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The Reproduction and Ecology of *Hypericum edisonianum*: An Endangered Florida Endemic

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ABSTRACT The reproduction and ecology of the narrow endemic and Florida endangered shrub *Hypericum edisonianum* (Edison's St. John's Wort) was investigated through field and greenhouse studies. *Hypericum edisonianum* exhibits a number of traits common to rare and geographically limited plant species including heavy reliance on clonal propagation to maintain local stands, passive seed dispersal resulting in a near-parent seed shadow, limited numbers of genetically unique individuals in its isolated seasonal-pond habitat, and likely self-incompatibility. In the field study, most flowers were produced by a small subset of the monitored ramets. Indeed, three ramets belonging to a single genetic individual accounted for 26% of all seed output from the 78 ramets monitored over a one-year period. In spite of strong seed production and germination, seedling establishment appears to occur episodically. The implication is that *H. edisonianum* is poorly equipped to withstand landscape drainage, agricultural and human development, and climate change. Such impacts will severely challenge the persistence of not only *H. edisonianum* but also many of the associated species inhabiting Florida scrub. Detailed information is needed about the population-genetic structure of *H. edisonianum* populations in order to understand its metapopulation structure. Protection of existing and potential *H. edisonianum* stands is crucial to the long-term preservation this species.

Key words: Clonal propagation, conservation, fire ecology, Florida scrub, reproductive ecology, seed dispersal, seed germination.

INTRODUCTION The question of why one species is well distributed and abundant while a closely related species is rare and has a narrow distribution has puzzled naturalists since at least the time of Darwin (1859). While ecologists are far from a thorough understanding of the causes of species rarity (Rabinowitz 1981, Bevill and Louda 1999), some evidence suggests that rare and geographically restricted taxa have suites of traits that differ from abundant and widely distributed taxa, including self-incompatibility, more reliance on asexual propagation, lower reproductive output, diploidy rather than polyploidy, limited competitive abilities, and reduced dispersal abilities (e.g., Kunin and Gaston 1993, 1997; Murray et al. 2002, Comita et al. 2010, Pandit et al. 2011). In addition to such inherent life-history traits, human-induced landscape change including drainage, fragmentation, habitat loss, and climate change can severely restrict the interactions of populations within a metapopulation, which in turn can reduce the size, distribution, and viability of individual populations (e.g., Bekker and Kwak 2005, Honnay and Jacquemyn 2007, Walck et al. 2011, Marini et al. 2012).

The reproduction and ecology of the narrow endemic plant *Hypericum edisonianum* (Small) W.P. Adams & N. Robson (Edison's St. John's Wort) was explored in order to gain insights into the reasons of its extremely limited geographic distribution and the likelihood of its persistence in a changing landscape. A small shrub that can form dense local patches, *H. edisonianum* is known to occur in only five counties of central peninsular Florida (Florida Natural Areas Inven-

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tory 2000, Wunderlin and Hansen 2003). Its distribution is focused in Highlands County with plants also found in adjacent Polk, Glades, DeSoto, and nearby Collier Counties (Wunderlin and Hansen 2008).

Classified as an endangered species by the state of Florida (Weaver and Anderson 2010; in imminent danger of extinction) and G2/S2 (imperiled globally due to extreme rarity/imperiled in Florida because of rarity, respectively) by the Florida Natural Areas Inventory, the conservation of *H. edisonianum* is a critical issue because drainage and large-scale agricultural and urban development are locally eliminating the species in parts of its range (Ward 1979).

Hypericum edisonianum has the potential to propagate via seed production as well as by clonal sprouting from underground rhizomes. The balance between these alternative propagation methods is important to both the demography and genetic structure of *H. edisonianum* populations. For example, if seed reproduction generates limited or episodic recruitment whereas clonal sprouts produce numerous genetically identical individuals (ramets), then *H. edisonianum* will appear locally abundant yet will be composed of relatively few genetic individuals (genets) with potentially limited genetic variability.

Accounts of the reproductive ecology of widespread *Hypericum* species are frequent in the literature particularly for the invasive, apomictic herb *Hypericum perforatum* L. (Mayo and Langridge 2003). Many genetic and demographic details are also known for the shrub *Hypericum canariense* L., which underwent rapid adaptive evolution of its reproductive phenology after its introduction to California and Hawaii (Dlugosch and Parker 2008). In contrast, little is known about the reproductive ecology of rare *Hypericum* species with the notable exception of *Hypericum cumulicola* (Small) W.P. Adams (e.g., Quintana-Ascencio et al. 1998, 2003; Evans et al. 2003, Trager et al. 2005). Almost nothing is known about the ability of *H. edisonianum* to produce viable seed, the distribution and fate of its seed, or the extent and persistence of its clonal connections. Several aspects of *H. edisonianum*'s ecology are reported including its flowering phenology, seed reproductive output, seed germination, and degree of clonality. Understanding its reproduction and ecology is crucial to its long-term conservation.

STUDY SITE AND METHODS

Study Site

The study locality, Archbold Biological Station (ABS; 27°10′50″N, 81°21′0″W, Highlands County, Florida, USA), is near the southern terminus of the several km wide but 160-km long Lake Wales Ridge, the most prominent topographic feature of the Florida peninsula. This region is home to a remarkably large number of endemic species and subspecies of plants and animals (Menges 1999). The climate is characterized by hot, wet summers and mild, dry winters. The highest monthly mean temperature (27.5°C) occurs in August and the lowest (16°C) in January. Long-term mean annual rainfall is 1,335 mm, of which 796 mm (60%) falls during a 4-month wet season (June through September; Abrahamson 2007). The rolling topography created by Paleo sandhills, beach ridges, and sand dunes with interspersed lowlands and seasonally flooded ponds, supports a range of vegetative associations (Abrahamson et al. 1984). Three factors predominate in the evolution and ecology of Lake Wales Ridge plants: climate, soil (acidic, nutrient-poor sands), and fire (which has frequent return intervals in most associations). These factors facilitated associations largely composed of sclerophyllous, evergreen species. The vegetation of the study area is appropriately considered as "old growth" because it has experienced little anthropogenic disturbance and has persisted for an estimated 50,000 years (Watts and Hansen 1994, Takahashi et al. 2011, 2012).

Study Species

The genus *Hypericum* (Clusiaceae) includes nearly 500 species that have a virtually worldwide distribution. As is true for most large genera, the abundance and distribution of individual *Hypericum* species varies remarkably among species. A number of *Hypericum* species are rare (e.g., *H. cumulicola*, *H. edisonianum*) while others are widely distributed and invasive (e.g., *H. perforatum*, *H. canariense*). Furthermore, reproductive strategies among *Hypericum* species vary widely. Some (e.g., *H. cumulicola*) reproduce exclusively via seed while others (e.g., *H. edisonianum*) spread locally via rhizomes. Chromosome numbers within the genus appear related to reproductive biology and growth habit. The base chromosome numbers

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(n) in *Hypericum* descend from 12, 10, 9, 8, to 7 with counts of n = 6 in a few species and polyploidy in select species (Robson and Adams 1968, Robson 1981). Apomixis occurs in some species including the invasive tetraploid *H. perforatum* (Matzk et al. 2001, 2003). Shrubby *Hypericum* species typically have chromosome numbers of n = 9 and n = 10, while herbaceous species' numbers are most often n = 7 and n = 8 (Crockett and Robson 2011). Specific counts for *H. edisonianum* are not available.

Hypericum edisonianum typically grows 1 to 1.5 m tall depending on water depth and time since fire (Abrahamson 1984, Abrahamson et al. 1984) with leafless lower stems and leafed (1–3 cm long oval evergreen leaves) multibranched upper stems. The species can occur in extensive, dense stands in seasonal ponds but occurs less abundantly in pine flatwoods depressions, wet prairies, cutthroat grass (*Panicum abscissum* Swallen) seeps, and along lake margins (see Myers and Ewel 1990 for details of these vegetation associations). The most extensive stands are found on poorly drained sandy sites that have low pH, little organic matter, and low nutrient status (Abrahamson et al. 1984, Van De Kerckhove 2002). Stands of *H. edisonianum* growing in seasonal ponds were used for our studies because of the low occurrence frequencies found in other associations.

Flowers have four yellow petals surrounding numerous stamens and four sepals, two of which are large and cover the remaining two narrow, tapered sepals. Flowers are borne throughout the year unless floral buds and flowers are injured by severe frost. The fruit is a small, pointed capsule that contains many seeds (Ward 1979, Robson 1996).

Seasonal Ponds

Seasonal ponds are rounded or irregularly shaped, shallow depressions from tens to hundreds of meters in diameter. These ponds vary extensively in the nature of their vegetation, which in turn reflects the depth and topography of the pond and type of soil (Abrahamson et al. 1984, Landman and Menges 1999, Lovell and Menges 2013). The hydroperiod (i.e., the period of standing water) of seasonal ponds at ABS is variable depending on pond elevation, basin topography, and rainfall patterns (Menges and Marks 2008). None is permanently flooded; some have water every summer and for longer periods in wetter years, and some contain water only in the wettest years (Abrahamson et al. 1984). The specific conditions of a given seasonal pond make it more or less prone to woody plant invasion (Landman and Menges 1999) and fire exclusion and/or drainage can result in appreciable shifts of pond-associated vegetation (Yahr et al. 2000). Common features of most seasonal ponds are a ring of saw palmetto (*Serenoa repens* (W. Bartram) Small) surrounding them and one or more zones of contained vegetation. The most common zonation encountered from center to edge are: (a) sparse maidencane (*Panicum hemitomon* Schult.) with *Sphagnum*, (b) *H. edisonianum*, often occurring in dense, nearly pure stands that are high and dry during the winter months, and (c) a marginal zone dominated by either dense cutthroat grass or sparse broomsedge (*Andropogon brachystachyus* Chapm. or *Andropogon* spp.) (Abrahamson et al. 1984).

Flower Production

The detailed ABS vegetation map that accompanies Abrahamson et al. (1984) delimits ABS seasonal ponds and also identifies seasonal ponds that contain high-density stands of *H. edisonianum*. Using the scale of that vegetation map (1 mm = 10 m), a 980 × 335 point grid was superimposed onto the map. A seasonal pond was selected for sampling whenever a pair of randomly generated numbers intersected a seasonal pond that contained *H. edisonianum*. During August 1985, the intersecting points were field located within the selected 26 seasonal pond locations (Figure 1). At each point, the three nearest *H. edisonianum* ramets were tagged with a numbered aluminum label for monitoring. Sampling more seasonal ponds, if fewer ramets per monitored pond, enhanced the number of genets examined since no genet would likely occur in multiple ponds.

The 78 tagged ramets (26 seasonal ponds × 3 ramets) were to be monitored on 58 days over the subsequent year starting in September 1985 and continuing until September 1986. Observation days were chosen with the stipulation that the maximum time between observations not exceed 10 days. However, observations ended up being limited to 35 observation days spanning 255 days because all floral buds, flowers, and developing capsules were destroyed by a severe frost on 23 December 1985 when the temperature dropped to –8°C. Flowering did not resume until 20 March 1986 (in contrast, flowering never

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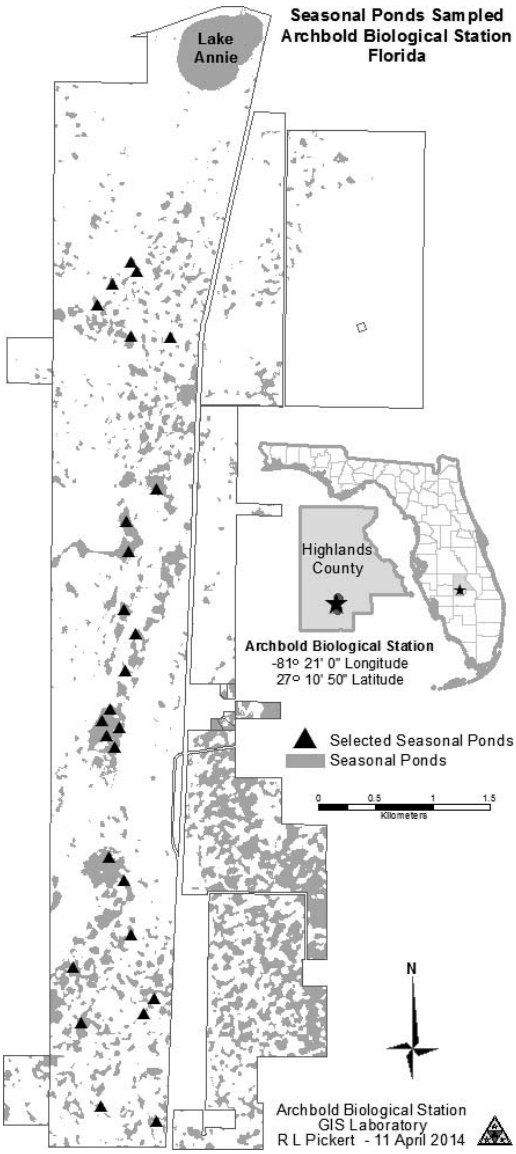


Figure 1. Locations of the 26 sampled seasonal ponds at Archbold Biological Station, Venus, Florida, USA.

ceased in the 1986–1987 winter during which time ABS recorded eight frosts, but none was colder than –2°C). At each observation, ramet height, distance of each focal ramet to its nearest neighbor, and the number of days that individual ramets stood in water were measured during the one-year observation period. Also recorded was the number of flowers in anthesis on each ramet. Several flowers on ramets were also tagged so that the duration of anthesis, ovule maturation, and seed dispersal could be determined.

For each of 78 observed ramets, a histogram was generated of the number of days on which there were no flowers, one flower, two, three, four, five, and six or more flowers. These histograms of observed flowering events were compared to expected numbers using the Poisson distribution to examine whether the production of a given flower is independent of previously or subsequently produced flowers within the same ramet. The fit of observed flowering events to those expected from the Poisson distribution were evaluated with the χ^2 goodness of fit test (Sokal and Rohlf 2012). Because of the high numbers of observations with zero flowers, the Poisson distribution did not match *H. edisonianum*'s distribution of flower production. However, the flowering patterns of most ramets did follow the "Poisson with added zeroes" distribution (Ridout et al. 1998, Johnson et al. 2005). Consequently, the Poisson with added zeroes model was used to examine the independence of flowering events. That is, whether the occurrence of one flowering event within a ramet affected the probability of subsequent flowering events.

Seed Banks

In order to assess the store of viable *H. edisonianum* seeds in the soil, 54 cores, 11.2 cm in diameter and 5 cm deep, were taken from the dense *H. edisonianum* zone (n = 18), the cutthroat grass zone (n = 18), and maidencane zone (n = 18) of three seasonal ponds. The soil from each core was spread over sterilized sand (2 cm deep) in a plastic tray with an area of 645 cm^2 (litter and rhizomes were discarded from these samples). All trays were kept in a greenhouse misting chamber at ambient temperature and light. Newly emerged seedlings of *H. edisonianum* were counted and removed at monthly intervals for 8 months.

Germination and Selfing Trials

Fifty sets of 25 mature, plump seeds (Figure 2) were collected monthly from September 1985 until September 1986 (incompletely formed, collapsed seeds were not used). Twenty-five sets were placed between moist Whatman #1 filter paper in a 9-cm glass petri dish each month and kept on a greenhouse bench under ambient temperature and light conditions. Petri dishes were checked daily for germination and moist-

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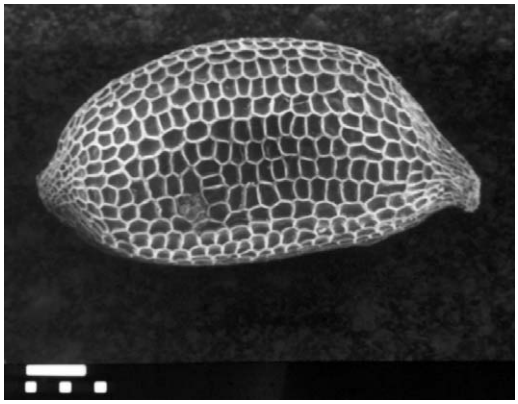


Figure 2. SEM image of a mature, plump seed of *Hypericum edisonianum*. Scale bar is equivalent to 100 μm.

ened as necessary. The remaining 25 sets were placed on top of a 1:1 sterilized sand-peat mixture in pots each month and placed in a misting chamber until cotyledons emerged (=germination), at which time the pots were moved to a greenhouse bench and watered daily. The number of days until germination and the number of seedlings were recorded.

In order to examine the ability of seedlings to become established, 25 seedlings, each approximately 4 cm tall, were transplanted in May 1986 (which was just prior to the rainy season) into three seasonal ponds. These transplant ponds contained no *H. edisonianum*, but did contain the congener *H. fasciculatum* Lamarck. Finally, plants were grown from seed to flowering in an Acadia University greenhouse to examine whether they could self-fertilize by placing pollen from a given plant onto the stigma of the same plant.

Post-Fire Recovery and Clonality

Following a 21 January 1977 prescribed fire that completely consumed all above-ground vegetation of an approximately 5-ha seasonal pond, a 7 $\times$ 20 m grid of 1 $\times$ 1 m quadrats was established within what had been an area of dense *H. edisonianum*. Ten of the 1 $\times$ 1 m quadrats were chosen by random design and the numbers of ramets within each quadrat was determined repeatedly on six occasions over a nearly 5-yr period (6 May 1977, 14 January 1978, 26 January 1979, 28 January 1980, 26 January 1981, and 25 January 1982). On the same dates, between 100 and 300 ramets were harvested at ground level from quadrats that were not adjacent to those used for the repeated density measurements or previous harvest and dried in a convection oven to constant mass to determine the mean above-ground dry mass of ramets.

In order to assess the extent and persistence of underground rhizome connections, all of the *H. edisonianum* ramets growing in a 7-m^2 plot within a seasonal pond were counted in January 1988. Subsequently, each of the contained ramets was carefully excavated and information recorded included whether a given ramet was connected via rhizome to one or more other ramets, the lengths of rhizome between ramets if connected to another ramet, and the total length of the ramet's attached rhizomes.

While examining the tagged ramets across the ABS seasonal ponds, S.P.V. realized that he could identify individual genets (i.e., the genetic individual composed of all ramets that originated from a single seedling) in the field using a combination of floral and vegetative morphologies. The shape and size of the outer sepals relative to the adjacent pair of leaves is constant within a genet, but the relationship differs among genets regardless of the age and the number of ramets within a genet. This is fortunate because rhizome connections between ramets are not persistent, which limits determining genetic association via excavation. Using this morphological relationship, S.P.V. estimated the numbers of genets composing *H. edisonianum* stands in 72 seasonal ponds distributed throughout Highlands County between September 1985 and September 1986.

RESULTS

Flowering Phenology

On any of the 35 observation days, only an average of one-third of the 78 tagged ramets had one or more flowers in anthesis. For the year, most ramets (59%, or 46 $\pm$ 8 ramets) bore no flowers on any given observation day, 13% of the tagged ramets (10 $\pm$ 5 ramets) had one flower, 5% (4 $\pm$ 2 ramets) had two flowers, and 4% (3 $\pm$ 2 ramets) had three flowers on each observation day (Figure 3). Remarkably, 26% of the 2,142 flowers observed throughout the year were from three ramets growing in one seasonal pond.

Observations of individually tagged flowers showed that flowers are short lived. Flowers were functional up to one day or less depending on temperature. During the warmer months (i.e., April to September), the petals typically unfurl at dawn, and, about 2 hr later, the anthers rupture

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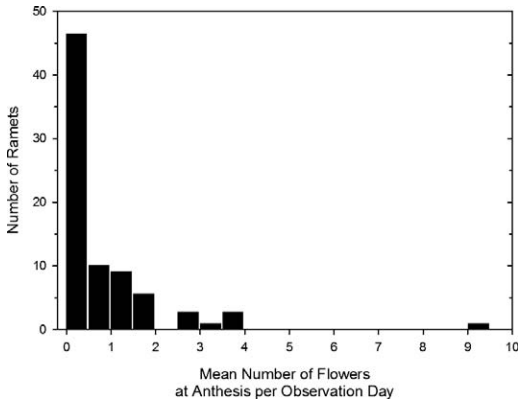


Figure 3. Histogram of the mean number of flowers at anthesis per observation day for 78 *Hypericum edisonianum* ramets growing in 26 seasonal ponds (3 ramets/pond) at Archbold Biological Station. Ramets were observed 35 times between September 1985 and September 1986.

and the stigma appears to become receptive to pollen. By noon, the anthers and petals begin to wilt and soon thereafter fall off. During the cooler months (i.e., October to March); however, the flowers open well after sunrise and may last until dusk depending on temperature.

The flowers of *H. edisonianum* are visited by at least ten insect taxa (Table 1). Of these, *Apis mellifera* accounted for more than three-quarters of all floral visitors at the study site. However, this frequency was likely influenced by the proximity of feral *A. mellifera* hives. Lacking feral *A. mellifera* hives, *Bombus impatiens* is the more frequent floral visitor (Deyrup, pers. comm. 2014). Insects alight on a flower's numerous anthers only momentarily and then move to the next flower brushing against the minute stigmas that stand on a stout style 1 to 2 mm above the encircling stamens. The efficacy of pollination was not tested nor was the impact on seed set by the introduced *A. mellifera*. This point needs study, especially to determine whether the honeybee is displacing native pollinators.

Flower Production

The histograms of the number of days on which there were no flowers, one, two, three, four, five, or six or more flowers for each of the 78 ramets revealed that on most days, ramets bore no or few flowers and on only a few days did ramets have higher numbers of flowers (Figure 4). The χ^2 goodness of fit tests associated with the Poisson with added zeroes distribution (Johnson et al. 2005) produced good fits between observed and expected flowering patterns for most ramets and particularly so for the higher yielding ramets. Some 86% of the 78 ramets, or all but 11 ramets, were acceptably fit using the Poisson with added zeroes distribution.

Yet, the mean number of flowers/ramet/day varied greatly among the observed ramets. The highest rate of flower production was nine flowers/day and the next highest was four flowers/day (Figure 3). The nine highest yielding ramets among the 78 monitored ramets accounted for over 50% of the observed flowers. As a consequence, the majority of the reproductive output was generated by a relatively small portion of ramets and hence, by few genets. This pattern of a limited number of ramets being responsible for the majority of floral reproduction was consistent throughout the year.

Self-Incompatibility

Hypericum edisonianum appears to be self-incompatible and hence, requires outcrossing. S.P.V. attempted selfing trials using several plants that were grown from seed to flowering in an Acadia University greenhouse. All selfing attempts failed with all ovules aborting before or by week 3. The suggestion that *H. edisonianum* is self-incompatible is preliminary. Confirmation will await controlled experiments.

Seed Set and Dispersal

Following anthesis, 58% of all flowers on the sampled field ramets set mature seed. Seed capsules matured on average in 34 ± 5 days ($n = 155$) following anthesis with each seed capsule containing an average of 62 ± 22 plump, brown seeds (or 39% of all seeds within capsules) and 98 ± 36 (or 61% of all seeds within capsules) incompletely formed, collapsed seeds. Once mature, seed capsules dehisce septicidally and as winds cause ramets to sway, seeds spill to the ground near the parent ramet. Seeds may be secondarily distributed by wind or water sheet flow when seasonal ponds flood. On two occasions, S.P.V. observed ants removing seeds from a seed capsule. While ants may occasionally disperse *H. edisonianum* seeds, the relationship with ants is more likely antagonistic with harvested seeds being consumed (Johnson et al. 1986, Keeler 1989).

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Table 1. Insect visitors to flowers of *Hypericum edisonianum* observed during September and October 1985 at the Archbold Biological Station, Venus, Florida, USA. Observations made during morning hours on 30 flowering ramets watched for six intervals of 15 min

Taxon	5 Sep	16 Sep	5 Oct	15 Oct	Total
Apis mellifera L.	39	38	7	16	100
Bombus impatiens Cresson			1	2	3
Augochloropsis sumptuosa Smith		2	1	1	4
Lasioglossum (Dialictus) surianae Mitchell	3				3
Halictid spp.		2	1	1	4
Anisomorpha buprestoides Stoll	8				8
Odontocorynus pulverulentus Casey		4			4
Vespa sp.				1	1
Volucella pusilla Macquart			1	2	3
Volucella nigra Greene			1		1
Total	**50**	**46**	**12**	**23**	**131**

Germination and Seedling Emergence

Forty-seven percent of the plump seeds germinated in the petri-dish and soil trials. Radicles emerged after an average of 30 ± 11 days (n = 50), cotyledons were visible after a mean of 33 ± 13 days, and apical meristems were visible after an average of 51 ± 22 days. Individual seedlings transplanted to 7-cm diameter pots on greenhouse benches grew slowly in the 1:1 sand: peat mixture, attaining a height of only ≈2 cm after 6 mo. None of the seedlings that were transplanted to seasonal ponds successfully established, in spite of being transplanted at the beginning of the rainy season. All seedlings were dead after one year.

The patterns of seedling emergence from the soil cores supported the suggestion that seeds do not disperse far beyond their parent. The 18 soil cores taken from the three *H. edisonianum* zones produced 49 seedlings over an 8-mo period or an equivalent of 277 seedlings/m^2. In contrast, the 18 cores removed from the three cutthroat grass zones and the 18 cores from the three maidencane zones yielded only 10 seedlings, or an equivalent of 28 seedlings/m^2. In spite of many hours of thorough searching, S.P.V. observed no seedlings in the field.

Seedling Production Estimates

Hypericum edisonianum's potential seed reproductive output can be approximated from the field results. The average ramet has the potential to produce ≈3,380 seedlings annually, given the following: (a) on average each ramet produces ≈200 flowers annually, (b) 58% of these flowers set seed, (c) each mature seed capsule contains, on average, 62 viable, plump seeds, and (d) 47% of these viable, plump seeds germinate. These numbers suggest that each m^2 within the dense *H. edisonianum* zone of seasonal ponds has the potential to produce ≈30,422 seedlings given field *H. edisonianum* ramet densities of 9 ± 11 ramets/m^2 (Abrahamson 1984). However, the reality appears several orders of magnitude less given that the soil cores from this zone produced only 277 *H. edisonianum* seedlings/m^2. It is likely that the majority of viable seeds are lost to a variety of factors including predation, pathogens, water-logging, desiccation, and/or fire.

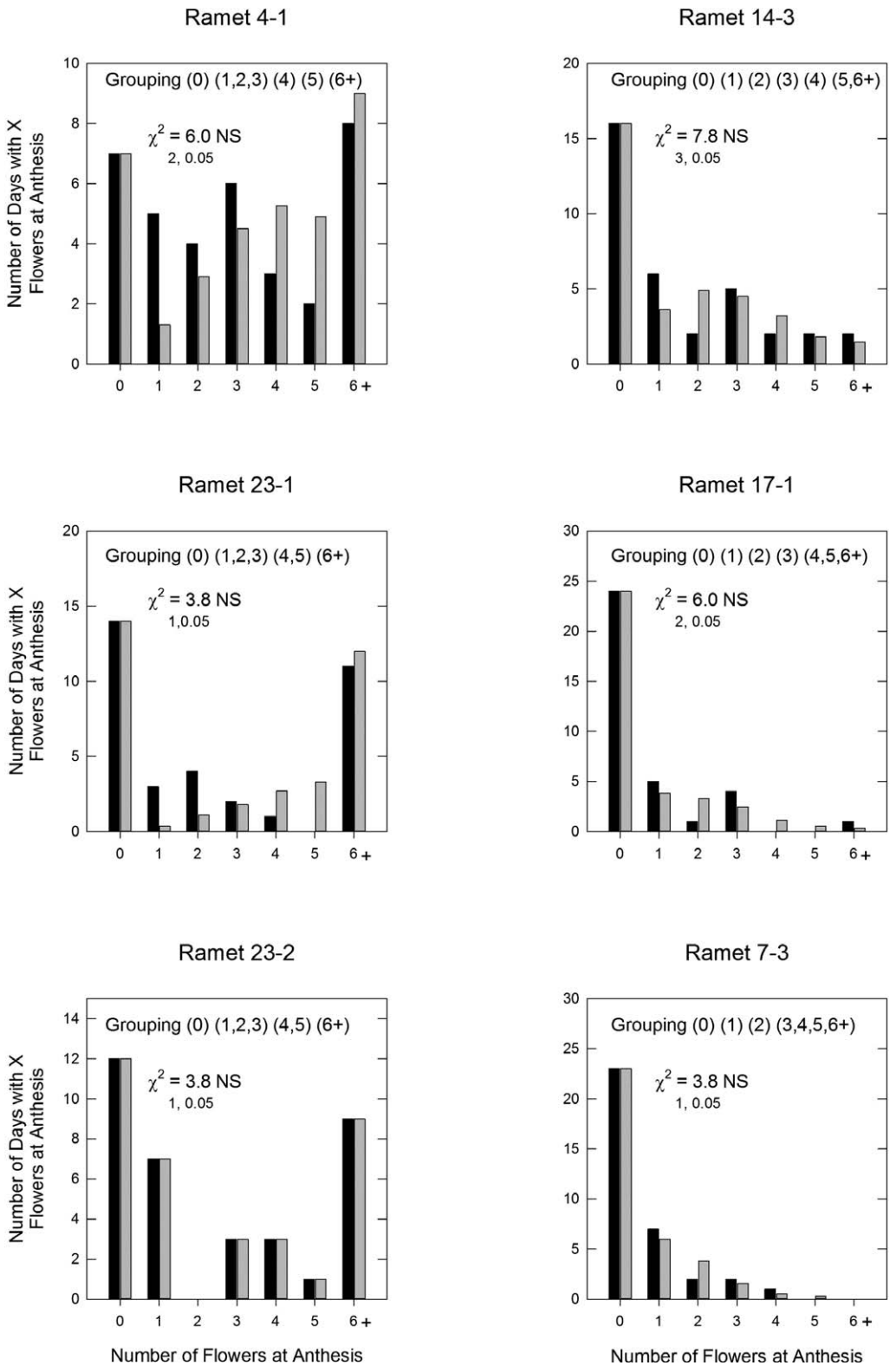
Size-Related Reproduction

At the outset of field observations on monitored ramets, mean ramet height was 91 ± 2 cm (n = 78) but during the subsequent year, three ramets died from apparent natural causes, and on 3 June 1986, 15 ramets were destroyed by a lightning-origin fire that consumed the vegetation in 5 of the 26 sampled seasonal ponds. By 3 March 1987, only 49 of the original 78 ramets remained alive and these had a mean height of 103 ± 3 cm. However, when the ramet heights for basal-sprouting replacement ramets are included, the

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Figure 4. Observed (black bars) and expected (light bars) number of days with a given number of flowers at anthesis for 78 *Hypericum edisonianum* ramets observed 35 times between September 1985 and September 1986. Expected numbers were generated by a Poisson with added zeroes distribution (Ridout et al. 1998, Johnson et al. 2005). The match of observed and expected numbers was examined with a χ^2 goodness of fit test. Ramet numbers were assigned using the seasonal pond number and then the number of the ramet sampled from each seasonal pond (e.g., Ramet 4-1 is from seasonal pond 4 and was the first ramet of the three ramets sampled in this pond).

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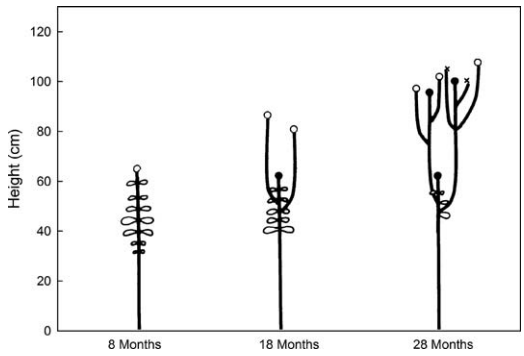


Figure 5. Post-fire aerial ramet development in *Hypericum edisonianum*. Ramets have a determinate growth pattern and new lateral branches arise from buds in the leaf axils. Legend: ○ = terminal flower, ● = ancient seed capsule, x = aborted apical meristem.

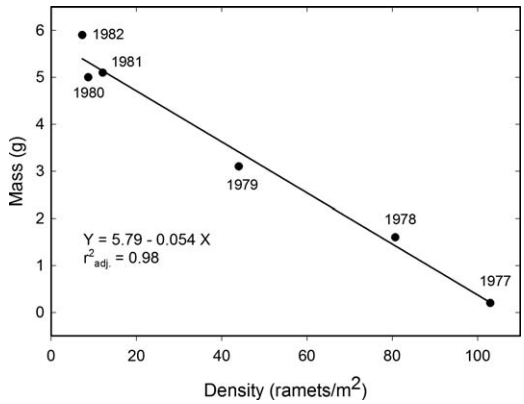


Figure 6. Relationship between above-ground ramet dry mass and ramet density following a 21 January 1977 fire that killed all above-ground ramets.

mean height on 3 March 1987 for 78 ramets was 87 ± 4 cm. Thus, for all intents and purposes, mean ramet height did not change appreciably from 22 August 1985 to 3 March 1987, in spite of the turnover of 63% of the original tagged ramets.

Ramet height was significantly correlated with flower production ($r = 0.51$, $p < 0.003$), however, this correlation is due to an allometric relationship in which the younger and thus smaller ramets have few flowers while older, larger, and multibranched ramets have greater numbers of flowers (Figure 5). When the data were adjusted for age, the correlation between ramet height and flower production became nonsignificant.

Post-Fire Ramet Recovery and Clonal Propagation

Above-ground portions of *H. edisonianum* are readily killed by fire but genets rapidly send up new ramets from underground rhizomes following fire (W.G.A., pers. obs.). While most of the new ramets produced following fire are closely associated with the fire-killed ramets, some appeared in new locations. This distinction is important since the latter facilitates occupation of new sites and potentially more space, and may benefit a genet's acquisition of additional resources (Menges and Kohfeldt 1995). Many ABS seasonal ponds have zones of *H. edisonianum* but the height and density of ramets within the zone depends in part on the time since fire and/or the depth and duration of standing water (long-term standing water can kill above-ground organs). At 4 mo, following a 21 January 1977 prescribed burn, an average ramet density of 103 ± 24 ramets/m^2 (mean ± s.d.) occurred within a series of permanent quadrats within a single seasonal pond. Mean ramet density declined sharply in quadrats over the next several years (Figure 6). By 4-yr postburn, mean density dropped more than an order of magnitude to 7 ± 12 ramet/m^2. Concurrent with the decrease in ramet density was an increase in individual ramet above-ground dry mass, which increased from 0.2 gm/ramet at 4-mo postburn to 5.9 gm/ramet after 4 yr. As ramets grew in mass, ramet leaves became smaller. Ramet leaves decreased from a mean of 26 ± 5 mm × 10 ± 2 mm (length × width, mean ± s.d.) at 4 mo to only 17 ± 2 mm × 7 ± 2 mm at 3-yr postburn. The observed decline in density was due to more factors than simply self-thinning (in the sense of the –3/2 power law; Weller 1990) given that several environmental factors such as long-standing, deep water and the impacts of pathogens and herbivores had obvious effects on plants.

Excavations showed that *H. edisonianum* is highly clonal given the amount of rhizome unearthed and that many ramets were connected via rhizomes to one or more other ramets. Excavation of 43 ramets found that 44% occurred in isolation (i.e., they had no underground connection to another ramet), but the majority (56%) were connected to other ramets. Some 33% of the ramets were connected to one other ramet, 9% were connected to three other ramets, and 14% were connected to five other ramets. The lengths of the rhizomes attached to isolated ramets ranged from 20 cm to 360 cm, with a

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mean of 140 ± 79 cm per ramet. For two-ramet-connected units, the lengths of rhizomes between connected ramets varied from as little as 1 cm up to 210 cm, with a mean of 120 ± 100 cm. The total rhizome lengths for all rhizomes on these two-ramet units varied from 27 cm up to 630 cm, with a mean of 253 ± 190 cm.

S.P.V.'s survey of 72 seasonal ponds in Highlands County suggests that the majority (54%) had stands of *H. edisonianum* composed of a single genet with numerous ramets, 22% of the seasonal ponds had two genets, 13% had three genets, and only 11% had four or more genets. Thus, although *H. edisonianum* appears to be locally abundant in seasonal ponds, the number of genets even at high-density sites is likely very limited.

DISCUSSION

Clonal Propagation, Seed Dispersal, Self-Incompatibility

The findings reported here indicate that *H. edisonianum* exhibits several traits that are frequently associated with rare and geographically limited species including heavy reliance on clonal propagation, limited dispersal ability, and possibly self-incompatibility. The ability to rapidly regenerate ramets is likely important given that *H. edisonianum*'s environment is highly prone to frequent fire (Abrahamson et al. 1984, Menges and Kohfeldt 1995) and lengthy periods of deep, standing water, both of which kill the above-ground portions of its genets (W.G.A., pers. obs.). Disturbances such as fire can reduce competition and the effects of herbivory and diseases. Quickly regaining photosynthetic input after above-ground organ loss via rapid ramet replacement potentially can enhance both genet fitness and persistence.

Seed dispersal by *H. edisonianum* appears passive with primarily local seed movement. Mature *H. edisonianum* seeds sink in water and consequently it is likely that many if not most seeds become embedded in sand near the parent unless moved horizontally by sheet flow during periods of flooding or by wind during dry periods. This conclusion is supported by the seed-bank analysis, which found that the vast majority of *H. edisonianum* seedlings were generated from the soil-core samples taken from the *H. edisonianum* zone. Limited numbers of viable seeds were present in the other seasonal-pond zones examined whether from the topographically higher cutthroat grass zone or the lower elevation maidencane zone. The strategy of having a dense seed shadow near the parent may be beneficial for plants that are narrowly adapted to specific abiotic and/or competitive conditions and where abiotic and/or biotic conditions change rapidly along gradients. However, this strategy could be highly detrimental if conditions change due to drainage or climate change.

Observations by S.P.V. coupled with those of Van De Kerckhove (2002) suggest that *H. edisonianum* may have episodic seedling recruitment. While S.P.V. found no seedlings in the field despite much searching during a 2-yr period, Van De Kerckhove reported seeing seedlings during one of her three field seasons. For plants that only episodically recruit, clonal propagation may facilitate maintenance of local stands. Clonal propagation enables genet persistence and growth between those periods when abiotic (e.g., water level, temperature) and biotic (e.g., competitive interactions) conditions are suitable for seed germination and seedling establishment.

The selfing trials, while preliminary, suggest that *H. edisonianum* requires outcrossing in order to produce viable seeds. If stands are composed of a limited number of genets, self-incompatibility could restrict the number of viable seeds produced. However, germination trials using soil-core samples taken from the field suggest that *H. edisonianum* has a relatively strong output of viable seeds. The caveat, however, is that this seed production is coming from a limited number of ramets, which in turn may restrict genetic variation among seeds and impact the performance of seedlings (Strauss and Karban 1994). The presence of limited genetic variation in *H. edisonianum* stands likely would be restrictive to population restructuring under conditions of environmental change and climate change.

Ramet Flower Production

The good fit between the expected number of days by given numbers of flowers at anthesis from the Poisson with added zeroes distribution and the observed numbers suggests independence of flower development within a given ramet, and implies that the production of one flower on a ramet does not appreciably enhance or diminish the probability of that ramet producing a second, third, or fourth flower. The model fit 86% of the observed ramets in spite of making no allowance for covariates such as the time of

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year, amount of rain, high and low temperatures, or wetness of the soil. Potential confounding variables such as daily low temperature and the length of time each ramet was in standing water were not correlated with the number of flowers on a given ramet. Thus, individual flowering events within a ramet appear to be reasonably independent of one another.

Yet, the high degree of variation recorded in flower production (i.e., mean number of flowers/ramet/day) among the observed ramets has the genetic consequence that a relatively small portion of ramets (and hence, few genets) generate the majority of the reproductive output. There is likely a significant genetic component to reproductive output among genets of *H. edisonianum*. Three of the four highest yielding ramets in this study were from the same genet and furthermore, the lowest yielding ramets also were typically from the same genets.

Genetic Diversity Within Stands

S.P.V.'s survey of seasonal ponds suggests that many seasonal ponds include only a single genet with numerous ramets while fewer ponds have two to several genets. Yet, Van De Kerckhove using amplified fragment length polymorphisms (AFLP) methodology reported that "unique haplotypes were scored for almost each individual [ramet] in each population [stand] found in the ABS property while populations [stands] outside ABS in Glades and DeSoto counties appeared to be slightly more homogeneous" (2002, p. 81). This conclusion may be erroneous given the high degree of rhizome connections among ramets found by excavation. Unfortunately, it is not possible to assess Van De Kerckhove's methodology because details of her methods were not provided. Amplified fragment length polymorphisms methodology has several well-known potential error sources including (a) contaminant fungal or bacterial DNA included with a sample, (b) somatic mutations among ramets of the same genet, and (c) AFLP errors (e.g., Takahashi et al. 2011, 2012). Any one of these errors, unless accounted for in the data analysis, can make samples appear genetically unique when they are not. Until another analysis of *H. edisonianum* genetic variation is available, it is best to err on the side of caution and assume that stands of *H. edisonianum* are composed of few genetically unique individuals. Although *H. edisonianum* appears locally abundant in seasonal ponds, the number of genets is likely very limited and hence, so is the amount of genetic variation present.

Constraints on Gene Exchange

Three features of *H. edisonianum*'s reproduction and ecology suggest the possibility that gamete exchange among genets is constrained. First, the number of flowers in anthesis on any given day is limited because individual flowers of *H. edisonianum* are short lived ($\leq$1 day) and flowering is spread throughout the year (barring severe freezes), rather than concentrated in a peak period of flowering. Synchronous flowering appears to enhance pollination efficiency in a number of species (Moreira et al. 2014). Second, on any given day most ramets bear no flowers; and third, relatively few ramets and hence few genets account for most of the reproduction. More than one-quarter of the 2,142 flowers observed were produced by only three ramets that S.P.V. believed belonged to the same genet. Nonetheless, *H. edisonianum* is not unique in having substantial portions of its seed output produced by few individuals. Vander Kloet and Cabilio (1984) obtained similar results in an eastern North American population of *Vaccinium corymbosum*, and Schaal (1980) observed a similar pattern for the winter annual *Lupinus texensis*.

Conclusions and Recommendations

Hypericum edisonianum possesses several reproductive traits that are common among rare and narrowly distributed plants. These traits include heavy use of clonal propagation, reduced seed dispersal, stands composed of few genetically unique individuals, and self-incompatibility (e.g., Kunin and Gaston 1993, 1997; Murray et al. 2002, Comita et al. 2010, Pandit et al. 2011). These and other traits suggest that although *H. edisonianum* can maintain its population structure under environmentally stable conditions, it will likely fare poorly with environmental change. This is reason for concern given that extensive drainage and agricultural and human development have severely impacted many areas that once supported stands of *H. edisonianum* and this development continues (Weekley et al. 2008). Furthermore, climate change threatens to modify the climate of Florida scrub and challenge the persistence of not only *H. edisonianum* but also many of the other scrub species. The Florida Natural Areas Inventory has mapped some 33 occurrences of *H. edisonianum* of which 5 are

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on lands protected by conservation easements, 11 occur on private land, and 17 occur within managed areas (A. Johnson, pers. comm. 2014).

This report offers some basic ecological information about *H. edisonianum* but in order to conserve this species in the long term, much more information is needed. A thorough genetic fingerprint screening is required to establish the genetic structure of *H. edisonianum*'s metapopulation. For example, are local stands composed of few genets as suspected and what fraction of these genets is exchanging gametes to produce seed crops? We also need to definitively determine if *H. edisonianum* is self-incompatible and better understand the interplay between floral visitors and viable seed set. Which floral visitors, for example, are most effective and how stable are their populations? Currently virtually nothing is known about the competitive abilities of *H. edisonianum* under field conditions, its relationships with herbivores and diseases, or the conditions required for establishment and maturation of its seedlings.

The available data suggest that a very limited number of genetic individuals are actively exchanging gametes in this apparent outcrossing species. While *H. edisonianum* appears capable of producing ample viable seed to maintain its seed bank, the fact that seedlings were observed in the field only episodically through multiple years raises concern. New genetic individuals appear to be infrequently added to seasonal ponds. Even though *H. edisonianum* is abundant locally because of its strong clonal propagation, there is good reason to be concerned about its conservation because of the potentially limited number of genets composing local populations, its extremely restricted geographic range, and the rapid loss and fragmentation of its habitat due to development.

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NOTE:

W.G.A. and his students conducted the field studies of ramet mass and density changes over time from 1977 through 1982, and on the extent of rhizome connections in 1988. W.G.A. prepared the manuscript and is responsible for interpretation of the findings.

S.P.V. did all field and greenhouse studies of floral phenology, flower and seed production, seed-bank contents, and seed germination during a sabbatical leave as an Archbold Fellow in 1985–1986. S.P.V. carried out additional studies on self-compatibility and germination at Acadia University, Wolfville, Nova Scotia from 1986 to 1990. S.P.V. died unexpectedly in January 2011 before this manuscript was prepared.

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