

RESEARCH PAPER

Micromorphology of the petals of the invasive weed, *Oxalis pes-caprae*

APOSTOLOS ARGIROPOULOS and SOPHIA RHIZOPOULOU*

Department of Botany, Faculty of Biology, National and Kapodistrian University of Athens, Athens, Greece

The alien, seedless *Oxalis pes-caprae* has spread and colonized many areas of the Mediterranean Basin, relying on vegetative reproduction. The flowering of *O. pes-caprae* is greatly accelerated by its exposure to sunlight. When the sun is shining, both sides of the petals of the funnel-shaped, open flowers of *O. pes-caprae* are exposed to the ambient conditions. In cloudy weather, only some portions of the abaxial petal surfaces of the trumpet-shaped, closed flowers of *O. pes-caprae* are exposed to the ambient conditions. The micromorphology of the petals of *O. pes-caprae* was imaged by using light, scanning and atomic force microscopy. In *O. pes-caprae*, conical cells are found only on the adaxial epidermis of the petals, which also consist of a narrow mesophyll with a loosely arranged parenchyma and convex cells on their abaxial epidermis. High-resolution imaging of the petal surfaces, using atomic force microscopy, revealed that the epidermal cells are further ornamented by submicron sculptures, indicating a different roughness, density, and arrangement of the folds between the adaxial and abaxial sides of the petals. Submicron sculpturing increases the surface area of the adaxial epidermal cells of the petals and the distances between the folds are almost equal to the visible waveband. On the abaxial epidermal cells, the distances between the folds are smaller than the subwavelength spectrum. The high and the negligible values of roughness that were obtained on the adaxial and the abaxial surfaces might facilitate the capture and the reflection of light, respectively.

Keywords: microsculpture, *Oxalis pes-caprae*, petal, surface, topology.

Oxalis pes-caprae L. (Bermuda buttercup), which is a native to the Cape region in South Africa (Aitken 2007; Oberlander 2009), was brought to Europe in 1757 (Lambdon 2009) and was introduced as an ornamental plant into Greece in 1787 (Sibthorp & Smith 1806). This species now has been widespread across the Mediterranean Basin and is a major weed in old fields, olive groves, disturbed areas, the well-drained, fertile soil of gardens, and grasslands (Petsikos *et al.* 2007; Arianoutsou *et al.*

2010; Verdaguer *et al.* 2010). *Oxalis pes-caprae* forms dense mats that prevent the growth of other species during the important for the Mediterranean habitats' early spring growth period (Damanakis & Markaki 1990; Petsikos *et al.* 2007; Vilà *et al.* 2008).

The introduced range of *O. pes-caprae* is seedless and reproduces asexually from underground bulbs (Lane 1984; Marshall 1987). *Oxalis pes-caprae* never has been known to bear fruit in the northern hemisphere (Galil 1968; Rottenberg & Parker 2004). The species blossoms during spring and a significant flowering mass is produced (Vilà *et al.* 2006; Castro *et al.* 2007; Verdaguer *et al.* 2010). The bright, yellow flowers of *O. pes-caprae* open only if the sun is shining and are visited by foraging bees, but their short-style morph implies illegitimate pollination only (Rottenberg & Parker 2004; Chapman 2007).

The epidermal cells of the flower petals constitute an important boundary between the mesophyll of the tissue and the external environment and usually they are

Communicated by T. Yoshioka.

*Correspondence to: Sophia Rhizopoulou, Department of Botany, Faculty of Biology, National and Kapodistrian University of Athens, Athens 15784, Greece.

Email: srhizop@biol.uoa.gr

The authors have no commercial interest in the findings that are presented.

Received 1 August 2010; accepted 19 January 2012

doi:10.1111/j.1445-6664.2012.00434.x

© 2012 The Authors

Weed Biology and Management © 2012 Weed Science Society of Japan

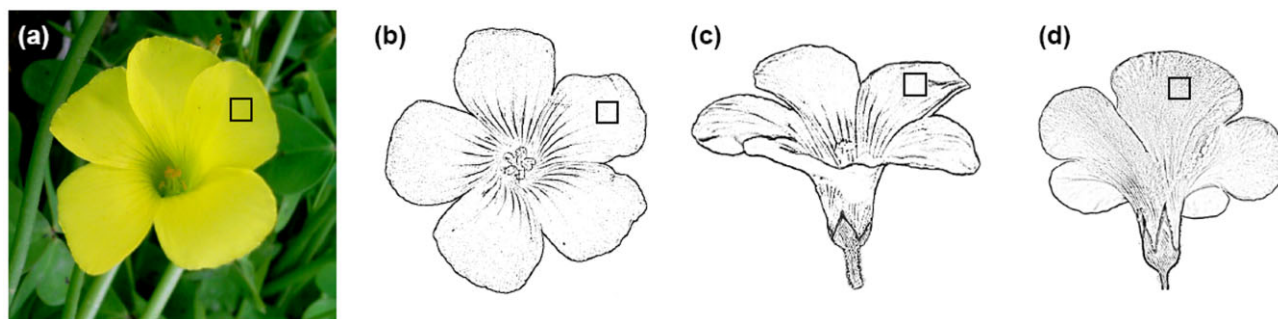


Fig. 1. (a) Solitary yellow flower of *Oxalis pes-caprae* and pencil sketches of (b) a funnel-shaped, open flower of *O. pes-caprae*, (c) the adaxial and (d) the abaxial petals' surfaces. The sampling region of the corolla, comprising five fully expanded petals of ~2 cm in length, is indicated by a square (© A. Argiropoulos).

covered by a multifunctional cuticle that has attracted the attention of several plant disciplines (Kay *et al.* 1981; van Doorn & van Meeteren 2003; Lee 2007; Li-Beisson *et al.* 2009). Also, the cuticle combines several aspects that are attributed to "smart" materials (Bargel *et al.* 2006; Kerstiens 2006; Bhushan 2009; Koch *et al.* 2009). Hence, the submicron patterns of petal surfaces have important applications to the rapidly growing and promising field of research for biomimetic materials (Fratzl 2007; Koch & Barthlott 2009); for example, humido- and thermo-responsive membranes were fabricated by mimicking the petals of the morning glory flower (Ma & Sun 2009).

In the present study, the micromorphology of the petal surfaces of *O. pes-caprae* is described, with the purpose of understanding the functional traits of the flowers of this asexual colonizer. In particular, the adaxial (inner) and the abaxial (outer) petal surfaces were examined with light microscopy, scanning electron microscopy, and atomic force microscopy (AFM), which according to the best of the authors' knowledge, has not been hitherto reported.

MATERIALS AND METHODS

The material was collected at the campus of the University of Athens in Greece (38°57.5'N, 23°48.0'E) during March 2009, coinciding with precipitation that exceeded 90 mm. The average monthly temperature is $14 \pm 2^\circ\text{C}$. Expanded petals were harvested from the flowers of *O. pes-caprae* L. (Oxalidaceae, Magnoliophyta), arranged in umbel-like inflorescences of densely colonized stands of the species. Also, the flowering of *O. pes-caprae* was observed on a regular basis every day during the blossoming period and the flowers exhibited a 5 day lifespan.

The anatomical study was carried out in the developed petal regions (Fig. 1a). Samples from the petal blade were cut carefully into square pieces (2 mm × 2 mm) and fixed in 3% glutaraldehyde in a Na phosphate buffer at a pH of 7, at room temperature, for 2 h. The plant material was washed three times by immersion in a buffer for 30 min each time. Then, it was postfixed in 1% OsO₄ in the same buffer at 4°C and dehydrated in acetone solution. The dehydrated tissues were embedded in SPURR resin (Serva, Heidelberg, Germany). Semithin sections of resin-embedded tissue (Ultratome III microtome; LKB Produkter, Bromma, Sweden) were stained in Toluidine Blue "0" in 1% borax solution, photographed, and digitally recorded with a light microscope (Zeiss Axioplan; Carl Zeiss, Thornwood, New York, USA) that was equipped with a video camera (Zeiss AxioCam MRc5). The dehydrated samples were dried at the critical point in a dryer (CPD-030; Bal-tec, Canonsburg, PA, USA), mounted with double adhesive tape on stubs, and sputter-coated with 20 nm of gold in a sputter-coater (SCP-050; Bal-tec). The adaxial (Fig. 1a,c) and the abaxial (Fig. 1d) epidermises of the petals were viewed with a scanning electron microscope (JSM 840; JEOL, Tokyo, Japan). The adaxial (3 μm × 3 μm) and the abaxial (0.5 μm × 0.5 μm) petal areas were imaged by using a tap mapping atomic force microscope (Multimode SPM; Veeco, Santa Barbara, CA, USA). Several parameters were analyzed and processed with the software package, Nanoscope III (Veeco), in order to detect detailed information about the surfaces of the petals. The quantitative measurements (means ± standard error) included the surface roughness, horizontal and vertical distances that represented the height of a step between the nanofolds, and the length between the markers, which represented the surface distance. The surface area ratio, representing the density of microfolding, was the percentage of the three-

dimensional surface, compared to the projected flat surface area, on the threshold plane. The traits were obtained from nine different samples.

RESULTS AND DISCUSSION

It was observed that the flowers of *O. pes-caprae* (Fig. 1a) open at approximately 10.00 AM if the sun is shining and close at 3.00 PM. In cloudy weather, the perianth remains twisted and closed throughout the day. Such synchronization might be under strong selection and adaptation.

The expanded petals possess epidermal cells with anticlinal walls on both the adaxial (Fig. 2a) and the abaxial (Fig. 2b) surfaces. In the funnel-shaped, open flowers of *O. pes-caprae*, the adaxial and the abaxial surfaces of the petals (Fig. 2c) are exposed to the ambient conditions. In the trumpet-shaped, closed flowers of *O. pes-caprae*, some portions of the abaxial petal surface (Fig. 2d) are exposed to the ambient conditions, while the twisted adaxial petal surface (Fig. 2c) is not exposed to the external environment.

In *O. pes-caprae*, the petals consist of a one-layered adaxial epidermis with conical cells (Fig. 2c), a one-layered abaxial epidermis with convex cells (Fig. 2d), and a narrow mesophyll with a loosely arranged parenchyma (Fig. 2e). The mesophyll's thickness ($32 \pm 1 \mu\text{m}$) is comparable with that of the adaxial epidermis ($35 \pm 1 \mu\text{m}$) and is substantially larger than that of the abaxial epidermis ($18 \pm 1 \mu\text{m}$).

It has been argued that the shape that would be optimal for absorbing the oblique rays would be conical and papillary (Brodersen & Vogelmann 2007; Glover 2007; Lee 2007). Conical epidermal cells, besides optimizing absorption, also scatter and diffuse the light reflected back from a loosely arranged mesophyll (Kay *et al.* 1981; Pfündel *et al.* 2006). The loosely arranged parenchyma of *O. pes-caprae* (Fig. 1e) might cause the diffusion of scattered light within the mesophyll, increasing the amount of usable light in the tissue. This is advantageous because it allows for greater electron capture by concentrated pigments, which absorb light energy, retain it for a few nano or microseconds, and produce heat (Miller *et al.* 2011). Furthermore, a mesophyll with large intercellular spaces could enhance the water status and turgor of the petals (Kay *et al.* 1981; Rhizopoulou *et al.* 2006).

It has been reported that the temperature of conical epidermal cells increases with the warming effect of solar irradiance and that this can mediate flower opening (McKee & Richards 1998; Glover 2007). For example, the temperature of the yellow petals of *Calendula arvensis* increases by exposure to sunlight, $\sim 2\text{--}4^\circ\text{C}$ above the temperature of the ambient air (Rejšková *et al.* 2010). Thus, solar radiation might be retained more effectively by the adaxial conical cells in comparison with the convex, abaxial epidermal cells of *O. pes-caprae* (Fig. 2e). It seems likely that foraging bumble bees prefer to visit warm flowers (Dyer *et al.* 2006; Whitney *et al.* 2009a). Also, the conical cells of petal epidermises facilitate the

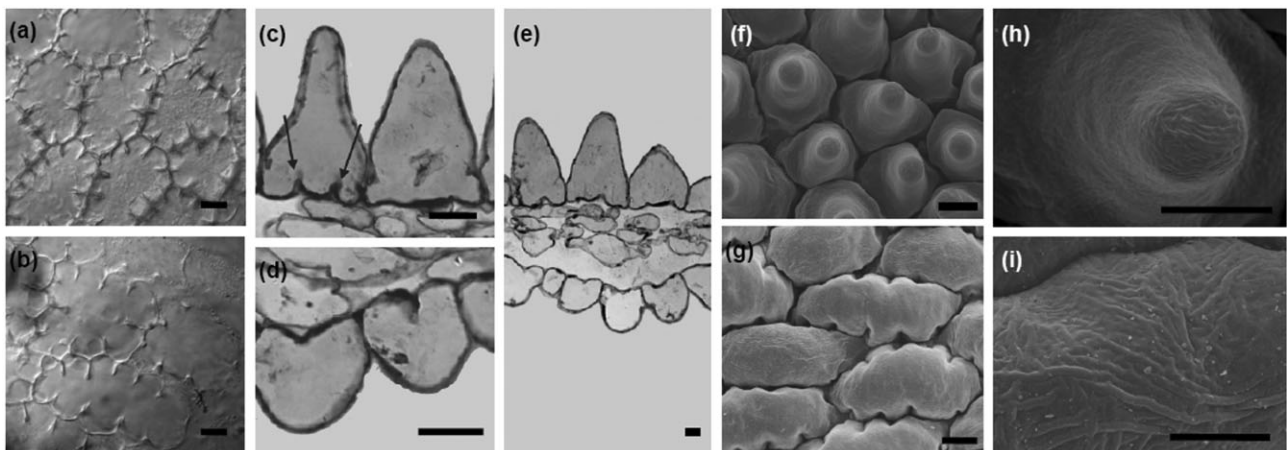


Fig. 2. Light micrographs of the paradermal section of the (a) adaxial and (b) the abaxial side of the petals of *Oxalis pes-caprae* with cells with anticlinal walls, light micrographs of a cross-section through the expanded region of the petals, (c) the adaxial epidermal cells (the arrowheads indicate the anticlinal walls), (d) the abaxial epidermal cells, and (e) the petal tissue, and scanning electron micrographs illustrating (f) the adaxial and (g) the abaxial epidermal cells and details of the profile of (h) the adaxial and (i) the abaxial relief of the epidermal cells of the petals. The scale bars represent $10 \mu\text{m}$.

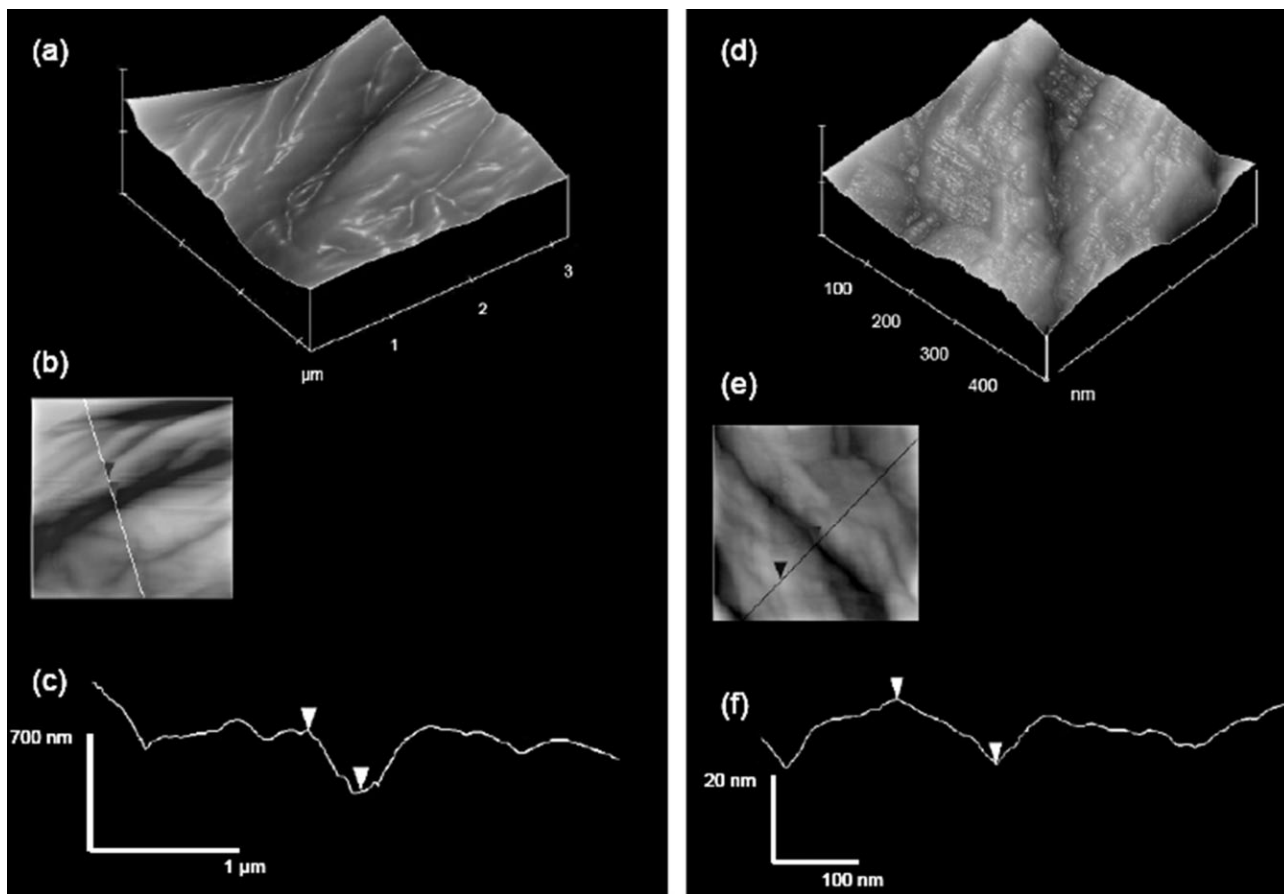


Fig. 3. Atomic force micrographs of the petal surfaces of *Oxalis pes-caprae* showing the three-dimensional profile of (a) the adaxial petal surface ($3\ \mu\text{m} \times 3\ \mu\text{m}$), (b) the integrated line of measured points on the plane profile, and (c) the profile view of the line section and the three-dimensional profile of (d) the abaxial petal surface ($0.5\ \mu\text{m} \times 0.5\ \mu\text{m}$), (e) the integrated line of measured points on the plane profile, and (f) the profile view of the line section.

physical handling of pollinators (Glover & Martin 1998; Whitney *et al.* 2009b; 2011).

Previous studies have indicated that the microsculpturing of the epidermal cells of petals influences the optical and adhesive properties of plant tissues (Wagner *et al.* 2003; Pfündel *et al.* 2006; Whitney *et al.* 2011). High-resolution imaging of both the adaxial and the abaxial petal epidermises of *O. pes-caprae* revealed a relief at the nanometer scale (Fig. 3). On the adaxial epidermis (Fig. 3a), the surface distance (Fig. 3b) between elevations (Fig. 3c) is higher than either the horizontal or the vertical distance (Table 1). In contrast, the horizontal distance of the abaxial surface is equal to the surface distance (Table 1). The relief of the abaxial petal epidermis (Fig. 3d,f) possesses a vertical distance that is 25.5-fold smaller than that of the adaxial surface, while the horizontal distance is 2.9-fold smaller than that of the adaxial surface.

High-resolution imaging using AFM revealed a microsculpturing that increases the size of the surface area of the adaxial epidermis by 56%, while that of the abaxial surface is increased by only 0.8%. Also, the distances between the folds are larger than the visible waveband on the adaxial surface and smaller than the subwavelength spectrum (i.e. $<150\ \text{nm}$) on the abaxial surface. A grating of periodically folded particles with sizes of $<150\ \text{nm}$ might cause interference (Whitney *et al.* 2009b); thus, light can be refracted and scattered via a range of wavelengths that are greater than the grating periodicity (Tucker & Garratt 1977). It seems likely that submicron structures of the abaxial surface compensate to some extent for the absence of light-trapping epidermal cell shapes (Pfündel *et al.* 2006).

The conical cells of the adaxial epidermis exhibit deep cavities that permit water droplets to flow easily into depressions (Wagner *et al.* 2003) and wet the sympetalous

Table 1. Estimates of the horizontal, vertical and surface distance, roughness, and surface area ratio of the examined tissues of *Oxalis pes-caprae*, using atomic force microscopy. Angles between the straight lines connecting the arrowheads with the horizontally positioned petals of *Oxalis pes-caprae*, using atomic force microscopy, are represented. The data are the means of five samples \pm standard error

Petal surface	Horizontal distance (nm)	Vertical distance (nm)	Surface distance (nm)	Roughness (nm)	Surface area ratio	Angle (°)
Adaxial	354 \pm 4	357 \pm 3	553 \pm 5	139 \pm 6	1.32 \pm 0.00	45 \pm 3
Abaxial	121 \pm 2	14 \pm 2	122 \pm 4	3 \pm 1	1.01 \pm 0.00	6 \pm 1

corolla of *O. pes-caprae*. The micromorphology of the adaxial petal surface might have developed to profit from sunshine and to not be harmed when exposed to unfavorable environmental conditions during the early spring-flowering period.

The flat abaxial epidermal cells of the petals (Fig. 2g) of *O. pes-caprae* seem to be less susceptible to wet conditions: the high-resolution imaging revealed a negligible roughness on the abaxial petal surface (Table 1), which minimizes the amount of water adhesion on the outer side of the petals. In contrast, the adaxial epidermal cells exhibit a 46-fold higher level of roughness than that of the abaxial epidermal cells, which might affect both the optical properties and the wettability of the petals' surface, thus making them vulnerable to water adhesion (Wagner *et al.* 2003; Feng *et al.* 2008; Polymeni *et al.* 2010). The topology of the petals of *O. pes-caprae* revealed a different micromorphology between the adaxial (Fig. 2h) and the abaxial (Fig. 2i) surfaces. Also, more intense forms were found on the adaxial surface, in comparison with those of the abaxial surface (Table 1).

The blossoming of *O. pes-caprae*, along with that of *Ashodelus aestivus*, *Sinapis arvensis*, and *Eruca sativa*, places the species among the early spring-flowering plants in the context of a Mediterranean-type ecosystem. In contrast to *O. pes-caprae*, the flowers of the above-mentioned native Mediterranean species remain open during their short lifespan and their petals are continuously exposed to the ambient conditions. It is noteworthy that the papillary epidermal cells of the petals of *A. aestivus*, *S. arvensis*, and *E. sativa* are covered by waxy, striated, and densely arranged nanoridges, which have a significant impact on the repellent properties of the short-lived, delicate tissues (Rhizopoulou *et al.* 2008; Argiropoulos 2009; Koch & Barthlott 2009; Koch *et al.* 2009).

The closed, fully developed flowers of *O. pes-caprae* open with the perception and the warmth of incident sunlight, which might involve a sensing of changing light intensity, perceived primarily by the petals' surfaces. Consistent with this view are the results in relation to *Oxalis*

martiana (Tanaka *et al.* 1989) and the flower-opening of other species, which is accelerated by exposure to sunlight (Sultan 2010 and references therein).

ACKNOWLEDGMENTS

This research was supported by funding from the General Secretary of Research and Technology, Athens, Greece (03 174 GSRT), which was granted to S.R. We thank A. Siakouli and E. Spanakis (Institute of Electronic Structure and Laser, Foundation for Research and Technology – Hellas, Crete, Greece) for their help with various techniques, K. Georghiou and P. Delipetrou for discussions about alien species in Greece, and E. Key Fowden for correcting an earlier draft of the manuscript.

REFERENCES

- Aitken R. 2007. The cape unveiled. In: *Botanical Riches, Stories of Botanical Exploration* (ed. by Aitken R.). Lund Humphries, London, 115–123.
- Argiropoulos A. 2009. [On the colour of flowers' petals] (PhD thesis). National and Kapodistrian University of Athens, Athens, Greece (in Greek with English abstract).
- Arianoutsou M., Bazos I., Delipetrou P. and Kokkoris Y. 2010. The alien flora of Greece: taxonomy, life traits and habitat preferences. *Biol. Invasions* **12**, 3525–3549.
- Bargel H., Koch K., Cerman Z. and Neinhuis C. 2006. Structure–function relationships of the plant cuticle and cuticular waxes – a smart material? *Funct. Plant Biol.* **33**, 893–910.
- Bhushan B. 2009. Biomimetics: lessons from nature – an overview. *Phil. Trans. R. Soc. A* **367**, 1445–1486.
- Brodersen C.R. and Vogelmann T.C. 2007. Do epidermal cells facilitate the absorbance of diffuse light? *Am. J. Bot.* **94**, 1061–1066.
- Castro S., Loureiro J., Santos C., Ater M., Ayensa G. and Navarro L. 2007. Distribution of flower morphs, ploidy level and sexual reproduction of the invasive weed *Oxalis pes-caprae* in the western area of the Mediterranean region. *Ann. Bot.* **99**, 507–517.
- Chapman D. 2007. *Oxalis*. *Southern Afr. Bulb Group Newslett.* **7**, 6–8.
- Damanakis M. and Markaki M. 1990. Studies on the biology of *Oxalis pes-caprae* L., under field conditions in Crete. *Zizaniology* **2**, 145–154.
- Dyer A.G., Whitney H.M., Arnold S.E.J., Glover B.J. and Chittka L. 2006. Bees associate warmth with floral colour. *Nature* **442**, 525.

- Feng L., Zhang Y., Xi J., Zhu Y., Wang N., Xia F. *et al.* 2008. Petal effect: a superhydrophobic state with high adhesive force. *Langmuir* **24**, 4114–4119.
- Fratz P. 2007. Biomimetic materials research: what can we really learn from nature's structural materials? *J. R. Soc. Interface* **4**, 637–642.
- Galil J. 1968. Vegetative dispersal in *Oxalis cernua*. *Am. J. Bot.* **55**, 68–73.
- Glover B.J. 2007. *Understanding Flowers and Flowering, An Integrated Approach*. Oxford University Press, Oxford.
- Glover B.J. and Martin C. 1998. The role of petal cell shape and pigmentation in pollination success in *Antirrhinum majus*. *Heredity* **80**, 778–784.
- Kay Q.O.N., Daoud H.S. and Stirton C.H. 1981. Pigment distribution, light reflection and cell structure in petals. *Bot. J. Linn. Soc.* **83**, 57–89.
- Kerstiens G. 2006. Water transport in plant cuticles: an update. *J. Exp. Bot.* **57**, 2493–2499.
- Koch K. and Barthlott W. 2009. Superhydrophobic and superhydrophilic plant surfaces: an inspiration for biomimetic materials. *Phil. Trans. R. Soc. A* **367**, 1487–1509.
- Koch K., Bhushan B. and Barthlott W. 2009. Multifunctional surface structures of plants: an inspiration for biomimetics. *Prog. Mater. Sci.* **54**, 137–178.
- Lambdon P.W. 2009. *Oxalis pes-caprae* L., Bermuda buttercup (Oxalidaceae, Magnoliophyta). In: *Handbook of Alien Species in Europe* (ed. by Drake J.A.). Springer Science and Business Media, Dordrecht, the Netherlands, 353.
- Lane D. 1984. Factors affecting the development of populations of *Oxalis pes-caprae*. *Weed Res.* **24**, 219–225.
- Lee D. 2007. *Nature's Palette, the Science of Plant Color*. The University of Chicago Press, Chicago.
- Li-Beisson Y., Pollard M., Sauveplane V., Pinot F., Ohlrogge J. and Beisson F. 2009. Nanoridges that characterize the surface morphology of flowers require the synthesis of cutin polyester. *Proc. Natl Acad. Sci. USA* **106**, 22 008–22 013.
- Ma Y. and Sun J. 2009. Humido- and thermo-responsive free-standing films mimicking the petals of the morning glory flower. *Chem. Mater.* **21**, 898–902.
- McKee J. and Richards A.J. 1998. Effect of flower structure and flower colour on intrafloral warming and pollen germination and pollen tube growth in winter flowering *Crocus* L. (Iridaceae). *Bot. J. Linn. Soc.* **128**, 369–384.
- Marshall G. 1987. A review of the biology and control of selected weed species in the genus of *Oxalis*: *O. stricta* L., *O. latifolia* H.B.K. and *O. pes-caprae* L. *Crop Prot.* **6**, 355–364.
- Miller R., Owens S.J. and Rørslett B. 2011. Plants and colour: flowers and pollination. *Opt. Laser Technol.* **43**, 282–294.
- Oberlander K.C. 2009. Molecular systematic study of Southern African oxalis (Oxalidaceae) (PhD thesis). Stellenbosch University, Matieland, South Africa.
- Petsikos C., Dalias P. and Troumbis A.Y. 2007. Effects of *Oxalis pes-caprae* L. invasion in olive groves. *Agric. Ecosyst. Environ.* **120**, 325–329.
- Pfändel E.E., Agati G. and Zerovic Z.G. 2006. Optical properties of plant surfaces. In: *Biology of the Plant Cuticle* (ed. by Riederer M. and Muller C.). Blackwell, Oxford, 216–249.
- Polymeni R., Spanakis E., Argiropoulos A. and Rhizopoulou S. 2010. Aspects on the relief of living surfaces using atomic force microscopy allow “art” to imitate nature. *Integr. Zool.* **5**, 218–225.
- Rejšková A., Brom J., Pokorný J. and Korečko J. 2010. Temperature distribution in light-coloured flowers and inflorescences of early spring temperate species measured by infrared camera. *Flora* **205**, 282–289.
- Rhizopoulou S., Argiropoulos A., Spanakis E., Gikas D., Alexandres N., Koukos D. *et al.* 2008. Visual perception of colourful petals reminds us of classical fragments. *Nature Precedings*. [Cited 16 January 2008.] Available from URL: <http://hdl.handle.net/10101/npre.2008.1523.1>
- Rhizopoulou S., Ioannidi E., Alexandres N. and Argiropoulos A. 2006. A study on functional and structural traits of the nocturnal flowers of *Capparis spinosa* L. *J. Arid Environ.* **66**, 635–647.
- Rottenberg A. and Parker S.J. 2004. Asexual populations of the invasive weed *Oxalis pes-caprae* are genetically variable. *Proc. R. Soc. Lond. B* **271**, S206–S208.
- Sibthorp J. and Smith J.E. 1806. *Florae Graecae Prodrum: Sive Plantarum Omnium Enumeratio Quas in Provinciis Aut Insulis Graeciae*, Vol. I. Richard Taylor, London.
- Sultan S.E. 2010. Plant developmental responses to the environment: eco-devo insights. *Curr. Opin. Plant Biol.* **13**, 96–101.
- Tanaka O., Murakami H., Wada H., Tanaka Y. and Naka Y. 1989. Flower opening and closing in *Oxalis martiana*. *Bot. Mag.* **102**, 245–253.
- Tucker C.J. and Garratt M.W. 1977. Leaf optical systems modelled as a stochastic process. *Appl. Opt.* **16**, 635–642.
- van Doorn W.G. and van Meeteren U. 2003. Flower opening and closure: a review. *J. Exp. Bot.* **54**, 1801–1812.
- Verdaguer D., Sala A. and Vilà M. 2010. Effect of environmental factors and bulb mass on the invasive geophyte *Oxalis pes-caprae* development. *Acta Oecol.* **36**, 92–99.
- Vilà M., Bartomeus I., Gimeno I., Traveset A. and Moragues E. 2006. Demography of the invasive geophyte *Oxalis pes-caprae* across a Mediterranean island. *Ann. Bot.* **79**, 1055–1062.
- Vilà M., Siamantziouras A.-S.D., Brundu G., Camara I., Lambdon P., Médail F. *et al.* 2008. Widespread resistance of Mediterranean island ecosystems to the establishment of three alien species. *Diversity Distrib.* **14**, 839–851.
- Wagner P., Fürstner R., Barthlott W. and Neinhuis C. 2003. Quantitative assessment to the structural basis of water repellency in natural and technical surfaces. *J. Exp. Bot.* **54**, 1295–1303.
- Whitney H.M., Chittka L., Bruce T.J.A. and Glover B. 2009b. Conical epidermal cells allow bees to grip flowers and increase foraging efficiency. *Curr. Biol.* **19**, 948–953.
- Whitney H.M., Federle W. and Glover B. 2009a. Grip and slip: mechanical interactions between insects and the epidermis of flowers and flower stalks. *Commun. Integr. Biol.* **2**, 505–508.
- Whitney H.M., Poetes R., Steiner U., Chittka L. and Glover B. 2011. Determining the contribution of epidermal cell shape to petal wettability using isogenic *Antirrhinum* lines. *PLoS ONE* **6**, e17576 1–e17576 5.