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REGULAR PAPER

A three-dimensional study of sub-foliar condensation in desert rhubarb (*Rheum palaestinum*, Polygonaceae)

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Background and aim – Desert rhubarb (*Rheum palaestinum* Feinbr.), a rare perennial plant endemic to Jordan and southern Israel, grows in areas with very low annual rainfall. It produces large leaves, atypical for a desert plant, that are tightly attached to the ground. The leaves have a unique morphology thought to be involved in water catchment and drainage systems along the central stem. The objective of this study was to simulate the leaf morphology of the rhubarb and investigate its function as a 'condensation trap'.
Methods – A field study was conducted on seven plants growing in one location in the desert of Jordan. Three-dimensional modelling software was used to identify the foliar architecture and the vapour-trapping and drainage system employed by the plant.
Results – The complex leaf morphology protects against excessive transpiration by self-shading, significantly increasing the surface area to maximise condensation mostly on the lower surface of the leaf, and to a lesser degree on the upper surface.
Conclusions – While previous scientific research has pointed to this plant's ability to irrigate itself, it has to a large extent been misunderstood how this self-irrigation system works. The rhubarb leaf must have evolved not as water catchment and drainage system but as a 'trap' for sub-foliage moisture. This method of self-irrigation by sub-foliar condensation has not been previously recognized in plants.

Key words – Desert rhubarb, 3D modelling, self-irrigation, sub-foliar condensation, moisture trap.

INTRODUCTION

The rare perennial plant species *Rheum palaestinum* Feinbr. (Polygonaceae), commonly known as desert rhubarb, is endemic to Jordan and southern Israel and grows in areas with low annual rainfall (Al-Eisawi 1998). It has an underground woody stem and grows mostly in shallow ravines of stony-sandy terrains during the winter and early spring in years with above-normal precipitation. It produces one to four rounded leaves, 20–60 cm in diameter, with a wrinkled surface (fig. 1).

The large leaf size of this species is atypical within arid ecosystems; in the presence of abundant sun, small leaf size is considered as one of the most common patterns of desert plants to decrease transpiration rates and increase water-use efficiency (Gibson 1996). The annual precipitation in Jordan's desert is less than 75 mm, and January is the wettest month (Tarawneh & Kadıoğlu 2002). A preliminary study of the relationship between precipitation patterns and leaf growth suggested complex and under-studied water-absorption strategies for plants growing in arid environments. Our personal observations showed some unique morphologies and timing patterns that perennial plants in the tableland desert of Jordan have developed as survival strategies. A previous study showed that the large size and surface morphology of rhubarb leaves help to create a self-irrigation system and increase rainwater harvesting by 16-fold compared to other desert plants (Lev-Yadun et al. 2008).

A simple leaf morphology can effectively drain rainwater without the need for wrinkles that dramatically increase leaf transpiration area, as has been shown for the lotus leaf (Barthlott & Neinhuis 1996). The leaf morphology of rhubarb may not play a crucial role in water collection, as rainfall is limited during its maximum growth period (March–April). Additionally, the leaves are tightly attached to the ground and the margins are bent downward to contact the soil; these morphological features favour the function of a vapour-trapping system under the leaf rather than water drainage on the upper surface.

Rainwater collection is related to the leaf horizontal catchment area and not to the surface area maximized by the wrinkles. Because the water absorption rate needs to be higher than the transpiration rate, rhubarb leaf wrinkles increase the leaf surface area relative to the leaf footprint and probably play a role in controlling leaf temperature that is directly connected to condensation.

The objective of this study was to simulate the leaf morphology of desert rhubarb using three-dimensional (3D) modelling software and to investigate its function as 'condensation trap'.

Figure 1 – *Rheum palaestinum* plant with two leaves (50 cm length). These large leaves represent a rare evolutionary trait, opposite to the reduced leaves of many desert plants.

MATERIAL AND METHODS

Study area and plant material

A field study was conducted northwest of Bayer in the eastern desert of Jordan (31°14′N 36°36′E; 840 m above sea level) during winter 2012 and spring 2013. Data were collected from seven desert rhubarb plants growing 4–10 m apart.

Foliar architecture

A typical leaf was drawn using SketchUp (Trimble, USA) 3D modelling software to calculate the increase in surface area as a result of leaf wrinkles and identify any functions other than light gathering or rainwater draining. Leaf wrinkles were represented as cones or pyramids, and the inclination angles were analysed to study water movement, particularly that of condensed droplets on the slopes of the lower surfaces. Computer 3D modelling was also used to identify the role of 'cooling' cones or pyramids that touch the ground and collect water from the condensation of soil vapour.

Leaf drainage

To study water drainage and the direction of the slope, half a litre of water was sprayed on five leaves of plants growing on different ground slopes. The water catchment areas and the direction of water flow within the surface 'valleys' were mapped. The amount of water that drained out of the leaves was measured at all drainage points below the midrib, towards the central stem or the leaf tip, and along the 'valleys' of the secondary veins of the entire leaf margin. The amount of water in the catchment areas was also measured to calculate the percentage of water that drained out from different points of the leaf margin, the midrib towards the central stem, and the amount that did not drain out. The horizontal footprint areas of the catchment subdivisions of each leaf were measured and compared to the amount of water in the catchment areas.

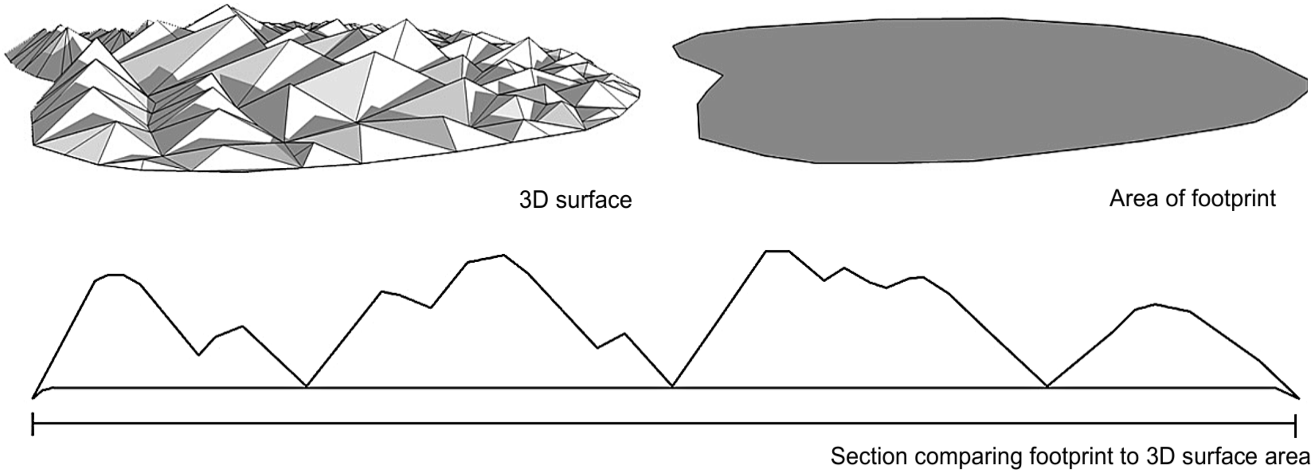

Figure 2 – *Rheum palaestinum* leaf wrinkles create a 3D surface area about double of the actual leaf footprint. Sub-foliar condensation remains the best candidate as an evolutionary driving force to explain this unique morphology.

Relationship between leaf morphology and the soil surface underneath the leaf

To study the relationship between the leaf morphology and the soil surface underneath the leaf, a small cavity in the ground (20 mm depth and 150 mm diameter) was dug under the leaf margin of four plants. The downward deformation of each leaf margin was measured for a period of three weeks during the full leaf-growth period.

Plant reactions to leaf inclination change

To identify plant reactions to changes in leaf inclination, stones (3–6 cm height) were placed underneath randomly selected leaves of two different plants. Parts of the leaves or even the entire leaves were elevated no more than 3 cm from the ground, which provided sufficient space to allow the wind to pass under the leaf and possibly to allow the leaf to readjust its morphology and close the gap. The leaves were observed for 30 d during March–April when they showed the maximum growth.

Effect of enhanced sealing between leaf and soil surface

Sand was placed around the leaves of two selected plants to further seal the space between the leaf and the soil surface. The general health of these plants was observed for 30 d, and the soil humidity underneath the leaves was measured and compared with that under leaves of plants that were not treated and others whose leaves were kept raised by twigs for the same period.

Study of self-shading

Pictures were taken at 1h-intervals from sunrise to sunset to study self-shading as a direct result of leaf surface morphology and to calculate the percentage of the leaf surface that was shaded.

Relationship between maximum rainfall and maximum leaf growth

Records of the Jordan Meteorological Department showed that precipitation during the past thirty years in the eastern desert was considerably inconsistent with regard to time and volume. Torrential rains that often occurred in November–February caused flash floods in the eastern desert to the northwest of Bayer (the main habitat of rhubarb), with often no precipitation recorded in March and April. To study the relationship between the monthly average rainfall and maximum leaf growth, the size of leaves from nine different plants was measured every 15 d, and the percentage of growth was calculated using the final maximum size.

RESULTS

Foliar architecture

Computer 3D modelling revealed that the leaf surface area was almost double the actual leaf footprint (fig. 2). The leaves had a unique morphology with wrinkles that resembled a mountainous area with deformed cones and pyramids. The wrinkles were found to function as a cooling system that condensed vapour from soil, especially during the evening

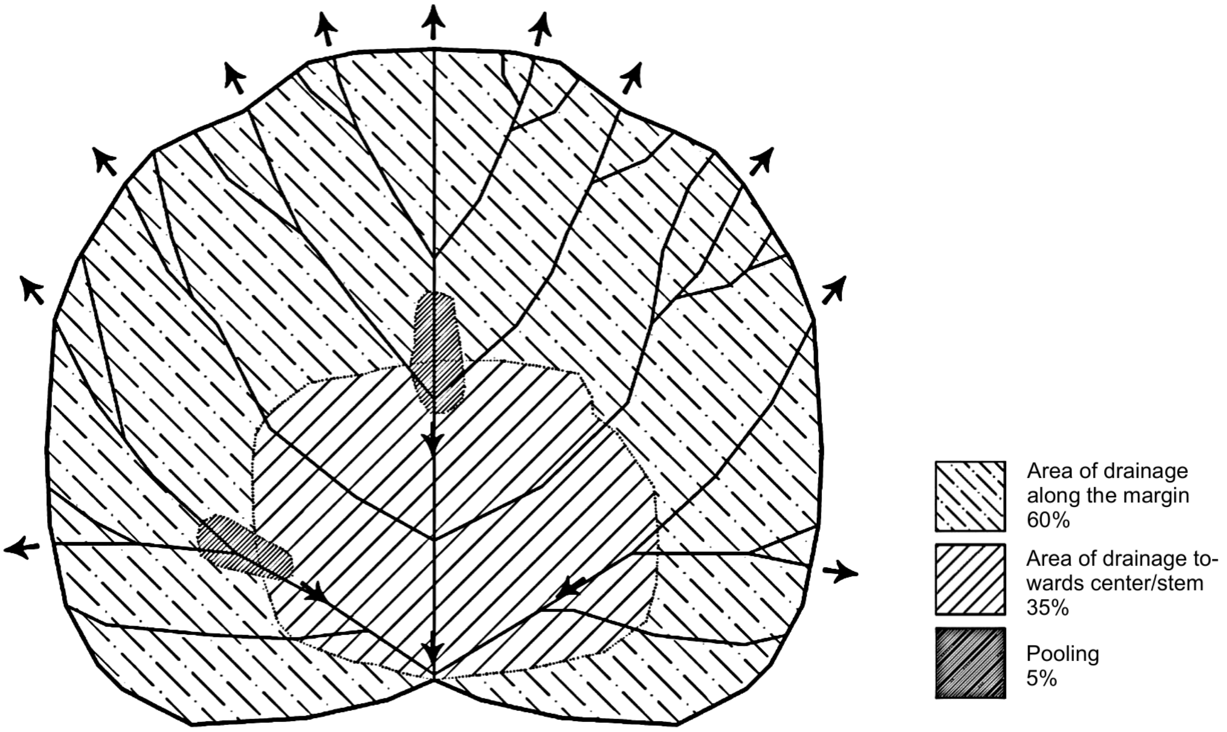

Figure 3 – If the *Rheum palaestinum* leaf acts as a rainwater catchment and drainage system, then why does only 35% of the water drain towards the main stem? A less wrinkled leaf will drain as well and save the plant any extra transpiration, which is least helpful in desert environment.

hours of a warm day when the soil temperature was higher than the air temperature.

Leaf drainage

Leaf morphology analysis showed that water drainage was inconsistent; it often occurred from different directions, whereas in one-leaf plants on a slight land inclination, 70% of drainage occurred away from the central stem. Catchment areas and watershed lines did not show any consistent drainage along the midrib and towards the central stem.

Overall, the average amount of water that drained out from different points of the leaf margin was 60%; 35% drained down the midrib towards the central stem, and 5% of the water did not drain out (fig. 3). These percentages were similar to the horizontal footprint areas of catchment subdivisions.

Relationship between leaf morphology and the soil surface underneath the leaf

Leaf margins remained tightly connected to the ground throughout the experimental period (fig. 4). The leaves showed a downward deformation of 12–16 mm that occurred either immediately or within the first 48 h to close the gap between the leaves and the cavities underneath.

Plant reactions to changes in leaf inclination

Leaf morphology was readjusted to close the gap between the leaf margin and the ground, resulting in drainage slopes away from the central stem. The readjustments occurred within the first 12 d after the placement of stones (fig. 5).

Effect of spacing between leaf and soil surface

Plants whose leaves were kept raised showed signs of dehydration and yellowing within 18 d of experimentation (fig. 6). Plants for which sand was placed around their leaves showed signs of better hydration and preserved their dark green colour for 14 d longer than the untreated plants (fig. 7). Soil humidity underneath the sand-covered leaves was noticeably higher, and the topsoil had a darker colour.

Study of self-shading

Analysis of the obtained photographs showed that self-shading ranged from 35% of the leaf surface at midday to 90% during the morning hours and before the sunset in March–

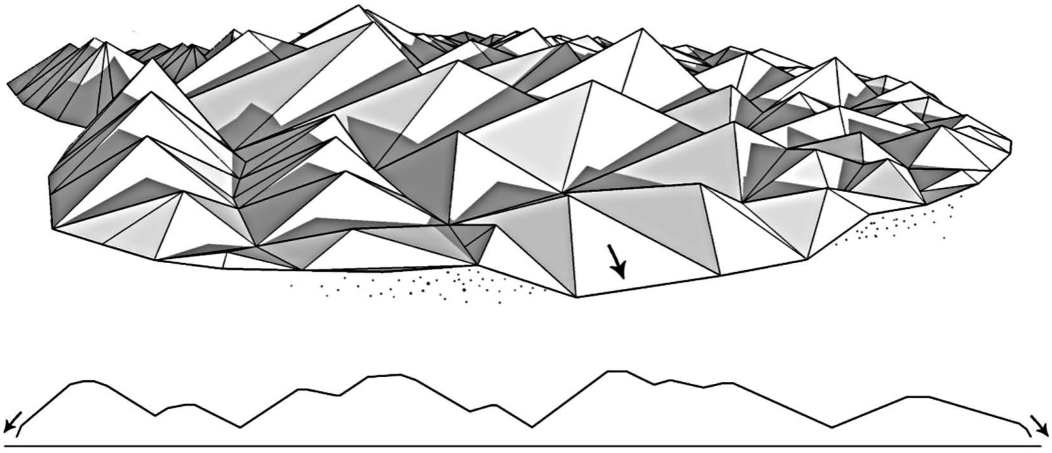

Figure 4 – A *Rheum palaestinum* leaf is tightly connected to the ground and does not allow desert wind to pass underneath. This highly articulated leaf-ground system or architecture has not been previously recognised as a survival strategy in plants.

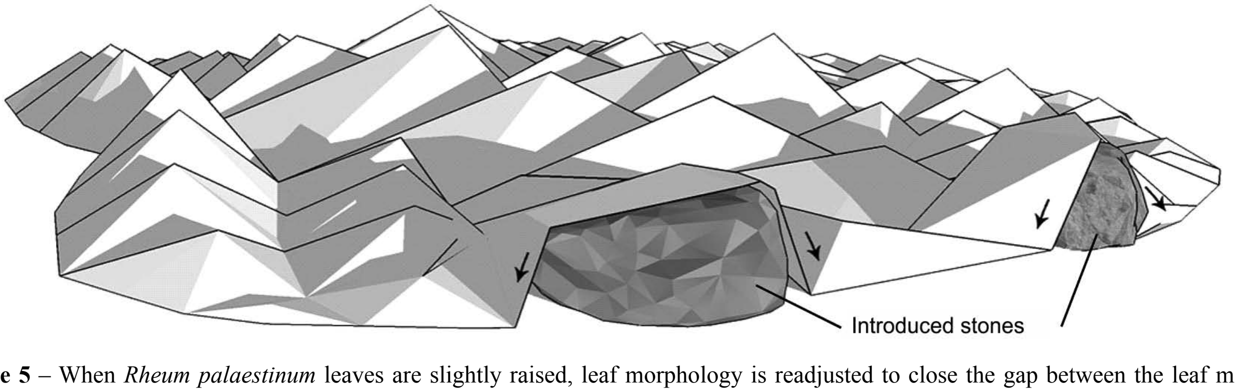

Figure 5 – When *Rheum palaestinum* leaves are slightly raised, leaf morphology is readjusted to close the gap between the leaf margin and the ground. The leaf keeps safeguarding the total vapour-trapping system, with the system's two main components: the purpose shaped geometry of the leaf, and vapour-providing ground.

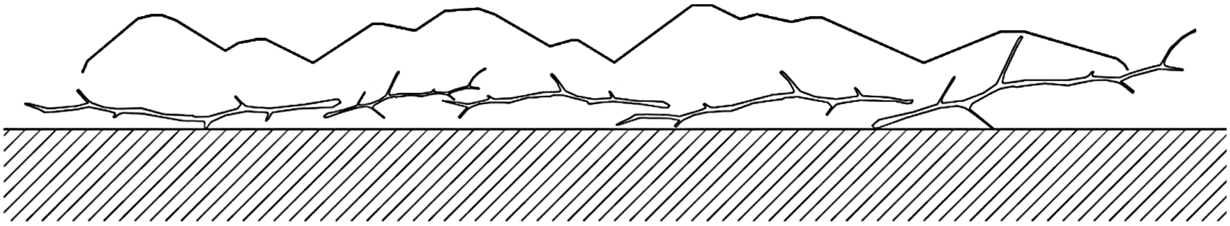

Figure 6 – When *Rheum palaestinum* leaves are completely raised, the plant is led to early dehydration and leaf yellowing; this shows that when the vapour-trapping mechanism is broken, the water balance is lost, even if inclination of leaf is better for any assumed rain drainage to central stem.

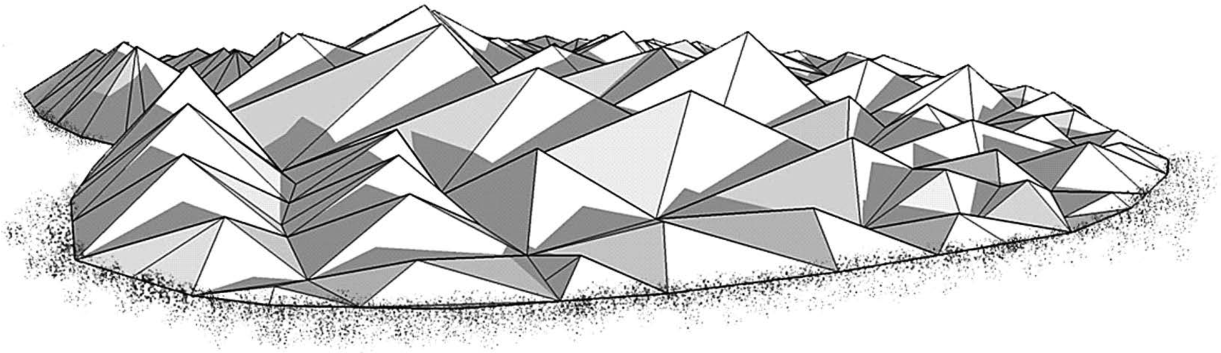

Figure 7 – When sand is placed along the margin of the leaf, the plant shows signs of better hydration. The tighter the marginal grip of the leaf to the ground the less vapour is escaping condensation.

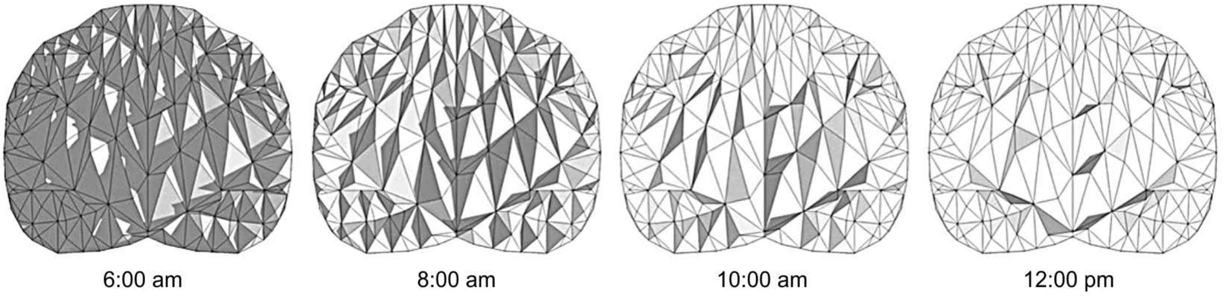

Figure 8 – Shadow analysis of 3D morphology at different times of the day. Leaf wrinkles clearly show a good function of self-shading, an additional secondary benefit to extend condensation hours into early morning and late afternoon.

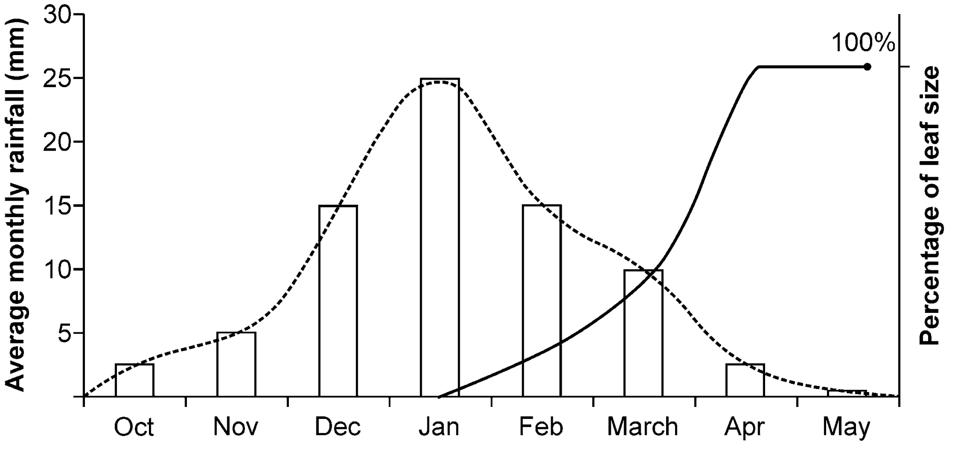

Figure 9 – Relationship between maximum rainfall and maximum leaf growth. The time of maximum leaf-size misses the maximum rainfall, and thus becomes a hydraulic liability if rain-drainage is given as the evolutionary cause of leaf size and geometry.

April, when the solar elevation angle was approximately 60° (fig. 8).

Relationship between maximum rainfall and maximum leaf growth

A time lag between maximum rainfall and maximum leaf size was observed. Full leaf growth occurred in March–April, which was three months later than the occurrence of maximum rainfall in December–January (fig. 9).

DISCUSSION

Desert rhubarb (*Rheum palaestinum*) produces large leaves, quite atypical for desert ecosystems that are tightly attached to the ground. The results showed that the complex leaf morphology that creates self-shading; protects against excessive transpiration, a feature that is highly advantageous within the desert environment; and significantly increases the surface area for condensation maximization. Rhubarb leaves function less as water catchment and drainage systems, and more as 'traps' of sub-foliage moisture, creating a self-irrigation system.

The self-irrigation system in rhubarb, provided by its large-sized leaves and leaf surface morphology, increases water absorption by 16-fold compared to other desert plants (Lev-Yadun et al. 2008). This study demonstrated that the desert rhubarb plant growing in an environment where rainfall is highly inconsistent, appears to have evolved a maximisation of both the footprint and surface area of leaves, even at the expense of transpiration rate, to attain consistent subfoliar condensation.

In arid environments, the amount of dew can exceed that of rainfall and dew may even serve as the only water source for plants (Agam & Berliner 2006). Leaf characteristics and surface structure or geometry have evolved to help plants absorb water from sources other than rain, such as the Namib desert grass *Stipagrostis sabulicola* (Pilg.) De Winter that absorbs fog water (Roth-Nebelsick et al. 2012). Many plants and animals in arid environments have developed purpose-shaped architecture, surfaces, and textures, often resulting in wrinkles with bumps and valleys, such as those of the desert beetle *Stenocara gracilipes* Solier (Guadarrama-Cetina et al. 2014).

The 3D geometry of the leaves points to another morphological adaptation related to the capture and absorption of water vapour. Characteristics such as the downward curving and ground-pressing leaf margins, and the strong leaf-ground attachment system, reveal a moisture capture system that prevents the evaporation of water harvested by sub-foliage condensation.

Desert plants with relatively large leaves have a leaf temperature lower than the air temperature (Smith 1978). Leaf wrinkles increase leaf area and maximize water uptake that occurs from the lower leaf face, while simultaneously decreasing the transpiration rate by providing self-shading. During the night, leaf wrinkles function as a cooling system that maximizes sub-foliage condensation and to a lesser amount collects dew above the leaf surface when sudden changes in weather occur. During the day, the wrinkles function as a self-shading system that protects the plant from high temperature differences, similar to other plant species grown in semi-arid environments (Valladares & Pugnaire 1999). Further studies focusing on the soil hydrology of stony terrains, where gravel mulch plays a key role in water retention and soil evaporation (Kaseke et al. 2012), may enable a better understanding of these unique characteristics of rhubarb.

High deserts (800–1000 m above sea level) are harsh environments, especially in January–February, when temperatures often decrease to below 0°C. Avoidance of frost probably plays a key role in the timing of foliage growth in many perennial plants, especially those with large leaves, grown in high-altitude arid and semi-arid environments (Jordan & Smith 1995).

Rhubarb normally grows from November to February immediately after torrential rains that saturate soils made deeper through eluviation. The leaves reach their maximum size in March–April, thereby avoiding January–February frost. This growth strategy enables this plant species to increase its water absorption by 16-fold (c. 400 mm) compared to other desert plants (c. 75 mm), possibly because of the self-irrigation system that is supported by the unique morphology of the leaves and their tight attachment to the ground. This self-irrigation system enables the plant to adapt in an environment where precipitation is greatly variable (Ghanem 1997) in terms of volume and time. Further studies of leaf structure may reveal characteristics of the lower epidermis and specific features of stomata that enable foliar water uptake (Limm et al. 2009).

While the results presented by Lev-Yadun et al. (2008) have successfully pointed to this plant's use of a unique self-irrigation system, their interpretation, on the other hand, appears to have missed the deeper and more complex secret of 'how' this system works. Their simplistic explanation remained above the leaf, while the plant's survival mechanism hides under the leaf, and in its firm pressing against the ground.

This type of leaf morphology appears to represent a recurrent general feature in the genus *Rheum*, possibly as a dormant, a stand-by 'plan-b', useful when climate borders shift into aridity. The population of desert rhubarb in Jordan may have evolved its unique morphological characteristics as a deviation from temperate genera that prevailed during the times of paleolakes of the Jordanian desert during the warmer and wetter Pleistocene periods, with as high precipitation as < 50–160 mm/y (Abed 2014). In other parts of the world, and under different habitat pressure and past geographical events, *Rheum* appears to use the same 3D leaf and ground system for self-irrigation. *Rheum tataricum* L.f. and other diversifications from the temperate genera can be found in the mountainous and desert regions of the Qinghai–Tibetan plateau (Wang et al. 2005, Sun et al. 2012). To assess whether rhubarbs evolved almost identical water-harvesting systems when faced by aridity and climatic harshness in different parts of the world, or is an ancestral feature that was present and adaptive in earlier common and continuous habitat during the Pleistocene and Miocene, is beyond the scope of the present study. However, the phylogenetic relationships of *Rheum* reported in Wang et al. (2005) and Sun et al. (2012) indicate that this morphology may be a plesiomorphic feature of the group that originated and evolved when *Rheum* started to diverge in the Miocene. The development to withstand arid conditions may be a more general feature of the genus *Rheum*, as other species (e.g. *Rheum tataricum*) seem to have exactly the same type of leaf morphology as seen in *Rheum palaestinum*.

For the future, other plants with large leaves that grow flat on the ground with a noticeable capping relationship with the soil, such as *Brunsvigia comptonii* W.F.Barker (Amaryllidaceae) or *Massonia depressa* Thunb. (Asparagaceae), and that grow in arid ecosystems with distinct seasonality and daily fluctuation of temperatures, may also be investigated to find out if they too have developed self-irrigation systems based on sub-foliar condensation. Furthermore, rhubarb creates a mini oasis and provides a water source for insects, small reptiles, rodents, and birds, especially in areas with no other vegetation cover. The self-irrigation system of rhubarb enables the exploration of new methods of cultivation and forestation of arid and semi-arid landscapes, using biomimicry approaches and possibly 'stimulated dependency' or 'stimulated symbiosis' methods. For instance, rhubarb could be used to support the germination and early growth of larger desert trees (such as *Pistacia atlantica* Desf. Anacardiaceae) in a completely biodegradable manner.

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