Un-
	ported License
CC BY-SA 4.0 I	Creative Commons Attribution-Share Alike 4.0 Inter-
	national License
Other	
TRL	Technology Readiness Level

Tab. 3. List of acronyms used in this paper, sorted alphabetically per topic.

A4: Declaration of elements used in images

Element	Meaning
1	
	Water displacement.
\rightarrow	Transition from one state to another.
\checkmark	Movement (open tip).
	Force (closed tip).
	Seeds.
° • •	Spores.
\bigcirc	Lump of pollen.
~	Stamen, stalk inside a flower (green) that con- tains the pollen at its tip. (yellow)

 Tab. 4. Explanation of informative parts of the figures in this paper.

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