Growth, reproductive phenology, and population structure in Syntrichia caninervis

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GROWTH, REPRODUCTIVE PHENOLOGY, 
AND POPULATION STRUCTURE IN 
SYNTRICHIA CANINERVIS

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Bachelor of Science
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ABSTRACT

Growth, Reproductive Phenology, and Population Structure in 
_Syntrichia caninervis_

by

Mary Lynn Bonine

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_Syntrichia caninervis_ is a dioicous bryophyte of the arid Southwest. It exhibits a phenology and growth rate similar to the related species _Tortula inermis_. Mean growth rate was 0.29 mm ± 0.04 (mean and S.D.). Expressing stems had a significantly greater growth rate than non-expressing stems, but no difference was detectable between males and females. The pattern of gametangial maturation is one of rapid perichaetial development, initiating in September and becoming receptive in March; and protracted perigonial development, initiating in October, developing to an immature state prior to over-summering, and completing maturation during the second fall and spring, with sperm dispersal from February to May. Abortion of gametangia is high (♀, 42-50%; ♂, 20-33%) and most likely linked to low levels of precipitation. Sporophyte maturation was unable to be effectively monitored due to a 100% abortion rate. The ratio of females to males was (2♀:1♂) in the 43% of stems that expressed. Spatial patterning of the sexes is significant, but segregation values were low.
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CHAPTER 1

INTRODUCTION

Defining Phenology and its Role

General Comments

Phenology is defined in the Merriam-Webster dictionary as the study of a periodic biological phenomenon. Stark (2002) refines this definition by designating it as the study of the timing of growth and reproductive events. Under this guise, a wide range of components of a species existence may be linked to almost any biological study containing a temporal component.

Phenological studies are useful to plant ecologists in a variety of ways. They are commonly used as one of several ways to describe growth forms for vascular plants, a means of describing life “strategies”, and the typically accepted format for describing relationships between seasonally observed phenomena and the climatic factors involved in such phenomena. These observations may reveal relationships along fine scale environmental gradients (i.e., edaphic factors, shade effects, and interspecific nutrient effects) or allude to larger scale trends (i.e., annual precipitation; mean, minima, and maxima of temperatures; radiation intensity), which may be more related to broad gradients such as latitude, longitude, and topographic effects.
When taking into consideration the range of overlapping environmental effects acting across a multitude of environmental scales, it quickly becomes apparent that it is quite challenging to factor out and determine their respective contributions to the overall phenological patterns. The goal of phenological studies is to elucidate the patterns of development, providing a foundation from which the ecologist may explore the causal factors. The broader categories of "reproductive ecology" and "life history" are the natural extension of these explorations combining both phenology and ecology.

Ideally, prior to making observations, one would attempt to establish which factors are of the most importance and on what scale these factors act. In this way, the phenologist would be able to pair examination of those specific elements with the phenological study. Unfortunately, the ecological parameters underlying many species distributions, particularly in bryology, are not well enough documented to determine which factors might be most profitable towards revealing the causation behind the phenological patterns. Vascular plant ecologists have established a variety of factors that may control phenology. Of particular importance in arid regions are, water availability, diurnal temperature variation, light regime, and energy balance (particularly as related to transpiration). Among vascular plants, there appear to be a few predominant phenological trends. These trends include the ephemeral, annual, and perennial strategies, with additional variation regarding deciduous versus evergreen tendencies (Barbour et al. 1987).
Bryophytes and Phenology

Morphological Concerns

Bryophyte phenology is affected by a similar range of ecological conditions as vascular plant phenology, but on a finer scale owing to their small stature. They are less able to "escape" the circumstances of their microhabitats, and due to their primitive configuration of tissues, are (under most circumstances) subjected to the full array of environmental fluctuations surrounding them (Richardson 1981). A primary example of this is their rhizoids, which fail to effectively transport water from the soil surroundings, due to a lack of advanced conductive tissues. The poikilohydric nature of bryophytes (dependent upon external water for growth and reproduction) restricts growth to mesic microsites conferring a favorable hydration status (Bates 2000). Structurally, stems and leaves possess few or no mechanisms by which to prevent water loss. Stems are comprised of a thin-walled epidermis which may lack or have a minimal cuticle. The cortex may or may not be differentiated into regions of various combinations of thin-walled and thicker-walled cells that may occupy the entire central region or surround central strands of varying complexity and conductive capability. The central strand varies between species as to the proportion of the cortex which it occupies, and though it may even contain primitive, vascular bundle-like cells, it is of doubtful conductive value to most stems. Leaves are simple, with one to a few cell layers and a costa or midrib several cell layers thick. Leaves may be variously appressed or spreading from the stem, lending characteristic form to many species in both the wet and dry states. Leaves come in a variety of shapes.
with various appendages and modes of stem insertion, suggested to be
advantageous for water conduction and retention during hydration (Flowers
1973). Leaf cells may also exhibit a variety of ornamentations that may assist in
gas exchange during desiccation.

Mosses grow in two primary configurations, prostrate (pleurocarpous) and
erect (acrocarpous), and exhibit wide variation in growth rates. Stem extension
rates may range from less than a single millimeter to almost 1 meter in length
over several seasons (Tallis 1959; Longton & Greene 1969a; Collins 1976;
Greene & Clayton-Green 1981; Miles et al. 1989). The species of study is of the
acrocarpous form, and so the effects of the pleurocarpous form on phenology will
only briefly be explored here. Species of pleurocarpous genera typically produce
a main axis and pinnately arranged lateral shoots and gametangia derived from
lateral buds. This leaves the apical cell available for indefinite indeterminate
growth (monopodial). Conversely, acrocarps must utilize this apical cell for
gametangial formation and thereby terminate the given stem with an
inflorescence. Following gametangial maturation (and sporophyte maturation, if
relevant), a lateral bud is typically stimulated to produce a new innovation
(vegetative branches). When only one bud is stimulated, its continued growth
may push the inflorescence to one side, giving the appearance of lateral
gametangia along a continuous stem; this is known as sympodial growth
(Richardson 1981). Multiple innovations may be stimulated following the
production of a terminal inflorescence, giving the appearance of dichotomous
branching, but this would be a misnomer since it is not the result of an even
division of an apical cell. Innovations may also be instigated by extremes of temperature, moisture, radiation, stem density, and breakage, damage, or death of the apex (Richardson 1981).

Perhaps the most significant capability of bryophytes is an extraordinary success and dependence upon vegetative reproduction (Newton & Mishler 1994). Bryophyte cells are totipotent, each having the ability to develop into a new individual under proper conditions. A single cell can eventually give rise to rhizoids, protonemata, and shoots. Through these means, an individual plant may give rise to numerous shoots, providing a pathway for both expansion of the genet and dispersal to new locations. The debate as to whether this type of dispersal should be considered growth or reproduction is ongoing (see Mishler 1988 for a thorough review). One point, however, is beyond debate—asexual reproduction is a significant and essential component in the survival of many species, in particular dioicous species. Understanding the mechanisms and consequences of a dependency on this type of reproduction require intense phenological study and attention to the broader effects regarding gene flow and species evolution.

**Bryophyte Reproductive Biology**

Dioicy and monoicy are terms unique to haploid organisms such as bryophytes. They describe species in which male and female sexes are expressed on separate plants and on the same plant, respectively. They also allude to the haploid nature of bryophytes in general and implicate the unique genetic consequences of these states. These terms have been used
interchangeably with haploid dioecy and haploid monoecy in an effort to facilitate understanding and communication across botanical fields, but debate continues as to standardization (see Zander 1984, Wyatt 1985, Allen & Magill 1987 for further discussion).

Dioicy is believed to be the primitive sexual condition for bryophytes, supported by evidence that many monoicous species are auto- or allopolyploid derivatives of dioicous species. In dioicous species, the haploid genome cannot be shielded from deleterious recessive alleles, and is thus exposed directly to selective pressures. However, the polyploid nature of many monoicous species may result in a dosage based expression, and provides a way for these species to conceal some genetic impediments. In addition, the monoicous condition decreases the required gamete dispersal distance thereby resulting in higher frequencies of fertilization. The latter advantage of monoicy may be particularly significant in extreme environments such as the southwest U.S. desert regions (Wyatt 1982; Stark 1983), where monoicous species are significantly greater components of xeric regions than dioicous species.

**The Moss Life Cycle**

Moss life cycles consist of a free living haploid gametophyte that produces haploid gametes through mitosis (Figure 1). Female and male reproductive structures (archegonia and antheridia, respectively) are normally housed within a group of modified leaves collectively referred to as perichaetia (♀) and perigonia (♂). Clusters of gametangia with their specialized leaves are also known as inflorescences. Sperm are carried on a film of water to the archegonium, where
Figure 1. Generalized moss life cycle.
they unite with the ovum in fertilization and produce a diploid zygote that is physiologically dependent upon the maternal gametophyte. While sperm do have a rudimentary flagellum, there is little indication that they have the ability to swim over more than a couple of centimeters to reach the ovum; however, sperm may have some limited directional control across this range, indicated by female dispersion of sucrose and other chemicals believed to attract sperm (Richardson 1981). Despite its dependency upon the gametophyte, the embryo, which develops into the sporophyte, is at least in part responsible for its own production of photosynthates, contributing in the neighborhood of 40% of its carbon budget (Proctor 1977). Sporophytes consist of a seta that serves to elevate the spore bearing tissue, and a capsule that produces meiospores. Sporogenous tissue in the capsule of the sporophyte undergoes meiosis and produces haploid spores which lack specialized dispersal mechanisms and are largely airborne. While a significant proportion (60-90%) of spores are dispersed in the immediate vicinity of the parent gametophyte, there are indications that long-range and even trans-oceanic dispersal may be possible based on spore bank evidence (Van Zanten 1976).

The initiation of archegonia (♀) and antheridia (♂) is affected by a variety of environmental and intrinsic factors, which include radiation, temperature, internal carbohydrate and hormone levels, and edaphic factors such as pH, moisture, nutrients, and minerals. Reaction to these factors can be species-specific. The factors that appear to be of the most importance in the desert ecosystem are
moisture, radiation, temperature, and carbohydrate levels (owing to the short duration of net carbohydrate assimilation in desert environments (Alpert 1979).

**Gametophyte Growth Rates**

**Trends and Contributing Factors**

Often, one of the stated goals of bryophyte phenology studies is the determination of growth rates, also referred to as stem elongation rates. Growth rates in species associated with xeric regions are typically low, with annual growth intervals less than 1 mm (*Syntrichia ruralis*, 2.67-2.96 mm/year, Mishler & Oliver 1991; *Tortula inermis*, 0.14 mm ± 0.04/year, Stark 1997; *Trichostomum swetii*, 0.18 mm ± 0.06, Stark & Castetter 1995) relative to more mesic species (ranging from less than 3 mm per year to 40-50 mm per year, Collins 1976, Miles et al. 1989, Imura & Iwatsuki 1989, Vitt 1989). Growth rates are extremely low in deserts, with the likely cause linked to water availability. Similarly, the lowest mesic report of 2.7 mm per year (Vitt 1989) comes from substrates unable to maintain a favorable hydration state.

Due to their poikilohydric nature, mosses are not only dependent on nutrient and radiation status, but severely limited by the availability of moisture. After a desiccation event, moisture is required for repair of internal and external membranes. However, plants are not always supplied with sufficient excess moisture to move beyond the repair stage and into a phase of net carbon assimilation and therefore growth (the carbon balance hypothesis; Alpert & Oechel 1985). Alpert and Oechel (1985) suggested that a minimum rain event of 4 mm is required for mosses to attain sufficient moisture status to begin
respiration in the arid U.S. Southwest, although less than 1 hour is required to pass into a phase of positive carbon gain (Oliver et al. 2000). Ideally, hydration must be available during daylight hours in order for mosses to expediently reach positive carbon balance, however there is evidence that mosses can begin recovery following night rain events (Alpert & Oechel 1985, Dilks & Proctor 1976).

The ability to tolerate desert hydration patterns is unique to true desiccation tolerant plants such as mosses, but even these organisms are considered rare within xeric habitats. Rarity of desiccation tolerant plants in xeric habitats is attributable to four main factors. First, rare severe drought cannot be endured by the majority of even the most resilient stems, leading to replacement of these stems by the spore bank and immigrant stems, which are probably less well adapted to these conditions in the short term; second, non-drought related extremes in temperature and nutrient contents often accompany the xeric character of these environments; third, competition between individuals is probably severe in order to procure and retain favorable sites; and fourth, the repetitive nature of the stress may further limit success (Alpert & Oechel 1985).

Workers have reported one (Lackner 1939) or two (Tamm 1953, Hägerup 1935, Jendralski 1955) periods of gametophyte growth per year in temperate climates. The initial period of growth typically coincides with the wettest time of year (Lackner 1939), with a secondary growth phase deriving from an innate pattern, independent of the external conditions (Hägerup 1935, see alternative viewpoint in Romose 1940). Pitkin (1975) reported a variety of growth rates
under seemingly uniform conditions, but noted that sampling may have been insufficient and lacking in uniformity. Pitkin also suggested that monthly rainfall means are a poor correlative measure and precipitation is better examined on a daily basis. Additionally, the author suggested using both precipitation and potential evapotranspiration as a better approach toward understanding growth patterns.

A few authors have reported notable differences in size between female and male individuals in angiosperms. For wind-pollinated angiosperms, if females have a higher investment in reproductive effort, there should be some discernable compensation in plant size (Ramadan et al. 1994). If females and males are equally sized, this brings into question how females are compromised or compensated for their higher reproductive investments. Potential explanations for this phenomenon include cost of sex, sex choice, maternal adjustment of the sex ratio, differential germination requirements, and active habitat selection or niche partitioning (Bierzychudek & Eckhart 1988). Dommee et al. (1990) reported no correlation of sex to size in 75% of the individuals sampled in a wind-pollinated annual. Generally, females allocate more energy to fruit maturation than males invest in pollen production (Willson 1983).

**Measurement Techniques**

Measurement of bryophyte growth intervals has historically been accomplished through a variety of methods both direct and indirect. Entire populations have been cropped to a consistent height and markers inserted to document successive growth or string has been tied to individuals and
subsequent growth measured directly (Longton & Greene 1969a). These direct methods are convenient for larger specimens, but as growth rates of xeric mosses have become of interest, alternative methods have been needed to detect shorter intervals. Indirect measurement is possible through careful dissection and interpretation of the chlorophyllous zones present along the stem in combination with inflorescence position and variations in leaf size. For acrocarpous species, because the development of an inflorescence terminates a given apical cell, gametangial position can demarcate growth intervals. Many species exhibit delicate variation in leaf morphology over the course of a growing season, and the careful observer can identify lateral buds to verify the delineations. For some species, these markers are accompanied by a subtle, but visually quantifiable, distinction in stem color (Figure 2). Stem color may provide evidence of two to three intervals of growth on specimens where other indirect growth indices are not available (Longton & Greene 1969a). These intervals are commonly referred to as the Green Zone (GZ), the entire chlorophyllous region, and the Recent Green Zone (RGZ), which refers only to the current season of photosynthetic tissue. An alternate system for naming these zones refers to the current season of growth as the GO segment, the previous as the G1 segment, and so on (G2, G3…). Both systems cause some amount of difficulty when crossing the boundary between two growing seasons as the GO segment now becomes the G1 segment and the RGZ is now the lower portion of the GZ.
Figure 2. Diagram of innate growth intervals (not to scale), after Stark (1997).
Phenological Patterns

Historical Perspectives

Interest in bryophyte phenological patterns began as casual observations regarding intermixed aggregates of species in the late 1800s. In particular, these remarks addressed timing of sporophyte appearance and release of spores. Individual plants were infrequently examined for specific phenophase and comments were often generalizations regarding seasonal appearance of structures. As phenology became recognized as a significant starting point for more sophisticated studies of ecology and reproductive biology, interest focused on the developmental times of antheridia and archegonia. These observations became valuable as taxonomic tools and environmental indicators and also provoked interest in population dynamics and breeding systems. Phenology also provided an interpretive basis for physiological responses on varying geographical scales, elucidated questions regarding sex dimorphism and novel sexual conditions, and suggested life history strategies (Miles et al. 1989, Stark 2002b). Mishler (1988) suggested that understanding reproductive biology is “critical in finding explanations for hypotheses of decreased genetic variation, phenotypic plasticity, pressures on mutation induced by haploid states, and ecological specificity.” Mishler also noted that these topics address questions regarding the function of sex in varying physiological and biotic environments—based on the diversity of reproductive mode and habitat specifications.
Nomenclature & Relevant Measures

Gametangia

Various schemes of assigning nomenclature to phenological phases have been proposed. As summarized in Table 1, foremost are those of Greene (1960), Bennett (1965), and Forman (1965), which have been variously adapted by more recent authors (Clarke & Greene 1970; Odu 1981; Imura 1994; Stark 1997, 2002). Initially, these classifications were looked upon as merely a tool of phase identification, but later numbers were assigned to the "phenophases" for the purpose of quantifying comparable differences in phases between and among populations.

Assignment of gametangial phases for archegonia and antheridia generally follows some variation of Greene (1960), and lists four phases. **Juvenile** gametangia are less than half the mean mature length, chlorophyllous, and cellular differentiation is minimal. Archegonia and antheridia are almost indistinguishable in mixed inflorescences, as well as being very similar to leaf primordia (Figure 3a). **Immature** gametangia are chlorophyllous, have attained at least half the mean mature length, and are differentiated into the vase-like archegonial and club-like antheridial forms (Figure 3b). Based on these conventions, the distinction between juvenile and immature gametangia must be done post-observation, and the distinction is somewhat arbitrary. The cap cells, which will disintegrate to permit entry into the archegonium and permit release of mature sperm from the antheridium, are intact in immature gametangia as the gametes develop. **Mature** gametangia continue to be chlorophyllous but cap
Table 1. Early phenological systems and current consensus scheme.

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cells in both archegonia and antheridia are ruptured. Ova are mature and receptive in the archegonium and dispersal of sperm takes place from the antheridium (Figure 3c). The final phase, dehisced, is typified by brown archegonia and antheridia. The archegonial neck canal is evident, and antheridia are empty and a translucent brown (Figure 3d). Gametangia which have failed to develop or are damaged are collectively classified as abortive, although if the specific cause can be determined, may be classified based on the specific cause of the failure. Values can then be assigned to each of the non-abortive phenophases to provide a quantitative measure of the mean phenophase of the sampled gametangia on a given sampling date. These data are usually represented graphically, with the predominant phenophase in large symbols and additional phenophases in proportionately smaller symbols relative to their prevalence.

Gametangial phenophases may be unequal in length and significant intervals of dormancy may transpire between stages. All gametangia of a given inflorescence may not mature at the same time. Initiation of gametangia can start along broad timelines of more than a year, although this extension may result in abortion of some gametangia. Initiation times are species specific and dependent upon a variety of environmental factors as discussed earlier. Ultimately, development concludes with a coordinated release of sperm from the antheridia and receptivity in the archegonia. Despite the specificity, there is some indication of broad geographic zones of similar developmental patterns and an effect of local climate and microclimate on maturation. Environmental effects

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on both gametangial and sporophytic maturation have been reported dating back to Wann (1925). Specifically, reports have been made regarding photoperiod (Voth & Hamner 1940), temperature (Benson-Evans 1964; Monroe 1965; Ridgeway 1967), and substrate (LaRue & Narayanaswami 1957; Crombie & Paton 1958). Reported patterns were summarized by Stark (2002b) in his review of bryophyte phenological studies. Stark noted wide variation in patterns of gametangial maturation, but stated that the most common pattern was one of archegonial initiation and maturation in a single spring/summer (1-2 months), antheridial initiation in fall/winter with over-wintering and maturation in spring/summer (6 months), and a fertilization period in summer (2 weeks to 4 months). Variations include: initiation of archegonia in fall/winter with maturation in spring/summer (6 months, but still preceded by antheridial initiation), additional rounds of antheridial initiation in spring/summer, initiation of antheridia in fall/winter but with a full year between initiation and maturation the following fall/winter (12 months), protracted sperm dispersal periods to maximize outcrossing in monoicous species, and prolonged periods of fertilization (up to 12 months). Some of these patterns are summarized in Figure 4.

The number, size, and abortion rate of gametangia produced per inflorescence are relevant to analyses of reproductive effort. The number of antheridia produced per perigonium often outnumbers the number of archegonia per perichaetium in a given species (Flowers 1973; Longton & Greene 1969a, b; Stark 1997, 2002b; Stark & Castetter 1995).
Figure 4 a-c. Common gametangial maturation patterns for archegonia (---) and antheridia (----) in a spring (♀)/fall (♂) pattern (a); a fall (♀)/fall (♂) pattern (b); and a fall (♀)/previous fall (♂) pattern (c). Based on northern hemisphere seasonality.
Gametangial size is ideally reported in terms of biomass, providing a comparison of assimilate investment; however, this is frequently not feasible considering their minute size. Evidence that biomass of antheridia exceeds that of archegonia is available in limited cases.

Stark et al. (2000) reported male allocation to perigonia as 0.0171 mg and to (unfertilized) perichaetia as 0.0027 mg. This accounted for approximately 1% and 0.1% of their total resource allocation per growth season, indicating a disproportionate allotment towards vegetative growth. Other limited evidence suggests this trend; hence, this level of effort is not customarily required and gametangial lengths suffice as a reasonable measure, comparisons then being restricted to an intragametangial level. Additionally, length measurements are already in place in order to provide distinction between juvenile and immature phenophases.

Some authors have chosen to omit rates of gametangial abortion; however, the prevalence of abortion could be important as an ecological indicator and for the purpose of examining the role of sexuality in species maintenance. Imura (1994) assessed developing, but not brownish, gametangia, which indicates that abortive gametangia may have been present though they were not reported as such. Greene (1960) addressed withered gametangia, but did not note whether these may actually have been abortive in nature. Duckett et al. (1982) noted, in a study not specifically related to reproductive biology, that many healthy-appearing antheridia are necrotic. This was particularly relevant for epiphytic species, another scenario in which water can be a limiting factor. Phenological
studies in xeric habitats have utilized this measure as an indication of male robustness (Stark 1997, Stark & Castetter 1995).

**Sporophytes**

The basis of distinctions among sporophyte phenophases is considerably more arbitrary; these stages create a continuum of development with fewer distinguishing features defining each phase. The phenophases are characterized by the maturation of several sporophytic features and their respective sizes. A brief explanation of terms is necessary here for better understanding of the phenophases. The archegonium is composed of a venter, the swollen vase-shaped portion, and a neck at the apex (Figure 5a). As the fertilized ovum within the archegonium matures, the haploid wall of the archegonium expands and encloses the growing embryonic axis within. The embryonic axis elongates and eventually ruptures, forming the calyptra and seta (Figure 5b). The calyptra acts as a shield for the developing embryo. The apex of the seta will expand to form a globose capsule with an inner area of sporogenous tissue and a cap which is designated the operculum. The capsule of many species has a "seam" encircling its mouth, the annulus, which assists in deoperculation (the detachment of the operculum), and rupturing of the annulus allows spore dispersal (Figure 5c).

Greene's (1960) phenological system identifies six primary phases (Figure 6), several of which he then subdivides into early and late. The first phase is identifiable by and named as *Swollen Venter* (SV) and is also indicated by a brown neck. Second, is *Calytra in Perichaetium* (CP), referring to the fact that
Figure 5. Archegonial and sporophytic terminology. Matured (dehisced) archegonium (a), developing embryo (b), sporophyte (c).

- a) Matured archegonium
  - ovum
  - venter

- b) Developing embryo
  - neck
  - calyptra (outer tissue)
  - embryo (within calyptra)

- c) Sporophyte
  - seta
  - operculum
  - annulus
  - capsule (theca)
Figure 6. Greene (1960) sporophyte phenophases (E = early, L = late).
the pre-calyptal tissue has expanded and elongated, but not beyond the confines of the shielding perichaetial leaves (if present). Prior to the rupture of the calyptra, this may be referred to as *Early CP*, and as the calyptra begins to emerge from the perichaetium, Greene identifies this as *Late CP*. Third, *Calyptra Intact* (CI), indicated by seta elongation that extends the calyptra beyond the perichaetial leaves early in the phase, and capsule expansion later, but with the calyptra intact throughout. When the calyptra falls, the fourth phase begins and is called, *Operculum Intact* (0I). This phase focuses on the maturation of the capsule and is suggestive of spore maturation. As the spores begin to mature, the operculum browns and the annulus develops a reddish-brown color. When the theca (capsule body) is less than half brown, it is called *Early 0I*, and when more than half brown *Late 0I*. When the spores are fully mature and spore dispersal is imminent, the operculum falls. This stage is *Operculum Fallen* (OF), and is relevant until three-fourths of the spores have dispersed. Finally, capsules that have dispersed at least three-fourths of their spores or are empty fall into the final category, *Empty and Fresh* (EF). This category only applies to capsules from the current maturation cycle; capsules from previous cycles would be categorized separately. The prevalence of abortive sporophytes is supposed, based on studies from mesic environments, to be rare, but is a relevant classification for desert mosses (Longton & Greene 1969a, b; Stark 1997, 2000a, 2001, 2002a, b; Stark & Castetter 1995) and has been added for the present study.
While Greene's system is convenient for a qualitative examination, it is not as convenient for quantitative assessment. It also leaves much room for debate when considering the subjective nature of distinctions between the early and late versions of each phase. Stark (1997, 2002) provides a consensus scheme for both gametophyte and sporophyte phenophases in Table 1 which will be utilized for this study. This system is not radically different from the original proposals, yet gives clear distinctions between phases and is neither too intensive nor too lax in forming reasonable divisions. By assigning numbers to each phase one can construct a quantitative analysis of data within and between populations.

As with gametangial development, the duration of each sporophytic phenophase is variable, yet remarkably well retained across the geographic range of most species (Stark 2002). These patterns are summarized by Stark (2002) into 6 general types approximated in Figure 7. Two of these groups may be categorized as rapid developing, including species with no resting phases in the maturation cycle. These species are either annuals, with ephemeral and variable timing of fertilization periods and rapid spore dispersal, or perennials, with a spring/summer fertilization and spore dispersal ranging from late summer to the following spring. A second pair includes species fertilized in spring, and segregated by the extent of development prior to over-wintering, with one developing to only the late embryo phenophase and the other to the meiotic/postmeiotic capsule phenophases. Of the final two groups, one is the exhibition of no discernable pattern and the other is the archetypical desert model. The xeric exemplars display patterns with fertilization in winter/spring,
Figure 7. Various patterns for sprophyte maturation. Annual (a); perennials with (b) rapid development, (c) over-wintering followed by rapid development, (d) rapid development followed by over-wintering, and (e) over-summering followed by moderately rapid development. Based on northern hemisphere seasonality.
maturation to the late embryo phenophase, over-summering, additional maturation in the following winter, and dispersal beginning the following spring.

**Population Demography**

For this study, demography of a population refers primarily to sex ratios and prevalence of reproductively successful individuals. The expectation in mosses is that spores are produced in a 1F:1M ratio in the capsule based on chromosomal sex determination and chromosome segregation during meiosis (Ramsey & Berrie 1982). Despite this expectation, both female-biased and male-biased sex ratios have been reported in the literature (Longton 1990; Wyatt 1994). A significant confounding aspect of sex ratios is the large proportion of non-expressing stems reported (Riemann 1972; Shaw et al. 1992). Regarding reproductive success, as measured by sporophyte frequency, low frequencies have been reported by many authors (e.g., Longton & Miles 1982; Rohrer 1982; Stark & Castetter 1987; Bowker et al. 2000).

**Spatial Patterning**

**Brief Review of Vascular Plant Literature**

The juxtaposition of females and males in space has been a topic of much interest recently. In particular, for vascular plants, discussion has focused around wind-pollinated dioecious species and the evolution of the dioecious habit in these species. This can fall under any or all the categories of spatial segregation of the sexes, niche partitioning, sex choice, differential mortality/survivorship, or resource partitioning. Trends indicate that females take
advantage of the more favorable habitats (Freeman et al. 1976). This may indicate higher costs of reproductive output for females and therefore a need for males to occupy less favorable sites and additionally to compete less with females in the more favorable sites. Cox (1981) suggests that two things must be true for spatial segregation to work for dioecious species. One, if females and males segregate to prevent intersexual competition, they must not become so separated that they fail to effectively fertilize. Two, if the evolution to dioecy in the species is segregation driven, the increased fitness caused by division of labor in this fashion must outweigh the disadvantages of dioecy. Bierzychudek and Eckhart (1988) point out that if the purpose of spatial segregation is to decrease intersexual competition, then intersexual competition must be more significant than intrasexual competition. Typically, intrasexual competition is dominant. Indeed, Bierzychudek and Eckhart (1988) suggest that true spatial segregation of the sexes (SSS) must meet 3 criteria. SSS should not be the result of differential mortality based upon habitat differences, there must be a clear mechanism driving segregation, and the segregation must be tested experimentally using reciprocal transplantation to distinguish intra- and intersexual competition from microhabitat mortality.

Bryophyte Applications

While it is intriguing to examine the causal factors behind SSS, bryophyte studies lack comprehensive examination of the presence or absence of SSS in natural populations. Clearly, in clonal organisms, expansion of a given genotype has the potential to create spatial segregation and large patches of a single sex.
In this scenario, genetic studies of the prevalence of specific genets within the population may be of more interest in the long term than superficial examination of sex-correlated segregation, but examination of the patterns (if present) on this level may be a necessary stepping stone to the genetic level.

Previous studies of population composition have been undertaken on both the superficial and the enzymatic/genotypic level, however the magnitude of the task of identifying all the individuals in a population, maintaining a record of their precise juxtaposition, and analyzing their relationships has been too daunting for any to undertake yet (including this researcher). One early study aimed at determining sex distributions looked at small clumps of individuals within larger populations and quantified sexuality within each clump. They did not, however, take any direct measurements of point-to-point distances between clumps or individuals and could only make an approximate conclusion that the sexes were intimately mixed, having found both males and females within most clumps (Bedford 1938). Wyatt (1977) assessed a single population of Atrichum angustatum (Brid.) B.S.G. through utilization of a grid system which sampled rows 10 cm apart and individuals along those rows at 1 cm intervals. From these data he was able to comment on the leptokurtic nature of gamete distribution (that gametes are dispersed within a few centimeters of the male.)

**Study Objectives**

The aims of the current study are to (1) identify the phenological pattern exhibited in S. caninervis, (2) determine the annual growth rate in a Mojave
Desert locale, (3) document the extent of gametangial and sporophytic abortion occurring in this extreme environment, and (4) establish the presence or absence of spatial pattern in sex expression and growth rate within various types of populations and within given proximities to observed demographic boundaries. Finer linkage of spatial pattern to specific, quantifiable microenvironmental trends represents a future goal.
CHAPTER 2

MATERIALS AND METHODS

Study Species

The study species is a bryophyte of arid regions including the western United States from Washington and southern Idaho south to New Mexico and Arizona (Flowers 1973) and Middle Eastern deserts. Syntrichia caninervis Mitt. is replaced by S. ruralis (Hedw.) Web & Mohr at higher elevations (Flowers 1973, Oliver et al. 2000). Growth form is compact to loose tufts or may occur scattered on open soil, and is distinguished from S. ruralis by its bistratose leaves. Plants are dioicous and acrocarpous, producing archegonia or antheridia in a single perigonium or perichaetium at the apex of the stem. Syntrichia caninervis is frequently found in association with the predominant shrub of the zone; in this case, Coleogyne ramosissima Torr. (blackbrush). Coleogyne ramosissima is predominant from 1200-1500 m elevation in the Mojave desert, overlapping with the adjacent Larrea tridentata-Ambrosia dumosa dominated community at the 900-1200 m elevation and the Pinus monophylla-Juniperus osteosperma dominated community at the 1500-1800 m elevations (Lei & Walker 1997). The positive correlation of Coleogyne to soil organic matter, lower under-shrub temperatures and greater fluctuation in soil temperatures in open areas reported
by Lei and Walker may be indicative in the relationship between Coleogyne and S. caninervis. The relationship between Coleogyne and S. caninervis may be a pseudo-symbiotic one, where establishment of Coleogyne is enhanced by S. caninervis' contribution to the organic matter of the soil in these regions and subsequent growth of Coleogyne provides protection from high temperatures and temperature fluctuations for S. caninervis, allowing proliferation of the species.

Syntrichia caninervis is a significant component of the desert biological crust, comprising 6.3% of soil cover in Nevada's Mojave Desert (Bowker et al. 2000). Bowker et al. (2000) documented a ratio of 14F:1M in expressing individuals, but acknowledged that due to the large number of non-expressing individuals (85%) this may not reflect the actual underlying genetic ratio, but merely the effective ratio for reproductive purposes. They also recorded an acute lack of sporophyte production, attributed largely to the low numbers of males present.

During the fall and winter of 1998-1999, approximately 450 populations of S. caninervis were sampled along a series of 5 transects (A – E) in a 1 hectare site near White Rock Spring, Spring Mountains, Red Rock NCA, Las Vegas, Nevada (elevation 1494m, T 20S, R58E). This site is adjacent to the study site used in the Bowker et al. (2000) analysis of sex expression, which remained advantageous owing to its protected status within a federal area. In the seven years previous to the study, annual precipitation averaged 25.23 ± 9.8 cm/year (mean ± one S.D.; Bowker et al. 2000). Precipitation was monitored on site throughout the study using a rain gauge secured in a Coleogyne shrub near several study populations. Evaporation of the precipitation water within the
gauge was prevented by leaving an oil film in the gauge after determining recent precipitation levels on each sampling date. Additionally, supporting precipitation and temperature data were supplied from the nearby Red Rock Canyon weather station (National Climatic Data Center).

For selection, populations were required to be at least 10 x 10 cm (L x W) and have a separation of 5 cm from other populations. One-centimeter diameter cores were taken from the densest portion of each population to determine the predominant sex. Stems were dissected from base to apex, carefully preserving inflorescences. If only females or males and non-expressing individuals were found in a given population, after a minimum of 10 stems were dissected, the population was given the designation Female, Male, or Non-expressing. If both a female and a male were recovered before reaching 10 dissections, the population was deemed Mixed-sex. Due to the previous findings in Bowker et al. (2000), in which all-male populations were found to be exceedingly rare, populations designated as purely Non-expressing or Male were resampled. This sampling was a haphazard collection of 10 individuals spanning the total area of the population.

Of a total of 186 populations that were sexed, only four populations were believed to be primarily composed of male and non-expressing stems. Three populations were mixed-sex (containing both males and females) and all remaining populations contained a mixture of female and non-expressing stems. No populations were entirely non-expressing based on these dissections. Using a random number table, four Female populations were selected for further study,
to accompany the three Mixed-sex populations and four Male populations available. Two of the three Mixed-sex populations contained high numbers of sporophytes from recent years. A map of the population locations is summarized in Figure 8 and basic population information is in Table 2.

Each population was carefully mapped using a 1 x 1 cm grid to designate population boundaries, densities, and location relative to its adjacent Coleogyne shrub. The grid and map provided the ability to realign the sampling grid and ensure systematic sampling of the populations on subsequent sampling dates.

Beginning January 1999, precipitation was closely monitored in anticipation of late winter rains. February provided the first rain event exceeding 4 mm, which has been noted as the minimum amount of precipitation required for full hydration of desert populations (Alpert & Oechel 1985). Following the rain event, each population was sampled using a random number table and grid coordinates from the earlier mappings. Individual ramets were removed in the field using fine forceps, attempting to disturb neighboring ramets as little as possible; if additional stems were removed along with the intended ramet, they were considered part of the sample. Here, a ramet is defined as single vegetative axis which may be branched or unbranched, and may or may not have organic attachments to other axes below the soil surface. Five randomly selected ramets (or ramet groups) from each population were placed in individually marked micropackets, allowed to air-dry if wet, and taken back to the lab. When young sporophytes became visible, additional ramets bearing sporophytes were haphazardly collected to provide a total of five specimens if they had not been
Figure 8. Red Rock NCA phenology populations.

- ♀ = female & non-expressing ramets
- ♂ = male & non-expressing ramets
- ♀♂ = female, male, & non-expressing ramets

Meters (E-W)
Meters (N-S)
Table 2. Red Rock NCA phenology populations.

<table>
<thead>
<tr>
<th>Population Name</th>
<th>Length x Width (cm)</th>
<th>Number of Ramets Sampled</th>
<th>Initial Sampling Sex Ratio</th>
<th>Designation</th>
<th>1997 Sporophytes</th>
</tr>
</thead>
<tbody>
<tr>
<td>A07</td>
<td>56 x 13</td>
<td>10</td>
<td>6♀:0♂:4NE</td>
<td>Mixed-Sex</td>
<td>yes</td>
</tr>
<tr>
<td>A13</td>
<td>56 x 26</td>
<td>10</td>
<td>1♀:0♂:9NE</td>
<td>Mixed-Sex</td>
<td>yes</td>
</tr>
<tr>
<td>B04</td>
<td>56 x 13</td>
<td>10</td>
<td>2♀:0♂:8NE</td>
<td>Female</td>
<td>no</td>
</tr>
<tr>
<td>B11</td>
<td>28 x 13</td>
<td>10</td>
<td>1♀:0♂:9NE</td>
<td>Female</td>
<td>no</td>
</tr>
<tr>
<td>B16</td>
<td>28 x 13</td>
<td>20</td>
<td>0♀:7♂:13NE</td>
<td>Male</td>
<td>no</td>
</tr>
<tr>
<td>B17</td>
<td>28 x 13</td>
<td>10</td>
<td>0♀:1♂:9</td>
<td>Mixed-Sex</td>
<td>yes</td>
</tr>
<tr>
<td>C08</td>
<td>28 x 13</td>
<td>20</td>
<td>0♀:6♂:14NE</td>
<td>Male</td>
<td>no</td>
</tr>
<tr>
<td>C09</td>
<td>28 x 13</td>
<td>20</td>
<td>0♀:6♂:14NE</td>
<td>Male</td>
<td>no</td>
</tr>
<tr>
<td>E01</td>
<td>56 x 13</td>
<td>20</td>
<td>0♀:6♂:14NE</td>
<td>Male</td>
<td>no</td>
</tr>
<tr>
<td>E02</td>
<td>28 x 13</td>
<td>10</td>
<td>1♀:0♂:9NE</td>
<td>Female</td>
<td>no</td>
</tr>
<tr>
<td>E04</td>
<td>28 x 13</td>
<td>10</td>
<td>1♀:0♂:9NE</td>
<td>Female</td>
<td>no</td>
</tr>
</tbody>
</table>

* NE = non-expressing
removed as part of the random sample. Samples were taken at least every 6 weeks, but more frequently if substantial rain events occurred. Care was taken that grid alignment was maintained on each sampling date to provide spatial data regarding the populations at the completion of the study. A low number of potentially significant precipitation events in 2001 caused sampling intervals to become attenuated to the minimum 6 week intervals. Sampling ended January 2002 due to time constraints on the length of the study.

**Laboratory Determinations**

Each micropacket was first examined for the number of ramets contained. If more than one ramet was present, a single ramet was selected randomly for dissection. Branched ramets were treated as a single unit regardless of whether the junction was below or above soil level. Using a stereomicroscope at 35x, hydrated ramets were denuded by removing single leaves from base to apex, detaching leaves carefully so as not to disturb inflorescences. If necessary, distal leaves subtending inflorescences were left intact until the rest of the stem was denuded, in order to prevent the shoot apex from detaching during dissection. Apices were thoroughly examined for presence of developing gametangia. Sex and number of inflorescences were noted. Each ramet was then placed on a slide micrometer (0.01 mm accuracy) and distances were recorded from the apex to each inflorescence. Length of the Green Zone and Recent Green Zone were also measured to the nearest 0.01 mm. Measurement
accuracy was within 0.02 mm on repeated trials and there was determined to be no discernable shrinkage of length in the Green Zone due to rewetting of stems.

**Determining Stem Elongation Rates**

A growth interval is defined as the stem distance between two inflorescences. Providing the individual expresses sex each year, this interval correlates to the period following expected gametangial fertility (when innovations were first observed, signifying the beginning of a new growth segment) through the following year of fertility (See Figure 9). However, for stems that did not produce gametangia (non-expressers), measurements taken from one season to the next had no clear delineation following the fertile period, resulting in the appearance that the RGZ/G0 had continued to expand when in reality, the RGZ was now the G1 segment with a new G0 developing. The segment that had been classified as G1 (while still greenish) was now the G2 segment. This new G0 growth was distinct on stems which had produced gametangia until after the July/August precipitation event, at which point recent green zones appeared to consist only of the new G0 (the previous G0 was now distinct as G1 and the previous G1 was now more or less indistinguishable from the other previous growth). This implies that the period from spring precipitation to fall precipitation is the period of resource transfer within the stem. As resources are removed from the G2 segment, it becomes indistinguishable from the previous growth seasons, and a demarcation develops between the new growth and the now G1 segment.

When a terminal archegonium was not fertilized, vegetative growth resumed from a subapical bud within the perichaetium. These buds have been observed
Figure 9. Stem elongation in expressing vs. non-expressing ramets. In the expressing ramet, the perichaetium provides a reference point to distinguish current growth from previous growth. In the non-expressing ramet, the growth appears contiguous.

Expressing Ramet

Non-expressing Ramet

terminal perichaetium

new innovations

unfertilized archegonium
in the related species *Tortula inermis* (Stark 1997). Providing sufficient hydration status and no fertilization, resumption of vegetative growth began immediately following the termination by archegonia. This suggests that for stems without terminal inflorescences, growth interval data from this time period may be relevant to both the G0 and G1, causing the potential for confusion. As mentioned previously, for this reason G0 data was not used.

**Determining Phenological Cycles**

Preliminary trials indicated that only current cycle (G0) perichaetia could provide reliable maturation data, while both current (G0) and previous (G1) cycle perigonia were relevant due to the two season requirement for initiation and maturation of the antheridia. G0 perichaetia and G0/G1 perigonia were wet-mounted for examination under a compound microscope fitted with an ocular micrometer. Archegonia and antheridia were counted within each inflorescence, measured to the nearest whole micrometer unit, photodocumented, and assigned a phenophase following Stark (1997, 2002a). Unused ramets and dissected stems were retained in the original micropackets, and mounted slides were retained in slide folders.

**Statistical Methods**

Ratios of females:males:non-expressing stems and female reproductive:non-reproductive stems were recorded for the population series, for each population type (Female, Male, Mixed-sex), and for each population. Stems were also

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scored based on functional sex during a given growth season to determine potential annual functional sex ratios.

Due to non-normality of the data set which was not correctable using the standard methods of normalization, G0 and G1 ramet lengths were assessed using a Kruskal-Wallis test for comparison of length between females, males, and non-expressing stems segregated by growth season. G1 lengths were also compared between growth seasons segregated by expression.

Number of inflorescences per stem, number of gametangia per inflorescence, and the majority phase of each inflorescence were calculated for each population, population type, and for the population series.

Individuals within populations were mapped using these data regarding growth rate, sex, and reproductive robustness. These graphs were then assessed for nearest neighbor distances and analyzed using a chi-square test following Pielou (1961). The resultant segregation values provide an estimate of the randomness of distribution of sexes within the population. If, as we currently assume, male and female spores are equally produced and randomly distributed, then aggregation would be attributable to either variation in rates of establishment, or unequal vegetative and reproductive success of individuals following establishment.

While the proximity of samples in this study might lead one to consider whether or not these samples are truly independent, samples are considered to be independent for the following reasons. First, due to their small size, sampling was destructive and stems could not be repeatedly sampled through the course
of the study. Second, competition is a phenomenon which is considered highly unlikely for mosses. A non-parametric two-way ANOVA supports this assumption for all of the populations at a p-value <0.05.
CHAPTER 3

RESULTS

Weather Data

Precipitation and temperature data collected at the Red Rock Canyon NCA weather station from 1961-1990 are displayed in Figure 10. This 30-year data set suggests two periods during which high levels of precipitation may occur in the Red Rock Canyon area. One period of high precipitation is during the late summer months of July and August, the traditional "monsoon" season. The second episode deposits less precipitation per diem, but over the extended period from November to April comprises a majority of the precipitation deposition for the year. Mean daily precipitation in the months of March and April frequently surpasses deposition during July and August. Actual rainfall data from the Red Rock Canyon NCA weather station from January 1998 through February 2002 is shown in Figure 11. Annual rainfall for the study period and data collected by Bowker et al. (2000) for the previous seasons is summarized in Table 3.

In the northern Mojave, temperatures climb during the spring months to reach their peak in July and slowly abate during the fall (Figure 10). The coincidence of high temperatures and high precipitation in July and August
Figure 10. Red Rock NCA Temperature and Precipitation 1961-1990.
Figure 11. Daily precipitation (cm) at Red Rock Canyon NCA 1998-2000.

<table>
<thead>
<tr>
<th>Year</th>
<th>Precipitation (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1990-1997 (mean) (Bowker et al. 2000)</td>
<td>25.23 ± 9.8</td>
</tr>
<tr>
<td>1998</td>
<td>44.83</td>
</tr>
<tr>
<td>1999</td>
<td>16.94</td>
</tr>
<tr>
<td><em>data not available for 01/1999</em></td>
<td></td>
</tr>
<tr>
<td>2000</td>
<td>22.53</td>
</tr>
<tr>
<td>2001</td>
<td>27.31</td>
</tr>
</tbody>
</table>

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creates a potential for rapid desiccation scenarios for mosses of the desert Southwest.

**Growth Rate**

Mean growth rate for all sexes and all growth seasons (1997-2000) was 0.29 mm ± 0.04, (mean and S.D., n = 1435). Growth rate partitioned by year and by sex is summarized in Table 4. Sample size for the 2001 growth season is small due to attenuation of sampling in 2001 and cessation in January 2002. Conclusions drawn from this data are consequently less supported, and will be only discussed briefly. Only G1 data was used in the analyses to prevent confusion as noted earlier.

Growth rate data as a function of sex expression and segregated into the 1997, 1998, 1999 and 2000 growth seasons are displayed in Table 5. These data suggest a significant association (regardless of the growing season) between sex expression and growth rate (p-values < 0.001 to 0.02). They do not, however, support any difference in growth rate between male and female individuals (p-values 0.235 to 0.740).

Growth rate as a function of growth season and segregated by expression is displayed in Table 6. The primary trend in these data suggests a significant difference between the 1997 growth season and other growth seasons for all expression classes (p-value < 0.001). However, these data do not support a difference in growth between 1998, 1999, and 2000 growth seasons (p-value 0.066 to 0.899); with the exception of female stems. Female stems were not
Table 4. Stem elongation rates (mm).

<table>
<thead>
<tr>
<th></th>
<th>All Stems</th>
<th>Non-expressers</th>
<th>Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Standard Deviation</td>
<td>Mean</td>
<td>Standard Deviation</td>
</tr>
<tr>
<td>All years</td>
<td>0.29</td>
<td>0.04</td>
<td>0.27</td>
<td>0.04</td>
</tr>
<tr>
<td>1997</td>
<td>0.31</td>
<td>0.05</td>
<td>0.29</td>
<td>0.06</td>
</tr>
<tr>
<td>1998</td>
<td>0.28</td>
<td>0.03</td>
<td>0.26</td>
<td>0.02</td>
</tr>
<tr>
<td>1999</td>
<td>0.28</td>
<td>0.03</td>
<td>0.26</td>
<td>0.02</td>
</tr>
<tr>
<td>2000</td>
<td>0.26</td>
<td>0.08</td>
<td>0.27</td>
<td>0.01</td>
</tr>
<tr>
<td>N</td>
<td>1435</td>
<td>634</td>
<td>516</td>
<td>285</td>
</tr>
</tbody>
</table>
Table 5. Comparison of growth rates between males, females, and non-expressing stems, for both G0 and G1

<table>
<thead>
<tr>
<th>Sample Sizes</th>
<th>Comparison of Growth Rates</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Non-Expressing</td>
</tr>
<tr>
<td>G1 1997-1998</td>
<td>206</td>
</tr>
<tr>
<td>G1 1998-1999</td>
<td>225</td>
</tr>
<tr>
<td>G0 1998-1999</td>
<td>225</td>
</tr>
<tr>
<td>G1 1999-2000</td>
<td>298</td>
</tr>
<tr>
<td>G0 1999-2000</td>
<td>298</td>
</tr>
<tr>
<td>G1 2000-2001</td>
<td>114</td>
</tr>
<tr>
<td>G0 2000-2001</td>
<td>114</td>
</tr>
</tbody>
</table>
Table 6. Comparison of growth rates by season, using G1 data only.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Indeterminate Ramets</td>
<td>206</td>
<td>298</td>
<td>114</td>
<td>16</td>
</tr>
<tr>
<td>Female Ramets</td>
<td>169</td>
<td>243</td>
<td>82</td>
<td>22</td>
</tr>
<tr>
<td>Male Ramets</td>
<td>91</td>
<td>125</td>
<td>60</td>
<td>8</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Indeterminate Ramets</td>
<td>p&lt;0.001</td>
<td>p&lt;0.001</td>
<td>p&lt;0.001</td>
<td>p=0.100</td>
<td>p=0.502</td>
<td>p=0.141</td>
</tr>
<tr>
<td>Female Ramets</td>
<td>p&lt;0.001</td>
<td>p&lt;0.001</td>
<td>p&lt;0.001</td>
<td>p=0.899</td>
<td>p=0.002</td>
<td>p=0.005</td>
</tr>
<tr>
<td>Male Ramets</td>
<td>p&lt;0.001</td>
<td>p&lt;0.001</td>
<td>p&lt;0.001</td>
<td>p=0.730</td>
<td>p=0.122</td>
<td>p=0.066</td>
</tr>
</tbody>
</table>
significantly different between the 1998 and 1999 growth seasons, however these seasons varied significantly from the 2000 growth season (p-values 0.002 and 0.005).

Gametangial Phenology

*Maturation Cycle*

Archegonia (♀) are initiated following a late summer rain event (August/September) and attain a juvenile to immature phenophase prior to the winter/spring precipitation events. Archegonia develop rapidly during the following rain events to achieve maturation in the spring (March). Archegonia which never reach a receptive state are considered abortive. Total time from initiation to a receptive state is approximately 6 months. Mean archegonial phenophase is reported in Figure 12a.

Antheridia (♂) are also initiated in late summer (August/September), but “over-summer” in the juvenile & immature phenophases. Additional maturation occurs during the following fall, increasing the proportion of antheridia in the immature phenophase. The first mature antheridia disperse their sperm in February, and dispersal continues through the archegonial period of receptivity into April (17 to 19 months after initiation). As with archegonia, antheridia that fail to disperse their sperm are regarded as abortive. Aborted gametangia were recorded during all months following initiation (Figure 12b).
Figure 12. Time course of gametangial maturation. Predominant phenophase for archegonia (a) and antheridia (b) is represented by the large symbol. Additional phenophases present in samples are represented by small symbols.
Number and size of gametangia

per inflorescence

Across populations, mean number of archegonia per perichaetium was 3.75 ± 2.5 (n = 105), and mean number of antheridia per perigonium was 14.35 ± 3.7 (n = 189). Length of gametangia is reported in Table 7. Mean length of each phase was compared to length of abortive gametangia (Table 8). For archegonia, there was no significant difference between length in the abortive phenophase (mean 524.6 µm ± 142.4) and immature, mature, or dehisced phenophases; however the least difference in length is between abortive and dehisced (mean 573.8 µm ± 196.2; H = 0.9, p-value = 0.332). For antheridia, the immature phenophase (mean 297.5 µm ± 71.2) shows the least difference in length from the abortive phenophase (mean 295.5 µm ± 91.9; H = 0.0, p-value = 0.958).

The proportion of abortive archegonia per perichaetium for the entire study period was 0.45 ± 0.42. The proportion of abortive antheridia per perigonium for the entire study period was 0.24 ± 0.14. Annual rates of abortive gametangia are reported in Table 9. There was no significant difference between the number of archegonia aborted from each year of maturation 1999-2001 (p = 0.063, n = 152); however, there was a significant difference between the number of antheridia aborted per perigonium between maturation in years 2000 and 2001 (initiated fall of 1998 and fall of 1999 respectively) and other years (Table 10).
Table 7. Mean gametangial lengths (µm), 1999-2001 collections combined.

<table>
<thead>
<tr>
<th></th>
<th>Archegonia</th>
<th>Antheridia</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean</td>
<td>st dev</td>
</tr>
<tr>
<td>Juvenile</td>
<td>168.8</td>
<td>61.5</td>
</tr>
<tr>
<td>n</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td>Immature</td>
<td>442.1</td>
<td>111.3</td>
</tr>
<tr>
<td>n</td>
<td>25</td>
<td></td>
</tr>
<tr>
<td>Mature</td>
<td>439.2</td>
<td>164.4</td>
</tr>
<tr>
<td>n</td>
<td>23</td>
<td></td>
</tr>
<tr>
<td>Dehisced</td>
<td>573.8</td>
<td>196.2</td>
</tr>
<tr>
<td>n</td>
<td>230</td>
<td></td>
</tr>
<tr>
<td>Abortive</td>
<td>524.6</td>
<td>142.4</td>
</tr>
<tr>
<td>n</td>
<td>152</td>
<td></td>
</tr>
</tbody>
</table>
Table 8. Comparison of maturing gametangial lengths to abortive gametangial lengths.

<table>
<thead>
<tr>
<th></th>
<th>Archegonia</th>
<th>Antheridia</th>
</tr>
</thead>
<tbody>
<tr>
<td>p-value</td>
<td>p-value</td>
<td>p-value</td>
</tr>
<tr>
<td>Juvenile</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>n</td>
<td>315</td>
<td>30</td>
</tr>
<tr>
<td>Immature</td>
<td>0.160</td>
<td>0.958</td>
</tr>
<tr>
<td>n</td>
<td>440</td>
<td>25</td>
</tr>
<tr>
<td>Mature</td>
<td>0.192</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>n</td>
<td>47</td>
<td>23</td>
</tr>
<tr>
<td>Dehisced</td>
<td>0.332</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>n</td>
<td>65</td>
<td>230</td>
</tr>
</tbody>
</table>
Table 9. Incidence of gametangial abortion.

<table>
<thead>
<tr>
<th>Year of Maturation</th>
<th>Archeogonia Mean % Abortive</th>
<th>S.D.</th>
<th>Antheridia Mean % Abortive</th>
<th>S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>49.60</td>
<td>41.80</td>
<td>33.22</td>
<td>29.08</td>
</tr>
<tr>
<td>2000</td>
<td>42.37</td>
<td>35.35</td>
<td>19.78</td>
<td>25.83</td>
</tr>
<tr>
<td>2001</td>
<td>47.26</td>
<td>40.73</td>
<td>19.09</td>
<td>12.87</td>
</tr>
<tr>
<td>2002</td>
<td>--</td>
<td>--</td>
<td>27.32</td>
<td>26.31</td>
</tr>
</tbody>
</table>
Table 10. Comparison of proportion of abortive gametangia in each season.

<table>
<thead>
<tr>
<th>Year of Maturation</th>
<th>Archegonia p-value</th>
<th>Archegonia n</th>
<th>Antheridia p-value</th>
<th>Antheridia n</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999 vs. 2000</td>
<td>0.175</td>
<td>103</td>
<td>&lt;0.001</td>
<td>110</td>
</tr>
<tr>
<td>1999 vs. 2001</td>
<td>0.346</td>
<td>96</td>
<td>&lt;0.001</td>
<td>115</td>
</tr>
<tr>
<td>1999 vs. 2002</td>
<td>--</td>
<td>--</td>
<td>0.020</td>
<td>94</td>
</tr>
<tr>
<td>2000 vs. 2001</td>
<td>0.103</td>
<td>105</td>
<td>0.786</td>
<td>157</td>
</tr>
<tr>
<td>2000 vs. 2002</td>
<td>--</td>
<td>--</td>
<td>&lt;0.001</td>
<td>133</td>
</tr>
<tr>
<td>2001 vs. 2002</td>
<td>--</td>
<td>--</td>
<td>&lt;0.001</td>
<td>138</td>
</tr>
</tbody>
</table>
Sporophyte Phenology

Maturation Cycle

Sporophyte development was observed among three cohorts, 1998, 1999 and 2000. Evidence of these fertilization events was apparent in March and April samples for the 1999 and 2000 sampling periods, during which embryos were observed somewhere in the early and late embryo phases. Sporophytes were not observed in the Seta Elongation phenophase. Because the distinction between early and late embryo phenophases is based on the embryos attaining one-half their final length (assessed at the onset of Seta Elongation), embryos could not be definitely categorized into one phase or the other. Unfortunately, no embryos fertilized in any of these years developed beyond late embryo.

Embryos from the 1998 cohort (collected in 1999, during their second season of maturation) did not develop beyond the late embryo phenophase, but were found in the abortive state. Embryos from the 1999 and 2000 cohorts remained in the late embryo condition through summer. In fall collections, calyptrae were unruptured, and sporophytes were withered and brown (abortive). There was evidence that successful maturation of fertilizations from the 1997 cohort had occurred, as withered sporophytes with empty capsules were present at the outset of the study. There was no record of successful maturation of a fertilized embryo from 1998-2001, from either the study populations or, by inspection, of the general Red Rock NCA region.
Number and size of sporophytes

per inflorescence

Among fertilized perichaetia from the 1998, 1999, and 2000 cohorts, usually one archegonium per inflorescence had been fertilized. Where multiple fertilizations had occurred, development ceased during the early embryo phenophase. No occurrences of successful polysety (development of two sporophytes by the same perichaetium) beyond early embryo were apparent. Sporophytes from all cohorts (abortive and viable) had a mean length of 1.63 mm ± 0.9 mm (n = 54); cohorts were not assessed individually due to small sample sizes.

Incidence of sporophyte abortion

For the study period, 85% of the embryos examined were abortive. The 15% that were not abortive were from collections made in March and April of each year, immediately following their fertilization. Based on samples taken in 1999, 2000, and 2001 of the 1998, 1999, and 2000 cohorts, respectively, rates of abortive sporophytes are estimated to be 100%. Within 6 months of fertilization of a given cohort, all sporophytes collected were abortive, supporting this hypothesis.

Population Demography/Sex Ratios

In total 57% of ramets sampled did not express sex in their lifetime. In the remaining ramets, either a perigonium or perichaetium had been produced at
some point during their life history. Actual counts of non-expressing, male, and female ramets are shown in Table 11. Sex ratios are summarized in Table 12. Expressing ramets had not necessarily expressed sex during the study period. In fact, the majority of ramets sampled had expressed sex prior to 1998. Two interesting calculations can be derived from this data. First, a determination of the frequency of sex expression can be made, as the number of inflorescences produced per ramet; in this case only ramets with at least 2.4 mm of stem length (approx. 8 years of growth) were examined. This data is summarized in Table 13. Secondly, using the stem elongation rate data, each inflorescence along the stem could be assigned an approximate year of maturation. This will be referred to in this study as the potential functional sex ratio for the given growth season. The reason it is potential is that since antheridia and archegonia are brown and withered after their periods of fertility, it could not be verified whether any gametangia successfully matured in the given season. Year of maturation is used as opposed to year of initiation because that is the year in which the individual would be potentially involved in sexual reproduction. Again, all stems with growth traceable back to 1992 (approx. 2.4 mm) were scored for functional sex ratio during each growth season. These data are summarized in Table 14.

Spatial Patterning

Each sample was mapped based on sex expression (Figure 13a-k). Nearest neighbor analysis (S-statistic, Pielou 1961) and chi-square analysis of contingency tables based on these maps are summarized in Table 15.
Table 11. Actual stem counts, all collections combined.

<table>
<thead>
<tr>
<th>Population Designation</th>
<th>Population Name</th>
<th>N</th>
<th>Non-expressing</th>
<th>Female</th>
<th>Female with Sporophytes</th>
<th>Male</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mixed-Sex</td>
<td>A07</td>
<td>112</td>
<td>44</td>
<td>60</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>A13</td>
<td>106</td>
<td>66</td>
<td>29</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>B17</td>
<td>102</td>
<td>29</td>
<td>43</td>
<td>21</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>B16</td>
<td>80</td>
<td>19</td>
<td>14</td>
<td>0</td>
<td>47</td>
</tr>
<tr>
<td></td>
<td>E01</td>
<td>109</td>
<td>66</td>
<td>10</td>
<td>2</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>C08</td>
<td>110</td>
<td>38</td>
<td>0</td>
<td>0</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td>C09</td>
<td>93</td>
<td>50</td>
<td>2</td>
<td>0</td>
<td>41</td>
</tr>
<tr>
<td>Male Only</td>
<td>B04</td>
<td>108</td>
<td>43</td>
<td>65</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>B11</td>
<td>104</td>
<td>33</td>
<td>64</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>E02</td>
<td>113</td>
<td>87</td>
<td>26</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>E04</td>
<td>113</td>
<td>56</td>
<td>57</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 12. Ratios of expressing, non-expressing, male, female, and reproductive ramets over the course of their lifetime.

<table>
<thead>
<tr>
<th>Sex Ratios</th>
<th>n</th>
<th>Non-Expressing: Expressing (% non-expressing)</th>
<th>Females: Males</th>
<th>% of Females Involved in Sexual Reproduction in Their Lifetime</th>
</tr>
</thead>
<tbody>
<tr>
<td>Community (All Growing Seasons Combined)</td>
<td>1899</td>
<td>1:21:1 (46.2)</td>
<td>2:1</td>
<td>10.8</td>
</tr>
<tr>
<td>By Population Type (All Growing Seasons Combined)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>392</td>
<td>1:1.27 (44.1%)</td>
<td>1:6.8</td>
<td>7.1</td>
</tr>
<tr>
<td>Female</td>
<td>438</td>
<td>1:1.02 (49.6%)</td>
<td>1:0</td>
<td>3.2</td>
</tr>
<tr>
<td>Mixed-Sex</td>
<td>320</td>
<td>1:1.30 (43.4%)</td>
<td>9:1</td>
<td>19.0</td>
</tr>
<tr>
<td>By Population (All Growing Seasons Combined)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A07</td>
<td>112</td>
<td>1:1.54 (39.9%)</td>
<td>33:1</td>
<td>9.1</td>
</tr>
<tr>
<td>A13</td>
<td>106</td>
<td>1:65:1 (62.3%)</td>
<td>4.7:1</td>
<td>12.1</td>
</tr>
<tr>
<td>B04</td>
<td>108</td>
<td>1:1.51 (39.8%)</td>
<td>1:0</td>
<td>0</td>
</tr>
<tr>
<td>B11</td>
<td>104</td>
<td>1:2.15 (31.7%)</td>
<td>1:0</td>
<td>9.9</td>
</tr>
<tr>
<td>B16</td>
<td>80</td>
<td>1:3.21 (23.8%)</td>
<td>1:3.4</td>
<td>0</td>
</tr>
<tr>
<td>B17</td>
<td>102</td>
<td>1:2.52 (28.4%)</td>
<td>1:2.52</td>
<td>32.8</td>
</tr>
<tr>
<td>C08</td>
<td>110</td>
<td>1:1.89 (34.5%)</td>
<td>0:1</td>
<td>-</td>
</tr>
<tr>
<td>C09</td>
<td>93</td>
<td>1:16:1 (53.8%)</td>
<td>1:20.5</td>
<td>0</td>
</tr>
<tr>
<td>E01</td>
<td>109</td>
<td>1:53:1 (60.6%)</td>
<td>1:2.6</td>
<td>16.7</td>
</tr>
<tr>
<td>E02</td>
<td>113</td>
<td>3.35:1 (77.0%)</td>
<td>1:0</td>
<td>0</td>
</tr>
<tr>
<td>E04</td>
<td>113</td>
<td>1:1.01 (49.6%)</td>
<td>1:0</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 13. Frequency of sex expression over the course of 8 years (approx. 2.4 mm stem length) for females and males.

<table>
<thead>
<tr>
<th>Population</th>
<th>Female Ramets</th>
<th>Male Ramets</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Frequency of Expression (# of years)</td>
<td>Frequency of Expression (# of years)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>% of ramets</td>
</tr>
<tr>
<td>A07</td>
<td>32</td>
<td>53.3</td>
</tr>
<tr>
<td>A13</td>
<td>24</td>
<td>82.8</td>
</tr>
<tr>
<td>B04</td>
<td>33</td>
<td>50.8</td>
</tr>
<tr>
<td>B11</td>
<td>34</td>
<td>53.0</td>
</tr>
<tr>
<td>B16</td>
<td>14</td>
<td>100.0</td>
</tr>
<tr>
<td>B17</td>
<td>36</td>
<td>83.7</td>
</tr>
<tr>
<td>C08</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>C09</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td>E01</td>
<td>8</td>
<td>100.0</td>
</tr>
<tr>
<td>E02</td>
<td>12</td>
<td>80.0</td>
</tr>
<tr>
<td>E04</td>
<td>29</td>
<td>46.2</td>
</tr>
<tr>
<td>Overall</td>
<td>224</td>
<td>60.5</td>
</tr>
</tbody>
</table>
Table 14. Functional sex ratios (Non-expressing:Female:Male) by population and for the study series approximated from the previous 2.4 mm of growth (≈8 years).

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>A07</td>
<td>11:1:0</td>
<td>1:0:0</td>
<td>9:1:0</td>
<td>11:1:0</td>
<td>5:1:0</td>
<td>6:1:0</td>
<td>10:1:0</td>
<td>6:1:0</td>
<td>8:1:0</td>
<td>10:1:0</td>
</tr>
<tr>
<td>A13</td>
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Figures 13a-k. Spatial pattern maps based on sex expression (lifetime).
♦ = non-expressing, ■ = female, △ = male, ○ = female w/ sporophyte

Population A07

Population A13

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Table 15. Summary of $\chi^2$ analysis of spatial patterns.

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CHAPTER 4

DISCUSSION

Weather Data

Precipitation data for the study period reflect the type of prolonged drought that may limit even desiccation tolerant species in xeric habitats. While there were 14 rain events of at least 1 mm during 1998, following years averaged only 6 events per year. In each year from 1998 through 2001, the number of 4 mm or greater rain events remained constant at 2 per year (the suggested minimum significant rain event (Alpert & Oechel 1985). However, total precipitation from all events was almost twice as high in 1998 as in the primary study years. Clearly, these plants were experiencing stressful conditions during these years, but without long term data, it is difficult to distinguish whether this is the "norm" or truly extreme. Because growth is observed in the absence of "sufficient" rainfall, these data suggest that, at least for this species, smaller hydration events may be effective toward growth and development. Also, the infrequency of hydration events reinforces the limited time frames during which growth occurs and the tremendous capacity the plants demonstrate to rapidly utilize their ephemeral resources as noted by Vitt (1989).
Examining this weather data and pairing it to the phenological pattern reveals which months are the principal growth periods for *S. caninervis*. Fall precipitation stimulates growth and initiation of both male and female gametangia. For expressing individuals, this results in archegonia maturing to the *immature phase* and males attaining the *juvenile* and sometimes *immature* state. Spring precipitation promotes additional growth in non-expressing individuals. Ideally, both non-expressing and expressing individuals must experience at least two considerable rain events during the spring months. The patterns observed in this study suggest that first event supports development of archegonia to the receptive *mature* state, and increases the ratio of *immature* to *juvenile* antheridia within perigonia (first year of maturation). The second event signifies the onset of the next growth season, with stems producing new innovations in both expressing and non-expressing stems. For males, a second year of development must occur before sperm are dispersed. For these individuals, the second series of fall rain events fuels an increase in length of the sterile innovation that was initiated during the previous spring and some additional development of antheridia from the *juvenile* to the *immature* phenophase. Again, the first spring precipitation event is responsible for the *mature* phenophase in antheridia, coinciding with the current year’s cohort of receptive archegonia. A second rain event in spring will again contribute to new innovations associated with the subsequent growth season.
Growth Rate

Growth rates for this species compare well to those for other xeric species, falling within the ranges reported of 0.14 mm to 3.0 mm per year (Mishler & Oliver 1991; Stark 1997; Stark & Castetter 1995). While only 48.6% of the variation in growth rates could be attributed to precipitation trends, it is commonly understood that precipitation patterns alone do not create the physiological complications experienced by desert organisms. The effect of the combination of both precipitation and temperature and/or radiation extremes must be taken into consideration for these organisms. The shorter elongation rates, 0.14 mm and 0.18 mm, reported by Stark (1997) and Stark and Castetter (1995) for two xeric monoicous species when compared to this study’s reported mean elongation of 0.29 mm may provide support to the theory that dioicous species allocate more resources to vegetative expansion than to sexual reproduction relative to monoicous species. Additional examination of this trend is warranted in both xeric and mesic species.

Examining non-expressing and expressing stems separately, there is evidence that expressing stems attain greater lengths than non-expressing stems. There are suggestions in the literature that sugar concentrations may play an important role in gametangial initiation, which may be a causal link to the correlation between growth rate and expression (Chopra & Rahbar 1982; Chopra & Bhatla 1983). Stark et al. (2001) found that individuals of S. caninervis require a biomass threshold of about 0.5 mg, with all individuals in excess of 2.0 mg expressing sex. Consistent with this, shorter stems (theoretically younger stems)
did tend to exhibit shorter growth rates. Young stems may not have the photosynthetic reserves available to transfer to new innovations and support increased growth rates. These issues are complicated by the clonal nature of the species. While there is ample documentation of the movement of resources between growing segments (Bates 2000), it is unknown to what extent ramets can transfer assimilate and/or resources between (connected) axes. The presence of a cause and effect relationship between stem age and elongation rates, and therefore expression, needs to be examined in vitro from spore or propagule isolates. Generation of individuals from spores is currently being explored for S. caninervis, however low levels of sporophyte production have hindered progress.

Males and females did not differ in growth rates. Because the mass of the perigonium is so much greater than that of the perichaetium, allocation towards gametangial production and maturation is probably more costly (in relation to total assimilate resources) for males than for females (Stark et al. 2000). This may be exhibited in other species by means of females displaying apparently greater growth rates than males (McLetchie & Puterbaugh 2000). This differential distribution of assets must be compensated for in some way. Possibly, the maturation of a perigonium creates a deficit of resources available for translocation to developing innovations. This potential deficit caused by production of a perigonium could impact subsequent growth seasons as a tradeoff. Species with such minute growth rates do not make feasible study subjects for this type of assessment due to the destructive nature of examination.
Larger species could provide useful insight using stems which can be repeatedly measured over many growth seasons to examine the effect of antheridial production on later growth and allocation. Molecular biology may also be a productive tool in exploring this question. Because the sexuality of non-expressing individuals cannot be determined, chromosomally or genotypically determined expression paired with growth rate examination could lead to evidence of growth rate variation within non-expressing stems (the expectation being that if males and females vary in elongation rates, this should be reflected prior to any realization of a minimum size).

In addition to an absence of successful sporophyte maturation, sample sizes were not sufficient to compare growth rate between females that had previously matured sporophytes to those that had not. However, exploration of trends regarding allocation and availability of resources following sporophyte maturation for such females should be informative in other species. Particularly, these data would be remarkable in relation to allocation and availability following perigonial development, because production of a sporophyte is about an order of magnitude more expensive than perigonial maturation.

Inspection of each class of individuals (male, female, and non-expressing) during individual growth seasons provided confirmation of the aforementioned correlations between males, females, and non-expressers. However, data from Table 6 may suggest a finer-scale pattern, at least for females. Precipitation during the 1997-1998 growth season was optimum relative to the other growth seasons, resulting in significantly greater growth rates. For males and non-
expressing stems, the decreased elongation rates generated from the 1998-2000 growth were not significantly different. Females, however, displayed some level of variation. Growth rates for females in 1998 and 1999 were not significantly different ($p = 0.899$); however, growth rate in 2000 was significantly greater than in either of these two preceding years (vs. 1998 $p = 0.002$; vs. 1999 $p = 0.005$). Precipitation in 2000 also exceeded the reported mean (27.3 cm versus 25.3 cm) for the first time during the study period. These data may suggest a greater sensitivity to moisture availability for females. This would also support the theory that females may be the more prevalent sex due to their ability to withstand less favorable conditions.

This species relies primarily on throughfall, resulting in a heterogeneous hydration pattern at the population level. As a result, it was not possible to chart a continuous timecourse for growth because growth intervals of individuals could not be tied to specific rain events.

Gametangial Phenology

Gametangial initiation and maturation are essentially dictated by hydration events and most likely coupled with genetic controls (Longton 1990). Initiation is triggered by a fall precipitation event, though potentially limited to stems realizing some minimum concentration of assimilates available for allocation to development of reproductive structures. Lesser precipitation events during the winter months may overlap with a period of genetically controlled developmental inactivity until more substantial spring rain events occur. These precipitation
events trigger additional maturation of archegonia and (second year) antheridia to the mature phenophase, dispersal of sperm, and potential fertilization.

Archegonia, with their relatively low prezygotic allocation requirements, initiate and mature in a 6-month period. Antheridia, having more sizeable requirements for maturation, mature in 17-19 months. Archegonia experience relatively few obstacles to successful maturation in a given growing season, though they must still negotiate the challenges of becoming fertilized, which is dictated by proximity to expressing and subsequently dispersing males. Antheridia, however, with their extended maturation periods have far greater potential for complications. That a male individual has initiated antheridial maturation does not ensure reproductive fecundity in the following growth season. If precipitation in the following growth season is insufficient, antheridia may not mature at the appropriate juncture, or may be aborted prior to the fertilization period in deference to the needs of the vegetative axis. Most antheridia subsist without notable compromise in maturation phase through the first "over-summering;" however, deficient fall rains in the following season can elicit severe abortive reactions. Even if fall precipitation is adequate, substandard spring rains can cause a failure in maturation.

Abortion of all gametangia which have failed to mature following the period of fertilization suggests the probability of genetic controls affecting phenophases. The presence of abortive archegonia was first noted in February and extended through July collections in every growth season. The presence of aborted antheridia was noted primarily after the first 6 months of development (March),
and the incidence of abortion increased over the following 12 months. This study presents one of the most significant incidents of gametangial abortion reported. Some authors have omitted abortive gametangia from their analyses, and as such, it is difficult to assess the relative significance of these results.

In other dioicous species studied, mean number of archegonia per perichaetium are as follows \((Polytrichum alpestre, 3-12, \text{and} Bryum argenteum, 2-17, \text{Miles et al. 1989}; Atrichum rhystophyllum, \text{mean} 4.52, \text{and} Pogonatum inflexum, \text{mean} 3.18, \text{Imura 1994}; Didymodon nevadensis, \text{mean} 10.7, \text{Zander et al. 1995}; Dicranum majus, \text{range} 1-23, \text{mean} 10.8 \pm 6.3, \text{Sagmo Salli et al. 1998}). \text{Mean number of antheridia per perigonium have previously been reported as well} (P. alpestre, >50, \text{and} Bryum argenteum, 8-38, \text{Miles et al. 1989}; Atrichum rhystophyllum, \text{mean} 94.0, \text{and} Pogonatum inflexum, \text{mean} 53.5, \text{Imura 1994}; Dicranum majus, 1 \text{per perigonium, Sagmo Salli et al. 1998}). \text{This study recovered a range from 1-8 archegonia per perichaetium and 3-21 antheridia per perigonium. Mean number of archegonia per perichaetium is considerably smaller and less variable than number of antheridia per perigonium. This trend is common among mosses, particularly in dioicous species (Longton & Greene 1969a; Stark 1983).}

\text{Mean length of archegonia and antheridia compared to mean length of abortive gametangia emphasize the critical control these organisms exert in order to maintain the vegetative axis. Survival to the next season and therefore the next potential opportunity to reproduce physiologically supercedes involvement in the current fertilization event. For males, it seems possible that}
the greatest assimilatory expenditure is required during the second season of maturation, and therefore the tendency should be for abortions to occur early in that season. The similarity in length between immature and abortive antheridia endorses this hypothesis. For females, it does not appear that any particular period of expense is excessive relative to others, at least for the prezygotic period. Data show that mean length of abortive archegonia is most similar to that of dehisced archegonia, suggesting that failure to mature at the appropriate point in time is the causal factor. These abortions are most likely under genetic control as opposed to physiological constraints.

Comparison of the percentage of abortive archegonia to the percentage of abortive antheridia provides evidence of an interesting pattern. Allocation studies would suggest that due to the higher expenditure of resources required for production of antheridia, a greater proportion of antheridia than archegonia should abort. Contrary to this hypothesis, Table 9 suggests otherwise. However, included in the given archegonial abortion counts are the proportion of archegonia which have been superceded by a fertilized archegonium. The revised data produce mean percent abortive rates slightly lower than previously presented (1998 = 37.6%, 1999 = 51.3%, 2000 = 35.1%). These data still suggest a higher rate of gametangial abortion for females than males, and are significantly higher than previous reports (4% for archegonia and 3% for antheridia, Stark 1997). This might suggest that just as females appear to have a lower response threshold to favorable environmental fluctuations and ability to be vegetatively productive under beneficial conditions; they may also have a
lower response threshold to unfavorable fluctuations, exhibited through increased abortion rates. This would be a potential explanation for the source of the hypothesized compensation necessary for males and females to attain equal levels of vegetative production. Alternatively, the expense of sporophyte maturation may be a causal factor in this trend, having multi-seasonal effects on ability to successfully mature a perichaetium for a given ramet.

Sporophyte Phenology

Following fertilization in each study year, early and late embryos were observed, but no embryos were observed to mature beyond this phenophase for the duration of the study. Two occurrences of multiple fertilizations within a single perichaetium were recorded; both incidents resulted in abortive sporophytes in the early embryo phenophase. Widespread abortion has been reported for at least two other xeric species (*Tortula inermis*, 66%, Stark 2002; *Grimmia orbicularis*, 50%, Stark 2001), however this is the first report of what was potentially an abortion of an entire cohort of sporophytes. This assertion is based on the congeneric (*sensu* Zander 1993) studies of *S. ruralis* (Mishler & Oliver 1991) and *T. inermis* (Stark 1997) combined with observations made by Stark (personal communication). *Syntrichia caninervis* is believed to fertilize in March, over-summer in a dormant state the following year, potentially undergoing some amount of maturation during the fall months. Capsules then rapidly develop and mature spores during the February-April period. Mature capsules collected during February 1998 appear to be a result of the 1997 fertilization
cohort (Stark personal communication). The extent of the period of spore dispersal is not known, although empty capsules were collected in early 1999 from the 1997 cohort (matured spores in 1998), implying that dispersal is complete in less than 12 months. The comprehensive nature of sporophyte abortion in this study strongly suggests that successful maturation of spores in rare for this species in this region.

Sex Ratios

*Syntrichia caninervis* has been examined regarding sex ratios on at least three previous occasions (Bowker et al. 2000; Stark et al. 1998, 2001). Reported percentages of non-expressing stems were 35% (Stark et al. 2001), 70% (Stark et al. 1998) and 85% (Bowker et al. 2000) compared with 57% for this study. This is most likely attributable to the selection of populations since the studies by Stark et al. (2001) and Bowker et al. (2000) used populations without selecting for presence of sex expression while Stark et al. (1998) used populations with at least one visible sporophyte. The current study ensured presence of expressing individuals prior to selection. A $\chi^2$ analysis of the present data provides support that the proportion of non-expressing stems is significantly higher in female-only populations ($p < 0.001$); the proportion of expressing individuals is artificially increased in this study by the use of male-only and mixed-sex populations.

Ratios of male and female expressing stems for each study series are expressed in Table 15. Again, selection of populations plays an important role in the outcome of these ratios. For example, if mixed-sex (sporophytic) populations
from this study are compared to sporophytic populations from Stark et al. (2001) study of sporophytic populations, sex ratios are almost identical (1♂:9♀ in this study versus 1♂:8♀, $\chi^2 = 0.181, p = 0.670$). The consistency in the results of these two studies reinforces the severe sperm limitation being experienced by females of *S. caninervis* in this area. Causal factors behind this discrepancy in prevalence are an area of ongoing research.

**Spatial Patterning**

The spatial data collected during this study and resultant data derivation suggest a strong need for additional study and probably a reanalysis of the appropriateness of the both the sampling method and statistical method used. While limited analysis of the segregation and/or aggregation of the sexes was possible, the segregation values (S-statistic) were small indicating a tendency toward randomness as opposed to either segregation or aggregation. Some uncertainty exists as to the confidence to place in this data as the statistic was extrapolated for use with three categories (female, male, and non-expressing) instead of only two as is typical; however, discrepancies were not resolved by comparing only expressing to non-expressing stems. In addition, the S-statistic requires additional modification to account for edge effect, which was not considered in this analysis. The analysis of these data was also not taken into consideration when developing a sampling scheme; therefore improved sampling techniques should be considered in the future. While the spatial analysis indicates simple randomness in this study, examination using a finer scale is
probably necessary. In combination with genetic study to better determine sex ratios regarding non-expressing stems and a more assured sampling technique, this could be a fertile area for future work.
CHAPTER 5

SUMMARY

*Syntrichia caninervis* is the second dioicous bryophyte to be examined in the desert Southwest. Its phenological pattern parallels that of the related species *S. ruralis*, but over a protracted time frame. Unlike the previous study of *S. ruralis* this species was examined in a very xeric environment and perhaps under rare, if not unique, patterns of precipitation. The minimal levels of hydration and sporadic occurrence of these events led to observations regarding growth rates and rates of sporophyte abortion more extreme than were expected by this researcher.

Growth rates averaged 0.29 ± 0.04 mm per year with rates in females and males exceeding the rates of non-expressers (0.30 ± 0.04 mm vs. 0.27 ± 0.04 mm). Over the course of the study, variation in growth rates was detected between the growth seasons. The highest growth rates corresponded with the highest levels of precipitation (1997, 0.31 ± 0.05 mm) and the lowest rates with the least precipitation (1998 & 1999, 0.28 ± 0.03 mm). Increased levels of precipitation toward the end of the study did not create corresponding increases in growth rate (2000, 0.26 ± 0.08 mm) suggesting lasting effects of periodic stress.
The phenological pattern is similar to that of other desert species studied. These desert species tend toward archegonial initiation in early fall (September) with antheridia initiating over a slightly longer period at the same time. Maturation time for archegonia is approximately 6 months with receptivity in early spring (March). Antheridia develop over a longer period of 16-19 months, releasing sperm concurrently with female receptivity in their second year of maturation. Gametangial abortion rates were higher than have been reported for other desert species. Sporophyte maturation was not observed during the course of this study. Fertilization was recorded in March each year and initial development began, however abortion rates were 100% by the following fall of each collection year when further maturation would have occurred. Due to these massive abortion rates, the completion of the maturation cycle could not be observed.

The existence of spatial patterns in these populations was supported in some cases; however, the segregation values were low, indicating small amounts of aggregation or segregation. I suggest that a more intensive sampling methodology is necessary to truly discern pattern in populations on this scale, an area of future interest.

Phenological studies like this one can be fruitful not only in their ability to answer questions regarding the developmental phases of an organism, but also to stimulate interest in parallel areas. This study has likewise created more questions to be answered. In particular, this study raises a question as to the levels of rainfall experienced by this throughfall reliant species on a regular basis.
Long term study is necessary to determine whether the extreme levels of abortion documented here were unique or ordinary. Also, questions are raised as to the long term effects of sporophyte maturation and recurring gametangial maturation on elongation of the vegetative axis. Finally, many questions still exist in regard to spatial patterns. These include what sampling methods and statistical analyses are best for examining bryophyte populations, what other factors may be involved in spatial patterns on this microscale, and, if interactions between reproductive and non-reproductive individuals do structure populations, what is the general pattern and how is it controlled.
LITERATURE CITED


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Tamm, C. O. 1953. Growth, yield, and nutrition in carpets of a forest moss (Hylocomium splendens). Meddn St. Skogsforsklnst 43:


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