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Plant movements as concept generators for the development of biomimetic compliant mechanisms

Running head: Plant movement biomimetics

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Synopsis

Plant movements are of increasing interest for biomimetic approaches where hinge-free compliant mechanisms (flexible structures) for applications e.g. in architecture, soft robotics, and medicine are developed. In this article, we first concisely summarize the knowledge on plant movement principles and show how the different modes of actuation, i.e. the driving forces of motion, can be used in biomimetic approaches for the development motile technical systems. We then emphasize on current developments and breakthroughs in the field, i.e. the technical implementation of plant movement principles through additive manufacturing, the development of structures capable of tracking movements (tropisms), and the development of structures that can perform multiple movement steps. Regarding the additive manufacturing section, we present original results on the successful transfer of several plant movement principles into 3D printed hygroscopic shape-changing structures ("4D printing"). The resulting systems include edge growth-driven actuation (as known from the petals of the lily flower), bending scale-like structures with functional bilayer setups (inspired from pinecones), modular aperture architectures (as can be similarly seen in moss peristomes), snap-through elastic instability actuation (as known from Venus flytrap snap-traps), and origami-like curved-folding kinematic amplification (inspired by the carnivorous waterwheel plant). Our novel biomimetic compliant mechanisms highlight the feasibility of modern printing techniques for designing and developing versatile tailored motion responses for technical applications. We then focus on persisting challenges in the field, i.e. how to speedboost intrinsically slow hydraulically actuated structures and how to achieve functional resilience and robustness, before we propose the establishment of a motion design catalogue in the conclusion.

<u>Keywords:</u> 4D printing, biomimetics, compliant mechanism, plant movements, responsive architecture

Plant movement actuation and biomimetics

Plants do not possess muscles, nerves or "real" (localized) hinges, yet they can perform a multitude of different and complex movements (Poppinga et al. 2013, 2016b) (Figure 1), which are driven by different types of actuation principles (and combinations thereof). Self-actuated motions can be driven by active or passive hydraulics (i.e., energy-costly or "free" water displacement processes between cells and tissues) and/or by the release of internal prestress (reviewed by Dumais & Forterre 2012; Forterre 2013), whereas externally actuated motions are driven by application of mechanical force, e.g. by pollinators, wind or raindrops. The respective motile plant structures often show high functional resilience, which makes them ideal candidates for the development of biomimetic compliant mechanisms (flexible structures) (Burgert & Fratzl 2009; Schleicher et al. 2015). All plant movement actuation principles have been subject to various biomimetic approaches, as concisely described in the following.

Active hydraulics require metabolic energy and comprise reversible turgor changes and irreversible growth processes, which are typically subject to tight physiological control and can be triggered by various types of external stimuli, e.g. touch, temperature or light. For example, many flower opening and closing processes fall into this movement category and are driven by differential growth processes. As has been shown in the lily cultivar *Lilium* 'Casa

Blanca' (Liang & Mahadevan 2011) (Figure 1A), the margins of the petals show excessive growth in contrast to the petal centers, causing strain gradients which force the petals to change their curvatures. By this edge actuation, the bud opens and the lily blooms. Growth processes have recently been abstracted and transferred into technical systems for robotics applications (Hawkes et al. 2017; Sadeghi et al. 2017). An exception from this group of externally triggered plant movements are autonomous motions (e.g., circumnutation), which are not triggered by external stimuli (Hill & Findlay 1981). Recent approaches have dealt with the technical implementation of circumnutation-like explorative movement in robotic tendrils (Nahar et al. 2017). Other active hydraulic plant motions, like the touch-induced folding of the *Mimosa* leaflets (Weintraub 1952), are based on the reversible change of turgor pressure in antagonistic motor cells. The involved osmotic actuation has been abstracted and transferred into several technical applications for movement generation (reviewed by Li & Wang 2017).

Passive hydraulic motions do not require metabolic energy. They are not stimuli-triggered but solely evoked by changing environmental conditions, mainly fluctuations in humidity. For example, the differential hygroscopic swelling/shrinking properties of tissues entail movement processes that can be found in many diaspore release mechanisms, e.g. in pinecones (Figure 1B), moss capsule peristomes (Figure 1C), and seed pods (reviewed by Elbaum & Abraham 2014; Elbaum 2018). The fact that the involved structures are sensor, actuator, and motile element all in one makes them highly interesting concept generators for biomimetic applications. The responsiveness of the developed technical actuators, e.g. to humidity, heat, or pH, can be "programmed" and adjusted by a tailored materials composition (Ionov 2014; Erb et al. 2013; Bargardi et al. 2014).

The speed of motile plant structures, which are actuated by active or passive hydraulics alone, relies on the timescale of diffusive water transport through the respective tissues and,

transport and, hence, are slower. Several intriguing plants overcome this poroelastic timescale paradigm by employing elastic instabilities (Skotheim & Mahadevan 2005). Here, foregoing deformation processes, induced e.g. by growth, cause the generation and storage of elastic energy in the respective structures, which are then prestressed. The release of the stored elastic energy acts as a speed boost, significantly enhancing the motion speed. Such movements are reversible when the respective structure can be prestressed again, or irreversible, when tissue is torn and the structure ruptures. Elastic instabilities can be found in many explosive diaspore dispersal mechanisms, like in the exploding fruits of touch-me-nots (*Impatiens* spp.) (Deegan 2012) and in carnivorous plants traps, which have to be fast enough to overcome their arthropod prey. A famous example from this group of plants is the Venus flytrap (*Dionaea muscipula*) (Figure 1D), where a geometrical change of its snap-trap lobes from concave (as seen from the outside) to convex enhances the snapping speed (Forterre et al. 2005). Such snap-buckling instabilities are widely used in biomimetic technical applications (Holmes & Crosby 2007; Lee et al. 2010; Hu & Burgueño 2015).

The plant itself cannot control externally actuated motions as they are driven by external power sources. Well-known examples from this group are the wind- or water-induced fluttering/streamlining movements of stems and leaves (Niklas 1999). The amount of mechanical force and the way it acts on the structure in combination with the structure's mechanical properties dictate the kind and duration of the respective movement. For example, there are very fast externally actuated motions, like the raindrop-powered oscillating lid of carnivorous pitcher plants (Bauer et al. 2015). Slow motions can be found, for example, in flowers with barrier structures, which mechanically interact with the respective pollinating animals (Córdoba & Cocucci 2011). The pollination mechanism of the bird-of paradise (Strelitzia reginae) comprises a torsional buckling-induced opening and closing of a petal

valve by the body weight of birds searching for nectar, which has been abstracted and transferred into a continuously adjustable biomimetic façade shading element (Flectofin, Lienhard et al. 2011) (Figure 2A).

Some plant movements comprise kinematic amplification mechanisms, where the actual motion is geometrically enhanced by curved-fold bending. This is, for example, known from the passive-hydraulically actuated opening and closing of ice plant (*Delosperma nakurense*) seed capsules (Harrington et al. 2011) and from the underwater snap-traps of the carnivorous waterwheel plant (*Aldrovanda vesiculosa*) (Figure 1E), which are actuated by active hydraulics and the release of prestress (Poppinga & Joyeux 2011; Westermeier et al. 2018). The curved-fold bending amplification of the *Aldrovanda* trap has been transferred into a kinetic façade shading element (Flectofold, Körner et al. 2017) (Figure 2B).

The above concisely summarized examples of plant movement actuation represent only a snapshot of the multitude of deformable systems that have evolved. A broader overview on this matter, highlighting the differences and similarities between plant-based and technical compliant mechanisms, is presented in Poppinga et al. (2016b). In the following, we highlight recent developments and breakthroughs and address persisting challenges in the field of plant movement biomimetics.

Current developments and breakthroughs

Implementation through additive manufacturing

4D printing of shape-shifting structures has become an emerging field (Gladman et al. 2016). To highlight the possible transfer of complex motions into 4D printed hygroscopic structures, we abstracted the modes of deformation of four exemplary plant movements and transferred them into technical demonstrators by Fused Filament Fabrication (FFF). These biomimetic

compliant mechanisms are passive-hydraulically driven, i.e. they adapt to environmental humidity, and are structurally based on actuating copolyester and resistance ABS plastic layers, following a methodology presented by Correa & Menges (2015) and Correa et al. (2015, 2020). The biological concept generators have been concisely introduced in the first paragraph: the lily flower with edge actuation (Figure 1A), the hygroscopic pinecone seed scale (Figure 1B), the aperture-like moss peristome (Figure 1C), the Venus flytrap snap-trap employing a snap-buckling instability (Figure 1D), and the snap-trap of the waterwheel plant with kinematic amplification (Figure 1E).

All hygroscopic structures were printed under dry and warm conditions (21°C, 18% RH) and undergo deformation when submerged in water (approx. 19°C). The edge growth-driven lily structure (Figure 3A, supplementary movie 1) consists of three artificial "petals", each possessing an actuating edge connected to a resistive middle part, based on the kinetic model by Schleicher et al. (2015). Hence, the edges are subject to water-induced swelling. Similar to the natural lily, the developing stresses during swelling drive the "blooming" of the demonstrator. The pinecone seed scale structure (Figure 1B, supplementary movie 2) is a large version of several prints already realized by Correa et al. (2020). It consists of an actuating lower layer and a resistive upper layer. The ca. 20 cm long demonstrator is fully capable of the reversible and repeatable bending deformation as seen in many pinecone seed scales, driven by the hygroscopic behavior of its functional bilayer architecture. The aperture structure (Figure 3C, supplementary movie 3) is a modular architecture composed of several flap-like structures, which are driven individually by passive hydraulics. In contrast to the biological concept generator, the "teeth" do not show complex multi-phase motion but gradually bend instead. Similar structures have already been implemented as architectural solutions (Correa & Menges 2017). A rapid curvature inversion can be seen in the flat, ringlike flytrap structure (Figure 3D, supplementary movie 4), taking place within a relatively

short timescale of a few minutes as compared to the overall motion duration (226 min). The kinematic amplification mechanism enabled by curved folds is present in the waterwheel structure (Figure 3E, supplementary movie 5). The curved fold is achieved by a change in stiffness between the actuator, composed of a wood polymer composite bilayer, and the lateral flaps printed with an oriented thermoplastic polyurethane (TPU) layer. Here, the 4D printed trap-like structure does not close, but smoothly opens during the wetting process.

As can be seen, the resulting 4D prints achieve similar modes of deformation as their biological counterparts, although in several examples the mode of actuation is different. Our biomimetic approach demonstrates that also complex origami-like folding, bending and buckling motions can be successfully transferred into technical systems via 4D printing. With the help of such diverse and on-demand printable deformation types, we believe that the establishment of a motion design catalogue for designing tailored compliant mechanisms will be possible. TOL.

Tracking movements (

Many plants are capable of tracking the sun with their flowers and/or leaves, as e.g. the sunflower (Helianthus annuus) (Atamian et al. 2016). Such tropistic movement behavior, which is dictated by the direction of the triggering stimulus (here: light), is based on adaptive asymmetric growth processes (reviewed by Harmer & Brook 2017). This is in contrast to nastic behavior, where the movement is structurally predetermined. Until recently, no synthetic material (or materials system) was intrinsically capable of detecting and tracking the direction of a stimulus. In a recent breakthrough article, Qian et al. (2019) developed the biomimetic omnidirectional tracker (SunBOT). Based on nanostructured stimuli-responsive polymers, SunBOT can aim and align to the incident light direction in 3D, which is rendered possible by a feedback loop rooted in the photothermal and mechanical properties of the

polymers. The versatility of technical biomimetic actuators could greatly benefit from the implementation of such tropistic behavior (see e.g. Mazzolai 2018). For example, smart architectural building skins incorporating both nastic and tropistic responses could act as adaptive and autonomous shading devices and humidity/venting controllers (Poppinga et al. 2018).

Structures that can perform multiple movement steps

Nastic plant motion typically comprises one movement step, which is fully executed upon triggering and actuation, like the opening of seed capsules. With only few exceptions (e.g., Stoychev et al. 2016), biomimetic motile structures consequently often also show only one movement step. However, some motile nastic plant structures pass through several phases of motion, but our knowledge on how these individual steps are connected and/or triggered is scarce. The steps could, for example, be characterized by different motion step durations, actuation principles, and divergent spatial deformation. For example, some hygroscopic moss peristome teeth are capable of slow bending as well as fast spore flicking motions (Gallenmüller et al. 2018). The fruit of the dynamite tree (*Hura crepitans*) shows slow desiccation-induced shrinkage and carpel deformation, which ultimately leads to explosive fruit dehiscence (Swaine & Beer 1977). In some cases, the discrimination of the different movement steps is difficult, as they altogether underlie one global complex movement process. This is for example the case in the Venus flytrap (D. muscipula), whose traps snap shut with a combination of active-hydraulically actuated trap lobe bending and passive snapthrough lobe curvature changes (Forterre et al. 2005). Recently, the complex two-phasic passive-hydraulic motion of the Bhutan pine (*Pinus wallichiana*) seed scale has been described (Correa et al. 2020). Upon drying, the initially wet scale first changes its transverse curvature and flattens. Upon further drying, the longitudinal curvature of the scale changes

and the scale bends. This biaxial, spatially complex movement pattern has been transferred into a 4D printed scale with a functional bilayer architecture, consisting of defined actuating (copolymers with embedded cellulose fibrils) and resistance layers (ABS polymer) (Figure 2C).

Understanding the biomechanical and functional-morphological properties of plant structures capable of the above-described multi-phasic motions and abstracting the principles behind the phenomena would allow for developing biomimetic structures with numerous tailored responses. The individual motions could either be structurally programmed into the biomimetic device for a sequential execution, e.g. along a humidity gradient, or for being "triggered" by achieving certain thresholds, e.g. in temperature or light. By this, multi-responsive motile structures, which could react in a variety of ways to several environmental factors as a single structure, would be possible.

Persisting challenges

Speed-boosting hydraulically actuated structures

Achieving reasonable motion durations is challenging for large biomimetic hydraulic structures due to the timescale of the required water displacement. This poroelastic timescale paradigm has so far been addressed by developing (super-)porous actuator hydrogels with faster response times (Bajpai et al. 2005; Ozmen & Okay 2005; Qiang et al. 2014) or by employing elastic instabilities as speed boosts (Holmes & Crosby 2007; Lee et al. 2010; Hu & Burgueño 2015; Stoychev et al. 2016). However, these measures are often accompanied by disadvantages like a reduction in mechanical strength of the structures or safety / controllability issues (especially regarding elastic instabilities). A possible solution was presented by Poppinga et al. (2018), where the development of a network of rigidly

connected, individually actuating units with fast individual response times was proposed. This network, if bathed in the triggering medium, would theoretically possess a fast overall response time. However, the difficulties and problems in developing such complex meta-architectures have not been addressed yet and, therefore, constitute exciting topics for future research.

In this context, it is important to note that the active transport of water in plants is also not yet (fully) understood. A well-known physiological process incorporating the "pumping" of water is guttation, i.e. the exudation of water droplets from uninjured leaves (Singh 2016).

However, this process is (most presumably) under tight physiological control and difficult to investigate. Active water displacement could probably be investigated very efficiently in the carnivorous genus *Utricularia*, which possesses submersed suction traps. Suction is based on the development of sub-ambient, trap-internal pressure (reviewed by Poppinga et al. 2016a), which is achieved by the energy-consuming pumping of water out of the elastically deformable trap body (Sasago & Sibaoka 1985a,b; Adamec 2011). After prey capture, the traps are ready to catch again within about 15 min once a sufficient sub-ambient pressure has been re-installed. The effective and continuous nature of the water pumping and the sheer number of traps per plant (often beyond the hundreds) could probably make *Utricularia* a very valuable model organism for studying the mechanisms involved in the water pumping. The active water transport is likely to be an effective and energetically optimized process with very high biomimetic potential in the context of the above-mentioned hydraulic actuators.

Functional resilience and robustness

The finding that millions-of-years old, fossilized conifer seed scales can still move (Poppinga et al. 2017) highlights their extraordinary functional resilience and robustness beyond any biological "purpose". Many materials (and materials systems) used for the construction of

technical biomimetic actuators are, however, prone to wear. For example, the repeated motion cycles are mechanically challenging and delamination may occur (see e.g. Correa et al. 2020). Functional fatigue has been observed as a result of repeated actuation through repeated mechanical or thermal loading (Lee et al. 2017), while the non-linear stress-strain behavior of plant fibers can be difficult to account for (Shah 2016). For wooden actuators, deterioration can occur due to UV decay, if left unprotected, or fungi may infest the structures in high humid applications (Reichert et al. 2015). These technical challenges are particularly important in the field of responsive architecture, where the structures should also be weatherresistant. This could be achieved by protecting the materials involved in actuation and movement by a flexible skin made of non-swellable material. By this, also the wear could be reduced. The toughness of the actuating material, for example hydrogels, could be enhanced by designing a fiber-based architecture, thereby also dictating an anisotropic swelling behavior and boosting actuation strength. To avoid delamination of tissues due to stresses and strains at the materials' interface, a strong adhesion by covalently linking the layers could be a solution. Recent approaches have already dealt, for example, with biologically functionalized, robust polymeric soft materials / silk protein actuators (Gil et al. 2010) and maleic anhydride polypropylene / plant fibers materials systems (Le Duigou et al. 2017).

Conclusion

Plants can help us to better understand how various types of actuation and modes of deformation can generate a multitude of tailored, hinge-free motions and motion sequences. By investigations of the combinations of plant deformation mechanisms and correspondingly weighted combinations of various actuation principles, a theoretical motion design framework can be established in the future. Depicting various shape-shifting methodologies within this framework would lead to a better understanding of the actuation controllability, functional

robustness and resilience to distortions, reversibility, energy efficacy, structural simplicity and (from an architectural point of view) aesthetics (Speck & Speck 2019). The possibility of a given mechanism to be scaled in size and/or to be distorted in shape could be further investigated by exploring the variety of structural "options" of a given mechanical motion principle (i.e., bauplan alterations), for example the structural variability (and, at the same time, functional consistency) of a certain motile plant structure (Schleicher et al. 2015). Such an approach could lead to a very powerful motion design "catalogue", where all mechanisms for motion actuation and control, the modes of deformation and involved energetics could be at hand. We are convinced that future in-depth investigations on the functional morphology and biomechanics of various motile systems from the plant kingdom will lead to exciting discoveries and cross-disciplinary biomimetic developments.

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Authors' contributions

All authors contributed to conception and design, analysis and interpretation of data, drafting and revising the article. SP developed the biomimetic concepts and analysis. DC and AM developed the responsive 4D printing concept. DC designed the 4DP bilayer structure, calculated the desired shapes and print paths, generated G-Code for printing, printed and prepared all samples. DC provided photographic images and time lapses of 4DP samples. SP provided photographic images of biological concept generators and wrote the first draft of the manuscript.

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Conflict of interest statement

The authors declare no conflicts of interest.

References

Adamec L. 2011. Functional characteristics of traps of aquatic carnivorous *Utricularia* species. Aquat Bot 95:226–33.

Atamian HS, Creux NM, Brown EA, Garner AG, Blackman BK, Harmer SL. 2016. Circadian regulation of sunflower heliotropism, floral orientation, and pollinator visits. Science 353:587-90.

Bajpai SK, Bajpai M, Sharma L. 2006. Investigation of water uptake behavior and mechanical properties of superporous hydrogels. J Macromol Sci A 43:507-24.

Bargardi FL, Le Ferrand H, Libanori R, Studart AR. 2016. Bio-inspired self-shaping ceramics. Nat Commun 7:13912.

Burgert I, Fratzl P. 2009. Actuation systems in plants as prototypes for bioinspired devices. Philos Trans A Math Phys Eng Sci 28:1541-57.

Córdoba SA, Cocucci AA. 2011. Flower power: its association with bee power and floral functional morphology in papilionate legumes. Ann Bot 108:919–31.

Correa D, Menges A. 2015. 3D printed hygroscopic programmable material systems. MRS Proc 1800:1016.

Correa D, Menges A. 2017. Fused filament fabrication for multi-kinematic-state climateresponsive aperture. In: Menges A, Sheil B, Glynn R, Skavara, editors. Fabricate 2017. London: UCL Press.

Correa D, Papadopoulou A, Guberan C, Jhaveri N, Reichert S, Menges A, Tibbits S. 2015. 3Dprinted wood. Programming hygroscopic material transformations. 3D Print Addit Manuf 2:106–16.

Correa D, Poppinga S, Mylo MD, Westermeier AS, Bruchmann B, Menges A, Speck T. 2020. 4D pine scale: biomimetic 4D printed autonomous scale and flap structures capable of multiphase movement. Phil Trans R Soc A 378:20190445.

Deegan RD. 2012. Finessing the fracture energy barrier in ballistic seed dispersal Proc Natl Acad Sci 109:5166–9.

Dumais J, Forterre Y. 2012. "Vegetable dynamicks": the role of water in plant movements. Ann Rev Fluid Mech 44:453–78.

Elbaum R. 2018. Structural principles in the design of hygroscopically moving plant cells. In: Geitmann A, Gril J, editors. Plant Biomechanics. Cham: Springer.

Elbaum R, Abraham Y. 2014. Microstructures of hygroscopic movement devices in plant seed dispersal. Plant Sci 223:124–33.

Erb RM, Sander JS, Grisch R, Studart AR. 2013. Self-shaping composites with programmable bioinspired microstructures. Nat Commun 4:1712.

Forterre Y. 2013. Slow, fast and furious: understanding the physics of plant movements. J Exp Bot 64:4745–60.

Forterre Y, Skotheim JM, Dumais J, Mahadevan L. 2005. How the Venus flytrap snaps. Nature 433:421–5.

Gallenmüller F, Langer M, Poppinga S, Kassemeyer H-H, Speck T. 2018. Spore liberation in mosses revisited. AoB PLANTS 10:plx075.

Gil ES, Park S-H, Tien LW, Trimmer B, Hudson SM, Kaplan DL. 2010. Mechanically robust, rapidly actuating, and biologically functionalized macroporous poly(N-isopropylacrylamide)/silk hybrid hydrogels. Langmuir 26:15614-24.

Gladman AS, Matsumoto EA, Nuzzo RG, Mahadevan L. 2016. Biomimetic 4D printing. Nat Mater 15:413–8.

Harmer SL, Brooks CJ. 2017. Growth-mediated plant movements: hidden in plain sight. Curr Opin Plant Biol 41:89–94.

Harrington MJ, Razghandi K, Ditsch F, Guiducci L, Rüggeberg M, Dunlop JWC, Fratzl P, Neinhuis C, Burgert I. 2011. Origami-like unfolding of hydro-actuated ice plant seed capsules. Nat Commun 2:1–7.

Hawkes EW, Blumenschein LH, Greer JD, Okamura AM. 2017. A soft robot that navigates its environment through growth. Sci Robot 2:eaan3028.

Hill BS, Findlay GP. 1981. The power of movement in plants: the role of osmotic machines. Q Rev Biophys 14:173–222.

Holmes DP, Crosby AJ. 2007. Snapping surfaces. Adv Mater 19:3589–93.

Hu N, Burgueño R. 2015. Buckling-induced smart applications: recent advances and trends. Smart Mater Struct 24:063001.

Ionov L. 2014. Hydrogel-based actuators: possibilities and limitations. Mater Today 17:494–503.

Körner A, Born L, Mader A, Sachse R, Saffarian S, Westermeier AS, Poppinga S, Bischoff M, Gresser GT, Milwich M, Speck T, Knippers J. 2018. Flectofold - A biomimetic compliant shading device for complex free form facades. Smart Mater Struct 27:017001.

Le Duigou A, Requile S, Beaugrand J, Scarpa F, Castro M. 2017. Natural fibres actuators for smart bio-inspired hygromorph biocomposites. Smart Mater Struct 26:125009.

Lee AY, An J, Chua CK. 2017. Two-way 4D printing: a review on the reversibility of 3D-printed shape memory materials. Engineering 3:663–74.

Lee H, Xia C, Fang NX. 2010. First jump of microgel: actuation speed enhancement by elastic instability. Soft Matter 6:4342–5.

Liang H, Mahadevan L. 2011. Growth, geometry, and mechanics of a blooming lily. Proc Natl Acad Sci 108:5516–21.

Lienhard J, Schleicher S, Poppinga S, Masselter T, Milwich M, Speck T, Knippers J. 2011. Flectofin: a hinge-less flapping mechanism inspired by nature. Bioinsp Biomim 6:045001.

Li S, Wang KW. 2017. Plant-inspired adaptive structures and materials for morphing and actuation: a review. Bioinspir Biomim 12:011001.

Mazzolai B. 2018. Growth and tropism. In: Prescott TJ, Lepora N, Verschure PFMJ, editors. Living machines: A handbook of research in biomimetics and biohybrid systems. Oxford University Press Scholarship Online.

Nahar D, Yanik PM, Walker ID. 2017. Robot tendrils: long, thin continuum robots for inspection in space operations. In: IEEE Aerospace Conference 2017, Big Sky, MT, p. 1–8.

Niklas KJ. 1999. A mechanical perspective on foliage leaf form and function. New Phytol 143:19–31.

Skotheim JM, Mahadevan L. 2005. Physical limits and design principles for plant and fungal movements. Science 308:1308–10.

Ozmen MM, Okay O. 2005. Superfast responsive ionic hydrogels with controllable pore size. Polymer 46:8119–27.

Poppinga S, Joyeux M. 2011. Different mechanics of snap-trapping in the two closely related carnivorous plants *Dionaea muscipula* and *Aldrovanda vesiculosa*. Phys Rev E 84:041928.

Poppinga S, Masselter T, Speck T. 2013. Faster than their prey: new insights into the rapid movements of active carnivorous plants traps. Bioessays 35:649–57.

Poppinga S, Zollfrank C, Prucker O, Rühe J, Menges A, Cheng T, Speck T. 2018. Toward a new generation of smart biomimetic actuators for architecture. Adv Mater 30:1703653.

Poppinga S, Weißkopf C, Westermeier AS, Masselter T, Speck T. 2016a. Fastest predators in the plant kingdom: functional morphology and biomechanics of suction traps found in the largest genus of carnivorous plants. AoB PLANTS 8:plv140.

Poppinga S, Nestle N, Šandor A, Reible B, Masselter T, Bruchmann B, Speck T. 2017. Hygroscopic motions of fossil conifer cones. Sci Rep 7:40302.

Poppinga S, Körner A, Sachse R, Born L, Westermeier AS, Hesse L, Knippers J, Bischoff M, Gresser GT, Speck T. 2016b. Compliant mechanisms in plants and architecture. In: Knippers J, Speck T, Nickel K, editors. Biomimetic research for architecture and building construction: biological design and integrative structures. Biologically-inspired systems. Heidelberg, Berlin: Springer. p. 169–93.

Qian X, Zhao Y, Alsaid Y, Wang X, Hua M, Galy T, Gopalakrishna H, Yang Y, Cui J, Liu N, Marszewski M, Pilon L, Jiang H, He X. 2019. Artificial phototropism for omnidirectional tracking and harvesting of light. Nat Nanotechnol 14:1048–55.

Qiang Z, Dunlop JWC, Qiu X, Huang F, Zhang Z, Heyda J, Dzubiella J, Antonietti M, Yuan J. 2014. An instant multi-responsive porous polymer actuator driven by solvent molecule sorption. Nat Commun 5:4293.

Sadeghi A, Mondini A, Mazzolai B. 2017. Toward self-growing soft robots inspired by plant roots and based on additive manufacturing technologies. Soft Robotics 4:211–24.

Sasago A, Sibaoka T. 1985a. Water extrusion in the trap bladders of *Utricularia vulgaris*. I. A possible pathway of water across the bladder wall. Botanical Magazine Tokyo 98:55–66.

Sasago A, Sibaoka T. 1985b. Water extrusion in the trap bladders of *Utricularia vulgaris*. II. A possible mechanism of water outflow. Botanical Magazine Tokyo 98:113–124.

Schleicher S, Lienhard J, Poppinga S, Speck T, Knippers J. 2015. A methodology for transferring principles of plant movements to elastic systems in architecture. Comput Aided Des 60:105–17.

Shah DU. 2016. Damage in biocomposites: stiffness evolution of aligned plant fibre composites during monotonic and cyclic fatigue loading. Compos Part A: Appl S 83:160–68.

Singh S. 2016. Guttation: mechanism, momentum and modulation. Bot Rev 82:149–82.

Speck T, Speck O. 2019. Emergence in biomimetic materials systems. In: Wegner LH, Lüttge U, editors. Emergence and modularity in life sciences. Switzerland, Springer Nature, p. 97–115.

Stoychev G, Guiducci L, Turcaud S, Dunlop JWC, Ioniv L. 2016. Hole-programmed superfast multistep folding of hydrogel bilayers. Adv Funct Mater 26:7733–9.

Swaine MD, Beer T. 1977. Explosive seed dispersal in *Hura crepitans* L. (Euphorbiaceae). New Phytol 78:695–708.

Weintraub M. 1952. Leaf movements in *Mimosa pudica* L. New Phytol 50:357–382

Westermeier A, Sachse R, Poppinga S, Vögele P, Adamec L, Speck T, Bischoff M. 2018. How the carnivorous waterwheel plant (*Aldrovanda vesiculosa*) snaps. Proc Roy Soc B 285:20180012.

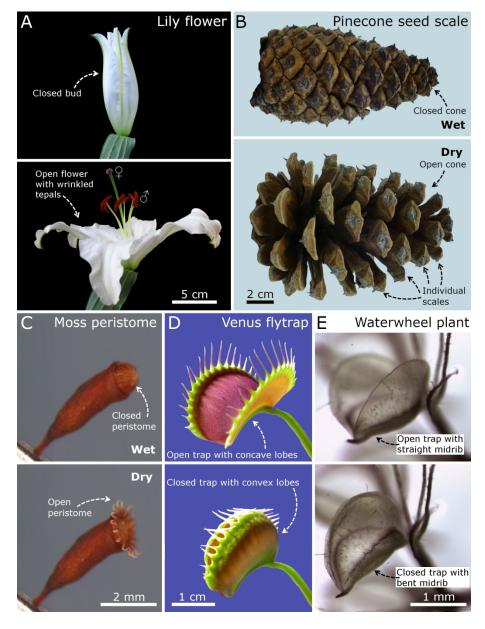
Figure legends

Fig. 1 Plant movements used as concept generators for the development of the 4D printed compliant mechanisms presented in this paper. A) The lily cultivar *Lilium* 'Casa Blanca' shows growth-based edge actuation of its petals, leading to flower opening and wrinkling of the petal edges. The male and female flower parts are indicated. B) The opening and closing of a pinecone, which consists of numerous seed scales arranged around a central cone axis, is based on differential swelling processes of the dead scale tissues, causing bending deformation. C) The hygroscopic peristome teeth situated at the opening of a moss capsule act as a modular aperture, allowing the spore release under favorable (and their retaining under unfavorable) environmental conditions. The image shows a spore capsule of Brachythecium populeum and is modified after Gallenmüller et al. (2018). D) The touchsensitive snap-trap of the Venus flytrap (*Dionaea muscipula*) rapidly catches incautious arthropod prey. The snapping speed is enhanced by snap-buckling comprising trap lobe curvature inversions from concave to convex (as seen from the outside of the trap). E) The underwater snap-trap of the Waterwheel plant (Aldrovanda vesiculosa) is also touch-sensitive. Triggering the trap entails bending deformation of the midrib and, simultaneously, trap closure due to the kinematically coupled trap lobes.

Fig. 2 Examples of motile biomimetic structures inspired by plant movements. **A)** The façade shading element Flectofin consists of two fins and a backbone. When the backbone is bend, the flaps move sideways due to torsional buckling. This system is based on the valvular pollination mechanism of the bird-of-paradise flower (*Strelitzia reginae*). Photo by Boris Miklautsch, workshop for photography, University of Stuttgart, with kind permission. **B)** The façade shading element Flectofold also consists of two fins and a backbone. Here, bending deformation of the backbone entails flapping of the fins due to kinematic coupling along

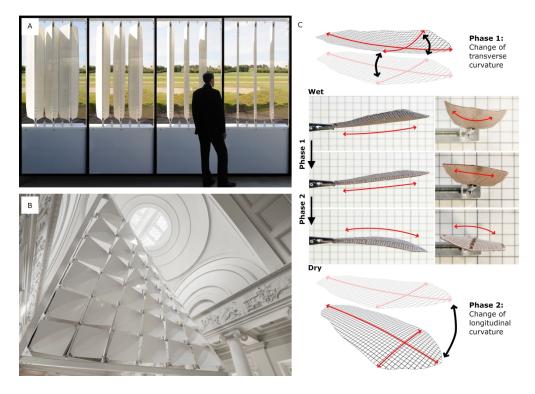
curved folds. The picture shows a Flectofold installation at the natural history museum Stuttgart, Rosenstein castle. Image © by ITKE Stuttgart, with kind permission. **C)** Inspired by the Buthan pine (*Pinus wallichiana*) seed scale, a 4D-printed artificial scale performs a biaxial two-phasic movement upon drying. In phase 1, the scale changes its transverse curvature, and in phase 2 the longitudinal curvature changes (the scale bends lengthwise). Image modified after Correa et al. (2020).

Fig. 3 4D printed, passive-hydraulically driven biomimetic compliant mechanisms. The respective biological concept generators are presented in Figure 1. Each structure was printed under dry and warm conditions (21°C, 18% RH). In the left images, the prints are initially submerged and start to absorb moisture until they are completely wetted in the rightmost images. A) Edge actuation-induced bending deformation in the lily structure. B) A large pinecone seed scale structure showing bi-directional bending deformation. C) Hygroscopic modular aperture structure based on several individually actuated sub-structures. D) Snapthrough of a flat, ring-like flytrap structure. The inlets are enlarged sections of the respective sub-images, showing the curvature inversion between t=117 min and t=121 min. E) The opening of an artificial waterwheel structure incorporates a kinematic amplification by curved fold bending.



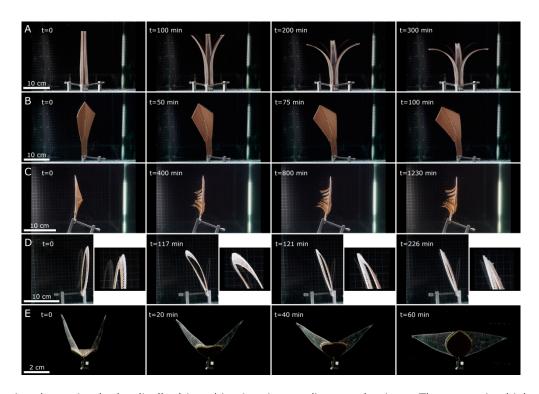
Plant movements used as concept generators for the development of the 4D printed compliant mechanisms presented in this paper. A) The lily cultivar *Lilium* 'Casa Blanca' shows growth-based edge actuation of its petals, leading to flower opening and wrinkling of the petal edges. The male and female flower parts are indicated. B) The opening and closing of a pinecone, which consists of numerous seed scales arranged around a central cone axis, is based on differential swelling processes of the dead scale tissues, causing bending deformation. C) The hygroscopic peristome teeth situated at the opening of a moss capsule act as a modular aperture, allowing the spore release under favorable (and their retaining under unfavorable) environmental conditions. The image shows a spore capsule of *Brachythecium populeum and is modified after Gallenmüller et al. (2018). D) The touch-sensitive snap-trap of the Venus flytrap (Dionaea muscipula) rapidly catches incautious arthropod prey. The snapping speed is enhanced by snap-buckling comprising trap lobe curvature inversions from concave to convex (as seen from the outside of the trap). E) The underwater snap-trap of the Waterwheel plant (Aldrovanda vesiculosa) is also touch-sensitive. Triggering the trap entails bending deformation of the midrib and, simultaneously, trap closure due to the kinematically coupled trap lobes.*

179x237mm (293 x 293 DPI)



Examples of motile biomimetic structures inspired by plant movements. A) The façade shading element Flectofin consists of two fins and a backbone. When the backbone is bend, the flaps move sideways due to torsional buckling. This system is based on the valvular pollination mechanism of the bird-of-paradise flower (Strelitzia reginae). Photo by Boris Miklautsch, workshop for photography, University of Stuttgart, with kind permission. B) The façade shading element Flectofold also consists of two fins and a backbone. Here, bending deformation of the backbone entails flapping of the fins due to kinematic coupling along curved folds. The picture shows a Flectofold installation at the natural history museum Stuttgart, Rosenstein castle. Image © by ITKE Stuttgart, with kind permission. C) Inspired by the Buthan pine (Pinus wallichiana) seed scale, a 4D-printed artificial scale performs a biaxial two-phasic movement upon drying. In phase 1, the scale changes its transverse curvature, and in phase 2 the longitudinal curvature changes (the scale bends lengthwise). Image modified after Correa et al. (2020).

180x129mm (611 x 611 DPI)



4D printed, passive-hydraulically driven biomimetic compliant mechanisms. The respective biological concept generators are presented in Figure 1. Each structure was printed under dry and warm conditions (21°C, 18% RH). In the left images, the prints are initially submerged and start to absorb moisture until they are completely wetted in the rightmost images. A) Edge actuation-induced bending deformation in the lily structure. B) A large pinecone seed scale structure showing bi-directional bending deformation. C) Hygroscopic modular aperture structure based on several individually actuated sub-structures. D) Snapthrough of a flat, ring-like flytrap structure. The inlets are enlarged sections of the respective sub-images, showing the curvature inversion between t=117 min and t=121 min. E) The opening of an artificial waterwheel structure incorporates a kinematic amplification by curved fold bending.

179x127mm (706 x 706 DPI)