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RESEARCH ARTICLE

The morphostructure of *Oxalis incarnata* bulbs

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Abstract

The morphostructure of the bulbs of *Oxalis incarnata* in the conditions of dormancy and the plant's growth and development are described. The plants were grown in two irrigation modes: 1) with regular irrigation during the year, and 2) with limited irrigation in March-October and without irrigation in November-February. The bulbs were analyzed by way of consequent detaching of the scales. Investigated bulbs always had four fleshy scales, while the number of coriaceous and membranous scales varied. Coriaceous scales, together with two fleshy outer scales, make a protective envelope of the bulb.

The overground shoot of *O. incarnata*, just like in other species of the genus, demonstrates monopodial growth and can produce up to five levels of lateral branches. Elongated parts of overground shoots serve for new territories' useful occupation, while shortened parts produce new particles. Resting buds (bulbils) of three types were observed in *O. incarnata*: underground axillary buds, overground axillary gemmae, and terminal gemma. Our investigations showed polyvariance both of organogenesis of the resting buds and ontogenesis of plants in general, depending on irrigation regimes. In the case of limited irrigation, the plants of *O. incarnata* shed the leaves and can produce terminal gemma. While in the case of regular irrigation during the year, they remain evergreen and form gemmae exclusively in the leaves' axils. We did not observe the formation of terminal gemmae in the case if axillary gemmae were present.

The root system of *O. incarnata* has a complex structure. It consists of two crowns of the filamentary roots, contractile roots, and additional adventitious roots located along the underground part of the shoot during its growth. Such structure of the root system probably ensures better absorption of the water.

Keywords: *Oxalis incarnata*, root system, bulb, gemmae, irrigation regime

Introduction

Cosmopolite genus *Oxalis* L. (Oxalidaceae R. Br.) comprises about 700 species (Knuth, 1930; Nesom, 2017). This is the only genus among dicots representing true bulbs. The genus *Oxalis* remains among the most diverse (Proches et al., 2006; Zietsman et al., 2009) but the least investigated in South Africa (Gebregziabher, 2004). *Oxalis incarnata* L., together with other 122 *Oxalis* species, is an endemic of the Cape Floristic Region (Freiberg & Manning, 2013). It is the only sylvatic endemic among all South African representatives of the genus. Accordingly to Salter (1944), *O. incarnata* belongs to the subsection *Subintegrae* of the section *Oppositae*. Oberlander et al. (2011) attributed it to the clade *Caulescent*, which is characterized by the presence of stem. This species is mostly distributed in a zone of coastal fynbos but also occurs in fragmented forests near the flowing water (Oberlander, 2009). It is a highly decorative plant, which is often introduced and even became a weed in many countries (Randall, 2017). Expansion of this species

observed in countries with a Mediterranean climate (Discover Life, 2020).

In South Africa, many species depending on local climatic conditions can demonstrate an evergreen or deciduous growing strategy (Proches et al., 2006). Similarly, *O. incarnata* can remain evergreen in well-hydrated places (Pacific Bulb Society, 2020).

Salter (1944) was the first, who outlined the importance of morphology of both overground shoots and bulbs for *Oxalis* systematics. Estelita-Teixeira (1982) and Zhila & Tymchenko (2014, 2016) investigated the structure of the bulbs of certain South American representatives of the genus. Pütz (1994) and Gebregziabher (2004) paid attention to bulbs' morphology in South African *Oxalis*. Nevertheless, despite the importance of such investigations for understanding the new territories' occupation mechanisms, bulbs' morphology of such aggressive weed as *O. incarnata* was not studied yet.

Material and methods

The bulbs of *O. incarnata* were received from the Botanical Garden of Karl-Franzens-University (Graz, Austria) and planted in 2015 at the M.M. Gryshko National Botanical Garden, National Academy of Sciences of Ukraine. Further investigations were carried out in 2016–2019. Plants were grown in pots in a cold greenhouse applying two irrigation modes: 1) with regular irrigation during the year, and 2) irrigation in March-October and without irrigation in November-February. Once per month, five plants were randomly taken for the analysis of bulbs' morphostructure. Scales of the bulbs were detached and investigated using the light microscope MBS-9. Provided description of the bulbs follows the terminology of Fedorov et al. (1962).

Results and discussion

The bulbs of *O. incarnata* are oval, hooked, 1.5–2 cm long, with brown, pubescent covering scales. The overground part of the stem is glabrous. Among other South African *Oxalis* representatives, *O. incarnata* is notable for branched, zig-zag shaped, up to 30 cm long stems, and axillary gemmae production.

Phyllotaxis is complex, distichous, and pseudo-whorled (Emshwiller, 1999). Some nodes demonstrate a strictly distichous position of the leaves. However, most of the shoot has a mix of elongated (up to 8 cm long) and significantly shortened internodes, where the nodes can gather up to ten leaves.

Leaves are compound trifoliate, with equal obovate leaflets, 4–16 × 5–22 mm each. The abaxial side of the leaves is punctate. Leaflets slightly pubescent, with reticulate ornamentation, often with irregular row of the oxalates seen along the margin. Leaf base partly surrounds the stem (almost 1/2 of the node) and continues into the stipule-like structures, which are about 3 mm long. Petioles are glabrous, 7–12 mm long (Nesom, 2017).

Solitary flowers are campanulate elongated, 13–22 mm long. Pedicels are as long as leaves, flaccid, with two opposite bracteoles. Corolla is pale-lilac, at the base – greenish. Sepals are slightly elongated (4–6 mm long), acute, coriaceous, pubescent, with oxalate deposits at the tips (Dreyer et al., 2006; Nesom, 2017).

Bulbous representatives of the genus *Oxalis* are sterile out of the natural range of their distribution. Supposedly, such species' reproduction goes only through the vegetative way due to pollination issues caused by introduced plants' clonal origin (Young, 1958). Similarly, *O. incarnata* tends to lose the heterostyly, and therefore – to lose the ability for cross-pollination, even in the natural conditions (Oberlander, 2009; Turketti, 2010). Vegetative propagation of such plants by bulbils became the primary way of their dispersion. Propagative bulbils develop both on the underground (Gray, 2011; Groom et al., 2017) and overground parts of the shoot. In the last case, bulbils (gemmae) can develop in the axils (Nesom, 2017) or at the shoot apex (Oberlander, 2009; Oberlander et al., 2009). Axillary gemmae also occur in some other South African *Oxalis* species, including *O. pocockiae* L. Bolus, *O. inaequalis* Weintroub, and *O. convexula* Jacq. (Oberlander et al., 2009; Pacific Bulb Society, 2020). Such axillary gemmae are also known for many other plants (Farrell, 2008). However, terminal gemmae are reported only for *O. incarnata* and look to be a unique feature of this species (Oberlander, 2009; Oberlander et al., 2009).

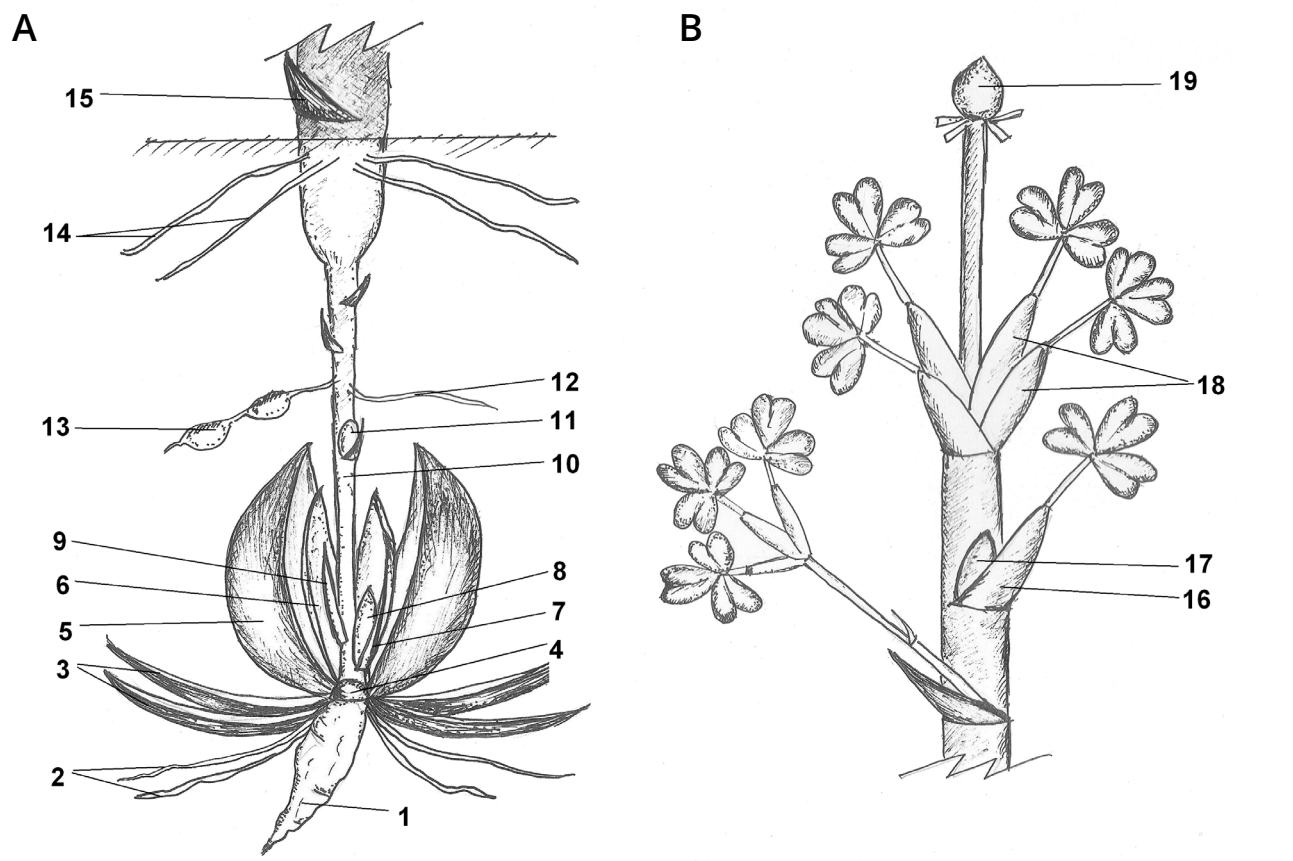

Figure 1. The bulb (**A**) and overground shoot (**B**) of *Oxalis incarnata*: **1** – napiform contractile root; **2** – filamentary roots (first crown); **3** – coriaceous scales; **4** – basal plate; **5** – outer thick fleshy scale; **6** – inner fleshy scale; **7** – first membranous scale; **8** – axillary bulbil in the axil of the first membranous scale; **9** – second membranous scale; **10** – first elongated internode; **11** – underground axillary bulbil; **12** – filamentary stem's root; **13** – stem's root with irregularly-thickened areas; **14** – stem's filamentary roots (second crown); **15** – the first scale of overground part of the shoot; **16** – trophophylls; **17** – axillary gemmae; **18** – leaves in a false whorl; **19** – terminal gemma.

The bulbs of South African representatives of the genus are considered as annual (Salter, 1944). During the vegetation season, the maternal bulb is wholly utilized to develop roots, shoots, and daughter bulbs. However, the bulbs' descriptions often differ even for the same *Oxalis* species, which probably depends on the ontogenetic stage when such a description has been performed. Salter (1944) and Gebregziabher (2004) reported South African *Oxalis* species to have the bulbs constructed from basal plate, coriaceous scales, fleshy scales, and young bulbil (the axillary bud of the next vegetation year). However, Pütz (1994) noted that the dormant bulb of *O. pes-caprae* L. has only coriaceous scales, fleshy scales, and undifferentiated terminal bud in its center. At the beginning of vegetation season, such terminal bud develops into the shoot with adventive roots and buds in the scales' axils.

The bulbs of *O. incarnata* are imbricate. In dormant conditions, the bulbs consist of a basal plate and few fleshy scales and terminal bud attached to this plate. After awake, the maternal bulb starts to produce filamentary roots around the basal plate, which form the first crown (Fig. 1A – 2 & 4). After that, one or two filamentary roots become thicker and form napiform contractile roots (Zhila & Tymchenko, 2016). The function of contractile roots in *O. incarnata* (Fig. 1A – 1) has been analyzed in detail by Thoday (1926) and Thoday & Davey (1932). In the bulbous representatives of the genus *Oxalis*, such roots usually serve to strengthen the plant in the soil and for the particular movement (Galil, 1968; Pütz, 1994). They also increase the absorption area near the soil surface (North et al., 2008). Moreover, it was noted that such contractile roots could serve as temporary (ephemeral) storage organs (Iziro & Hori, 1983). In general, the

genus's bulbous representatives' root system combines features of both monocots and dicots (Zhila & Tymchenko, 2016).

South African *Oxalis* have no regular leaves (trophophylls) attached to the bulb's basal plate; all trophophylls are located in the overground shoot nodes (Oberlander et al., 2009). When the plant has already developed overground shoot in the phase of active growth, *O. incarnata* develops up to six coriaceous scales at the basal plate (Fig. 1A – 3). Such coriaceous scales are 3.5–4.0 mm wide and 3.0–3.2 mm long, with three veins, shortly pubescent on the abaxial side (with denser pubescence at the tips) and glabrous – on the adaxial one. Coriaceous scales cover four fleshy scales (Fig. 1A – 5 & 6). Two outer fleshy scales are more prominent and thicker, 17.0–20.0 mm long, and the other two inner fleshy scales are much smaller (8.0–11.0 mm long) and thinner. Coriaceous scales, together with two flashy outer scales, make a protective envelope of the bulb. The number of fleshy scales in *O. incarnata* always remains invariable, while the number of coriaceous scales can vary. Resting buds can develop in the axils of both coriaceous and flashy scales.

In *O. incarnata*, the terminal bud forming the overground shoot, just like in other species of the genus, demonstrates monopodial growth (Jeannoda-Robinson, 1977; Shorina, 1983; Chub, 2008). Two first internodes of the shoot are shortened; here are located very narrow and thin membranous scales. The first membranous scale is longer (2.5–3.0 mm long) and holds the better-developed axillary bulbil, which is elongated and with a sharp tip. The second membranous scale is much smaller, and the second bulbil forms much later (Fig. 1A – 7–9). The next internode (Fig. 1A – 10) is elongated, and the node holds the scale (0.5–0.8 mm long) with spherical axillary bud (Fig. 1A – 11). Later, this bud grows and goes out of the bulb. Consequent elongated internodes hold the scales, all about 1 mm long but vary in their width. The number of these internodes, hidden under the ground, depends on the depth of sowing.

The underground part of the shoot located between the bulb and the soil surface form the filamentary roots, which are often irregularly utricular and can ramify (Fig. 1A – 12–13). This part of the shoot has a whitish color.

The frontier internode (partly located in the ground and partly open) is significantly thickened. It holds many adventitious filamentary roots, which form the second crown (Fig. 1A – 14). Below this crown, the internode is pinky, while above this level, it becomes greenish. All other shoot elements are located over the ground.

The overground shoot of *O. incarnata* is monocyclic and survives only one vegetation season (about six months). The first overground node still forms a membranous scale, which is more prominent (3.5–4.0 mm long) than previous ones (Fig. 1A – 15). The next leaves gradually obtain the structure of the regular trophophylls. The lower leaves are undeveloped (the leaf base is well developed, but the petioles and laminae are not developed). The middle formation leaves are already well developed, have flashy base, pronounced cylindrical petiole, and three leaflets (Fig. 1B – 16). The internodes here are elongated, 6.5–8.0 cm long.

The main shoot can ramify and produce up to five levels of lateral branches. Lateral shoots have a similar organization – the first internode is shortened (up to 1 mm long), and the first leaf is undeveloped, but all the next internodes are elongated, and the leaves are developed.

In the case of regular irrigation during the year, the plants of *O. incarnata* remain evergreen and form gemmae in the leaves' axils (Fig. 1B – 17). In this case, shoots actively ramify and, caused by elongated internodes, lie down. They also produce additional points of rooting in short internodes. As a result, several grounded clones with their own root systems and developed axillary gemmae (bulbils) in the pseudowhorled leaves' axils are present at the end of vegetation season. These axillary gemmae can serve for vegetative propagation in the next year or complete the existing plant's shoot system.

In the case of seasonal irrigation, the plants of *O. incarnata* shed the leaves and can produce terminal gemma (Fig. 1B – 19). We did not observe the formation of such terminal gemmae in the case if axillary gemmae were present. Each terminal gemma consists of three outer coriaceous and four inner fleshy scales and the bud inside of these scales. Below such terminal gemma, shoot forms several significantly shortened internodes, the basal

of which can bear up to five regular leaves or narrow scales. The uppermost shortened internode bears three broad scales with three rudimental axillary buds.

At the end of the vegetative season, the overground shoots die, the gemmae (either terminal or axillary) shed away and produce new plants in the next vegetation season.

Conclusions

1. The root system of O. *incarnata* has two crowns of filamentary roots and contractile and additional adventitious roots, ensuring better water absorption.

2. Resting buds are represented by three types – axillary underground buds, axillary overground gemmae, and terminal overground gemmae.

3. Gemmae can continue the growth and ramify during the current season on the mother plant. Otherwise, gemmae can serve for vegetative propagation and produce the new plant in the next season.

4. In the case of regular irrigation, the vegetative propagation of O. *incarnata* realizes with the help of axillary underground buds and axillary overground gemmae. In the case of insufficient irrigation, it can be performed through the axillary underground buds and terminal gemmae.

5. Elongated internodes serve adjacent territories' occupation, while shortened ones – for effective rooting and production of the new particles with gemmae.

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Морфоструктура цибулин *Oxalis incarnata*

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У роботі описана морфоструктура цибулини *Oxalis incarnata* як у стані відносного спокою, так і в процесі росту і розвитку упродовж вегетаційного періоду. Рослини утримувалися у двох режимах поливу: 1) рівномірного протягом року; 2) змінного (полив у березні-жовтні, без поливу у листопаді-лютому). Цибулини аналізували шляхом послідовного видалення лусок. Досліджені цибулини завжди мали чотири соковиті луски, в той час як кількість шкірястих і перетинчастих лусок варіювала. Шкірясті луски разом з двома зовнішніми соковитими, очевидно, виконують захисну роль.

Надземний пагін *O. incarnata*, як і в інших представників роду, демонструє моноподіальне галуження і може продукувати до п'яти рівнів бічних пагонів. Видовжені ділянки надземного пагона можуть

полягати і вкорінюватися, захоплюючи прилеглі території, тоді як вкорочені ділянки відповідають за вкорінення і формування парціальних особин. Залежно від місця закладання у *O. incarnata* можуть спостерігатися бруньки поновлення (цибулинки) трьох типів: аксилярні підземні, аксилярні надземні виводкові і термінальні виводкові. Рослинам цього виду притаманна як поліваріантність проходження органогенезу бруньок поновлення, так і поліваріантність онтогенезу рослин в цілому залежно від режимів зволоження. У випадку обмеженого поливу, рослини можуть скидати листки і формувати термінальні повітряні виводкові бруньки. За дотримання режиму постійного поливу протягом року формуються повітряні бруньки поновлення лише у пазухах листків, а рослина залишається вічнозеленою. Одночасного утворення аксилярних повітряних виводкових цибулинок і термінальних повітряних виводкових цибулинок не спостерігалося.

Коренева система *O. incarnata* має складну структуру і складається з двох корон зі шнуроподібних коренів, а також контрактильних коренів та додаткових коренів сформованих уздовж осі пагона при його підземному наростанні. Така її структура, ймовірно, покликана забезпечити краще поглинання води.

Ключові слова: *Oxalis incarnata*, коренева система, цибулина, виводкові цибулинки, режим зволоження