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Ontogenetic features of *Sternbergia vernalis* and dynamics of its bulb development

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Abstract

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This study addresses the limited understanding of underground morphogenesis and adaptive mechanisms in the endangered geophyte *Sternbergia vernalis* (Miller) Gorer & J.H. Harvey. To characterise its bulb development, we cultivated wild specimens collected from the northeastern Greater Caucasus *ex situ* at a soil depth of 20 cm. During the 2023–2024 growing seasons, we combined phenological observations, stereomicroscopic examination of anatomical sections, and graphical analysis of renewal-bud development. Mature bulbs comprised 15–20 fleshy scales formed over four consecutive growing seasons and had 7–9 cm-long neck. Floral differentiation began in May, when soil temperature reached 34°C, and the first floral shoot was initiated by late June. Renewal-bud growth continued from July to early September despite high temperatures, root absence, and dry summer conditions. These findings indicate that *Sternbergia vernalis* does not undergo true physiological dormancy; instead, slow underground morphogenesis continues throughout the annual cycle. Sustained bulb development and early preformation of vegetative and reproductive organs appear to support survival, regeneration, and reproduction in arid and variable environments. Bulb development was also linked to soil temperature and moisture, highlighting the species' responsiveness to climatic change.

Keywords: adaptation, bulb development, geophyte, morphogenesis, ontogeny.

INTRODUCTION

Rare bulbous geophytes are particularly vulnerable to habitat fragmentation, land-use change, and prolonged drought associated with climate change. *Sternbergia* species often have narrow ecological requirements, restricted distributions, and limited competitive ability (Pasche & Kerndorff, 2002; Peruzzi et al., 2008). Effective conservation therefore requires detailed knowledge of their morphology, phenology, reproductive biology, and responses under *ex situ* conditions (Youssef et al., 2017; Gürbüz et al., 2009). More broadly, conserving rare and endangered geophytes is increasingly important as anthropogenic pressures reduce floristic and genetic diversity (Aliyev et al., 2004; Bakhshiyev, 2015; Shevchenko, 2005).

Bulbous geophytes commonly survive seasonal adversity through underground storage organs and a period of physiological or physical dormancy.

In many genera, including *Tulipa*, *Narcissus*, and *Galanthus*, above-ground senescence is followed by a marked reduction in growth and metabolic activity. However, dormancy varies across geophytes: in some Mediterranean and Western Asian taxa, future vegetative and reproductive organs continue to differentiate within the bulb while the plant appears inactive aboveground. Tissue-level dynamics, the multiyear contribution of bulb scales, and how such continuous development under arid conditions is integrated remain insufficiently understood (Aedo et al., 2013; Pasche & Kerndorff, 2002; Peruzzi et al., 2008; Youssef et al., 2017).

Although researchers have partially documented the morphology and conservation status of *Sternbergia vernalis*, its detailed ontogenetic pathway or the apparently continuous development of its storage organs have not been systematically characterised. In particular, it remains unclear how reserve tissues of different ages support renewal-bud and floral development without a distinct period of physiological dormancy.

Conservation planning for rare plants depends on knowledge of their distribution, ecology, population decline, and responses to environmental pressures (Asadova, 2020; IUCN, 2001). Cultivation under controlled conditions can clarify adaptation and reproduction and inform propagation and reintroduction strategies (Asadova, 2019, 2020; Aliyev et al., 2004; Yip et al., 2006). Such information is especially relevant under increasing climatic variability, when morphological indicators may help assess adaptive capacity (Asadli et al., 2025).

This study aimed to characterise the ontogenetic and seasonal development of *Sternbergia vernalis* through phenological observations, morphological and anatomical examination of bulbs, and quantitative assessment of renewal-bud growth. Specifically, we evaluated whether bulb morphogenesis continued during the post-vegetative period conventionally regarded as dormancy, documented changes in the renewal bud, bulb scales, vegetative organs, floral shoots, and bulbils across successive developmental stages, and examined their temporal association with soil temperature and moisture. We interpreted the potential adaptive significance of continuous bulb development indirectly from these developmental and environmental relationships.

MATERIALS AND METHODS

We selected *Sternbergia vernalis*, an endangered species in Azerbaijan, as the study organism. The investigation addressed four questions: (i) whether bulb development continues throughout the annual cycle, including the period conventionally regarded as dormancy; (ii) which ontogenetic changes occur in the bulb and renewal bud at successive developmental stages; (iii) how uninterrupted bulb morphogenesis supports the formation of vegetative and reproductive organs; and (iv) whether continuous bulb development constitutes an adaptive strategy under arid environmental conditions.

We collected specimens from the species' natural range in the northeastern Greater Caucasus, Azerbaijan, and cultivated them *ex situ* in the introduction plot of the Central Botanical Garden of the Azerbaijan National Academy of Sciences (ANAS). The bulbs were planted at a soil depth of 20 cm.

Throughout the cultivation period, we applied identical agronomic practices to all experimental plants to ensure uniform growing conditions. Phenological observations encompassed both the vegetative growth period and the subsequent post-vegetative stages of underground development.

To investigate ontogenetic development, we monitored the plants regularly throughout the growing season. We assessed underground developmental processes by excavating 3–5 bulb samples at each observation stage. The bulbs were carefully cleaned and subjected to detailed morphological and anatomical analyses. We examined their internal structure using a stereomicroscope after preparing longitudinal sections.

During the study, we evaluated a series of morphological characteristics describing bulb development. These included the number, arrangement, colour, and thickness of bulb scales; the developmental stages of the renewal bud; the sequence of differentiation of assimilating leaves and floral shoots; and bulbil formation and development. In addition, we systematically recorded the distribution of reserve nutrients among the bulb scales and morphological changes throughout the growing season.

The dimensions of the renewal bud, leaf primordia, and floral shoots were measured using a stereomicroscope equipped with a millimetre scale. We recorded measurements at each observation stage and

used them to construct graphs illustrating renewal-bud development. We then performed comparative analyses across developmental stages.

We monitored the progression of underground developmental stages in relation to soil temperature and moisture throughout the observation period. We indirectly evaluated the potential adaptive significance of continuous bulb development by comparing the timing of renewal-bud growth, organ differentiation, root absence or emergence, and bulbil development with prevailing soil conditions. Evidence of continued morphogenesis during hot and dry post-vegetative periods, followed by accelerated growth after lower temperatures and increased moisture, was interpreted as indicating a potential adaptive role. We did not directly measure survival, fitness, or reproductive success. We systematically organised, comparatively analysed, and used the data to establish the sequence of developmental stages and their temporal relationships with environmental conditions.

We statistically analysed renewal-bud height using measurements from five bulbs examined during each observation period. Results were expressed as the mean ± standard deviation (SD) and processed using Microsoft Excel. We descriptively evaluated the number of bulb scales and the developmental characteristics of assimilating leaves and floral shoots.

RESULTS

Seasonal dynamics of bulb development

The underground developmental phase of *Sternbergia vernalis* began immediately after senescence of the aerial organs and roots. The bulbs remained at a soil depth of approximately 20 cm, where soil temperature reached about 34°C. At the end of the growing period, renewal buds and floral primordia for the following season began to form. In contrast, the autumn renewal bud continued developing within the bulb.

At this stage, mature bulbs comprised 15–20 fleshy white scales formed over four consecutive growing seasons. The bulb neck, formed by persistent leaf sheaths, was 7–9 cm long.

The seasonal growth patterns of the first and second renewal buds are shown in Fig. 1. Both buds continued to develop underground after completion of the growing period. The first renewal bud increased steadily in length throughout the observation period, whereas the second developed more slowly and remained considerably smaller.

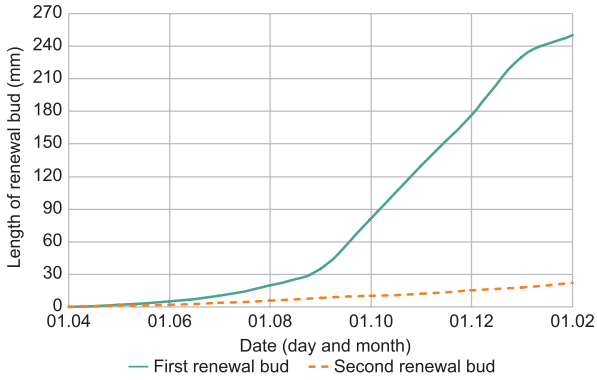


Fig. 1. Seasonal growth dynamics of the renewal buds of *Sternbergia vernalis* during 2023–2024.

Table 1. Growth dynamics of the renewal bud in *Sternbergia vernalis* during 2023–2024. Data are presented as mean ± standard deviation (n = 5) for five bulbs examined in each observation month

No.	Month	Mean (mm)	SD
1.	June	1.36	0.11
2.	July	2.54	0.11
3.	August	3.52	0.33
4.	September	4.20	0.16
5.	October	4.80	0.27
6.	December	6.22	0.62
7.	February	7.12	0.72

Quantitative measurements confirmed continued renewal-bud growth throughout the observation period. Mean bud height increased progressively, accompanied by changes in bulb-scale number and in the development of assimilating leaves and floral shoots. The means and standard deviations in Table 1 show generally low variation among the five bulbs examined at each observation point.

Ontogenetic development of the renewal bud

Each mature bulb produced one to two scale leaves and four to seven assimilating leaves annually. Scale leaf length varied with planting depth. The bulb scales were fleshy and firm, with reserves distributed throughout. During the fourth growing season, reserves in the peripheral scales were gradually depleted. After senescence of the aerial organs, cataphylls and assimilating leaves became difficult

to distinguish because second- and third-year leaves functioned as storage scales. First-year bulbils developed in the axils of second-year scales while remaining attached to the parent bulb.

At the onset of underground development, the renewal bud was approximately 5–7 mm high and enclosed by the scale leaf. Above it, assimilating leaf primordia surrounded the apical meristem, and several subsequently elongated to form leaf-blade rudiments.

Floral organ differentiation for the following year began in May. Concurrently, the peripheral scales formed during the fourth growing season were progressively depleted and developed into the brown protective tunic. By late June, the first floral shoot for the following growing season was initiated, and the primordium of a second floral shoot was visible. In some bulbs, development of the second floral shoot stopped early.

Internal structure of the bulb during underground development

Between 8 and 15 June, the floral shoot primordium appeared as a broad protuberance with a bifurcated apex corresponding to the future bract. Approximately ten days later, the first floral shoot increased in size, and the second became distinguishable.

By early July, the renewal bud was approximately 5 mm high. It contained the protective scale leaf, three assimilating leaf primordia approximately 4 mm long, two floral shoots measuring 1.4 and 0.7 mm, respectively, and the apical primordium of the fourth assimilating leaf. The bract completely enclosed the floral shoot.

In early June, the fourth-year bulb scales were almost completely depleted, whereas the lowermost scales from the third growing season began to degenerate. The renewal bud contained a short scale leaf, median leaf primordia, and a floral shoot primordium approximately 1.7 mm long. The primordium of the fourth assimilating leaf was visible above the floral shoot.

Development of vegetative and reproductive organs

Vegetative and floral organs differentiated by early June. From July to early September, the renewal bud continued to grow gradually despite elevated soil temperatures and the absence of roots.

By early September, the lower third-year bulb scales were progressively depleted and fragmented. A thin, brown, transparent sheath enclosed the floral shoot, and bulbils formed during the second growing season became exposed as the surrounding scales degenerated.

During this period, the renewal bud reached approximately 12.6 mm in length. It comprised the scale leaf, five assimilating leaves approximately 9.8 mm long, and a floral shoot approximately 7 mm long. The floral organs, including the ovary, stamens, and ovule, were already differentiated, although the staminal filaments and style remained short. Additional assimilating leaf primordia for the subsequent growing season were visible within the apical meristem.

By late September, increased soil moisture and lower soil temperature coincided with rapid renewal-bud elongation. Root primordia became visible on the basal plate, and intercalary leaf elongation accelerated.

At this stage, the assimilating leaf primordia and floral organs were yellowish, with occasional green pigmentation. Second-year bulbils had partially separated from the third-year scales but remained connected to the parent bulb through vascular attachments.

By late September, the scale leaf measured approximately 17 mm, the first assimilating leaf 16 mm, the fertile leaf 6 mm, and the floral shoot 11 mm. The floral shoot stem continued to elongate; the outer stamens measured approximately 3 mm, and primordia of the second floral shoot were visible.

Development during autumn and emergence of the aerial shoot

By late October, the renewal bud, floral shoot, assimilating leaves, and bulbil primordia grew rapidly. Meiosis in the stamens was complete by this stage.

In early November, vigorous root development began following autumn precipitation. The renewal bud elongated through the bulb neck and gradually became visible externally. During the same period, green pigmentation developed in the upper portions of the leaves and floral shoot.

Leaf primordia for the next annual cycle also differentiated within the renewal bud, while new bulbils continued to develop in the axils of second-year bulb scales.

By late November, the bulb comprised approximately 17 scales formed during the preceding three

growing seasons, together with the newly formed renewal bud for the subsequent growing season. The scale leaf was approximately 11.5 cm long, whereas the floral shoot measured approximately 9.5 cm.

Emergence of the renewal shoots above the soil surface marked the onset of the aerial phase, which included vegetative growth, flowering, and fruiting. During this phase, assimilates accumulated in the basal regions of the assimilating leaves and subsequently supported development of the renewal bud and floral shoot for the following annual cycle.

Leaves emerged more rapidly than the other organs. During flowering, the assimilating leaves elongated gradually, whereas the floral shoot grew more rapidly and eventually exceeded the leaves in height. Flower production continued throughout the flowering period, which lasted approximately 35–60 days, from January to February and occasionally into March.

DISCUSSION

Continuous bulb development throughout the annual cycle

The observations indicate that bulb development in *Sternbergia vernalis* continues throughout the annual cycle, including the post-vegetative period conventionally regarded as dormancy. Although the aerial organs and roots senesced, underground morphogenesis remained active. The renewal bud continued to increase in size during summer, floral primordia differentiated progressively, and new vegetative structures developed before emergence of the aerial shoot.

These findings answer the first research question by showing that *Sternbergia vernalis* does not undergo complete developmental arrest during the post-vegetative period. Instead, morphogenesis continues within the bulb, indicating that the underground phase is an active stage of ontogeny rather than true physiological dormancy. This continuous development allows the formation of the organs required for the following growing season well before they emerge above ground.

Ontogenetic changes during bulb development

Successive observations revealed an ordered pattern of ontogenetic development within the bulb. The renewal bud developed progressively through successive stages involving the differentiation of scale leaves, assimilating leaves, floral shoots, root primordia, and bulbils. At the same time, reserves stored in older bulb scales were progressively depleted as new organs developed.

The coexistence of organs formed in different growing seasons indicates close integration of storage, vegetative development, reproductive differentiation, and clonal propagation. The simultaneous presence of growing renewal buds, differentiating floral organs, storage tissues, and bulbils shows that organogenesis continues across marked seasonal changes in soil temperature and moisture.

The gradual depletion of fourth-year bulb scales, together with reserves contributed by third-year bulb scales, illustrates the sequential mobilisation of stored resources. The bulb therefore functions not only as a storage organ but also as a dynamic developmental system coordinating organogenesis over several consecutive growing seasons.

The descriptive statistics are consistent with the anatomical observations. The generally small standard deviations indicate limited variation in renewal-bud growth among the bulbs examined, supporting the interpretation that continued underground development is a recurrent feature of *Sternbergia vernalis* (Table 1).

Adaptive significance of uninterrupted bulb morphogenesis

The observed developmental pattern suggests that uninterrupted bulb morphogenesis may contribute to adaptation in *Sternbergia vernalis*. Floral organs differentiate several months before flowering, and continued renewal-bud development during the underground phase may reduce reproductive dependence on short-term environmental conditions during the aerial growing season.

Early formation of assimilating leaves and reproductive structures enables rapid shoot emergence after seasonal decreases in soil temperature and increases in soil moisture following autumn precipitation. This strategy allows the species to exploit the relatively short period of suitable temperature and soil moisture characteristic of its natural habitats. Furthermore, continued underground growth during periods of high soil temperature and temporary root absence indicates that

development depends primarily on reserves accumulated during previous growing seasons.

The results answer the third research question by showing that uninterrupted bulb morphogenesis supports continuous formation of vegetative and floral organs. A substantial part of the developmental programme is completed underground before the aerial phase begins. This temporal separation between organ differentiation and emergence may buffer organ formation against short-term environmental variability. Because we did not experimentally measure survival, fitness, or reproductive success, this adaptive interpretation remains a hypothesis supported by developmental and environmental observations.

Ecological and conservation implications

The ontogenetic characteristics identified in this study provide insight into the potential ecological significance of continuous underground development in *Sternbergia vernalis*. Multiyear reserve storage, preformation of vegetative and floral organs, and vegetative propagation through bulbils may jointly support persistence under seasonal drought and environmental variability.

Bulbil formation during successive developmental stages may provide an additional mechanism for population maintenance, particularly when seed-based recruitment is limited. However, we did not quantify its contribution to long-term population persistence; this requires direct demographic investigation.

Taken together, these observations support the interpretation that continuous bulb development contributes to developmental continuity under arid and climatically variable conditions. However, they do not provide direct evidence of increased survival, regeneration, or reproductive success.

From a conservation perspective, *ex situ* cultivation and reintroduction programmes should account for continuous underground development. Because morphogenesis continues throughout the post-vegetative period, disturbance during this phase may affect the differentiation of vegetative and floral organs. Knowledge of the timing and sequence of bulb development may therefore inform propagation, transplantation, and monitoring, although its practical benefits require testing under conservation conditions.

Overall, the bulb of *Sternbergia vernalis* integrates resource storage, vegetative growth, reproductive differentiation, and clonal propagation within a continuous ontogenetic process. Morphological development persisted during the post-vegetative period, distinguishing this phase from complete developmental dormancy. Preformation of vegetative and reproductive structures before above-ground emergence may improve performance under arid and environmentally variable conditions, but confirming this adaptive interpretation requires direct physiological and demographic evidence.

These findings provide a developmental basis for further experimental studies of dormancy, resource allocation, and environmental responses in *Sternbergia vernalis*, as well as for refining conservation practices.

This study shows that *Sternbergia vernalis* exhibits continuous bulb development throughout its annual cycle, indicating the absence of true physiological dormancy. During the underground phase, the renewal bud, assimilating leaves, floral organs, and bulbils develop sequentially within the bulb, ensuring uninterrupted morphogenesis across successive growing seasons.

Author contributions. V.M.A. contributed to the study design, field observations, and data interpretation. V.S.B. conducted the anatomical analyses and contributed to data analysis. K.A.A. analysed the data and drafted the manuscript. Z.J.M. supervised the study and critically revised the manuscript. E.M.G. and A.O.M. provided expert guidance, contributed to the critical review and revision of the manuscript, and offered valuable suggestions to improve the scientific quality of the work. All authors read and approved the final version of the manuscript.

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