THE EFFECT OF FLOWERING SYNCHRONY AND FLORAL DISPLAY ON THE

REPRODUCTION OF A GYNODIOECIOUS ALPINE CUSHION PLANT,

SILENE ACAULIS (CARYOPHYLLACEAE)

by

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Departmental Honors Thesis

Appalachian State University

Submitted to the Department of Biology

in partial fulfillment of the requirements for the degree of

Bachelor of Science

May, 2018

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ABSTRACT

Flowering plant populations have various reproductive systems, potentially influencing the effects of different ecological factors on reproductive success. Gynodioecious systems include female plants that only produce seeds and hermaphroditic plants that produce both seeds and pollen. We tested whether floral display and flowering synchrony with conspecific neighbors affected the reproductive success of each sex in a gynodioecious species, *Silene acaulis*. Furthermore, we explored how varying the spatial scale and type (which sexes included in the neighborhood) of the neighborhoods used to define synchrony affected its correlation with fruit production. We observed four sites of this alpine cushion plant throughout the 2016 and 2017 flowering periods at Niwot Ridge, Colorado. We counted open flowers every other day and the total number of flowers and fruits produced at the end of each season for 628 individuals. Female plants had significantly higher raw fruit production and per-flower fruit set than hermaphrodites. The total number of flowers produced by an individual was positively correlated with fruit set, suggesting that individuals that produce more flowers are more likely to be pollinated. We found a positive correlation between synchrony of flowering and raw fruit production, however the mechanism behind that relationship is still unknown. Varying the spatial scale or type of neighborhood by which we calculated synchrony scores had no effect on synchrony's relationship with fruit production, however we still recommend that future studies on the effects of flowering synchrony carefully consider the effect of neighborhood size. Understanding the factors that influence the reproductive success of a gynodioecious population clarifies the processes that may influence populations' responses to climate change.

Key words: *Silene acaulis,* synchrony, reproduction, alpine, phenology

ACKNOWLEDGEMENTS

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INTRODUCTION

Reproductive success is a critical component of life history for many plants. Because plants are mostly sessile organisms, and individuals cannot migrate, reproduction provides the only means of population persistence other than survival. The rate at which new individuals are added to a population must equal or exceed the rate at which individuals die, else the population will decline to extinction over time. Reproduction allows for seed dispersal, and, if a local population goes extinct, dispersal from nearby populations can recolonize the empty patch of suitable habitat, providing a "rescue effect" that aids in metapopulation persistence (Hanski 1998). However, connectivity between subpopulations is necessary for the rescue effect to occur. Connectivity is lacking for plant species without a long-range dispersal mechanism, which means that patches of suitable habitat have no mechanism of being recolonized after a local population is extinguished (Eriksson 1996).

While short-term reproductive success is not as vital in populations of long-lived species that have the ability to endure periods of adverse reproductive conditions (Eriksson 1996), it is nevertheless a factor affecting the probability of persistence of those populations. Thus, the study of factors that influence seasonal reproductive success in a population of a long-lived species helps shed light on how the population may respond to changes in those factors.

Within a season, pollinators visit flowering plants in a non-random fashion. If a plant is pollen limited, an increase in pollination services is expected to increase its seed and/or fruit set (Ashman *et al.* 2004; Burd 1994; Bierzychudek 1981). Bumble bees visit plants with large floral displays more often than plants with smaller displays, and visit proportionally similar or fewer flowers per visit on many-flowered plants than few-flowered plants (Ishii, Hirabayashi, & Kudo 2008; Grindeland, Sletvold, & Ims 2005; Miyake & Sakai 2005; Mitchell *et al.* 2004; Ohashi & Yahara 2002, 1998; Vrieling *et al.* 1999; Goulson *et al.* 1998; Vaughton & Ramsey 1998; Conner & Rush 1996; Ohara & Higashi 1994; Eckhart 1991; Klinkhamer & de Jong 1990), suggesting that plants with larger floral displays receive more diverse pollen loads.

Synchronously flowering patches of conspecifics can increase pollinator visitation and access to pollen donors (Hegland & Boeke 2006; Ghazoul 2005; Grindeland, Sletvold, & Ims 2005; Waites & Ågren 2004; Ollerton & Diaz 1999; Dreisig 1995; Kunin 1993; Klinkhamer & de Jong 1990), or can conversely cause intraspecific competition for pollinators (Steven *et al.* 2003). Thus, conspecific flowering synchrony can have positive, negligible, or negative effects on reproductive success that vary by study system (Kempe 2015; Ison *et al.* 2014; Pires, Silva, & Freitas 2014; Parra-Tabla & Vargas 2007; Buide, Díaz-Peromingo, & Guitián 2002; McIntosh 2002; Ollerton & Lack 1998; Augspurger 1983).

We chose to investigate the role of conspecific flowering synchrony and individual floral display in an ecologically important native alpine perennial, *Silene acaulis*, in the Colorado Rocky Mountains. In harsh alpine and arctic environments, cushion plants like *S. acaulis* provide favorable microclimates that facilitate establishment of both native and non-native plants (in *S. acaulis*: Molenda, Reid, & Lortie 2012; Antonsson, Björk, & Molau 2009; and in other species: Reid, Lamarque, & Lortie 2010; Cavieres *et al.* 2007) as well as arthropods (Molenda, Reid, & Lortie 2012), thereby stabilizing species diversity within the habitat (Badano *et al.* 2006). However, the cumulative area of alpine habitat is expected to shrink as climate warms and lower elevation species invade mountaintops (Dirnböck, Essl, & Rabitsch 2011), and with that native alpine species are projected to be displaced (Halloy & Mark 2003). *Silene acaulis* is at particularly high risk of displacement due to its low growth rate and fecundity (Morris & Doak 1998), and low tolerance to shade, which would be introduced by encroaching tree lines expected with climate warming (Dirnböck, Essl, & Rabitsch 2011; Gehrig-Fasel, Guisan, & Zimmermann 2007).

The decline or total loss of *S. acaulis* from an alpine community could have negative downstream impacts on organisms that typically establish in its cushion. Reproduction and seed dispersal provide the only mechanism by which *S. acaulis* could shift to higher elevations to find more suitable habitat as climate warms, thus it is important to understand factors that might significantly impact its fecundity. The relative importance of floral synchrony to the reproductive success of *S. acaulis* in the Rocky Mountains is currently unknown, but synchrony has been shown to have a positive role in a European population (Kempe 2015).

Study questions

Using a gynodioecious population of *S. acaulis* found in the Rocky Mountains, four main questions are explored in this thesis:

1. **Does plant sex affect reproductive success?**
    Prediction: Females will produce more fruits and higher per-flower fruit sets than hermaphrodites due to a higher allocation of resources towards female functions.

2. **Does individual floral display affect reproductive success?** More specifically, does the total number of flowers a plant produces correlate with its fruit set?
    Prediction: Fruit set will increase with floral display due to many-flowered plants receiving more pollinator services than few-flowered plants.

3. **Does the spatiotemporal flowering synchrony of an individual with its conspecific neighbors affect its reproductive success?**
    Prediction: Synchrony will correlate positively with fruit production because synchronously flowering patches attract more pollinators and synchronously flowering plants have more access to nearby pollen.

4. **Does the relationship between flowering synchrony and reproductive success change depending on the scale or type of neighborhood used to define synchrony?** In this question, scale refers to the radius of the neighborhood and type refers to which sexes of plants are included as neighbors (both sexes or only hermaphrodites).
    Predictions: Synchrony defined by larger-scale neighborhoods will correlate more positively with fruit production than synchrony defined by small-scale neighborhoods because the main pollinator of *S. acaulis*, *Bombus sylvicola*, responds to flowering density at larger scales (Thomson 1981). Synchrony defined by hermaphroditic neighborhoods will correlate more positively with fruit production than synchrony defined by both-sexed neighborhoods because synchrony with specifically pollen donors (hermaphrodites) gives an individual more access to pollen, which should increase fruit production if the population is pollen limited.

METHODS

Study location and species

This study was conducted at the Mountain Research Station, Niwot Ridge (Front Range), Colorado in the summers of 2016 and 2017 as part of a National Science Foundation Research Experience for Undergraduates (REU) internship. The focal species, *Silene acaulis* (Caryophyllaceae), is a perennial, moss-like cushion plant with a circumboreal arctic and alpine distribution (Jones & Richards 1962), and is a common member of tundra habitat in North America's Rocky Mountains (Shykoff 1988). Individuals are extremely long-lived (the oldest cushions are estimated to be over 300 years old) and grow very slowly, however they can experience significant diebacks from year to year (Morris & Doak 1998). Each cushion posses a singular tap root and dense, green foliage occuring in rosettes (Jones & Richards 1962). *Silene acaulis* produces many small (9-12 mm in diameter) rose-pink flowers, and various populations have been characterized as subdioecious (Hegi 1981; Müller 1883), dioecious (Gleason & Cronquist 1963), or gynodioecious (Morris & Doak 1998; Shykoff 1992, 1988). The *S. acaulis* that occur in the Rocky Mountains (variety *subacaulescens* (FN Williams) CL Hitchc. and Maguire) exhibit a gynodioecious breeding system (Delph 2004; Delph & Carroll 2001; Marr 1998; Morris & Doak 1998; Shykoff 1992, 1988) with females tending to produce more (Shykoff 1988) and higher quality (Delph 2004) seeds than hermaphrodites. Hermaphrodites are protandrous, with anthers typically dehiscing one to two days after anthesis, and self-compatible, while females are obligate outcrossers (Shykoff 1988). The main pollinators of *S. acaulis* are alpine bumble bees, specifically *Bombus sylvicola* queens (Marr 1997; Shykoff 1992), however moths, flies, ants, and beetles (Delph & Carroll 2001; Marr 1997) also regularly visit their flowers. Seeds are dispersed locally by gravity and, to a certain extent, by wind, although they do not bear specialized structures to aid wind dispersal (Gehring & Delph 1999).

Selection of observational sites

Four sites (SN1, SN2, SN3, and SN4; Fig A1) of *S. acaulis* were selected on Niwot Ridge, CO (40.05˚N, 105.59˚W) in 2001 by Doak and Morris (2010) as part of a long-term demographic study and lie on an elevational gradient (3540 – 3613 m) completely above treeline. The sites also vary by microhabitat ranging from fellfield to dry meadow, with two sites lying on the West

Knoll and two on the East Knoll separated by a shallow valley. Each site has three to five transects (~20 x 1 m each) in which every individual *S. acaulis* has been permanently tagged (or, in the case of small individuals, marked with colored toothpicks due to low survival rates) and given an X-Y location relative to the transect line, where X is the distance along the transect line and Y is the distance perpendicular to the line. Precise GPS locations of the start and end of each transect allowed the use of each individual's X-Y mapping to determine its absolute location in ArcMap 10.4.1 (ESRI 2016; Fig. A2). We used the Generate Near Table tool to identify each plant's neighbors for five different neighborhood radii (0.5 m, 1 m, 3 m, 5 m, whole site; see Fig. A3). Although there are over a thousand tagged individuals on Niwot Ridge, data were only collected from individuals in two transects of each site for the purposes of this study, which totaled 628 plants.

Flowering phenology and synchrony indices

We collected flowering phenology data in 2016 and 2017 by counting the number of open flowers on each plant ($N = 628$ and 495 in 2016 and 2017, respectively) during regular surveys every 2-5 days during the flowering season (June 15-July 14 in 2016, June 15-July 17 in 2017). Flowers were considered open if pollinators could use them (petals at least 45˚ open) and closed if stigmas (in the case of females) and both stigmas and anthers (in the case of hermaphrodites) were wilted. The sex of each flowering plant was recorded and verified with records from previous years. We excluded plants for which sex could not be determined or was determined to be different in 2016 and 2017 from analyses that required the sex of the plant. With the phenology data collected, we were able to determine the day of year of first flower, last flower, and peak flower (the day on which the most flowers were recorded) for each individual and site. We also calculated each individual's flowering period (day of last flower - day of first flower) and each site's flowering period (the day the last plant no longer had open flowers - the day the first plant was recorded having open flowers). Each individual's proportional flowering period was calculated by dividing its flowering period by its site's flowering period.

Flowering synchrony (heretofore referred to as synchrony) was measured using an index that takes into account the proportion of open flowers on the focal plant that overlapped temporally with open flowers on its neighbors. The synchrony index (SI_p) was calculated with the equation,

$$SI_p = 1 - 0.5 \sum_{d=1}^{D} \left| \frac{F_{pd}}{F_{ps}} - \frac{F_{nd}}{F_{ns}} \right|$$

(Kempe 2015; Mahoro 2002), where F_{pd} and F_{nd} are the number of flowers open on focal plant p and on all of its neighbors n, respectively, on day d; D is the number of days that flowers were counted for an individual; and F_{ps} and F_{ns} are the total number of flowers produced during the season by focal plant p and all of its neighbors n, respectively (Kempe 2015). The index outputs values from zero to one, where one is the most synchronous an individual could be and zero is not synchronous at all (i.e., the individual only flowered while all of its neighbors had no flowers). Ten different synchrony indices (heretofore referred to as SI) were calculated for every plant which varied by the type of plants considered to be neighbors (hermaphrodites only or all conspecifics) and the spatial scale of the neighborhood (0.5 m, 1 m, 3 m, 5 m, and whole site radii; see Fig. A3). We distinguished the SIs defined by only hermaphroditic neighbors because only hermaphrodites can act as pollen donors for outcrossing, suggesting that females (obligate outcrossers) might have a specific reproductive response to being synchronous with hermaphrodites. Hereafter, the different SIs will be referred to by their scale and which sexes of neighbors are included such that 3 m SI (hermaphrodites) and Site SI (both sexes) indicate the SIs calculated with a 3 m radius of hermaphroditic neighbors and with a whole site radius of either sexed neighbors, respectively. Plants were given an SI of 'NA' if they were never recorded having flowers or if they had no neighbors at the given scale (this occurred most often in 0.5 m SI (hermaphrodites)).

Defining reproductive success
Doak and Morris (2010) have conducted yearly censuses of this population at the end of each summer season since 2001, in which they count each plant's fruits and measure the major (longest, a) and minor (perpendicular to the major axis, b) axes (if the plant had more than 20 rosettes). The area of the cushion is calculated as the area of an ellipse ($A = \pi ab$). The yearly censuses have continued up to and including the 2017 season. We also recorded the total number of flowers a plant produced during the 2016 and 2017 yearly censuses (on July 29 in 2016 and July 31 in 2017) as the total number of open, wilted, and fruiting flowers. This total flower count allowed us to calculate per-flower fruit set (hereafter referred to as fruit set) as the fruit count divided by the total flower count. Fruit set can be thought of as the proportion of flowers that

become a fruit. Raw fruit count may be considered a better measure than fruit set to compare reproductive success between plants in this system because the total flower counts ranged from 1 to 428, so in a pair of plants that both had a fruit set of 0.75, one could have had 3 out of 4 total flowers become fruits and the other could have had 300 out of 400 total flowers become fruits. However, fruit set may be a better metric to compare pollinator activity between plants. The total flower count was used as a metric for floral display, and either raw fruit production or fruit set was used as the measure of reproductive success depending on the question we were exploring.

Statistical analyses

General protocol

We checked data distributions for normality using Shapiro-Wilk normality tests before selecting parametric or nonparametric versions of each statistical test used. Variances of data distributions were compared using *F*-tests. For analyses comparing two groups (e.g., females and hermaphrodites or 2016 and 2017) with unequal variances and/or non-normal distributions, we used Mann-Whitney *U*-tests, whereas *t*-tests were used for groups with equal variances and normal distributions. In some cases, linear models were created to identify significant predictor variables for a response variable and analyses of variance (ANOVAs) or analyses of covariance (ANCOVAs) were used on those models to identify any significant interactions between predictor variables. All correlations were tested using Pearson product-moment correlations that output the correlation coefficient as Pearson's *r*.

All analyses were done in R version 3.3.1 (R Core Team 2016). Most figures were made in base R or with the R package ggplot2 (Wickham 2009), and the correlogram in figure 11 was made with the corrplot package (Wei & Simko 2017).

Assessing differences in reproductive success between the sexes

The number of fruits an individual plant produced each year from 2003 to 2017 was averaged and those averages were subsetted by sex. Data from 2001 and 2002 were excluded because the number of plants for which fruit production data was collected was substantially lower in those years ($N = 22$ in 2001 versus $N = 307$ in 2003). The variances of mean raw fruit production for females and hermaphrodites were not equal ($F = 0.42408$, $P < 0.0001$, Female df = 264,

Hermaphroditic df = 133), and Shapiro-Wilk normality tests suggest that neither female (W = 0.60425, $P < 0.001$) nor hermaphroditic (W = 0.62687, $P < 0.001$) means followed a normal distribution. Therefore, a one-tailed Mann-Whitney U-test was used to compare mean fruit production of the sexes.

Total flower production was collected along with fruit production in 2016 and 2017, and each plant's fruit set was calculated for those years as the number of flowers divided by the number of fruits. The data were subsetted by year (2016 and 2017) and sex (female and hermaphroditic), and an F-test concluded that the variances of fruit set for females and hermaphrodites were not equal in 2016 (F = 1.603, female df = 128, hermaphroditic df = 264, P = 0.001452) nor in 2017 (F = 1.5483, female df = 81, hermaphroditic df = 139, P = 0.02394). Shapiro-Wilk normality tests suggest that none of the subsets followed a normal distribution: 2016 female fruit sets (W = 0.95403, P = 0.0002489), 2016 hermaphrodite fruit sets (W = 0.91557, $P < 0.0001$), 2017 female fruit sets (W = 0.89003, $P < 0.0001$), and 2017 hermaphrodite fruit sets (W = 0.81741, $P < 0.0001$). Therefore, one-tailed Mann-Whitney U-tests were used to compare fruit sets between the sexes for both 2016 and 2017.

The relationship between floral display and fruit set
Since total flower production data were only collected in 2016 and 2017, analyses in this section only include plants that flowered in 2016 and/or 2017. An ANCOVA of the linear model, Fruit set ~ TotFlr + Year + Sex + TotFlr:Year + TotFlr:Sex + Year:Sex, where TotFlr is the total number of flowers a plant produced in a season and colons represent interactions, was conducted to identify any significant interactions between predictor variables (Table 3). No interaction terms were significant, suggesting that the effect of total flower production on fruit set did not vary by sex or year, and that the effect of sex on fruit set did not vary by year, so the correlation between total flower production and fruit set was run on a dataset including data from both sexes and years (N = 969).

The relationship between flowering synchrony and fruit production
Separate ANCOVAs of the linear model, Fruit ~ SI + Sex + Site + Year + SI:Sex + SI:Site + SI:Year, where Fruit is raw fruit production and colons represent interaction terms, were run for

each of the ten different SIs to identify any significant interactions between predictor variables. SI, site, sex, and year were significant predictors of fruit number in all ten models, but SI did not interact with sex, site, or year in seven of the models (Table 4). The 3 m SI (both sexes) did, however, have significant interactions with sex, site, and year. Similarly, 3 m SI (hermaphrodites) had significant interactions with sex and year, and 5 m SI (both sexes) had a significant interaction with year. Since some significant interactions occurred between certain SIs and sex, year, or site, separate correlations were run between each SI and raw fruit production for the complete dataset as well as data subsetted by sex, year, or site.

To test whether the effect of SI on fruit production changed with different neighborhood scales (1 m to whole site radii) or type (both sexes or hermaphrodites only), a separate regression was run for each SI on the linear model, Fruit ~ SI. The 0.5 m SIs were excluded because they would have reduced the sample size for all correlations from 498 to 428. These regressions were run for the complete dataset (Fig. 5 & 6, Table 5), the data subsetted by sex (Fig. 7, Table 6), the data subsetted by year (Fig. 8, Table 7), and the data subsetted by site (Fig. 9, Table 8). Correlations were compared using Z-tests that required Pearson's r to be transformed to Fisher's z prior to comparisons (Meng, Rosenthal, & Rubin 1992).

RESULTS

Assessing differences in reproductive success between the sexes
A one-tailed Mann-Whitney U-test concluded that the mean number of fruits female plants produced (mean = 13.25) from 2003 to 2017 was significantly higher than that of hermaphroditic plants (mean = 8.50, $W = 21026$, $P = 0.0013$, df = 397, Fig. 1, Table 1). However, the number of individuals for which fruit production was recorded varied each year (see df column in Table 1), so one-tailed Mann-Whitney U-tests testing if females produced more fruits than hermaphrodites were also conducted for each year separately (Fig. 2, Table 1). Females produced significantly ($P < 0.05$) more fruits than hermaphrodites in 2006, 2009, 2010, 2013, 2016, and 2017, and tended ($P < 0.1$) to produce more fruits in 2011 and 2015. While hermaphrodites had higher averages of fruits produced than females in 2005 and 2012, their means were not significantly different.

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One-tailed Mann-Whitney U-tests were used to compare fruit sets between the sexes in 2016 and 2017 and concluded that females had significantly higher fruit sets than hermaphrodites in both 2016 ($W = 23472$, $P < 0.0001$, df = 392) and 2017 ($W = 7059.5$, $P = 0.0019$, df = 220, Fig. 3, Table 2). Plants in 2016 tended to have higher fruit sets than plants in 2017 ($W = 49082$, $P = 0.0056$, df = 614).

A t-test concluded that female plants (mean = 9.40 days) had open flowers on their cushions for significantly fewer days than hermaphroditic plants (mean = 11.53 days, $t = -3.987$, $P < 0.0001$, df = 350.21).

The relationship between floral display and fruit set

There was a significant positive correlation between total flower count and fruit set when plants of different sexes and years were run in the same regression ($r = 0.2928$, $t = 9.5213$, $P < 0.0001$, df = 967, Fig. 4).

The relationship between flowering synchrony and fruit production

Figures 5-9 and tables 5-8 show that all SIs correlated positively with raw fruit production, no matter how the data were subsetted, although a few correlations in the subsetted analyses were non-significant (see Fig. 7 & 9). This suggests that, overall, synchrony has a positive correlation with fruit production.

Tables 9 and 10 show the results of pairwise correlation coefficient comparisons of the correlations between SI and fruit production for neighborhood type and scale, respectively (for the complete dataset only). The non-significant differences in r-values in these figures and tables suggest that the correlation between SI and fruit production did not change with the scale or type of the neighborhood used to define the SI.

To understand why the correlation between fruit production and SI did not vary by which SI was used, correlations were performed between Site SI and the other four scales (0.5, 1, 3, and 5 m radii) for SIs using both sexed neighbors (Fig. 10A) and only hermaphroditic neighbors (Fig. 10B) and results for all correlations are reported in Table 11. The correlations strengthen as the

radii for each SI increase (i.e., become more similar to the Site SI radius). A correlogram was created to go one step further in showing how each type of SI correlated to every other SI (Fig. 11). The results of all 55 correlations shown in the correlogram are reported in Table 12. All correlations between SIs were significant and strongly positive (all r > 0.6 and P < 0.0001). The strongest correlations were between SIs of similar scale and type (e.g., Site SI (both sexes) and Site SI (hermaphrodites)), while the weakest correlations were between SIs using radii of opposing scale and type (e.g., Site SI (both sexes) and 0.5 m SI (hermaphrodites)).

Since each SI is calculated with an equation that takes into account the proportion of open flowers on the focal plant that overlapped temporally with open flowers on its neighbors, we thought the strong positive correlations between each SI might have to do with the flowering period of an individual plant relative to its site's flowering period. Hermaphroditic plants (mean +/- SE = 0.3768 +/- 0.0103) flowered for a higher proportion of their site's flowering period than female plants (mean +/- SE = 0.3166 +/- 0.0145, t = -3.39, P = 0.0004, df = 322.69, Fig. 12). Furthermore, the proportional flowering period of an individual had a significant positive correlation with its Site SI (both sexes) (r = 0.5269, t = 13.411, P < 0.0001, df = 468, Fig. 13).

DISCUSSION

Assessing differences in reproductive success between the sexes
We initially asked whether the sex of individuals in a gynodioecious population of *Silene acaulis* affects reproductive success. Female plants in our study had higher raw fruit production and fruit sets than hermaphrodites on average (Figs. 1-3), which supports the hypothesis that females are more reproductively successful than hermaphrodites. These results are consistent with other studies on sexual polymorphisms in *S. acaulis* (Delph 2004; Shykoff *et al.* 2003; Delph & Carroll 2001; Shykoff 1992, 1988). The disparity between sexes is likely due to a higher allocation of resources towards producing fruits by females than by hermaphrodites (see discussion in Burd 1994). For example, though Shykoff (1988) found no difference in individual flowering periods between the sexes, we found that hermaphroditic plants flowered for two days longer than females on average, suggesting that hermaphrodites may need to allocate more resources towards flower maintenance than females. Hermaphrodites also allocate resources

towards male functions, such as producing pollen (Charlesworth & Charlesworth 1981) and producing larger flowers than females (Philipp, Jakobsen, & Nachman 2009; Shykoff *et al.* 2003). Females can instead allocate resources towards fruit and seed development (Shykoff *et al.* 2003; Sakai *et al.* 1997; Burd 1994).

Differential rates of inbreeding may provide an alternative or additional hypothesis to explain higher reproduction rates in *S. acaulis* females. Shykoff (1988) showed that offspring from female *S. acaulis* have higher survival rates than those of outcrossed hermaphrodites, which in turn have higher survival rates than selfed hermaphrodites, suggesting that the superiority of females' offspring can be partially, but not completely, attributed to inbreeding depression in hermaphrodites (see Sun & Ganders 1986 for further support of this hypothesis). Shykoff (1992) showed that female *S. acaulis* flowers recruit more pollen tubes than hermaphroditic flowers, which increases gametophytic competition that favors fit pollen genotypes, thereby increasing offspring fitness, as well as probability of fertilization, of female flowers. Male-sterility (being female) in plants is thought to follow cytoplasmic inheritance, suggesting that sex expression is inherited maternally (Laporte *et al.* 2001). Delph & Carroll (2001) suggest that ecological factors such as site quality impact the maintenance and frequency of females in populations even though Gouyon *et al.* (1991) posit that cytoplasmic inheritance should not be affected by any ecological factor. Since females in the Niwot Ridge population have significantly higher reproductive success than hermaphrodites when measured by both raw fruit production and fruit set, and female fruits produce higher quality seeds that produce more successful offspring, it is clear that females play an important role in increasing the overall reproductive success and fitness of this gynodioecious population by reducing inbreeding depression and maintaining genetic diversity among individuals (Sakai *et al.* 1997). Hence, the maintenance of females is likely due to both genetic (e.g., cytoplasmic inheritance and inbreeding depression) and ecological (e.g., pollination intensity and site quality) factors.

The relationship between floral display and fruit set
Our second question was: does the floral display, measured by total number of flowers, a plant produces affect its reproductive success? The significant positive correlation between total flower count and fruit set (Fig. 4) suggests that individual flowers on a plant with a high number

of flowers are more likely to become fruits than flowers on a plant with a low number of flowers. It is widely observed that floral display size is an important visual signal for pollinators at multiple scales from large patches to individual plants (Ishii, Hirabayashi, & Kudo 2008; Grindeland, Sletvold, & Ims 2005; Thomson 1981). All else being equal, individual plants with more flowers should provide greater visual and olfactory cues at short distances making those plants both more attractive to pollinators and a better actual investment; many-flowered plants are therefore more likely to experience greater visitation and pollination services compared to those with a smaller display.

While bumble bees visit many-flowered plants more often, they visit a similar or lower proportion of flowers on those plants than on few-flowered plants (Ishii, Hirabayashi, & Kudo 2008; Grindeland, Sletvold, & Ims 2005; Miyake & Sakai 2005; Mitchell *et al.* 2004; Ohashi & Yahara 2002, 1998; Vrieling *et al.* 1999; Goulson *et al.* 1998; Vaughton & Ramsey 1998; Conner & Rush 1996; Ohara & Higashi 1994; Eckhart 1991; Klinkhamer & de Jong 1990), which indicates that flowers on many-flowered plants receive more diverse pollen, increasing gametophytic competition and fertilization probability of flowers on those plants (Shykoff 1992), thereby increasing fruit set. An alternative and untested hypothesis to explain the observed relationship between total flower count and fruit set could be that plants that have enough resources to produce many flowers are more likely to have enough resources to successfully convert those flowers into fruits after being pollinated, which is likely the case if the population is not pollen limited. We intend to assess the relative contributions of resources and pollination to reproductive success in the upcoming data-collection season.

The relationship between flowering synchrony and fruit production
Our third question was: does the spatiotemporal flowering synchrony of an individual with its conspecific neighbors affect its reproductive success? The overall positive, albeit weak, correlation between every type of SI and fruit production (Fig. 5-9), suggest that plants that flower synchronously with their conspecific neighbors have a higher reproductive success. These results support our prediction and could support the hypothesis that neighborhood floral display synchrony acts to attract pollinators to the neighborhood, thereby increasing pollinator visitation to and reproductive fitness of plants in that neighborhood. It could also support the hypothesis

that higher flowering synchrony increases reproductive success by giving plants in a neighborhood more access to pollen donors. For either of these hypotheses to be supported, the population must be under some degree of pollen limitation, otherwise more access to pollen donors and/or more frequent pollinator visitation would not alter reproductive success. Unfortunately, we have yet to experimentally assess pollen limitation in this population, which means we are not able to directly distinguish effects of pollen limitation and resource limitation on reproductive success. The only other study on the effects of flowering synchrony on reproductive success in *S. acaulis,* done by Kempe (2015), also reports a positive correlation between synchrony and reproductive success and attributes that relationship to pollen limitation, based on observed pollen limitation in another nearby population of *S. acaulis* 13 years prior (Alatalo & Molau 2001). Nevertheless, the potential for either or both the pollinator attraction or the pollen donor hypotheses to be valid exists and warrants further study.

Our fourth question was: does the relationship between flowering synchrony and reproductive success change with the neighborhood scale or type (which sexes of neighbors are included) by which flowering synchrony is defined? Here, the positive relationship between SI and fruit production did not differ depending on which scale or type of neighborhood was used, no matter how the dataset was subsetted (i.e., by year, sex, or site; Figs. 5-9 and Tables 9 & 10).

Since the correlations between fruit and SIs of different sized neighborhoods were not different (Fig. 6; also see Fig. 5 & Table 10), the prediction that synchrony at larger scales would be better predictors for reproductive success is not supported. The main pollinator of *S. acaulis*, *Bombus sylvicola*, responds to flowering densities at around 500 m^2 patch sizes (Thomson 1981), which is about the size of our sites. If the hypothesis that synchrony increases reproductive success by attracting pollinators to the neighborhood were supported, and pollinators are expected to respond to larger neighborhood sizes, we would have expected SIs defined by larger neighborhoods to have stronger correlations with fruit production than SIs defined by smaller neighborhoods. Therefore, our results do not support the hypothesis that synchrony increases reproductive success via pollinator attraction. However, as later discussed, *S. acaulis* may not be an ideal system to use when trying to identify the mechanism by which synchrony and reproductive success are related.

These results also fail to support our prediction that the effect of SI on reproductive success would vary by neighborhood type (what sexes were considered neighbors). Since the correlations between fruit and SIs of both sexed neighborhoods and hermaphroditic neighborhoods were not different (Fig. 6; also see Fig. 5 & Table 9), the hypothesis that synchrony increases reproductive success via pollen donor access is not supported. If the hypothesis were supported, we would have expected to see stronger correlations between fruit and SIs (hermaphrodites) than SIs (both sexes). Specifically, we expected synchrony with hermaphroditic neighbors to be a larger factor in female than in hermaphroditic reproductive success because females are obligate outcrossers that rely on hermaphrodites as pollen donors while hermaphrodites are self-compatible, however those correlations were no different (Fig. 7). This could suggest that the population is not pollen limited, however we did not test for pollen limitation directly.

The strong positive correlations between Site SI and the other neighborhood scales (Fig. 10) as well as among all pairwise SIs (Fig. 11) provide insight into why the effect of synchrony did not change with neighborhood scale or type. Since all types and scales of SIs are highly correlated, it makes sense that the correlations between each distinct SI and fruit production would not differ much. The strong positive correlation between proportional flowering period (individual flowering period divided by its site's flowering period) and Site SI (Fig. 13) helps to elucidate why all SIs are so highly correlated. Individual *S. acaulis* in this population seem to keep their flowers open for high proportions of their site's flowering period (Fig. 12), suggesting each site and the whole population are considered highly synchronous.

Perhaps plants that flower for a lower proportion of their population's flowering period, or where the whole population is less synchronous, might exhibit more variable synchrony indices at different scales, which would allow for the detection of fine-scale impacts of floral display synchrony on reproductive success. To get an idea of how relatively short this population's flowering period is (our sites averaged 4.2 weeks), Arroyo, Armesto, & Villagran (1981) reported that alpine species at 3550 meters-above-sea-level (similar to our sites) in the Chilean Andes had an average population flowering period of 10.8 weeks. The proportionally long flowering period of individuals in the Niwot Ridge population (individuals averaged 10.8 days,

around a third of their site's flowering period) may serve as a bet-hedging strategy to increase the chance of pollinator visitation in an alpine habitat documented to have low levels of insect diversity and activity (Bingham & Orthner 1998; Ashman & Schoen 1994).

The yearly minimum temperature on Niwot Ridge has been increasing for the past two decades, and the minimum and maximum July temperatures have been increasing over the past six decades (McGuire *et al*. 2012). These temperature shifts could lengthen growing periods for plants due to earlier onset of spring events, such as last frost, leafing, and flowering, and later onset of fall events, such as first frost and leaf color change (Linderholm 2006; Menzel *et al*. 2006; Robeson 2002; Menzel & Fabian 1999). If the overall flowering period of the population on Niwot Ridge increases, more fine-scale impacts of floral synchrony on reproductive success may be seen if the population as a whole becomes less synchronous, with plants in highly synchronous patches potentially receiving more visits from pollinators than plants in less synchronous patches due to variable pollinator attraction.

Conclusions

We add to the collection of studies that describe the mechanism by which females are maintained in a gynodioecious population, that is, by having significantly higher reproductive fitness than hermaphrodites. Further, we observe a positive relationship between total flower production and per-flower fruit set, however the mechanism behind that relationship cannot be distinguished by this study in its present form. It is clear that flowering synchrony is a significant predictor of reproductive success in this population, however the mechanism by which that relationship exists is not yet understood. These three factors, sex, flower production, and flowering synchrony, are significant predictors of reproductive success and should be considered when attempting to make a parsimonious model for predicting reproductive success of individuals in this population.

Future studies on the impacts of floral display and flowering synchrony on reproductive success should experimentally assess pollination limitation by hand-pollinating a few plants at each site to compare fruit production between natural and hand-pollinated plants. This would help the researcher distinguish between the relative effects of resource and pollination limitation on reproductive success (Burd 1994; Bierzychudek 1981) and would thereby strengthen any

hypotheses implicating pollen or resource limitation as factors influencing trends in reproductive success. Furthermore, if a researcher wishes to study how the spatial scale of flowering synchrony alters the relationship between synchrony and reproductive success, we recommend they choose a study system in which individual plants have short flowering periods relative to their population so that fine-scale variation in flowering schedule can be detected.

TABLES

Table 1. The results of one-tailed Mann-Whitney U-tests comparing the fruit production of females and hermaphrodites each year from 2003 to 2017 and their average fruit production over those years (last row). The p-values for years in which females produced significantly more fruits than hermaphrodites ($P < 0.05$) are bold, and years in which females tended to produce more fruits than hermaphrodites ($P < 0.1$) are italic.

Year	p-value	df	Mean (females)	Mean (herm)	SE (females)	SE (herm)
2003	0.3489	305	22.73	15.42	4.88	2.32
2004	0.7034	319	6.93	5.98	1.72	0.88
2005	0.7132	331	16.61	17.25	3.15	2.38
2006	**0.0001**	329	8.53	4.53	1.51	0.80
2007	0.3204	256	7.00	6.53	1.12	0.91
2008	0.8474	351	6.52	5.97	1.50	0.78
2009	**0.0021**	358	34.69	19.80	6.54	2.73
2010	**0.0001**	360	33.37	13.63	5.58	1.68
2011	*0.0564*	361	5.41	4.06	1.02	0.61
2012	0.7944	371	3.13	3.30	0.87	0.54
2013	**0.0438**	371	3.73	2.65	0.81	0.44
2014	0.3246	376	12.57	8.36	2.74	1.28
2015	*0.0716*	384	17.21	11.09	2.39	1.26
2016	**0.0017**	397	26.51	18.07	4.36	1.97
2017	**0.0418**	325	10.40	6.63	1.58	0.94
Average	**0.0013**	397	13.25	8.50	1.84	0.85

Table 2. The results of one-tailed Mann-Whitney *U*-tests comparing the fruit set of females and hermaphrodites in 2016 and 2017. The *p*-values for years in which females produced significantly more fruits than hermaphrodites ($P < 0.05$) are bold.

Year	*p*-value	df	Mean (females)	Mean (herm)	SE (females)	SE (herm)
2016	**<0.0001**	392	0.4479	0.2589	0.0257	0.0142
2017	**0.0019**	220	0.3743	0.2285	0.0369	0.0227

Table 3. The p-values of each term from an ANOVA of the linear model, Fruit set ~ TotFlr + Year + Sex + TotFlr:Year + TotFlr:Sex + Year:Sex, where TotFlr means the total number of flowers a plant produced in a season. Significant ($P < 0.05$) p-values are bold, and nearly significant ($P < 0.1$) p-values are italic.

	TotFlr	Year	Sex	TotFlr:Year	TotFlr:Sex	Year:Sex	Residuals
p-value	**<0.0001**	**0.0009**	**<0.0001**	0.4587	0.8948	*0.0764*	-
F-value	34.993	11.109	60.105	0.5498	0.0175	3.1505	-
df	1	1	1	1	1	1	661

Table 4. The p-values of each term from an analysis of covariance (ANCOVA) of the linear model, Fruit ~ SI + Sex + Site + Year + SI:Sex + SI:Site + SI:Year. The synchrony index (SI) used for each model is specified, and significant ($P < 0.05$) terms for each model are bold. The residual degrees of freedom (df) for each model are also reported.

SI used in model	SI	Sex	Site	Year	SI:Sex	SI:Site	SI:Year	df
0.5 m SI (both)	**0.0103**	**0.0023**	**0.0013**	**<0.0001**	0.5952	0.2911	0.5819	462
0.5 m SI (herm)	**0.0021**	**0.0023**	**0.0102**	**0.0003**	0.4384	0.1832	0.3527	416
1 m SI (both)	**0.0006**	**0.0012**	**0.0013**	**<0.0001**	0.1094	0.3316	0.1709	486
1 m SI (herm)	**0.0006**	**0.0009**	**0.0012**	**<0.0001**	0.1227	0.2474	0.3935	486
3 m SI (both)	**<0.0001**	**0.0001**	**0.0014**	**<0.0001**	**0.0336**	**0.0389**	**0.0071**	486
3 m SI (herm)	**<0.0001**	**0.0002**	**0.0015**	**<0.0001**	**0.0494**	0.0954	**0.0495**	486
5 m SI (both)	**<0.0001**	**0.0002**	**0.0012**	**<0.0001**	0.0938	0.0565	**0.0341**	486
5 m SI (herm)	**<0.0001**	**0.0002**	**0.0021**	**<0.0001**	0.3724	0.1076	0.1404	486
Site SI (both)	**0.0001**	**0.0003**	**0.0006**	**<0.0001**	0.6468	0.1025	0.0981	486
Site SI (herm)	**0.0003**	**0.0004**	**0.0013**	**<0.0001**	0.9858	0.4296	0.2236	486

Table 5. The results from a regression of the linear model, Fruit ~ SI, where SI refers to the specific synchrony index used in the regression. Significant ($P < 0.05$) correlations have their *p*-value in bold. These tests correspond to Figs. 5 & 6.

SI used in test	r	r^2	*p*-value	t	df
1 m SI (both)	0.1478	0.0219	**0.0009**	3.3291	496
3 m SI (both)	0.2051	0.0421	**<0.0001**	4.6674	496
5 m SI (both)	0.1842	0.0339	**<0.0001**	4.1727	496
Site SI (both)	0.1651	0.0272	**0.0002**	3.7270	496
1 m SI (herm)	0.1472	0.0217	**0.0010**	3.3137	496
3 m SI (herm)	0.1898	0.0360	**<0.0001**	4.3045	496
5 m SI (herm)	0.1689	0.0285	**0.0002**	3.8166	496
Site SI (herm)	0.1537	0.0236	**0.0006**	3.4648	496

Table 6. The results from a regression of the linear model, Fruit ~ SI, subsetted by sex, where SI refers to the specific synchrony index used in the regression. 'Fems' refers to females and 'Herms' refers to hermaphrodites. Significant ($P < 0.05$) correlations have their *p*-value in bold. These tests correspond to Fig. 7.

SI used in test	Sex	r	r^2	*p*-value	t	df
1 m SI (both)	Fems	0.2050	0.0420	**0.0067**	2.7469	172
3 m SI (both)	Fems	0.2756	0.0759	**0.0002**	3.7599	172
5 m SI (both)	Fems	0.2412	0.0582	**0.0013**	3.2599	172
Site SI (both)	Fems	0.1731	0.0300	**0.0223**	2.3055	172
1 m SI (herm)	Fems	0.2053	0.0421	**0.0066**	2.7508	172
3 m SI (herm)	Fems	0.2618	0.0685	**0.0005**	3.5574	172
5 m SI (herm)	Fems	0.2035	0.0414	**0.0071**	2.7265	172
Site SI (herm)	Fems	0.1478	0.0218	*0.0517*	1.9596	172
1 m SI (both)	Herms	0.1302	0.0170	**0.0190**	2.3566	322
3 m SI (both)	Herms	0.2014	0.0406	**0.0003**	3.6891	322
5 m SI (both)	Herms	0.1958	0.0383	**0.0004**	3.5829	322
Site SI (both)	Herms	0.2308	0.0533	**<0.0001**	4.2566	322
1 m SI (herm)	Herms	0.1341	0.0180	**0.0158**	2.4275	322
3 m SI (herm)	Herms	0.1831	0.0335	**0.0009**	3.3412	322
5 m SI (herm)	Herms	0.2113	0.0446	**0.0001**	3.8788	322
Site SI (herm)	Herms	0.2342	0.0548	**<0.0001**	4.3227	322

Table 7. The results from a regression of the linear model, Fruit ~ SI, subsetted by year, where SI refers to the specific synchrony index used in the regression. Significant ($P < 0.05$) correlations have their p-value in bold. These tests correspond to Fig. 8.

SI used in test	Year	r	r^2	p-value	t	df
1 m SI (both)	2016	0.1407	0.0198	**0.0140**	2.4705	302
3 m SI (both)	2016	0.2114	0.0447	**0.0002**	3.7583	302
5 m SI (both)	2016	0.1753	0.0307	**0.0022**	3.0943	302
Site SI (both)	2016	0.1509	0.0228	**0.0084**	2.6533	302
1 m SI (herm)	2016	0.1314	0.0173	**0.0220**	2.3031	302
3 m SI (herm)	2016	0.1824	0.0333	**0.0014**	3.2245	302
5 m SI (herm)	2016	0.1512	0.0229	**0.0083**	2.6582	302
Site SI (herm)	2016	0.1415	0.0200	**0.0135**	2.4839	302
1 m SI (both)	2017	0.2124	0.0451	**0.0030**	3.0113	192
3 m SI (both)	2017	0.2347	0.0551	**0.0010**	3.3450	192
5 m SI (both)	2017	0.2775	0.0770	**0.0001**	4.0020	192
Site SI (both)	2017	0.2923	0.0854	**<0.0001**	4.2349	192
1 m SI (herm)	2017	0.2328	0.0542	**0.0011**	3.3176	192
3 m SI (herm)	2017	0.2617	0.0685	**0.0002**	3.7579	192
5 m SI (herm)	2017	0.2856	0.0816	**0.0001**	4.1293	192
Site SI (herm)	2017	0.2800	0.0784	**0.0001**	4.0422	192

Table 8. The results from a regression of the linear model, Fruit ~ SI, subsetted by site, where SI refers to the specific synchrony index used in the regression. Significant ($P < 0.05$) correlations have their *p*-value in bold. These tests correspond to Fig. 9.

SI used in test	Site	r	r^2	*p*-value	t	df
1 m SI (both)	SN1	0.1599	0.0256	**0.0498**	1.9777	149
3 m SI (both)	SN1	0.1371	0.0188	*0.0932*	1.6896	149
5 m SI (both)	SN1	0.1522	0.0232	0.0622	1.8792	149
Site SI (both)	SN1	0.1693	0.0287	**0.0377**	2.0968	149
1 m SI (herm)	SN1	0.1672	0.0280	**0.0401**	2.0706	149
3 m SI (herm)	SN1	0.1510	0.0228	*0.0643*	1.8640	149
5 m SI (herm)	SN1	0.1604	0.0257	**0.0491**	1.9840	149
Site SI (herm)	SN1	0.1770	0.0313	**0.0297**	2.1948	149
1 m SI (both)	SN2	0.0728	0.0053	0.4138	0.8199	126
3 m SI (both)	SN2	0.1548	0.0240	*0.0810*	1.7590	126
5 m SI (both)	SN2	0.1662	0.0276	*0.0608*	1.8918	126
Site SI (both)	SN2	0.2060	0.0424	**0.0197**	2.3624	126
1 m SI (herm)	SN2	0.0810	0.0066	0.3633	0.9124	126
3 m SI (herm)	SN2	0.1367	0.0187	0.1238	1.5493	126
5 m SI (herm)	SN2	0.1435	0.0206	0.1060	1.6280	126
Site SI (herm)	SN2	0.1932	0.0373	**0.0289**	2.2101	126
1 m SI (both)	SN3	0.1769	0.0313	**0.0266**	2.2382	155
3 m SI (both)	SN3	0.2587	0.0669	**0.0011**	3.3347	155
5 m SI (both)	SN3	0.2432	0.0592	**0.0021**	3.1222	155
Site SI (both)	SN3	0.2106	0.0443	**0.0081**	2.6820	155
1 m SI (herm)	SN3	0.1637	0.0268	**0.0405**	2.0656	155
3 m SI (herm)	SN3	0.2311	0.0534	**0.0036**	2.9577	155
5 m SI (herm)	SN3	0.2183	0.0477	**0.0060**	2.7856	155
Site SI (herm)	SN3	0.1658	0.0275	**0.0380**	2.0932	155
1 m SI (both)	SN4	0.1958	0.0383	0.1273	1.5462	60
3 m SI (both)	SN4	0.2625	0.0689	**0.0393**	2.1069	60
5 m SI (both)	SN4	0.1777	0.0316	0.1671	1.3986	60
Site SI (both)	SN4	0.1493	0.0223	0.2468	1.1695	60
1 m SI (herm)	SN4	0.2811	0.0790	**0.0269**	2.2685	60
3 m SI (herm)	SN4	0.2658	0.0706	**0.0368**	2.1356	60
5 m SI (herm)	SN4	0.1300	0.0169	0.3138	1.0159	60
Site SI (herm)	SN4	0.1517	0.0230	0.2391	1.1891	60

Table 9. The results of each pairwise correlation comparison for neighborhood type (i.e., whether both sexes or only hermaphrodites were considered neighbors). The correlation coefficients (*r*) represent the correlation between the given SI and fruit production. There was no significant difference between the correlation coefficients of each SI type at any scale. The sample size (n) was 498 for all correlations.

First SI	First *r*	Second SI	Second *r*	Fisher's *z*	*p*-value
1 m SI (both)	0.1478	1 m SI (herm)	0.1472	0.0108	0.9914
3 m SI (both)	0.2051	3 m SI (herm)	0.1898	0.2513	0.8016
5 m SI (both)	0.1842	5 m SI (herm)	0.1689	0.2476	0.8044
Site SI (both)	0.1651	Site SI (herm)	0.1537	0.1828	0.8550

Table 10. The results of each pairwise correlation comparison for neighborhood size (i.e., what neighborhood radius was used to define the SI). The correlation coefficients (*r*) represent the correlation between the given SI and fruit production. There was no significant difference between the correlation coefficients of any SI size combination. The sample size (n) was 498 for all correlations.

First SI	First *r*	Second SI	Second *r*	Fisher's *z*	*p*-value
1 m SI (both)	0.1478	3 m SI (both)	0.2051	-0.9303	0.3522
1 m SI (both)	0.1478	5 m SI (both)	0.1842	-0.5876	0.5568
1 m SI (both)	0.1478	Site SI (both)	0.1651	-0.2776	0.7814
3 m SI (both)	0.2051	5 m SI (both)	0.1842	0.3427	0.7318
3 m SI (both)	0.2051	Site SI (both)	0.1651	0.6528	0.5139
5 m SI (both)	0.1842	Site SI (both)	0.1651	0.3100	0.7566
1 m SI (herm)	0.1472	3 m SI (herm)	0.1898	-0.6898	0.4903
1 m SI (herm)	0.1472	5 m SI (herm)	0.1689	-0.3507	0.7258
1 m SI (herm)	0.1472	Site SI (herm)	0.1537	-0.1055	0.9160
3 m SI (herm)	0.1898	5 m SI (herm)	0.1689	0.3391	0.7345
3 m SI (herm)	0.1898	Site SI (herm)	0.1537	0.5843	0.5590
5 m SI (herm)	0.1689	Site SI (herm)	0.1537	0.2452	0.8063

Table 11. The results of correlations performed between site-scale SI and the other four scales (0.5, 1, 3, and 5 m radii) for SIs using both sexed neighbors (Fig. 10A) and only hermaphroditic neighbors (Fig. 10B). All *p*-values are less than 0.0001 and are in bold to indicate significance ($P < 0.05$).

First SI	Second SI	r	r^2	*p*-value	t	df
	0.5 m SI (both)	0.6296	0.3964	**<0.0001**	17.6050	472
Site SI	1 m SI (both)	0.6849	0.4690	**<0.0001**	20.9320	496
(both)	3 m SI (both)	0.8749	0.7655	**<0.0001**	40.2409	496
	5 m SI (both)	0.9295	0.8639	**<0.0001**	56.1159	496
	0.5 m SI (herm)	0.6028	0.3633	**<0.0001**	15.5912	426
Site SI	1 m SI (herm)	0.6547	0.4287	**<0.0001**	19.2906	496
(herm)	3 m SI (herm)	0.8512	0.7245	**<0.0001**	36.1198	496
	5 m SI (herm)	0.9166	0.8402	**<0.0001**	51.0722	496

Table 12. The results of each correlation in the correlogram (Fig. 11), in which each synchrony index (SI) is correlated with every other SI. All *p*-values are less than 0.0001 and are in bold to indicate significance ($P < 0.05$).

First SI	Second SI	r	*p*-value	df
0.5 m SI (both)	0.5 m SI (both)	1.000	NA	473
0.5 m SI (herm)	0.5 m SI (both)	0.897	**<0.0001**	427
1 m SI (both)	0.5 m SI (both)	0.813	**<0.0001**	473
1 m SI (herm)	0.5 m SI (both)	0.741	**<0.0001**	473
3 m SI (both)	0.5 m SI (both)	0.723	**<0.0001**	473
3 m SI (herm)	0.5 m SI (both)	0.702	**<0.0001**	473
5 m SI (both)	0.5 m SI (both)	0.687	**<0.0001**	473
5 m SI (herm)	0.5 m SI (both)	0.661	**<0.0001**	473
Site SI (both)	0.5 m SI (both)	0.630	**<0.0001**	473
Site SI (herm)	0.5 m SI (both)	0.608	**<0.0001**	473
0.5 m SI (herm)	0.5 m SI (herm)	1.000	NA	427
1 m SI (both)	0.5 m SI (herm)	0.765	**<0.0001**	427
1 m SI (herm)	0.5 m SI (herm)	0.815	**<0.0001**	427
3 m SI (both)	0.5 m SI (herm)	0.726	**<0.0001**	427
3 m SI (herm)	0.5 m SI (herm)	0.725	**<0.0001**	427
5 m SI (both)	0.5 m SI (herm)	0.687	**<0.0001**	427
5 m SI (herm)	0.5 m SI (herm)	0.687	**<0.0001**	427
Site SI (both)	0.5 m SI (herm)	0.615	**<0.0001**	427
Site SI (herm)	0.5 m SI (herm)	0.603	**<0.0001**	427
1 m SI (both)	1 m SI (both)	1.000	NA	497

1 m SI (herm)	1 m SI (both)	0.917	**<0.0001**	497
3 m SI (both)	1 m SI (both)	0.802	**<0.0001**	497
3 m SI (herm)	1 m SI (both)	0.795	**<0.0001**	497
5 m SI (both)	1 m SI (both)	0.756	**<0.0001**	497
5 m SI (herm)	1 m SI (both)	0.738	**<0.0001**	497
Site SI (both)	1 m SI (both)	0.685	**<0.0001**	497
Site SI (herm)	1 m SI (both)	0.669	**<0.0001**	497
1 m SI (herm)	1 m SI (herm)	1.000	NA	497
3 m SI (both)	1 m SI (herm)	0.776	**<0.0001**	497
3 m SI (herm)	1 m SI (herm)	0.801	**<0.0001**	497
5 m SI (both)	1 m SI (herm)	0.738	**<0.0001**	497
5 m SI (herm)	1 m SI (herm)	0.750	**<0.0001**	497
Site SI (both)	1 m SI (herm)	0.658	**<0.0001**	497
Site SI (herm)	1 m SI (herm)	0.655	**<0.0001**	497
3 m SI (both)	3 m SI (both)	1.000	NA	497
3 m SI (herm)	3 m SI (both)	0.977	**<0.0001**	497
5 m SI (both)	3 m SI (both)	0.952	**<0.0001**	497
5 m SI (herm)	3 m SI (both)	0.931	**<0.0001**	497
Site SI (both)	3 m SI (both)	0.875	**<0.0001**	497
Site SI (herm)	3 m SI (both)	0.866	**<0.0001**	497
3 m SI (herm)	3 m SI (herm)	1.000	NA	497
5 m SI (both)	3 m SI (herm)	0.936	**<0.0001**	497
5 m SI (herm)	3 m SI (herm)	0.947	**<0.0001**	497
Site SI (both)	3 m SI (herm)	0.846	**<0.0001**	497
Site SI (herm)	3 m SI (herm)	0.851	**<0.0001**	497
5 m SI (both)	5 m SI (both)	1.000	NA	497
5 m SI (herm)	5 m SI (both)	0.975	**<0.0001**	497
Site SI (both)	5 m SI (both)	0.929	**<0.0001**	497
Site SI (herm)	5 m SI (both)	0.919	**<0.0001**	497
5 m SI (herm)	5 m SI (herm)	1.000	NA	497
Site SI (both)	5 m SI (herm)	0.906	**<0.0001**	497
Site SI (herm)	5 m SI (herm)	0.917	**<0.0001**	497
Site SI (both)	Site SI (both)	1.000	NA	497
Site SI (herm)	Site SI (both)	0.987	**<0.0001**	497
Site SI (herm)	Site SI (herm)	1.000	NA	497
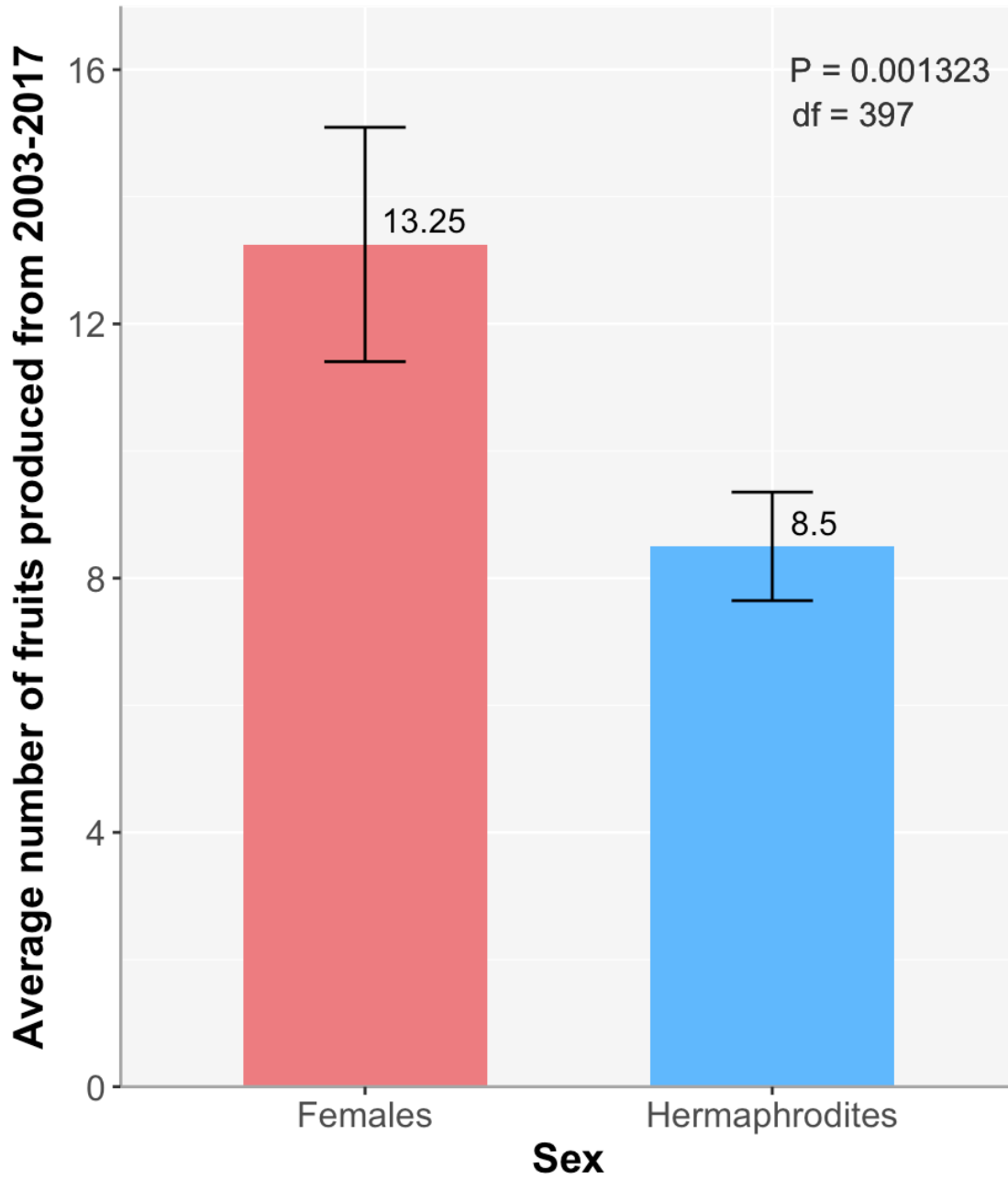
Figure 1. The average number of fruits female plants produced from 2003-2017 ($W = 21026$, $P = 0.0013$, df = 397). Error bars are +/- one standard error from the mean.
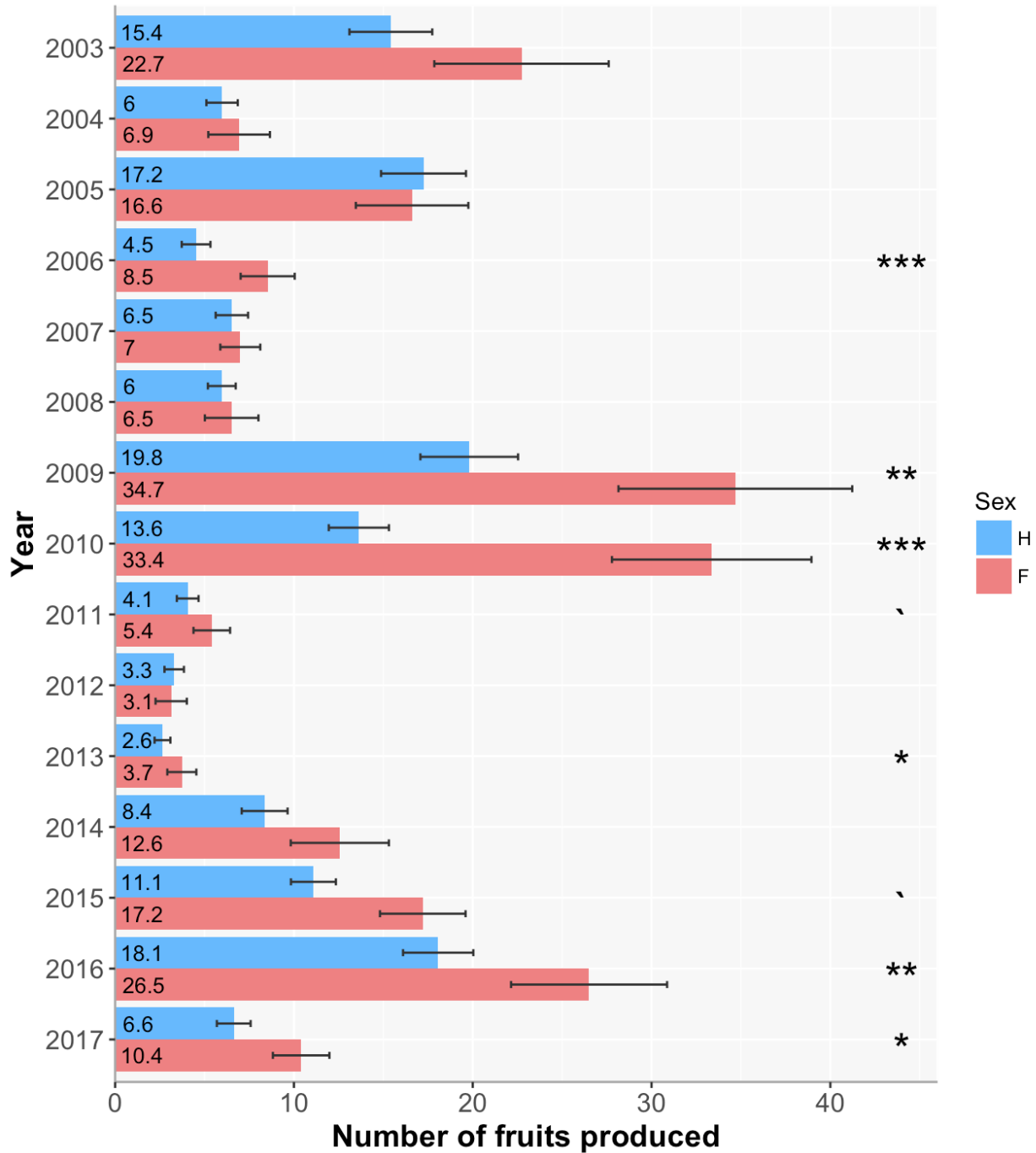
Figure 2. The means +/- one standard error of the number of fruits produced by female (F, red) and hermaphroditic (H, blue) individuals for each year from 2003 to 2017. Years in which females produced significantly more fruits than hermaphrodites are coded as follows: ' *** ' for $P < 0.001$, ' ** ' for $P < 0.01$, ' * ' for $P < 0.05$, and ' ` ' for $P < 0.1$.
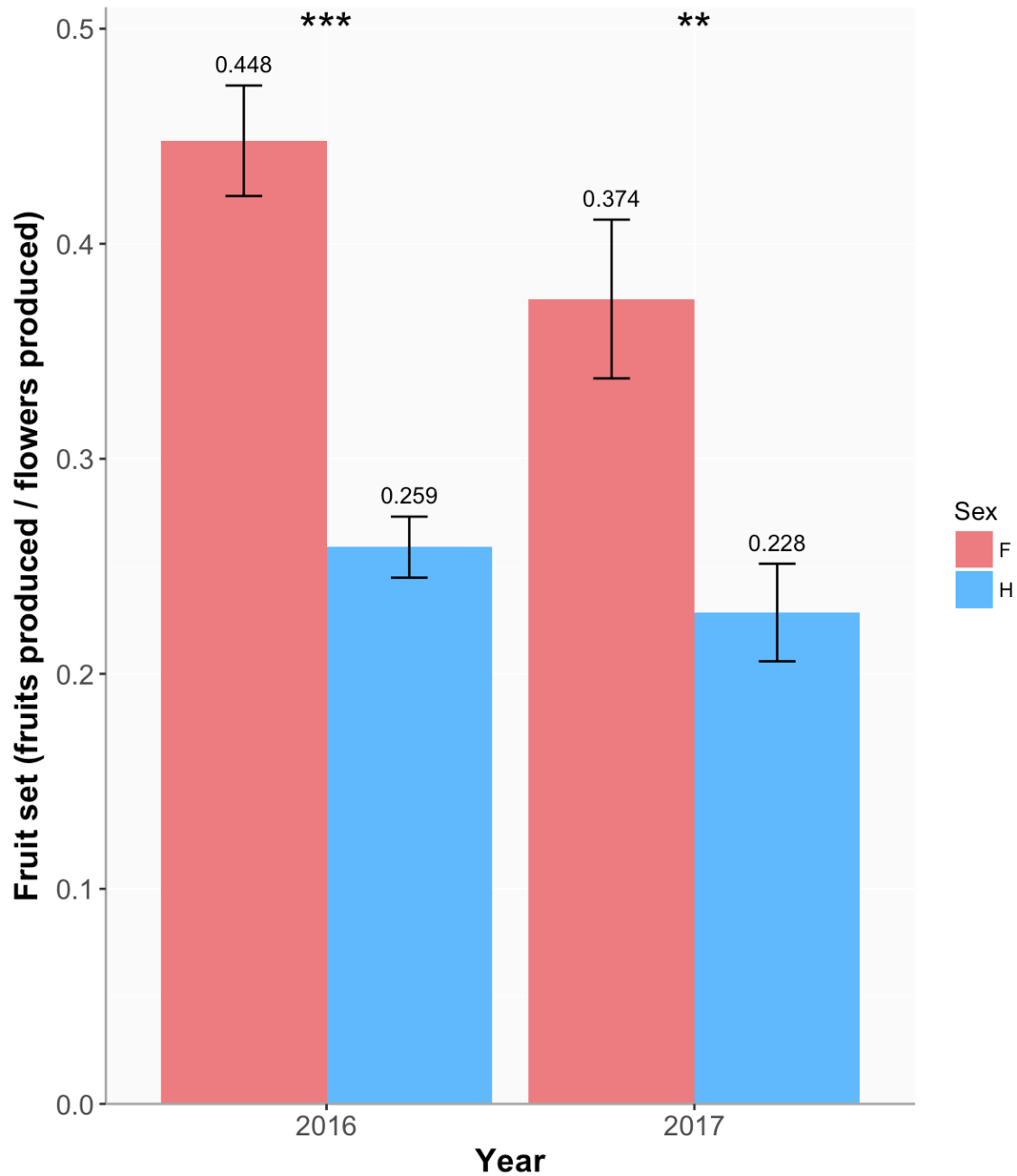
Figure 3. The means +/- one standard error of the fruit set of females (F, red) and hermaphrodites (H, blue) in 2016 and 2017. Asterisks indicate difference between the sexes as determined by a one-tailed Mann-Whitney *U*-test and are coded as follows: ' *** ' for $P < 0.001$, ' ** ' for $P < 0.01$. Plants in 2016 tended to have higher fruit sets than plant in 2017 ($W = 49082$, $P = 0.0056$, df = 614).
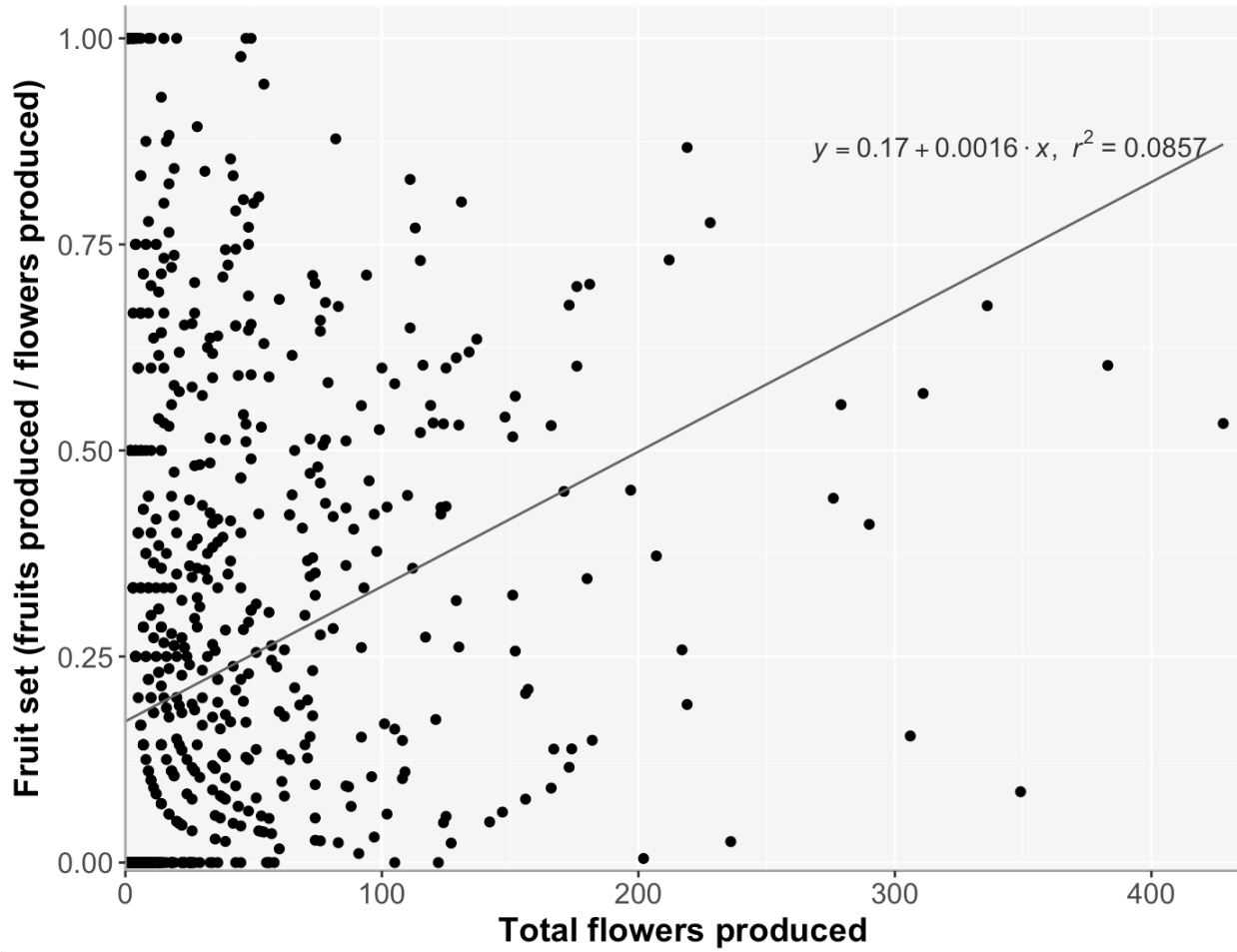
Figure 4. The relationship between total number of flowers produced by a plant and fruit set with sexes and years pooled ($r = 0.293$, $t = 9.5213$, $P < 0.0001$, df = 967).

The equation shown in the figure: $y = 0.17 + 0.0016 \cdot x$, $r^2 = 0.0857$
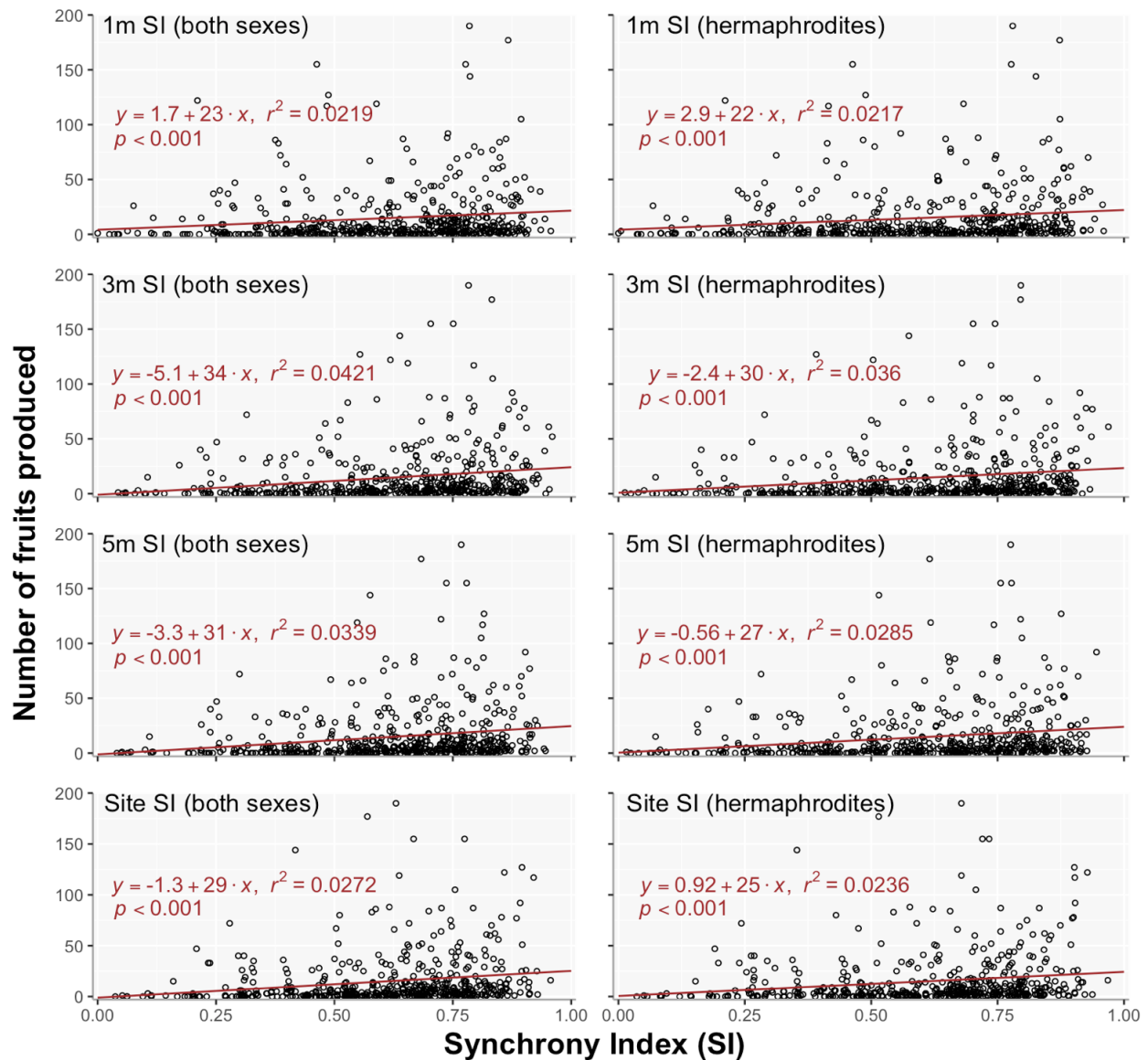
Figure 5. The relationship between SI and raw fruit production per plant, where SI signifies the synchrony index used in the regression. Eight different SIs were calculated for each plant using different neighborhood types (hermaphrodites only or both sexes) and neighborhood radii (1 m, 3 m, 5 m, or whole site); see also Fig. 6 and Table 5.
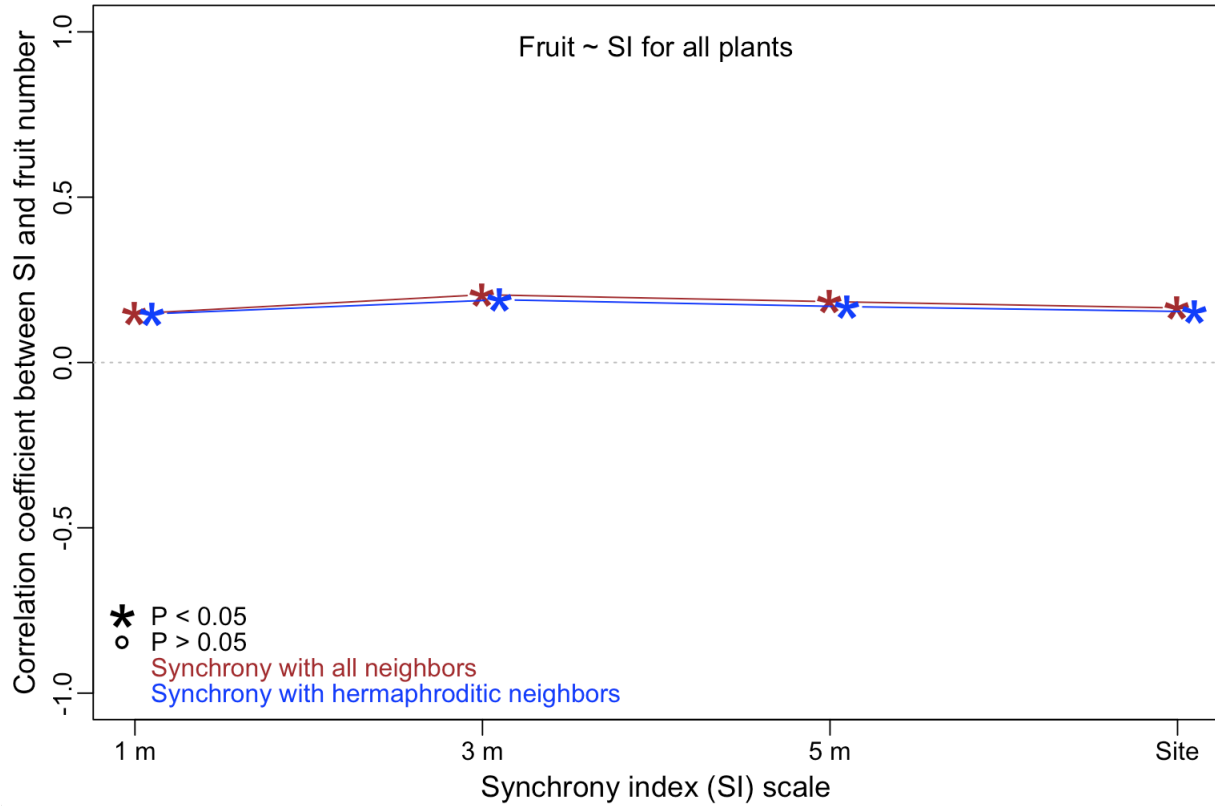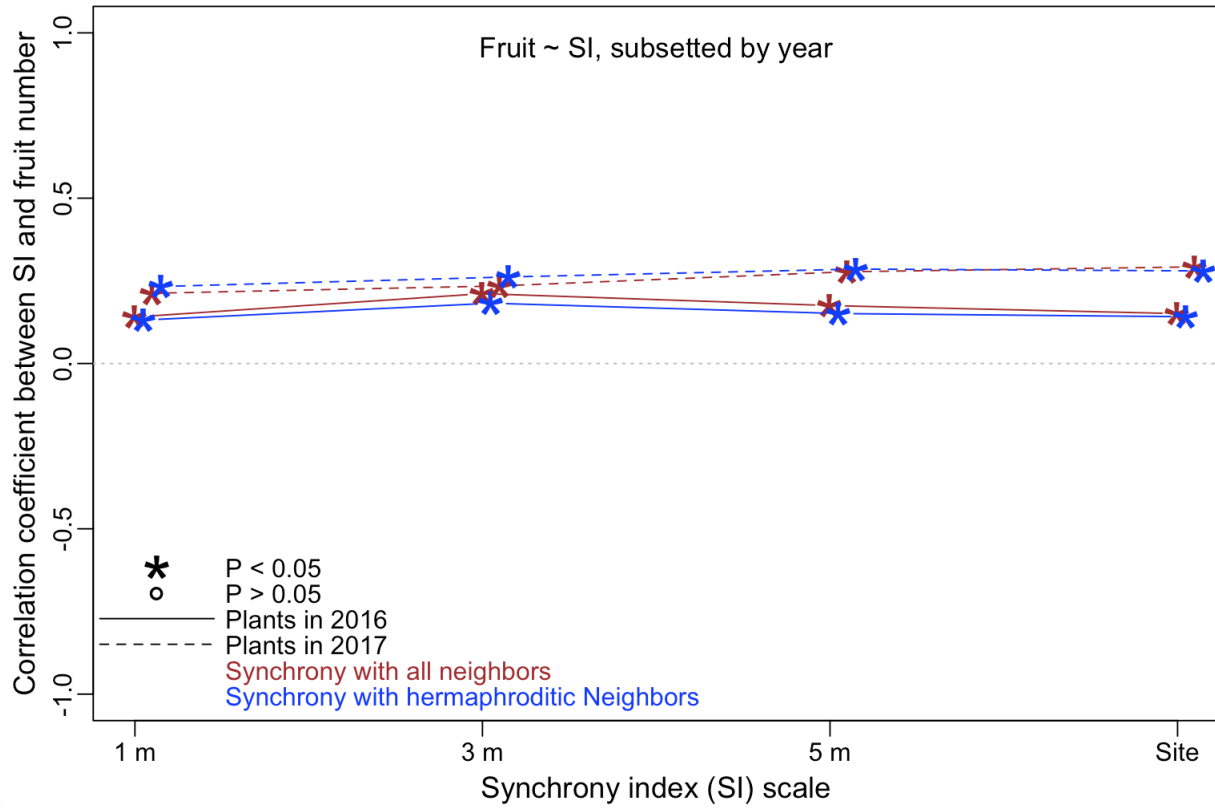
Figure 6. The correlation coefficients (*r* values) for the regression, Fruit ~ SI, where SI signifies the synchrony index that was used in the regression. The eight points represent different SIs based on their scale (radius of the neighborhood) and whether all neighbors (red) or only hermaphroditic neighbors (blue) were used in the calculation of the SI; see also Table 5.
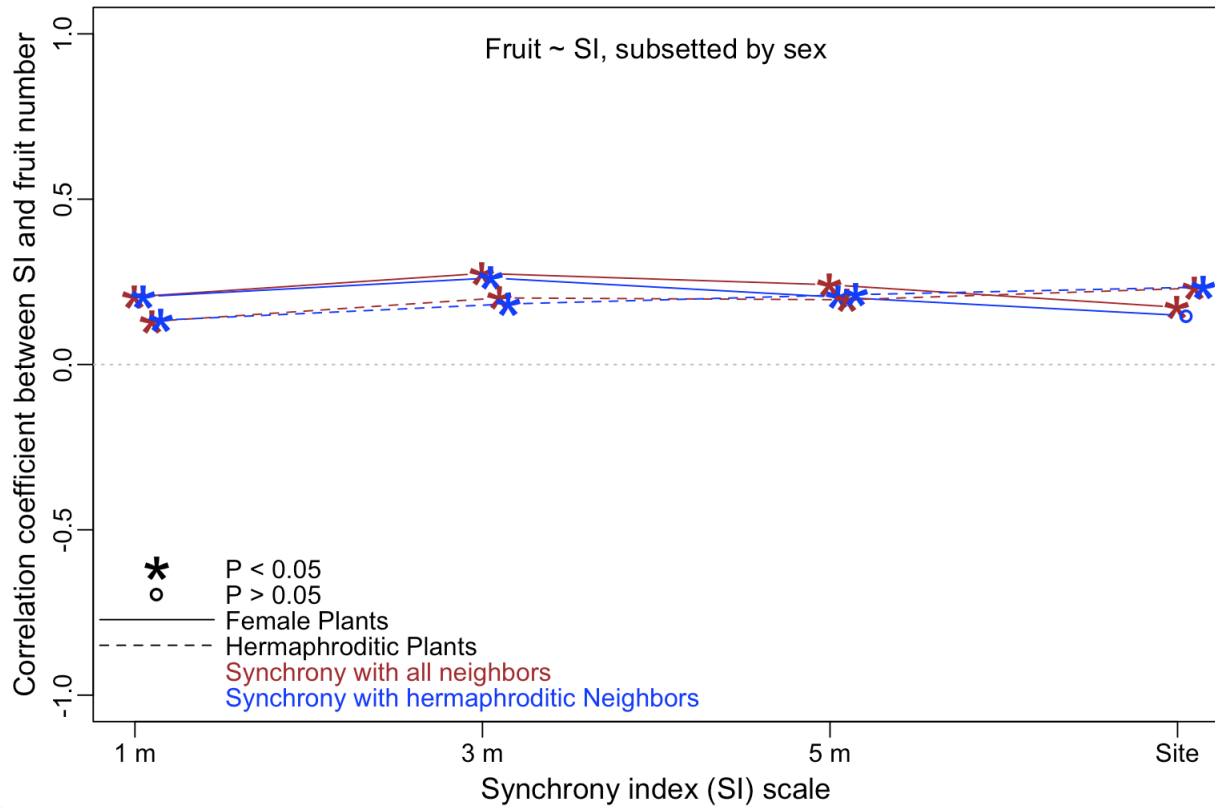
Figure 7. The correlation coefficients (*r* values) for the regression, Fruit ~ SI, subsetted by sex, where SI signifies the synchrony index that was used in the regression. The eight points represent different SIs based on their scale (radius of the neighborhood) and whether all neighbors (red) or only hermaphroditic neighbors (blue) were used to calculate the SI; see also Table 6.
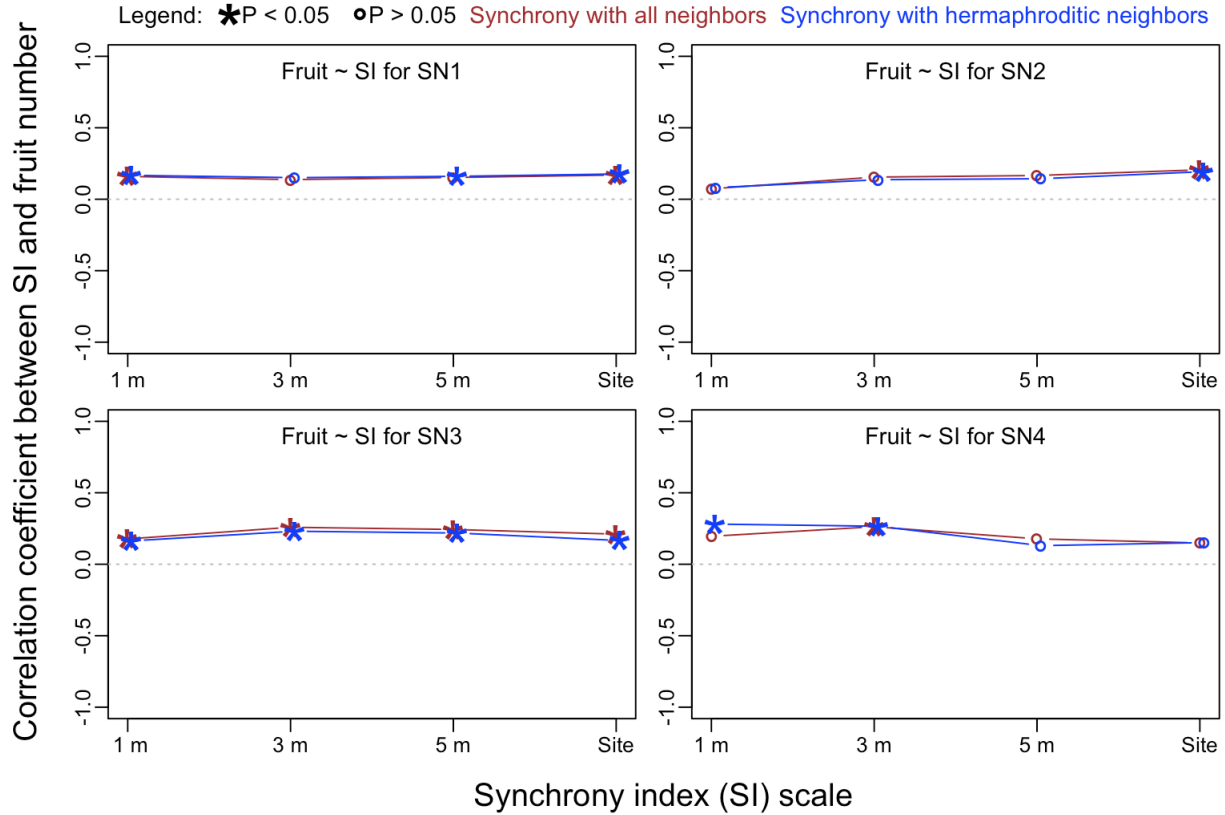
Figure 8. The correlation coefficients (*r* values) for the regression, Fruit ~ SI, subsetted by year, where SI signifies the synchrony index that was used in the regression. The eight points represent different SIs based on their scale (radius of the neighborhood) and whether all neighbors (red) or only hermaphroditic neighbors (blue) were used to calculate the SI; see also Table 7.

Figure 9. The correlation coefficients (*r* values) for the regression, Fruit ~ SI, subsetted by site, where SI signifies the synchrony index that was used in the regression. The eight points represent different SIs based on their scale (radius of the neighborhood) and whether all neighbors (red) or only hermaphroditic neighbors (blue) were used to calculate the SI; see also Table 8.
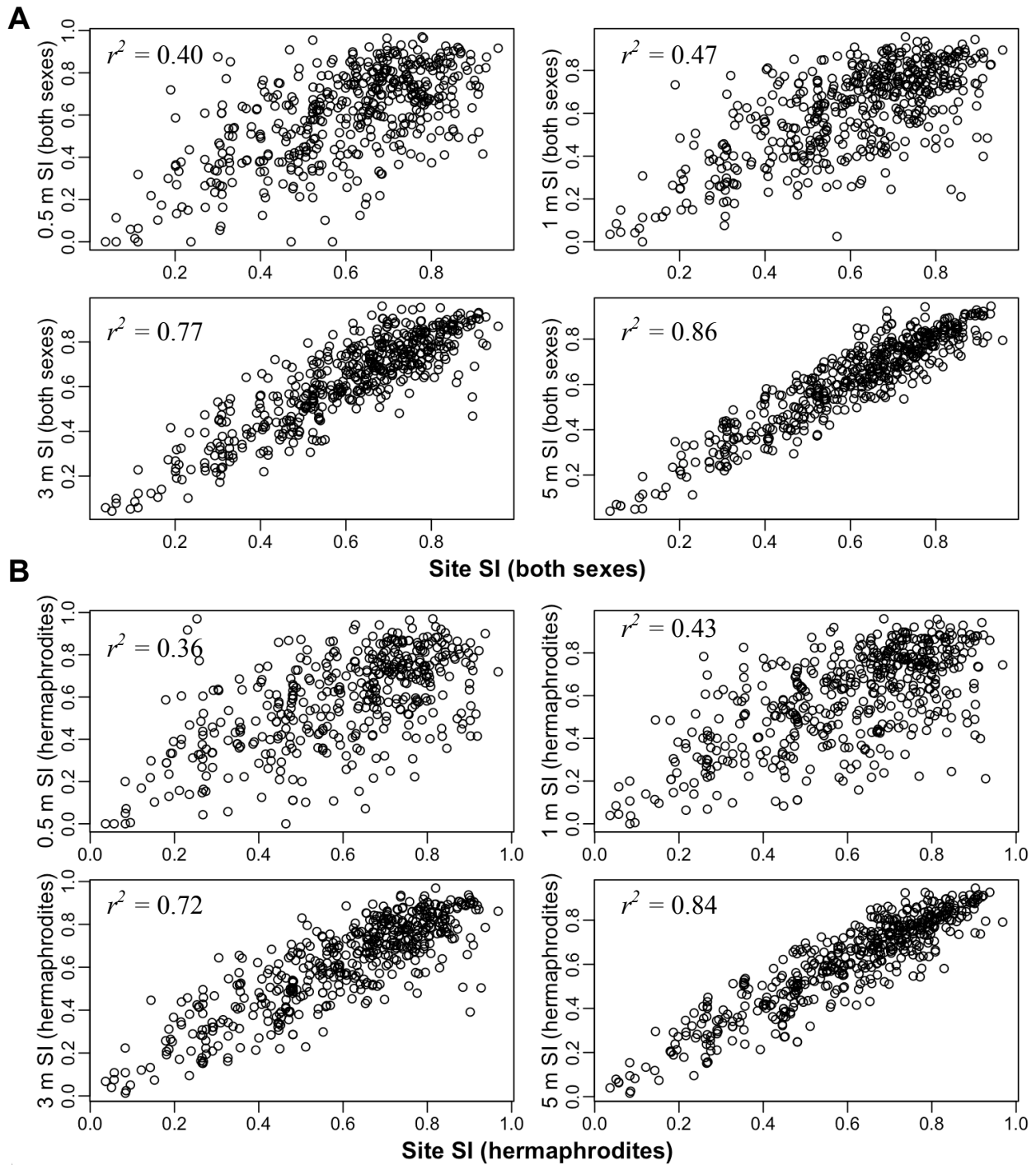
Figure 10. The relationship between site SI and smaller scale SIs (0.5, 1, 3, and 5 m radii) when SIs include all neighbors (A, upper) or hermaphroditic neighbors only (B, lower); see also Table 11.
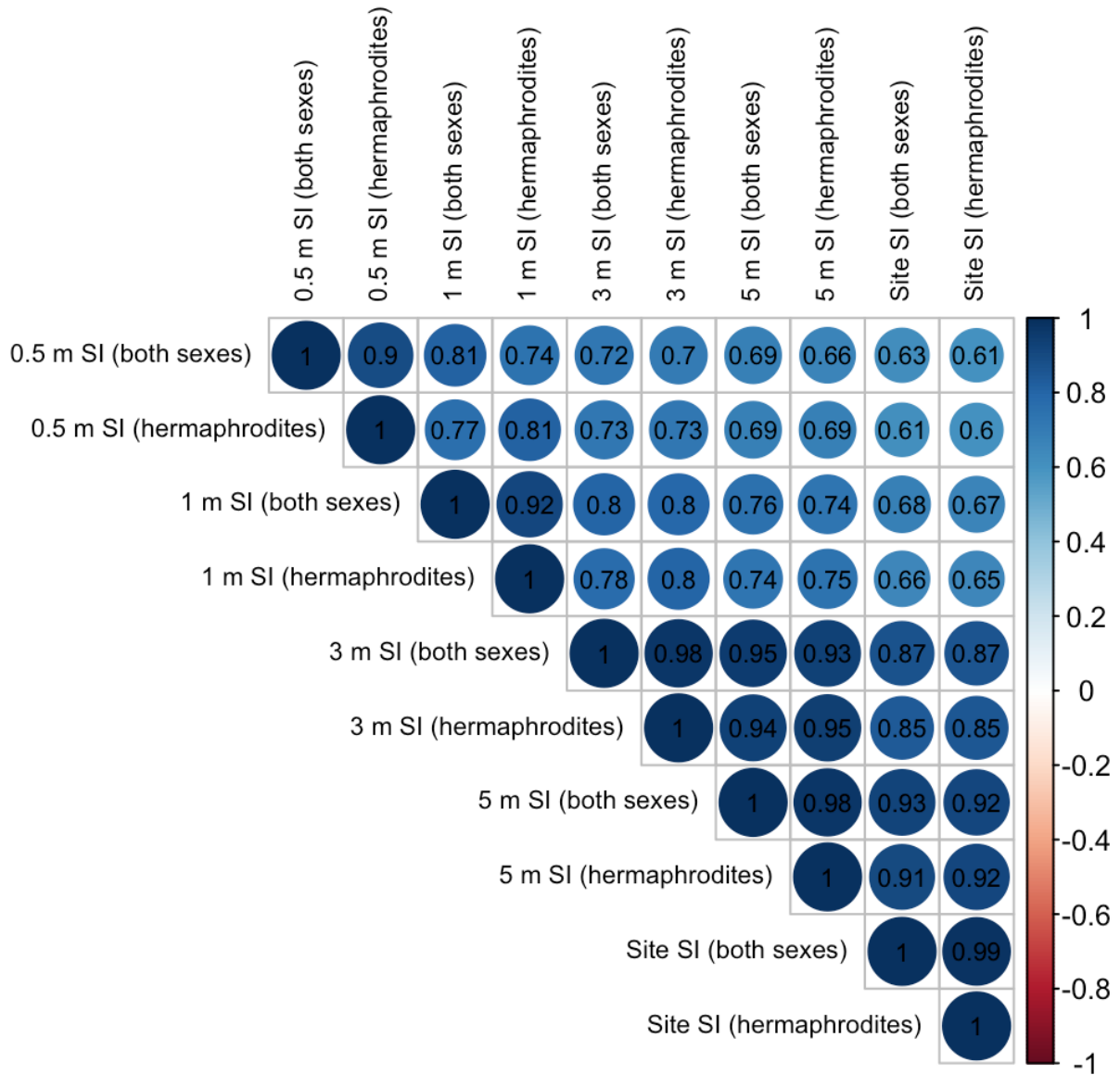
Figure 11. Correlogram showing the correlations among SIs. Color varies with correlation coefficient from red to blue (for *r* values from -1 to 1, respectively). All correlations are significant ($P < 0.0001$) and the results of each correlation are summarized in Table 12.
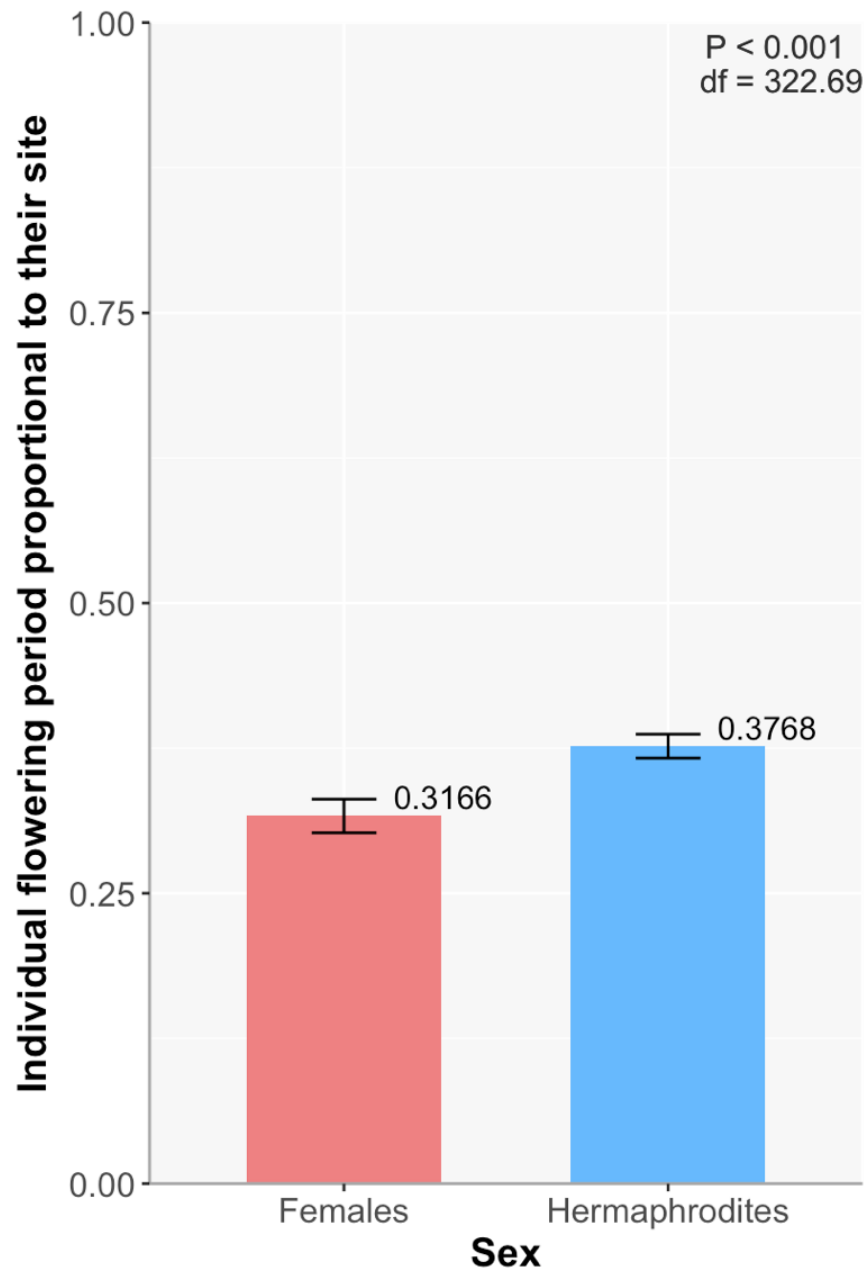
Figure 12. The proportion of total site flowering time that female and hermaphroditic plants were in bloom (had at least one flower open). Error bars are +/- one standard error from the mean.
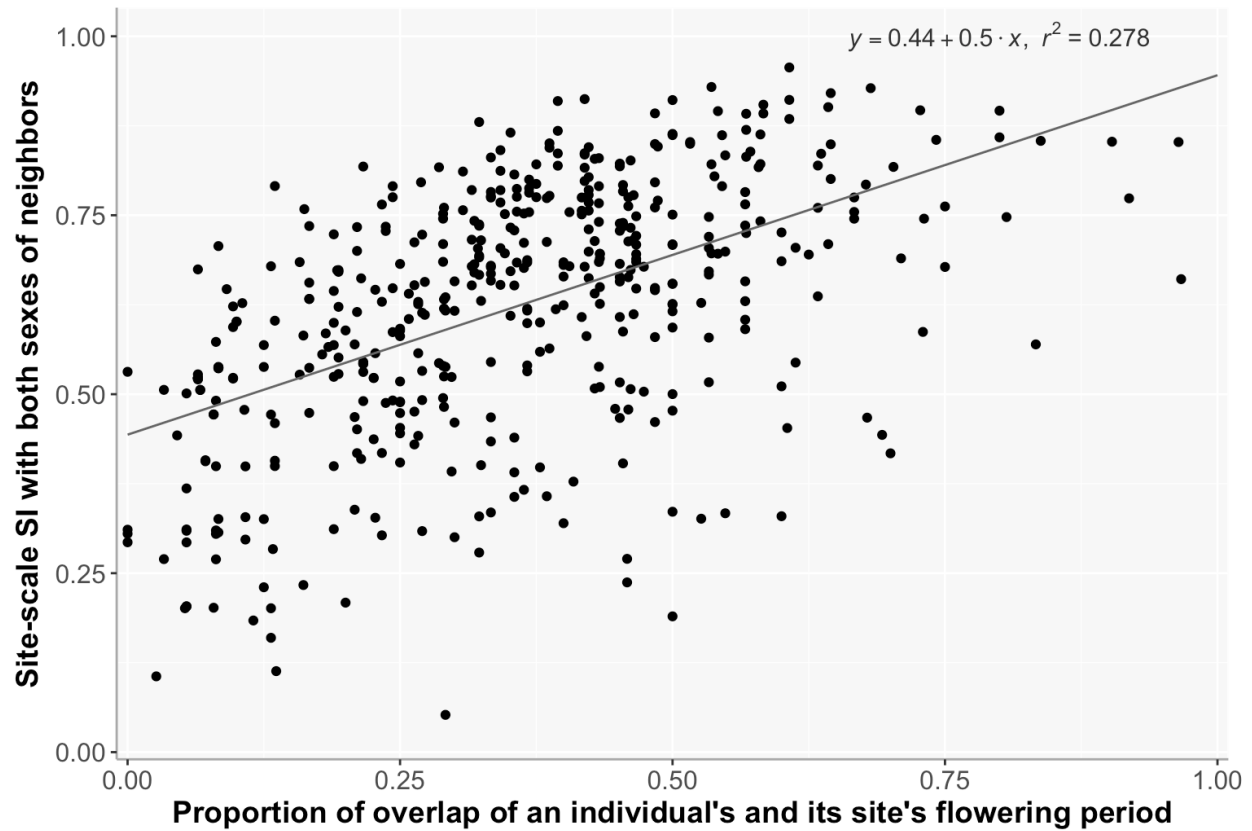
Figure 13. The relationship between proportional overlap of flowering period (an individual's flowering period / its site's flowering period) and site-scale synchrony index (SI) when including both females and hermaphrodites as neighbors ($r = 0.5269$, $t = 13.411$, $P < 0.0001$, df $= 468$).

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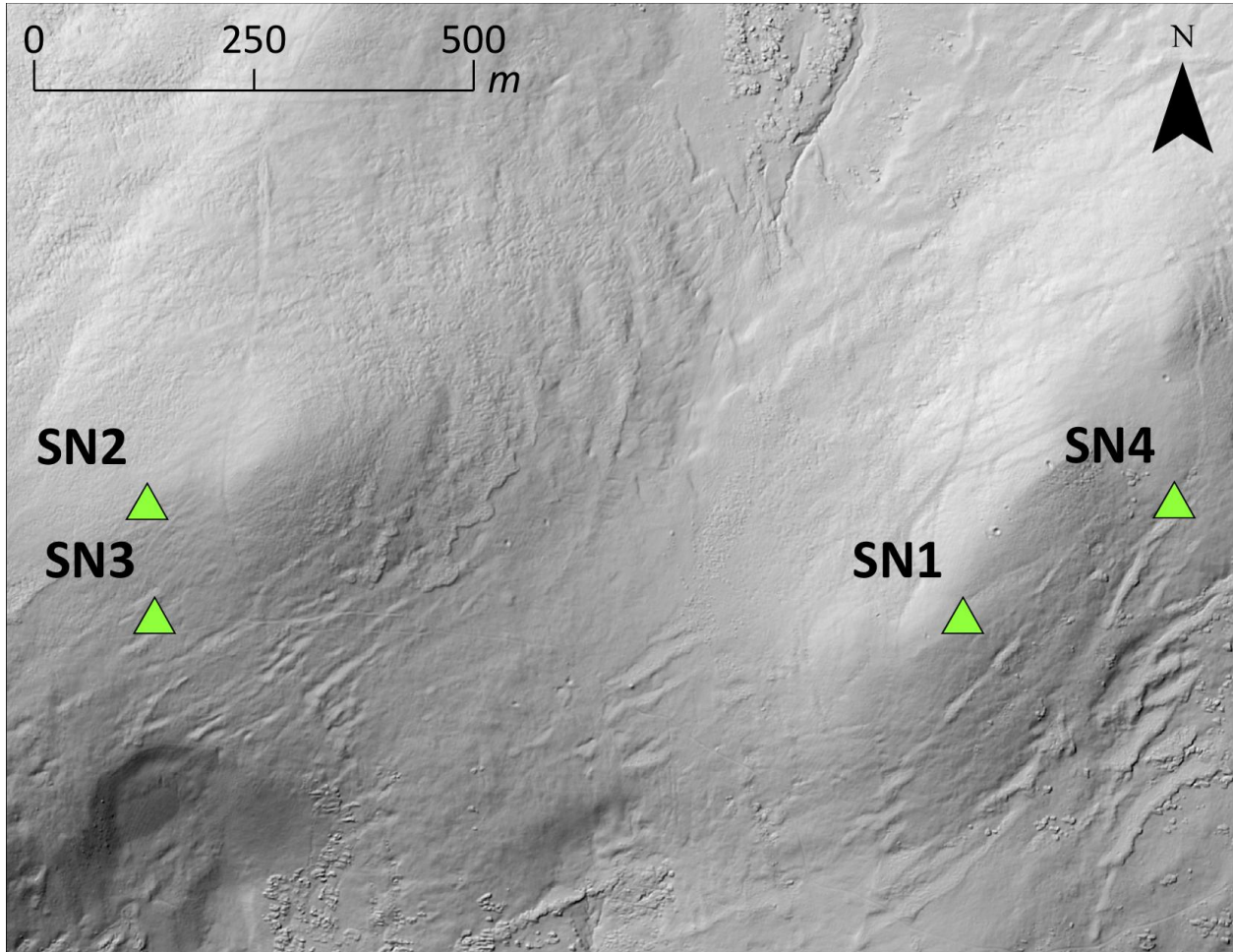
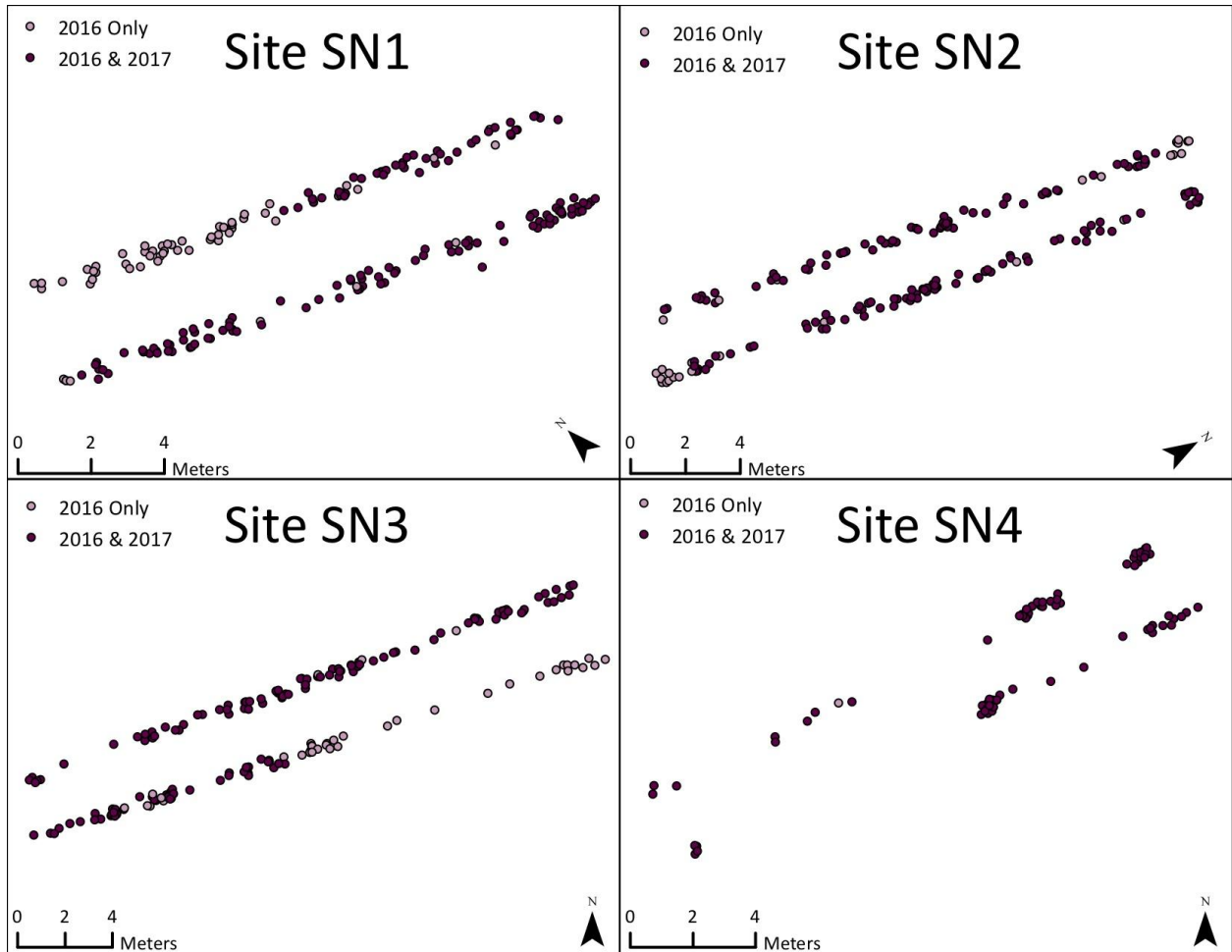Figure A1. The locations of the four sites on Niwot Ridge, CO. Shading indicates topography.

Figure A2. Maps of all *S. acaulis* individuals for which phenology data was collected in 2016 only (pink) and both 2016 and 2017 (purple).
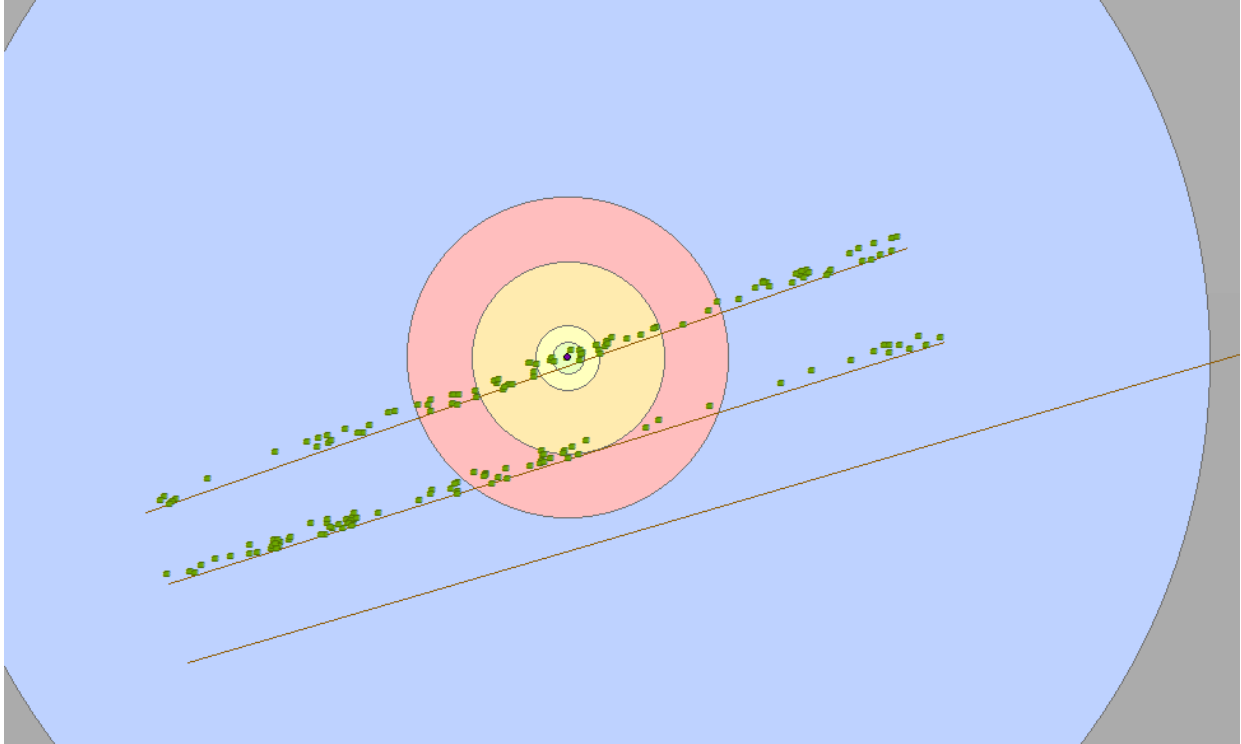
Figure A3. An example of the five different radii that were used to identify the neighbors of just one focal plant. The Generate Near Table tool in ArcMap 10.4.1 does something similar to this for each plant. The colors, green, yellow, orange, red, and blue, represent the 0.5 m, 1 m, 3 m, 5 m, and whole site radii, respectively, and the purple dot indicates the focal plant. The lines indicate transects within the site, and only the plants in two transects are shown because those were the ones included in this study.