adansonia

2020 • 42 • 13

Gender expression in *Sedum praealtum* A. DC. (Crassulaceae) in Central Veracruz, Mexico

Angélica María HERNÁNDEZ-RAMÍREZ

art. 42 (13) — Published on 21 September 2020
www.adansonia.com

PUBLICATIONS SCIENTIFIQUES
MUSÉUM NAL HIST NATURELLE

Directeur de la publication / *Publication director*: Bruno David
Président du Muséum national d'Histoire naturelle

Rédacteur en chef / *Editor-in-chief*: Thierry Deroin

Rédacteurs / *Editors*: Porter P. Lowry II; Zachary S. Rogers

Assistant de rédaction / *Assistant editor*: Emmanuel Côtez (adanson@mnhn.fr)

Mise en page / *Page layout*: Emmanuel Côtez

Comité scientifique / *Scientific board*:

P. Baas (Nationaal Herbarium Nederland, Wageningen)
F. Blasco (CNRS, Toulouse)
M. W. Callmander (Conservatoire et Jardin botaniques de la Ville de Genève)
J. A. Doyle (University of California, Davis)
P. K. Endress (Institute of Systematic Botany, Zürich)
P. Feldmann (Cirad, Montpellier)
L. Gautier (Conservatoire et Jardins botaniques de la Ville de Genève)
F. Ghahremaninejad (Kharazmi University, Téhéran)
K. Iwatsuki (Museum of Nature and Human Activities, Hyogo)
K. Kubitzki (Institut für Allgemeine Botanik, Hamburg)
J.-Y. Lesouef (Conservatoire botanique de Brest)
P. Morat (Muséum national d'Histoire naturelle, Paris)
J. Munzinger (Institut de Recherche pour le Développement, Montpellier)
S. E. Rakotoarisoa (Millenium Seed Bank, Royal Botanic Gardens Kew, Madagascar Conservation Centre, Antananarivo)
É. A. Rakotobe (Centre d'Applications des Recherches pharmaceutiques, Antananarivo)
P. H. Raven (Missouri Botanical Garden, St. Louis)
G. Tohmé (Conseil national de la Recherche scientifique Liban, Beyrouth)
J. G. West (Australian National Herbarium, Canberra)
J. R. Wood (Oxford)

Couverture / *Cover*:
Réalisée à partir des Figures de l'article/*Made from the Figures of the article*.

Adansonia est indexé dans / Adansonia *is indexed in:*
- Science Citation Index Expanded (SciSearch®)
- ISI Alerting Services®
- Current Contents® / Agriculture, Biology, and Environmental Sciences®
- Scopus®

Adansonia est distribué en version électronique par / Adansonia *is distributed electronically by:*
- BioOne® (http://www.bioone.org)

Adansonia est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Adansonia *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:* ***Geodiversitas***, ***Zoosystema***, ***Anthropozoologica***, ***European Journal of Taxonomy***, ***Naturae***, ***Cryptogamie*** **sous-sections** ***Algologie***, ***Bryologie***, ***Mycologie, Comptes Rendus Palevol***

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél.: 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

© Publications scientifiques du Muséum national d'Histoire naturelle, Paris, 2020
ISSN (imprimé / *print*): 1280-8571/ ISSN (électronique / *electronic*): 1639-4798

Gender expression in *Sedum praealtum* A. DC. (Crassulaceae) in Central Veracruz, Mexico

Angélica María HERNÁNDEZ-RAMÍREZ
Centro de EcoAlfabetización y Diálogo de Saberes, Universidad Veracruzana,
Avenida de las Culturas Veracruzanas No.1. Colonia Emiliano Zapata,
C.P. 91060, Xalapa (Veracruz)
angehernandez@uv.mx

Submitted on 20 September 2019 | accepted on 19 March 2020 | published on 21 September 2020

Hernández-Ramírez A. M. 2020. — Gender expression in *Sedum praealtum* A. DC. (Crassulaceae) in Central Veracruz, Mexico. *Adansonia*, sér. 3, 42 (13): 241-247. https://doi.org/10.5252/adansonia2020v42a13. http://adansonia.com/42/13

ABSTRACT

Inflorescence type and design determine the position of reproductive meristems and sequence of flowers opening. I examined the gender expression over two entire flowering seasons in *Sedum praealtum* A. DC. (Crassulaceae) in Central Veracruz, Mexico. Specifically, I studied the floral longevity, sexual-phase duration, flower opening within an inflorescence and sex ratio in the species. I observed that the 8-days flower initiated in male-phase and then switched to female-phase. An extended time of pollen presentation by gradual anthers dehiscence caused an incomplete protandry in the species. The basal-positioned floral buds reached anthesis sooner than the distal-positioned floral buds, resembling an acropetal flowering sequence. Inflorescences production ceased in the middle of the flowering season, whereas flower opening remained constant over reproductive season of the species. The opening of flowers in successive cohorts linked to changes in the flower sexual-phase phenology caused an initial sex expression toward maleness and a balanced sexual expression from the peak to the end of reproductive season in the population sampled. This study highlights the important influence that variations in onset and duration of sexual-phase of flowers can have on sex expression in flowering plants.

KEY WORDS
Dichogamy,
incomplete protandry,
sexual-phase,
sex ratio,
stonecrop.

RÉSUMÉ

Expression du genre dans Sedum praealtum *A. DC. (Crassulaceae) dans le centre de Veracruz, au Mexique.*
Le type et l'architecture de l'inflorescence déterminent la position des méristèmes reproducteurs et la séquence d'ouverture des fleurs. J'ai examiné l'expression du genre pendant deux saisons de floraison entières chez *Sedum praealtum* A. DC. (Crassulaceae) dans le centre de Veracruz, au Mexique. J'ai en particulier étudié la longévité florale, la durée de la phase sexuelle, l'anthèse au sein d'une inflorescence et le sex-ratio chez l'espèce. J'ai observé que la fleur de 8 jours commençait en phase mâle et passait ensuite en phase femelle. Une durée prolongée de présentation du pollen par la déhiscence progressive des anthères a provoqué une protandrie incomplète chez l'espèce. Les bourgeons floraux en position basale ont atteint l'anthèse plus tôt que ceux en position distale, évoquant une séquence de floraison acropète. La production d'inflorescences a cessé au milieu de la saison de floraison, alors que l'ouverture des fleurs s'est poursuivie pendant toute la saison de reproduction de l'espèce. L'ouverture des fleurs dans les cohortes successives est liée aux changements de la phénologie de la phase sexuelle des fleurs et a provoqué un décalage de l'expression sexuelle initiale vers la masculinité et ultérieurement une expression sexuelle équilibrée du pic à la fin de la saison de reproduction dans la population échantillonnée. Cette étude souligne l'influence importante que les variations dans l'apparition et de la durée de la phase sexuelle des fleurs peuvent avoir sur l'expression sexuelle des plantes à fleurs.

MOTS CLÉS
Dichogamie,
protandrie incomplète,
phase sexuelle,
sex ratio,
orpin.

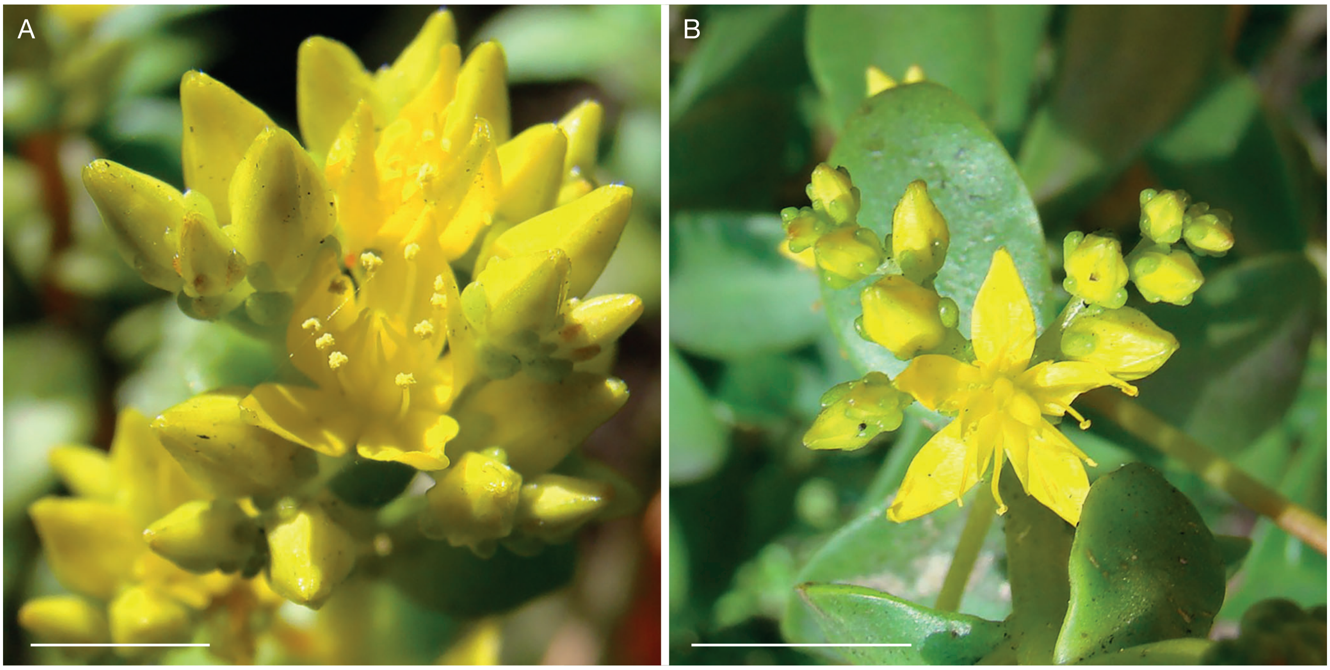

Fig. 1. — Male-phase and female-phase flowers of *Sedum praealtum* A. DC. (Crassulaceae). **A**, Male-phase flower with dehiscent anthers; **B**, Female-phase flower with expansion of the stigmas. Photos by Angélica Hernández-Ramírez. Scale bars: 0.5 cm.

INTRODUCTION

One of the most extraordinary manifestations of plant evolution and diversification is its diversity in gender expression, varying from all male flowers/individuals at one extreme, through different co-sexuality levels, to all female flowers/individuals at the other extreme (Lloyd 1980). Gender expression is derived from activation of the reproductive meristems positioned within an inflorescence in some plant species (Diggle 2003; Obeso 2002). On these plants, the inflorescence architecture determines the position of reproductive meristems, whereas the inflorescence development program gives rise to the flower opening sequence (Lloyd & Webb 1986; Brunet & Charlesworth 1995; but see Sargent & Roitberg 2000; Ishii & Harder 2012). In dichogamous plants, the temporal separation of sexual functions of flowers causes a predictable shift in gender expression across flowering season (from male-biased to female-biased in protandrous species, or from female-biased to male-biased in protogynous species; Lloyd & Webb 1986; Brunet & Charlesworth 1995).

Crassulaceae (stonecrops) is a morphologically diverse and complex family of succulent plants with approximately 1400 species. The family has a widespread distribution with five centers of diversity located in Mexico, Macaronesia, the Mediterranean basin, eastern Asia and southern Africa (reviewed by Thiede & Eggli 2006). The genus *Sedum* L. and its derivatives are the most successful, least specialized, and polyphyletic members of the family (Hart 1997; Thiede & Eggli 2006).

From the traditional taxonomy perspective, the genus *Sedum* is typified by the determinate growth pattern of its inflorescences (reviewed by Thiede & Eggli 2006). In the determinate inflorescence type of *Sedum*, main shoot ends in a flower, while growth remains though lateral axes below the terminal reproductive structure (Thiede & Eggli 2006; Hernández-Ramírez 2017). Furthermore, the members of the genus exhibit a conserved modular development, due to growth determination of its inflorescences occurs by a reiteration of structured-modules along the main stem (Thiede & Eggli 2006; Hernández-Ramírez 2017). With regard to flower bud development, the apical meristem develops from a vegetative growth stage to a reproductive stage in a basipetal sequence, initiating in succession from the apex to the base (Wyatt 1983; Thiede & Eggli 2006; Hernández-Ramírez 2017). The flower is usually actinomorphic with corolla differentiated into sepals and petals, having two whorls of stamens (Wyatt 1983; DeChaine & Martin 2005; Thiede & Eggli 2006; Hernández-Ramírez 2017). Protandry, when male function of flowers precedes female function of flowers has been reported in the genus (Wyatt 1983; Thiede & Eggli 2006).

Previous work has shown that inflorescence architecture has been accountable for variation in the male investment and female investment at flower level in the species (Hernández-Ramírez 2017). Given that inflorescence architecture seems to be determinant in the reproductive traits in *S. praealtum* A. DC., the species appears to be a good model to explore the gender expression under a differentiated modular approach (at flower, inflorescence and plant level), because it would be constrained by the inflorescence type, as for as reproductive structures depend upon where and when they are produced within the inflorescence (architectural effects hypothesis; Diggle 2003; Hernández-Ramírez 2017; and references there in).

The aim of this study was to study whether there is a predictable pattern in the gender expression according to flower and inflorescence type in *Sedum praealtum* (Crassulaceae) in Central Veracruz, Mexico. In view of dichogamy may cause a predictable shift in the sexual-phase of flowers (Lloyd & Webb 1986; Brunet & Charlesworth 1995), I hypothesized that *Sedum praealtum* would exhibit a protandrous flower, with a gender expression from male to female at flower level, as well as at individual level across flowering season (i.e., from maleness at the beginning of flowering season to femaleness at the end of flowering season; Lloyd 1980; Wyatt 1983; Diggle 1997, 2003; Thiede & Eggli 2006; Hernández-Ramírez 2017).

MATERIAL AND METHODS

Study population

Sedum praealtum A. DC. (Crassulaceae) is a succulent perennial plant endemic to Mexico. Synonyms of the species include: *Sedum dendroideum* subsp. *praealtum* (A. DC.) R.T. Clausen, 1959, and *Sedum dendroideum* Moc. & Sessé ex D.C., 1828 subsp. *dendroideum.* The original type description of the species was given from specimens collected in Mexico and grown in Geneva. Thus, it is needed to locate appropriate type specimens that represent the vegetative and floral traits of the species. This action currently is in processes.

The population of the species is located in Tlacolulan municipality, Veracruz, Mexico (19°39'46"N, 96°58'34"W). The study was carried out in 2017 and 2018. Previous work has reported that male investment in the flowers decreased from a distal-positioned to basal-positioned within inflorescences, whereas the opposite pattern was observed in the female investment in the flowers (Hernández-Ramírez 2017). The flowering season occurs from January to April. A complete description of the study area and population may be found in Hernández-Ramírez (2017).

Sex expression at flower level in the species

To characterize the sexual expression at flower level in the species, I randomly selected 20 plants from the study population. I chose and tagged at random one floral bud per plant. I daily monitored and recorded the sexual-phase of flower until it withered according to Lloyd & Webb (1986). As male phase precedes female one, the male phase was recorded from the date of the first dehiscence of an anther to the last dehiscence of an anther (Fig. 1A). The female phase was recorded from the date of expansion of the stigmas to the change of stigmatic papillae condition (Fig. 1B). The same protocol was repeated once a week during the period of flowering of the species (lasting 4 months; from January to April) over two years of survey. Differences in the sexual phase duration or flower longevity were assessed using Mann-Whitney test and Kruskal Wallis test (Zar 1999).

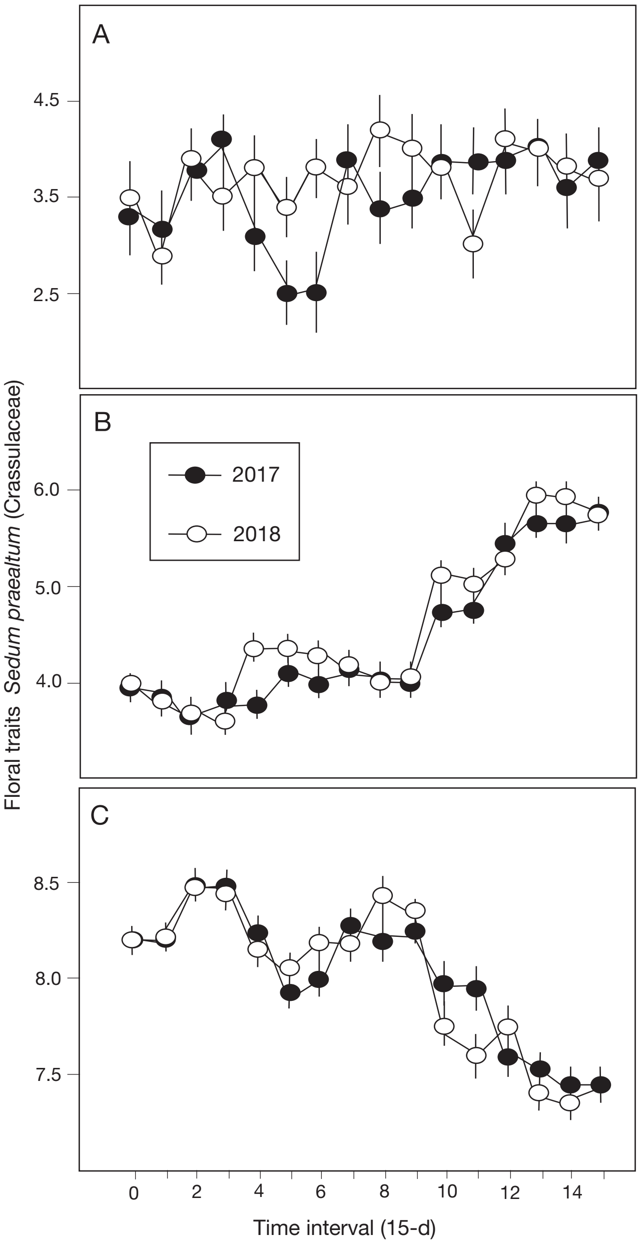

Fig. 2. — Floral traits in *Sedum praealtum* A. DC. (Crassulaceae). **A**, Floral longevity (days); **B**, Onset of female-phase flowers (days); **C**, Female-phase duration (days). Values are means ± SE.

Sex expression at inflorescence level in the species

The timing and sequence of the flowers opening were used to characterize the sexual expression at inflorescence level in the species. For that, I randomly selected one inflorescence from ten plants of a similar size. Five basal-positioned floral buds and five distal-positioned floral buds were tagged and monitored daily until flower's anthesis. The beginning of observation was recorded as time zero (floral buds tagging). The date of flower's anthesis was recorded as days elapsed from the beginning of observation to flower opening. Survival Analysis was used to determine how long did floral buds take to open (Muenchow 1986). Kaplan-Meier product-limit non-parametric method was used for the computation of

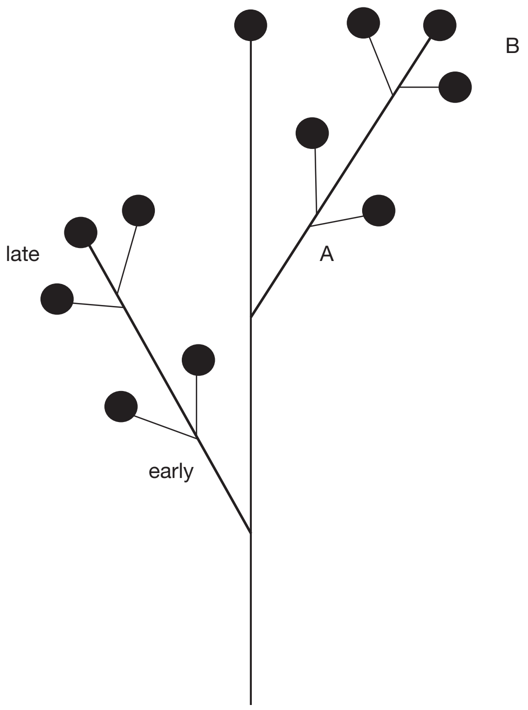

Fig. 3. — Scheme of inflorescence architecture of *Sedum praealtum* A. DC. (Crassulaceae). **A**, Basal-positioned floral buds; **B**, Distal-positioned floral buds.

probabilities of flower opening after beginning of observation. Lon-rank (Mantel-Cox) non-parametric statistic was used for testing differences in flower opening probabilities according to its position within the inflorescence.

Sex expression across flowering season in the species

I used the number of produced inflorescences and the sex ratio to characterize the variation in gender expression over time in the species. For that, I counted the total number of produced inflorescences in each tagged plant (20 randomly selected plants). Each count was performed once a week from January to April in two consecutive years. Furthermore, I randomly selected and tagged one inflorescence per plant. I recorded the sexual phase of each flower within the inflorescence once a week from 13:00 to 16:00 hrs according to Lloyd & Webb (1986). Due to male-phase function is extended through flower lifespan, I calculated the proportion of flowers that were in female-phase as a measure of sex ratio by each tagged plant (i.e., number of female-phase flowers/total number of flowers).

Repeated-measures nested ANOVAs were used to analyze differences between years in the number of produced inflorescences per plant or sex ratio per plant (Zar 1999). In the model, year was treated as a fixed factor and the plant was nested in the year factor. The number of produced inflorescences per plant or the sex ratio per plant were the repeated measures (response variables).

All statistical analyses were run using general linear modeling with SuperANOVA and StatView (Abacous Concepts 1989, 1996).

RESULTS

Sex expression at flower level in the species

The flower is yellow at anthesis but it changes to brown at the end of its lifespan. The flowers were open eight days (Mean ± SE; 8.05 ± 0.03 d; n = 640). There were not differences in the floral longevity between years and over flowering season (U = 48959.50, p = 0.33, H = 22.05, p = 0.10; respectively; Fig. 2A).

S. praealtum flowers are hermaphrodite, a flower begins in male-phase (anther dehiscence) and then it activates female-phase (expansion of the stigmas). When flowers open, all anthers are not dehiscen and the stigma is not receptive (closed stigmas). In the population sampled, dehiscence of anthers took place *c.* 7 h after flower opening and pollen grains were continuously released throughout flower's lifespan. The stigma became expanded (receptive) on average 3.0 days after flower opening and it remained so for 3-6 days, then the flower wilted (Mean ± S.E.; 3.0 ± 0.03 d, n = 640 onset of female-phase and 5.01 ± 0.04 d, n = 640 female-phase duration; Fig. 2B, C). Thus, pollen release (male-phase) were overlapped with stigma receptivity (female-phase) in *S. praealtum.*

There were not differences in the female-phase onset neither the female-phase duration between years (U = 47732.00, p = 0.14, and U = 50706.5, p = 0.83; Fig. 2B, C). A high variation in the female-phase onset and female-phase duration were observed across flowering season (H = 361.7, p < 0.0001, and H = 271.4, p < 0.0001). Furthermore, opposite trends were observed between female-phase onset and female-phase duration across flowering season of the species (Fig. 2B, C).

Sex expression at inflorescence level in the species

Floral buds took 12.8 days to reach anthesis (i.e., flower opening, 12.8 ± 0.35 S.E., n = 100). There were differences in the probabilities of floral buds opening according to its position within the inflorescence (Chi = 92.08, p < 0.0001; Fig. 3). Specifically, the basal-positioned floral buds were opened sooner than the distal-positioned floral buds (9.48 ± 0.16, n = 50 basal-position flowers and 16.37 ± 0.17, n =50, distal-positioned flowers; Fig. 4).

Sex expression across flowering season in the species

S. praealtum produced on average 7.7 inflorescences per plant (7.7 ± 0.14 S.E., n = 640). Results of the repeated-measures ANOVA showed a variation in the inflorescence production across flowering season (F = 279.85, p < 0.0001). The production of inflorescences reached its asymptote two months earlier in 2018 than in 2017 (factor interaction effect: F = 7.48, p < 0.0001; Fig. 5A). A similar inflorescence production was observed between years (F = 3.21, p = 0.08). Plant identity did not contribute to explain the observed differences in inflorescence production across time (F = 0.55, p = 0.86).

Each plant began by opening approximately two flowers per inflorescence, then successive cohorts of flowers opened at various time intervals, reaching its asymptote at the end of flowering season (F = 619.72, p < 0.0001; Fig. 5B). Variation in flower production was similar between years and among

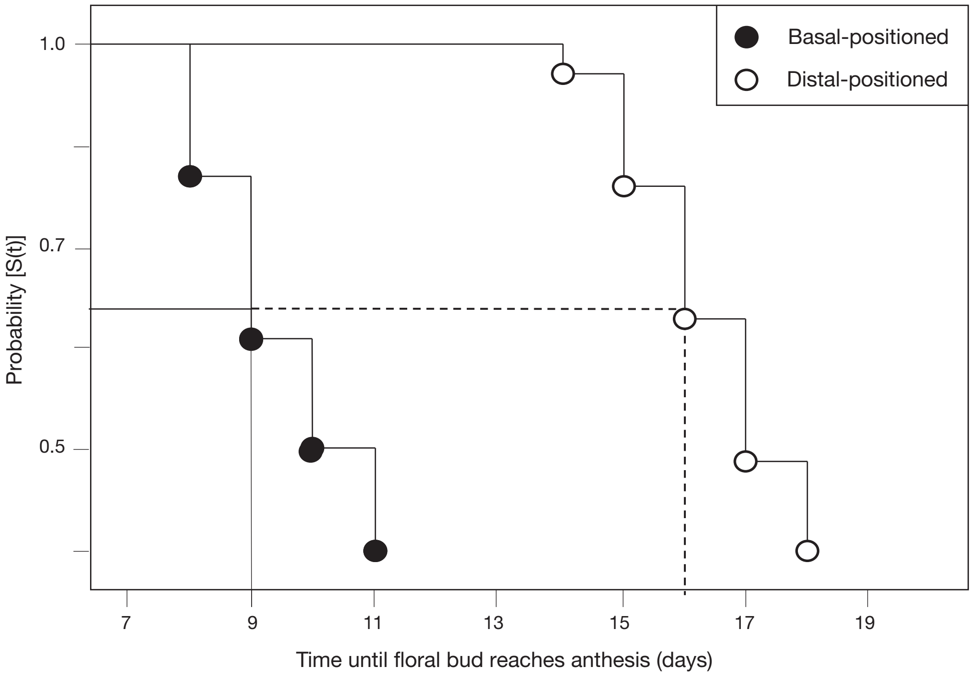

Fig. 4. — Comparison between basal-positioned floral buds (black circles) and distal-positioned floral buds (white circles) in its probability of reaching anthesis during observation period. The S(t) abbreviation is the probability that a floral bud has not opened. Time until floral bud reaches anthesis refers to the time elapsed since the begin of the observation period. Solid line shows mean of time that basal-positioned floral buds open, and dashed line shows mean of time that distal-positioned floral buds open.

individuals sampled (year effect: F = 0.10, p = 0.74; individuals nested in year effect; F = 1.57, p = 0.32). A higher flower production was observed in 2018 than in 2017 at the end of flowering season (factor interaction effect: F = 1.92, p = 0.01).

The pattern of flower development in multiple cohorts and the sequential hermaphroditism of flowers caused a variation in sex ratio across time. A male-biased gender was observed at the beginning of flowering season, whereas the sex ratio was balanced from the peak to the end of flowering season (F = 189.06, p < 0.0001; Fig. 5C). A similar pattern of gender variation was observed between years and among individuals sampled (year effect: F = 0.04, p = 0.83; individuals nested in year effect; F = 1.10, p = 0.51). Factor interaction was not significant in the model (factor interaction effect: F = 0.81, p = 0.58).

DISCUSSION

S. praealtum flowers exhibited a male-female sequential hermaphroditism, but an extended time of pollen presentation by gradual anther dehiscence caused an incomplete protandry in the species. To my knowledge, this is the first study that demonstrate an overlapped male and female functions in genus *Sedum*. The observed gradual dehiscence of anthers could enhance pollen transfer among flowers in the species (reviewed by Harder & Wilson 1994). Thus, *S. praealtum* flowers seem to operate with an extended pollen-dispatching mechanism. Protandry has been recognized as a strategy that improves outcrossing rate by reducing pollen-pistil interference within a flower (Lloyd 1980; Lloyd & Webb 1986; Brunet & Charlesworth 1995). The observed incomplete protandry in *S. praealtum* flowers could be more than just a mechanism that avoids self-fertilization, which requires future research.

Traits related to growth pattern have contributed to a number of dichotomies involving vegetative and reproductive traits in the taxonomy of *Sedum* (Hart 1997; Thiede & Eggli 2006). Whilst the developmental pattern of inflorescences usually typifies where and when floral buds are produced, the flower anthesis seems to be modeled, at least to some extent, by other factors beyond the determinate growth pattern of inflorescences in *S. praealtum*. Hernández-Ramírez (2017) observed that flowers within lateral branches were opened earlier than those within main axis. This study confirms previous observation, i.e., the flowers opening sequence within inflorescence resembles an acropetal flowering sequence (flower opening in sequence from the bottom to the top). Although the inflorescence growth pattern determines the position of floral buds, it does not determine the sequence of flower opening within the inflorescence.

In *S. praealtum*, the inflorescence production reached its asymptote at the middle of the flowering season, whereas an extended opening of flowers was observed through reproductive season. Although, the asynchronous development of the pre-existing reproductive meristems (both active and those remaining quiescent) contributed to explain the continuous opening of flowers over reproductive season, the differences between floral bud production timing and flower opening timing could compensate for architecture and modularity constraints linked to its inflorescence type. A similar phenom-

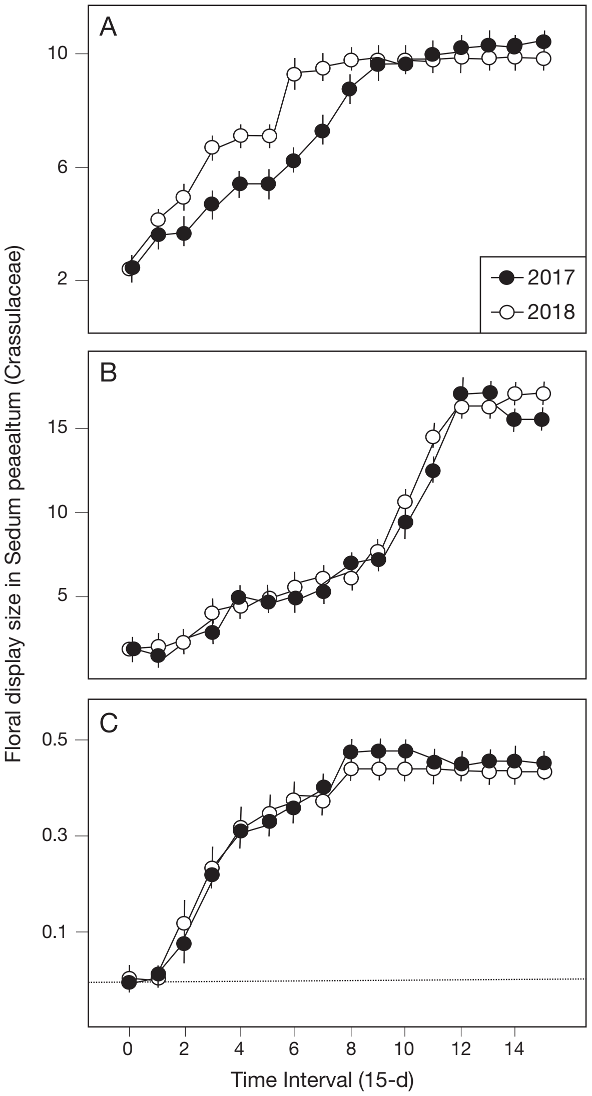

Fig. 5. — Floral display size in *Sedum praealtum* A. DC. (Crassulaceae): **A**, number of inflorescences; **B**, number of flowers; **C**, sex ratio (female-phase flowers/ total number of flowers). Values are means ± SE.

enon was reported in several species, including members of the Brassicaceae, Gentianaceae, Lythraceae, Orobanchaceae family (reviewed by Obeso 2002). It is well known that both endogenous factors (modification of transcriptional programs associated with gene expression; Lemmon *et al.* 2016), and exogenous factors may modify the development program of reproductive meristems within inflorescence (reviewed by Harder & Wilson 1994). Within the exogenous factors, the pollinators identity and behavior (reviewed by Harder & Wilson 1994), as well as differences in resource allocation (Lloyd & Webb 1986; Brunet & Charlesworth 1995) could modify the development program of flowers within an inflorescence. Specifically, theory suggest that adjusting the flower opening and extended pollen presentation in plants would be favored when pollinators were frequent and less efficient to pollen transfer (Castellanos *et al.* 2006). Hernández-Ramírez (2017) documented that *S. praealtum* exhibited pollen limitation, whereas investment allocation to flowers was not constrained by changes in resources status in the species. Thus, the atypical development program of flowers within the inflorescence linked to extended pollen presentation in *S. praealtum* might be at least partially attributable to the identity and behavior of pollinators. Regardless of what factors are operating in the development program of flowers within an inflorescence in *S. praealtum*, the inflorescences production cessation and the flowers opening continuity over flowering season suggest a potential trade-off between the elements that composed the floral display size. Identify the selection pressures and mechanisms that modulate floral display size in the species are potential avenues for future researches.

Typically, protandry promotes a predictable gender shift from maleness to femaleness in plants (Lloyd & Webb 1986; Brunet & Charlesworth 1995). Nonetheless, *S. praealtum* exhibited an initial sex expression toward maleness, but changes in the phenology of flowers modified the expected pattern of femaleness at the end of the flowering season. Specifically, late-produced flowers did become functionally female 1-2 days later than early-produced flowers. Furthermore, some late-produced flowers wilted before becoming female, modifying the expected female-biased ratio at the end of flowering season. In the species, the abortion of late-produced flowers may be a strategy that allows to reallocate resources and enhance fruit development of already pollinated female flowers (Lloyd & Webb 1986; Brunet & Charlesworth 1995; Hernández-Ramírez 2017). Although the mechanism underlying the modification of sex-phase of late-produced flowers requires future research, the results obtained in this study confirm that dichogamous species are able to modify its gender expression by changing the flower sexual-phase duration (Schoen & Ashman 1995; Routley & Husband 2005; Castro *et al.* 2008). The change of sexual-phase phenology of flowers over flowering season has also been noted in a number of species, including *Chamerion angustifolium* (L.) Holub (Sargent & Roitberg 2000) and *Delphinium glaucum* S. Watson (Ishii & Harder 2012). I hypothesized that *Sedum praealtum* would exhibit a protandrous flower, with a gender expression from male to female at flower level, as well as at individual level across flowering season (i.e., from maleness at the beginning of flowering season to femaleness at the end of flowering season). Based on the observed results, the hypothesis was rejected in the study population.

The results obtained in this study revealed that *S. praealtum* produced incomplete protandrous flowers developing in an acropetal sequence within an inflorescence. The species displayed a maleness sex expression at the beginning of flowering season, whereas a balanced gender expression was observed from the middle to the end of flowering season. The timing of reproductive meristem development, onset of sexual-phase and sexual-phase duration were the flower phenology traits that modified the gender expression in *S. praealtum* Thus, this study highlights the important effect that flower phenology traits may have on sex expression change under a modular approach in flowering plants.

Previous research has documented variation in the gender investment of flowers located at different position within the inflorescence in the species. Current research showed that floral traits associated with dichogamy, as well as flower opening sequence modified the sex expression in spite of inflorescence developmental pattern constraint of *Sedum*. The observed atypical pattern of flowering within the inflorescence in *S. praealtum* may be useful to understand the internal mechanisms regulating flowering and their interaction with pollinators. Understanding those mechanisms and its consequences would be usefulness for controlling time of flower opening and pattern of flower opening in domesticated plants.

Acknowledgements
I thank Guadalupe Hernández for her logistic support in field. I thank Thierry Deroin, Emmanuel Côtez, and an anonymous reviewer for improving an earlier version of this manuscript.

REFERENCES

ABACOUS CONCEPTS 1989. — Abacous Concepts. SuperAnova Reference. Abacous Concepts, Berkeley, California.

ABACOUS CONCEPTS 1996. — Abacous Concepts. StatView Reference. Abacous Concepts, Berkeley, California.

BRUNET J. & CHARLESWORTH D. 1995. — Floral Sex Allocation in Sequential Blooming Plants. *Evolution* 49: 70-79. https://doi.org/10.1111/j.1558-5646.1995.tb05959.x

CASTELLANOS M. C., WILSON P, KELLER S. J., WOLFE A. D. & THOMSON J. D. 2006. — Anther evolution: pollen presentation strategies when pollinators differ. *The American Naturalist* 167: 288-296. https://doi.org/10.1086/498854

CASTRO S., SILVEIRA P. & NAVARRO L. 2008. — Effect of pollination on floral longevity and costs of delaying fertilization in the out-crossing *Polygala vayredae* Costa (Polygalaceae). *Annals of Botany* 102: 1043-1048. https://doi.org/10.1093/aob/mcn184

DECHAINE E. G. & MARTIN A. P. 2005. — Marked genetic divergence among sky island populations of *Sedum lanceolatum* (Crassulaceae) in the Rocky Mountains. *American Journal of Botany* 92: 477-486. https://doi.org/10.3732/ajb.92.3.477

DIGGLE P. K. 1997. — Extreme preformation in alpine *Polygonum viviparum*: an architectural and developmental analysis. *American Journal of Botany* 84: 154-169. https://doi.org/10.2307/2446077

DIGGLE P. K. 2003. — Architectural effects on floral forms and function: a review, in STUESSY T., HÖRANDL E. & MAYER V. (eds), *Deep Morphology: Toward a Renaissance of Morphology in Plant Systematics*. Koeltz, Königstein: 63-80.

HARDER L. D. & WILSON W. G. 1994. — Floral evolution and male reproductive success: optimal dispensing schedules for pollen dispersal animal-pollinated plants. *Evolutionary Ecology* 8: 542-559. https://doi.org/10.1007/BF01238257

HERNÁNDEZ-RAMÍREZ A. M. 2017. — Architectural effects on floral traits in *Sedum praealtum* D.C. (Crassulaceae) in Mexico. *Haseltonia* 23: 35-38. https://doi.org/10.2985/026.023.0105

ISHII H. S. & HARDER L. D. 2012. — Phenological associations of within- and among-plant variation in gender with floral morphology and integration in protandrous *Delphinium glaucum*. *Journal of Ecology* 100: 1029-1038. https://doi.org/10.1111/j.1365-2745.2012.01976.x

LEMMON Z. H., PARK S. J., JIANG K., ECK J. V., SCHATZ M. C. & LIPPMAN Z. B. 2016. — The evolution of inflorescence diversity in the nightshades and heterochrony during meristem maturation. *Genome Research* 26: 1676-1686. https://doi.org/10.1101/gr.207837.116

LLOYD D. G. & WEBB C. J. 1986. — The avoidance of interference between the presentation of pollen and stigmas in angiosperms. I. Dichogamy. *New Zealand Journal of Botany* 24: 135-162. https://doi.org/10.1080/0028825X.1986.10409725

LLOYD D. G. 1980. — The distribution of gender in four angiosperm species illustrating two evolutionary pathways to dioecy. *Evolution* 34: 123-134. https://doi.org/10.1111/j.1558-5646.1980.tb04795.x

MUENCHOW G. 1986. — Ecological use of failure time analysis. *Ecology* 67: 246-250. https://doi.org/10.2307/1938524

OBESO J. R. 2002. — The cost of reproduction in plants. *New Phytologist* 155: 321-348. https://doi.org/10.1046/j.1469-8137.2002.00477.x

ROUTLEY M. B. & HUSBAND B. C. 2005. — Responses to selection on male-phase duration in *Chamerion angustifolium*. *Journal of Evolutionary Biology* 18: 1050-1059. https://doi.org/10.1111/j.1420-9101.2005.00896.x

SARGENT R. D. & ROITBERG B. D. 2000. — Seasonal decline in male-phase duration in a protandrous plant: a response to increase mating opportunities? *Functional Ecology* 14: 484-489. https://doi.org/10.1046/j.1365-2435.2000.00453.x

SCHOEN D. J. & ASHMAN T.-L. 1995. — The evolution of floral longevity: resource allocation to maintenance versus construction of repeated parts in modular organisms. *Evolution* 49: 131-139. https://doi.org/10.1111/j.1558-5646.1995.tb05965.x

'T HART H. 1997. — Diversity within Mediterranean Crassulaceae. *Lagascalia* 19 (1-2): 93-100. http://hdl.handle.net/11441/63144

THIEDE J. & EGGLI U. 2006. — Crassulaceae, in KUBITZKI K. (ed.), *The Families and Genera of Vascular Plants*. Vol. 9. Springer, Hamburg, Germany: 83-118.

WYATT R. 1983. — Reproductive Biology of the Granite Outcrop Endemic *Sedum pusillum* (Crassulaceae). *Systematic Botany* 8: 24-28. https://doi.org/10.2307/2418559

ZAR J. H. 1999. — Biostatistical Analysis. Fourth Edition. Prentice Hall, Ann Arbor, 929 p.

Submitted on 20 September 2019;
accepted on 19 March 2020;
published on 21 September 2020.