2011

Life History and Demography of Trillium ovatum Pursh. (Liliaceae) in Western Montana

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LIFE HISTORY AND DEMOGRAPHY OF TRILLIUM OVATUM PURSH. (LILIACEAE) IN WESTERN MONTANA

By

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Bachelor of Arts, University of Montana, Missoula, MT, 1991

Thesis

presented in partial fulfillment of the requirements for the degree of

Masters in Interdisciplinary Studies

The University of Montana
Missoula, MT

Spring 2011

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Life history and demography of *Trillium ovatum* Pursh. (Liliaceae) in Western Montana

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*Trillium ovatum* is a long-lived, spring ephemeral that grows in moist forest habitats of the western United States. Extensive investigations of *Trillium*, including *T. ovatum*, have been accomplished, yet no prior studies of *T. ovatum* have been conducted at the eastern edge of its distribution in Montana, where populations experience increased aridity and highly variable climatic conditions as compared to other regions where it occurs. This study examines life-history characteristics and demography of *T. ovatum* in three representative populations that were sampled over 9 growing seasons to determine: 1) life history stages, stage class structure, and yearly transitions among stage classes; 2) age and size of plants and relationships among age, size, and stage class; 3) minimum age of reproduction and fecundity; 4) forest structure and site characteristics.

Life-history stages of *T. ovatum* include: cotyledon; one-leaf vegetative; three-leaf vegetative (juvenile); three-leaf reproductive (flowering); and three-leaf nonflowering regressive stages. Juvenile plants comprise the majority of each population. Flowering plants represent the only means of reproduction, and plants are slow to reach sexual maturity, which takes a minimum of 18 years. Age and number of seeds produced are positively correlated with individual plant size. Yearly fecundity measures of fruit set, number of seeds produced per plant, and seeds per square meter are highly variable. *Trillium* exhibit stage class regressions, with an average of 27% of reproductive adults periodically retrogressing to a nonflowering stage. Dormancy was observed in all adult stage classes. Mortality is generally low (<1.5%), and yearly tallies of new plants showed that more plants were ‘recruited’ into the population than died, but no clear changes in population density were documented during the period of this study.

*Trillium ovatum* face many of the same threats as other forest understory species—logging, overharvest for horticultural/medicinal use, competition from nonnative species, and overgrazing. Low fecundity and recruitment may limit the ability of these populations to recover from stress or mortality events, and make them sensitive to climatic changes and increases in fire disturbances that are likely to occur in this region. Continued long-term monitoring will be invaluable for understanding responses of long-lived forest understory species to the complex interplay of these environmental stresses.
ACKNOWLEDGEMENTS

I would like to thank Steve Shelly, Diane Pavek, John Pierce, Tiffany Knight, Erik Jules, Peter Stickney, Mark Roberts, and Nan Vance for their willingness to share their botanical (and *Trillium*) expertise. I would also like to thank Michael Gundale, Tom DeLuca, Dexter Roberts, Tabitha Graves, Kelly Chadwick, Dave Affleck, Tempe Regan, who bravely and beautifully made her first botanical drawings, Marlene Hutchins for formatting the life-cycle drawings, members of the Clark Fork Chapter of the Montana Native Plant Society, and Fred Allendorf for sending me his birthday-walk *Trillium* picture every year (which reminded me to get my data collection sheets ready!). Most importantly, I would like to thank my very patient committee—Paul Alaback, Steve Siebert, and Rustem Medora—for their support and encouragement. And big thanks to my mom for her time spent on this project, as well as her love of all things biologic.

I could not have gathered all this data without my invaluable volunteer field crew (in other words, the best lunches were had with the following): Cathy Ream, Michael Meyer, Jennifer Rackley, Sarah McClain, Beth Judy, Nicole Dunn, Paul Lackner, Dori Gilels, Erin Cuniff, Robbie Liben, Martha Kimmick, and Dan Dorn.

This project received research support from the Montana Native Plant Society Small Grants Program, Five Valleys Audubon Society Phillip L. Wright Memorial Research Award, Matthew Hansen Endowment (Wilderness Institute, School of Forestry, University of Montana), and the National Garden Club Scholarship Program.
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Chapter 1

Ecology, life-history characteristics, and the effects of disturbance on
Trillium ovatum Pursh. (Liliaceae)

ABSTRACT

Trillium ovatum Pursh. (Liliaceae) is a long-lived, spring ephemeral that grows in moist, coniferous forest habitats of the western United States. It is a member of the Trillium, or pedicellate, subgenus—bearing a single white flower on a pedicel. These flowers represent the only means of reproduction, as there is no asexual clonal growth in this species, and plants are slow to reach sexual maturity, presumably when a threshold of rhizome size is attained, which can take a minimum of 15-18 years. Each flower produces a capsule containing one to 150 seeds, each of which bears an oily food body, called an elaiosome, that is attractive to ants, yellow jackets (Vespula vulgaris), and other insects, which aids in seed dispersal. Seeds require one cold period for germination, at which time only the root emerges, and another cold period for cotyledon emergence the following year. The life-history stages of T. ovatum include a cotyledon stage, one-leaf vegetative stage, three-leaf vegetative (juvenile) stage, three-leaf reproductive (flowering), and three-leaf nonflowering regressive stage. Trillium exhibit stage class regressions (e.g. three-leaf flowering individuals transitioning to three-leaf nonflowering regressive stage), as well as extended dormancies—the lack of aboveground growth for one or more years. Trillium ovatum face many of the same threats as other forest understory species—anthropogenic disturbance such as logging and overharvest for horticultural and medicinal use, competition from nonnative invasive plant species, and overgrazing by deer, to name a few. Baseline long-term research of this species is necessary to understand population dynamics in the face of ecosystem change and to address conservation issues surrounding the health and welfare of long-lived understory species in general. Extensive investigations of Trillium, including T. ovatum, have been accomplished, yet no prior studies of T. ovatum have been conducted at the eastern edge of its distribution in Montana, where populations experience increased aridity and highly variable climatic conditions as compared to other regions where T. ovatum occurs. This chapter reviews basic biologic features of T. ovatum, and threats to populations.

Distribution and habitat

Western trillium (Trillium ovatum Pursh.) is an herbaceous perennial plant found in mesic forested sites from southern British Columbia and southwestern Alberta, southward through the Cascades in Washington and Oregon, western Montana, Idaho, Colorado, and Utah, to the California Coast Range as far as Monterey.

Distribution of *Trillium ovatum* in Montana is generally in the western part of the state (west of the continental divide), but there are a few disjunct populations in eastern Montana documented with specimens in the University of Montana Herbarium. One specimen was collected at Our Lake (39 miles northwest of
Choteau) in Teton County, blooming at 7000 feet elevation on June 30, 1963. This site is approximately 10 miles east of the Continental Divide, and the label notes read “wet soil”. Another specimen collected east of the Continental Divide is from 5,000 feet elevation at Limekiln Canyon in Beaverhead County and was collected by Blankinship on June 1, 1905. Fruiting and flowering plants were on the specimen sheet and label notes mentioned “low rich woods.” An additional oddity was collected by Mrs. Moore in July of 1889 (flowers and fruits) from Pyrenees, which is an historical post office listing in Deer Lodge County (the post office closed in 1891). While this is located just west of the Continental Divide, it is an outlier, perhaps taking advantage of a mesic site at high elevation (the late blooming indicating high elevation). All of these collections deserve attention and follow-up in the interest of *T. ovatum* populations living at the extreme edge of their distribution, and to investigate whether these populations still exist in the face of changing climatic conditions, disturbance regimes, and other ecological conditions.

It is interesting to note that chromosome patterns of allocycly within and between populations show differences within the species associated with two regions—the Pacific coast region of western North America (CA, OR, WA, BC) and the Rocky Mountain region (MT, ID). Pacific coast populations show homogeneity within
each population and clinal variation between populations. Rocky Mountain populations are relatively heterogeneous in chromosome composition and show no regular pattern of variation between populations with respect to chromosome type (Fukuda and Channell 1975). Fukuda (1990) also found that populations of *T. ovatum* in the Pacific coast region exhibit a generally high inbreeding level, whereas populations from the Rocky Mountain region are apparently outbreeding.

**Species description**

Traditional botanists place the *Trillium* genus in the Liliaceae family, but many modern botanists consider it part of a separate Trilliaceae family (Case and Case 1997, Ohara 1989), a classification arising from some major characteristics of *Trillium* such as net venation of the leaves (true lilies display classic monocot parallel-veined leaves), sepals and petals of different colors, among others (Case and Case 1997). Two subgenera of *Trillium* are recognized—the *Trillium* subgenus, or the pedicellate trilliums (flowers borne on pedicels), and the *Phyllantherum* subgenus, also known as the sessile trilliums (flowers sessile). Sessile flowered species tend to grow on alluvial floodplain and depend, to a great degree, on vegetative reproduction, whereas the pedicellate-flowered species tend to occur in mesic temperate forests and reproduce exclusively by seed (Ohara et al. 1990). *Trillium ovatum* is a member of the *Trillium* subgenus (*Grandiflorum*...
subgroup (Samejima and Samejima 1987)), and shares many attributes of other members of this subgenus. *Trillium grandiflorum*, or Great White Trillium, is native to eastern North America and is the closest relative to *T. ovatum*. Studies on *T. grandiflorum* and other Trillium species (particularly those of the *Trillium* subgenus) are incorporated in this summary to explore biological possibilities for this genus as a whole, and *T. ovatum* specifically.

*Trillium ovatum* has glabrous aerial parts. Underground rhizomes produce one stem annually with either one or three leaves (depending on the life-history stage), occasionally two or three stems are produced in older plants (Jules 1997b, 1998). Rhizomes are horizontal to somewhat erect, short, thick, fleshy, and develop white, fleshy adventitious roots in the spring (UBC Bot. Garden 1977). The stem is simple, erect, fleshy, and 20-46cm tall. The base of the stem is sheathed with a few short scale-like leaves and there is a horizontal whorl of three ovate-shaped leaves with acute apices just below the terminal flower (in reproductive age plants) (Kawano et al. 1992, Lackschewitz 1991, Samejima and Samejima 1987, UBC Bot. Garden 1977). Stem buds for the next season are laid down during active growth season from February to late July (Brandt 1916). Leaves are ovate to broadly-ovate, clear green, entire, sessile, and 5-15cm long and wide (Lackschewitz 1991, UBC Bot. Garden 1977).
Each shoot bears a single erect, pedicellate flower that opens soon after plant emerges in spring (Jules 1997a, Levkovitz 1984, Mesler and Lu 1983), which is April to May in British Columbia, and as early as February or March or as late as July in other parts of the range (Lackschewitz 1991, UBC Bot. Garden 1977).

Flower buds for not only the next growing season, but also for two or more subsequent seasons, are visible in the autumn prior to blooming (Brandt 1916).

Flowers are perfect, regular, solitary, bractless, and terminal on a pedicel arising from the center of the leaves (Lackschewitz 1991, UBC Bot. Garden 1977). Three green sepals are narrower and shorter than the three petals, which are lanceolate and white, or sometimes light pink, becoming deep rose to purplish with age (Goodspeed and Brandt 1916, Griffiths and Ganders 1983, Jules 1997a, Lackschewitz 1991, Levkovitz 1984, Samejima and Samejima 1987, UBC Bot. Garden 1977). Multiple-petaled mutants exist—different mutants have a different multiple of the basic number three—as well as dwarf mutants that have been found throughout the range of the species—these plants are much smaller than normal, and the flowers are reportedly pink when they open (Griffiths and Ganders 1983).

*Trillium* flowers lack abscission tissue, so all flower parts remain attached to the receptacle until after fruit maturation (Berg 1958).
The fruit is a fleshy, globose to ovoid capsule that is greenish-brown and 1.2 to 2.5cm in diameter at maturity (Berg 1958, Mesler and Lu 1983, UBC Bot. Garden 1977). The fruit ripens to produce one to more than 150 seeds, each of which is ovoid and 3-5mm in length (Brandt 1916, Mesler and Lu 1983, UBC Bot. Garden 1977). The ventral or concave side of each seed bears a conspicuous, oily, white or yellow appendage, called an elaiosome, which equals or surpasses the volume of the seed and often overarches or encloses half of the seed (Berg 1958). The elaiosome is attractive to ants, yellow jackets (Vespula vulgaris), and other insects (Berg 1958, Jules, 1998, Mesler and Lu 1983, Ohara 1989), and after short exposure to air, shrinks and becomes less attractive (Berg 1958).

**Life-history characteristics**

Life-history stages of *Trillium ovatum* include: cotyledon stage, one-leaf vegetative stage, three-leaf vegetative (juvenile) stage, three-leaf reproductive (flowering) (Jules 1997b, Kawano 1992), and three-leaf nonflowering regressive stage (Chapter 2) (Fig. 1). The cotyledon stage is easy to distinguish from the one-leaf stage—cotyledons exhibit an oblong to lanceolate shape and one-leaf plants display the typical ovate-shaped leaves of this species (Kawano et al. 1992). Marked cotyledons were observed to remain in the cotyledon stage for more than one year (personal observation for *T. ovatum* in Montana), but more data collection
will be necessary to understand if this is a normal part of the life-history. It is not clear how long *T. ovatum* persist in the one-leaf stage class in Montana, but these plants tend to be very small (averaging 2.2cm long and 1.5cm wide) (unpublished data), in sharp contrast to other studies that define the one-leaf stage as having a range of size classes (Kawano et al. 1992) (see Chapter 2 discussion). Similar to populations elsewhere, the three-leaf juvenile stage does exhibit a wide range of sizes in Montana from very small (dime-sized) to very large (hand-sized) plants (personal observation for *T. ovatum* in Montana). Transition to the reproductive (flowering) stage occurs at a minimum age of 18 years in Montana (unpublished data, see Chapter 2), but this transition likely depends more on individual plant size and resources than age. Flowering plants are generally the largest plants in these populations, although some small plants flower as well (personal observation for *T. ovatum* in Montana). *T. ovatum* exhibit stage class regressions—reproductive plants undergo a reverse transition to a nonflowering regressive stage (Goodspeed and Brandt 1916, Jules 1997b, Kawano 1992, personal observation for *T. ovatum* in Montana). Plants in the regressive stage are generally larger and more likely to flower again. A few cases have been noted of one-leaf plants that have transitioned to a small three-leaf juvenile stage, reverting to a one-leaf stage (personal observation for *T. ovatum* in Montana, and see also Ohara and Kawano 2005 for *T. camschatcense* in Japan). Dormancy, defined as the lack of above-
ground growth for one or more years, has been observed in this species (Goodspeed and Brandt 1916, Jules 1997b). Dormancy in every three-leaf stage class has been observed in Montana, with most plants returning to aboveground status in the following year or two (Chapter 2). Many individual plants exhibit repeated dormancy every other year (or so), and there are some plants that reappear after being in a dormant class for 3-5 years consecutively (personal observation for *T. ovatum* in Montana).

Stem production creates an annual constriction on the rhizome and no clonal reproduction occurs, so the age of plant can be determined. Age estimates for older plants are underestimates because most plants greater than 30 years of age have lost small portions of their rhizome due to decay (Brandt 1916, Jules 1997a and b). *T. ovatum* plants range up to 72 years old and individuals do not become reproductive until they are at least 15 years old (Jules 1997a), although the University of British Columbia Botanical Garden (1977) reports that seedlings undergo at least three to five years of vegetative growth before the first flowers are produced. It was not clear whether the UBC results were from garden experiments or populations in their native habitat. Horticultural applications report that, in ideal conditions, flowers will appear in 4-7 years (Deno 1993, Cullina 2000, Phillips 1985).
Fig. 1. Life cycle of *Trillium ovatum*. Clockwise from top left: fruit, seeds with attached elaiosome, cotyledon, small one-leaf vegetative, large one-leaf vegetative, small three-leaf juvenile, medium three-leaf juvenile, large three-leaf juvenile, reproductive, and nonflowering regressive stages. (Sketches by Tempe Regan, arrangement by Marlene Hutchins).
Patrick (1973) observed similar rhizome characteristics in *Trillium grandiflorum*, a close relative of *Trillium ovatum*. He described aging the plants by “counting the embedded annular remnants of the sheathing cataphylls,” and also added that it is difficult to determine the exact number of years represented at the apical end of the rhizome, as it takes three to four years from the time that an aboveground shoot appears to the time the scar of that shoot becomes a visible part of the rhizome (after the remnant cataphyll bases embed and tissue enlarges with stored starch to maintain the uniform diameter of the rhizome). He reported that the average age of a mature rhizome is 20 to 25 years, and the age of the living part of the rhizome with a flowering shoot is no more than 35 years.

Hanzawa and Kalisz (1993), while studying *T. grandiflorum*, found that reproductive plants were significantly older (X=22.8 years) than nonreproductive plants (X=13.3 years), and that reproductive plants also had significantly larger rhizome volumes and total leaf areas. Reproduction in the population they studied occurred once plants reached a threshold of rhizome volume or leaf area. They found that the two measures of plant size--total leaf area and rhizome volume, were better predictors of plant reproductive status than was the plant age.
Reproductive ecology

Recruitment of offspring in *Trillium ovatum* is exclusively dependent upon sexual reproduction (Jules 1997a and b, Kawano et al. 1992), and plants are self-incompatible, and cross-pollination by insects is necessary for seed production (Jules 1997b, 1998, Levkovitz 1984). The flowers do not produce nectar, although several insects forage for their pollen. Jules (1998) found that pollination is accomplished primarily by sap beetles (Nitidulidae), two species of bumble bees (Apinae), rove beetles (Staphylinidae), flower long-horned beetles (Lepturinae) and honey bees (*Apis mellifera*). In addition, crab spiders (Thomisidae), often inhabit the corolla tubes of trillium, and geometer moths (Geometridae) covered in pollen are sometimes found captured by these spiders in the morning, indicating that moths probably pollinate flowers at night (Jules 1997b, 1998). Levkovitz (1984) similarly found that northern California populations of trillium are cross-pollinated by several species of small, hairy beetles. She noted that *T. ovatum* flowers are cantharophilous (adapted for pollination by beetles), due to their large, open morphology (beetles are not capable of complex flower handling), white color, fruity scent, and pollen rewards.

Lubbers and Lechowicz (1989) found that seed production in *Trillium grandiflorum*, under conditions of carbohydrate limitation, will proceed at the
expense of storage in rhizomes. They posited that allocation of resources to current reproduction, at the expense of survival and future reproduction, possibly reflects the selective effects of unpredictable year-to-year availability of pollinators for this spring ephemeral. Lapointe (1998) monitored carbohydrate content in the stem and rhizome of *Trillium erectum* during an entire growing season (May-November), and found that rhizome starch reserves were replenished quickly in the spring and maintained constant levels until senescence of above-ground plant parts in the fall. Accumulation of reducing sugar in the stem increased rapidly for the first three weeks of growth, then decreased slowly over the summer until fruit maturation, when sugar levels dropped drastically. Additionally, stems at the beginning of the fruiting stage were harvested and maintained in aqueous solution after leaf removal until fruits were fully mature—demonstrating fruit development without leaves or rhizome. Lapointe’s study (1998) shows that temporary carbohydrate accumulation in the stem of *T. erectum*, as well as rapid replenishment and long-term storage of carbohydrate reserves in the rhizome, early in the spring takes advantage of higher irradiances before canopy closure, which has been found in other spring ephemerals (Risser and Cottam 1968). It would seem that no comparison would exist for these eastern species of deciduous forests with western species in coniferous forests, but *T. ovatum* appears to take advantage of being the first plant to emerge by completing its bloom cycle (and pollination)
before the larger understory plants (shrubs and tall herbs) leaf out (personal observation for \textit{T. ovatum} in Montana).

Levkovitz (1984) reported relatively low (32\%) average seed set in natural \textit{T. ovatum} populations as compared to hand-pollinated populations, partially caused by self-incompatible pollen deposition on stigmas that interrupt cross-pollination. The number of seeds matured is dependent on plant resources, and the proportion of investment of resources in seed production is not a function of plant size (Levkovitz 1984, see also Ohara et al. 1990). Four species of \textit{Trillium} (\textit{T. grandiflorum}, \textit{T. erectum}, \textit{T. undulatum}, and \textit{T. sessile}) examined by Kawano et al. (1986) showed that the number of propagules produced per plant was clearly dependent on the size of the plants (individual biomass).

Numerous studies of \textit{Trillium} species confirm that seeds often drop (and subsequently germinate) just below parent plant (Berg 1958, Kawano et al. 1992, Ohara 1989, Ohara and Kawano 2005, and personal observation for populations in Montana). \textit{Trillium} are myrmecochorous and each seed bears an elaiosome that is an attractive food source for numerous species of ants (Berg 1958, Mesler and Lu 1983), yellow jackets (\textit{Vespula vulgaris}) (Jules 1998), and other insects, such as solitary ground beetles (Carabidae) (Ohara 1989). Generally speaking, insects do
not destroy the seeds, and while ground beetles and small ants eat the elaiosome and leave the seed in place (ultimately interfering with dispersal) (Berg 1958, Ohara 1989, Ohara and Higashi 1987), large ants and yellow jackets act as dispersal agents by transporting seeds with elaiosomes to their nests (Berg 1958, Jules 1996, 1998). Berg (1958) observed ants carrying *Trillium* seeds 15 meters away from experimental seed depots to their nests and subsequent disposal of seeds by carrying them out of the nest after removing elaiosomes. Yellow jackets forage over much greater distances than ants, and will therefore influence both the dispersal ability of plants and the genetic and demographic structure of populations (Jules 1996). Mesler and Lu (1983) found that *T. ovatum* populations in second-growth redwood forests of northern California had limited dispersal—most seedlings occurred in mixed-age clusters near potential parents. In their study, ants were absent or rare at some sites, and in sites where they were present, ants removed elaiosome before returning to nest. They concluded that dispersal adaptations of *T. ovatum* probably evolved in forests where seed-carrying ants were more common.

While Berg (1958) noted that harvester ants (*Aphaenogaster subterranea*) collect *Trillium* seeds for food and likely destroy the seed, dispersal by other species of ants (myrmecochory), yellow jackets, and other insects can potentially provide
several benefits for the species such as escape from seed predators, dispersal to superior germination sites, and reduced intra-specific competition. Ant-dispersed *T. tschonoskii* populations exhibit proportionally more 3-leaf than 1-leaf (younger) individuals at distances greater than 60cm from the parent plant as compared to closer to parent plants, indicating reduced seedling mortality, through reduced competition, due to relatively short dispersal distances (mean 64cm) by ants (Higashi et al. 1989). There is evidence of *T. ovatum* seed predation by rodents (Jules 1997b, Jules and Rathcke 1999, Mesler and Lu 1983), which could act as a strong selective force favoring elaiosome-bearing seeds when seeds dispersed into ant or yellow jacket nests are less likely to be found by foraging rodents (Jules 1997b).

Dispersal of seeds by deer has been described as an important factor in long-distance, post-glacial migration of *Trillium grandiflorum* and *Trillium erectum* (Vellend et al. 2003, 2006). *Trillium* seeds remain viable after passing through the digestive tract of white-tailed deer (*Odocoileus virginianus* Zimm.), and the seed shadow modeled by Vellend et al. 2003 showed that most seeds dispersed by deer will be at least several hundred meters, and occasionally up to greater than three kilometers, from the parent plant. Frugivory of *Trillium ovatum* by deer has been
observed in Montana (personal observation), thus deer likely act as long-distance dispersers of seed for this species as well.

Seed germination requirements for *Trillium ovatum* include moisture and stratification (Jules 1997b, UBC Bot. Garden 1977). Seeds require one cold period (winter) for germination, at which time only the root emerges, and another cold period for cotyledon emergence (Jules 1997b). The University of British Columbia Botanical Garden (1977) found that, by planting the seeds as soon as they are ripe (preferably straight from the capsule without drying out), the need for a second cold treatment seems to be eliminated. Older seed may not germinate for two to three years (UBC Bot. Garden 1977). Deno (1993) found that Gibberellic Acid-3 stimulated germination after seeds had already undergone fluctuating temperature treatments. Deno’s (1993) experiments also indicate that light has no effect on *Trillium* seed germination. Seedling establishment requires moisture and absence of disturbance (UBC Bot. Garden 1977).

Garden observations by Goodspeed and Brandt (1916) found that *Trillium ovatum* rarely send up more than one shoot annually and “almost never produce new individuals asexually.” Although no clonal reproduction has been observed in *T. ovatum* in Montana (personal observation), rhizome wounding in *T. grandiflorum*
has been shown to produce bulblets, which can be subsequently divided and planted (Phillips 1985), and it appears that Goodspeed and Brandt (1916) were able to grow *T. ovatum* plants from divided rootstock. It is possible, therefore, that *T. ovatum* surviving disturbance to the rhizome could produce new plants.

**Effects of disturbance**

Demographic changes in *Trillium ovatum* populations due to habitat fragmentation from logging have been observed in southwestern Oregon. The amount of fragmentation strongly influences species composition and the type of fragmentation strongly influences species abundance and the relative number in each response group (Jules et al. 1999). There is evidence of changes in population sizes of *T. ovatum* due to logging (Jules et al. 1999). Jules (1998) found that the process of logging and conifer replanting in the Siskiyou Mountains of Oregon resulted in high mortality (approximately 97.6%) and almost no recruitment of individuals in clearcut sites. The remaining plants were not recruiting new individuals, even in sites clearcut 30 years prior to the research (Jules 1997a, Jules 1997c, Jules 1998). Reduced recruitment could not be attributed to a lack of seeds, as reproductive plants produced an average of 24 seeds, or an average of 0.003 seeds per m$^2$ (Jules 1997a, Jules 1997c). In addition, the hot, dry summers and conditions between fragments were too extreme for establishment of plants (Jules 1997a).
Trillium ovatum are restricted to, or closely associated with, remnant patches of late-successional or old-growth forest, which provide a less suitable habitat than their original range (Jules 1997a, Jules 1997b, Jules et al. 1999). Clearcut-forest edges have been shown to create compositional changes in the understory flora up to 60 meters or more from the boundary in the Klamath Mountains (Frost 1997). Jules (1997a, 1997c, 1998) showed that Trillium populations in forest remnants within approximately 65 meters of forest-clearcut edges have had almost no recruitment of young plants since the time of the adjacent clearcutting, while the forest interior populations contained higher recruitment levels. Projections based on these recruitment estimates indicate that edge populations will decline in size, eventually going extinct, and that interior populations will not decline (Jules 1998). When viewed from this angle, it is probable that the mechanism of demographic change is a combination of reduced seed set and survivorship of seedlings near edges (Jules 1998). Studies of Japanese species show similar results—limited recruitment near forests edges due to microclimatic conditions of T. camschalcense (Ohara et al. 2006, Tomimatsu and Ohara 2004), and larger populations, with possibly fewer edge effects have higher proportions of seedlings (Tomimatsu and Ohara 2002).
Edge effects also alter several plant-animal and plant-pollinator interactions (Jules 1997b). A study by Jules and Rathcke (1999) elucidates that pollinators, including common beetles and bees, appear to be either less abundant or less effective near edges. This study also identified two factors that appear to responsible for reduced recruitment near edges: decreased seed production due to changes in pollination and increased seed predation by rodents (see also Jules 1997b and Tallmon et al. 2003). This suggests that plant population declines associated with fragmentation are due to subtle interspecific interactions, rather than to direct alteration of the physical environment (Jules and Rathcke 1999).

Kahmen and Jules (2005) studied the recovery of *T. ovatum* following clearcut logging across a 424-year chronosequence and found a significant positive relationship of population size and stand age, suggesting that recovery may take centuries, and depends on a sufficient number of individuals surviving the disturbance event. In contrast, Jenkins and Webster (2009) found that population structure of *T. erectum* primary and post-logging secondary forests in the southern Appalachian Mountains were similar—logging did not eliminate this species, and even though secondary forests contained more low density patches that had less complexity of spatial structure, these populations had higher densities of young plants, which could indicate that these populations are still expanding 80 years
after timber was harvested. Their additional studies in the old-growth forests of Great Smoky Mountains National Park show that populations of *T. grandiflorum*, *T. erectum*, and *T. vaseyi* exhibit stable spatial distributions and a high degree of spatial aggregation over long time periods, and individual plant aggregations were multi-aged (Webster and Jenkins 2008).

Physical disturbance such as logging has many visible, as well as imperceptible, long-term consequences for forest ecosystems. The effects of climate change have likely caused subtle shifts to populations that need be studied and followed through time. Phenology, particularly time of flowering, will be an excellent indicator of shifts in basic reproductive biology of any given species. Routheir and Lapointe (2002) found that initiation of emergence (development and bud burst) in *T. erectum* in the spring is closely linked to temperature. Thus, changes in temperature could alter phenological schedules. Routher and Lapointe (2002) studied the impact of overstory canopy closure on size and growth rate of this species in deciduous maple forests of Quebec, Canada. They found a south to north gradient with decreased plant biomass, annual growth rate, and investment to reproduction—indicating that the shorter length of the high light period in early spring had negative effects on growth and reproduction in northern sites, which could explain the northern distribution limit of this species (Routher and Lapointe
While *T. ovatum* in Montana does not grow in a deciduous forest habitat, it does experience canopy cover closure in the form of shrubs and other species in the herb layer. Shifts in the timing of canopy closure could have large implications for this species in terms of timing of budburst, pollination biology, and use of light for resources, etc. Additionally, downhill distributional shifts in elevation driven by changes in climatic water balance have been described for plants species in California (Crimmins et al. 2011), and considering that *Trillium* species are highly dependent on water, this is yet another aspect of climate change to take into consideration.

**Deer**

White-tailed deer overpopulation in the eastern North America has led to the decimation of forest ecosystems, particularly understory native plant communities. Overgrazing by deer has dramatically impacted forest diversity, abundance and population structure of many species, and facilitated invasion by exotic plant species (Alverson et al. 1988, Jenkins et al. 2007, Knight et al. 2009, Rooney et al. 2004). Popular magazines have run titles such as “Oh, Deer” (Discover, Ness 2003) and “Wanted: More Hunters” (Audubon, Williams 2002) to bring attention to this problem. The March 2003 Discover magazine article quotes writings of Aldo Leopold (1949), “Just as a deer herd lives in mortal fear of its wolves, so does a mountain live in mortal fear of its deer,” and went on to list *T. grandiflorum*
as “collateral damage” (Ness 2003). Research in these ecosystems shows that *Trillium* are a preferred food plant for grazing deer (Anderson 1994, Augustine and Freligh 1998, Knight 2004), who browse almost exclusively on large three-leaf plants (both reproductive and nonreproductive) that once consumed, don’t regrow in the same season (Augustine and Freligh 1998, Knight 2003, Rooney and Gross 2003, and personal observation for *T. ovatum* in Montana). Herbivory of plants can occur from the time that plants emerge and early in the growing season, which removes reproductive plants that could potentially produce seed, through the time of seed production, when fruits can be ingested and dispersed (Rooney and Gross 2003, Vellend et al. 2006, and personal observation for *T. ovatum* in Montana).

Deer herbivory of the large three-leaf stage classes has a strong negative impact on population growth rate (\(\lambda\)) in *T. grandiflorum* (Knight 2004, Rooney and Gross 2003). Augustine and Freligh (1998) found that sites with high densities of deer consistently had over a 50 percent deer-caused reduction in reproduction during the growing season, and population structures were skewed toward small plants. Plants rarely die, but in the year(s) following early-season grazing, plant size, either height (Anderson 1994), or leaf area (Augustine and Freligh 1998, Knight 2003, Lapointe et al. 2010 for *T. erectum*) is consistently reduced and plants are less likely to flower (Knight 2003 and 2007). Plant size (stem height, leaf length,
and leaf area) is positively correlated with reproductive output (Anderson 1994, Augustine and Frelich 1998, Knight 2003), suggesting that the reductions in plant size due to grazing could reduce future reproductive success. Chronic herbivory by deer of *T. catesbaei*, a habitat generalist, in the Western Great Smoky Mountains National Park caused truncated age structures, and flowering in smaller and younger plants, and may eventually lead to local extirpation of this species (Jenkins et al. 2007). Additionally, Collard et al.’s (2010) studies of deer exclusion zones show overall slow recovery of understory vegetation, as well as incomplete recovery of individual species such as *T. erectum* after eight years of deer exclusion. Exhaustive studies of the impacts of deer browsing on *T. ovatum* are nonexistent, but potential localized overgrazing could be a factor in the demography of this species.

**Medicinal use**

Medicinal use of *Trillium* by Native Americans includes dermatological applications, eye medicines, and for childbirth, which is why it is often called Bethroot (or Birthroot) (Bown 1995, Gunther 1973, Moerman 1981, Moerman 1998, Schenck and Gifford 1952, Turner et al. 1990). Moerman (1998) refers to *Trillium ovatum* as “Pacific Trillium,” and lists specific uses by a number of coastal tribes. He documents the Karok and Quileute use of plant juice or scraped bulbs in a poultice for skin boils and extensive use of fresh and dried roots for eye
medicine by Lummi, Paiute, Skagit, and Thompson tribes, as well as a poultice of pounded rhizome applied as love medicine (Moerman 1998). The Skagit also considered the plant poisonous (Moerman 1998). Roots of *T. ovatum* are currently used by herbalists for uterine bleeding, particularly after birth (Anon., pers. comm., Moore 1995). Moore (1995) also suggests its use by males with an acute episode of benign prostatic hypertrophy. Active constituents of *Trillium* include steroidal saponins, particularly trillin (diosgenin monoglucoside) and trillarin (diosgenin diglucoside), and tannins (Bown 1995, Brendler et al. 1997, Moore 1995).

Growing interest in herbal medicines has created a market for wild herbs, which, in turn has lead to overharvest of many plant populations. In response, the 1999 Montana State Legislature passed Senate Bill 178 in an attempt to secure seven native plant species. Because the root of *T. ovatum*, one of the seven listed species, is used for medicinal purposes, population disturbances can be extreme, as a greater number of large, reproductive-age plants are removed, which is common practice for root harvesters (Nantel et al. 1996). There is a concern among herbalists that the unsustainable harvest of these older plants will decimate populations in a very short time (Anon., pers. comm.). Education about *Trillium* ecology and more restrictions, such as the Montana Law and British Columbia’s Dogwood, Rhododendron, and Trillium Protection Act (1996), will likely be
necessary to maintain this species. Even laws are often limited, as in the case of
the Montana law, the moratorium on harvest lasted only three years, and no
funding was provided to implement it. Additionally regulation of forest herb
harvest is difficult and generally low on the list of priorities of overburdened forest
managers.

Conservation

The *Trillium* genus is admired by the general public and scientists alike throughout
its native range in Japan and North America. The reproductive biology and life-
history characteristics of these spring ephemerals are fascinating and lend well to
research as study systems in the forest understory. Indeed, extensive investigations
of *Trillium*, including *T. ovatum*, have been accomplished, yet no prior studies of
*T. ovatum* have reached the eastern edge of its distribution in Montana, where
populations experience increased aridity and highly variable climatic conditions as
compared to other regions where *Trillium* occur. *Trillium* populations are also
limited in their range within Montana, as they are closely associated with the
relatively rare and fragmented riparian and seep habitats in montane forests. Forest
habitats in Montana are not immune to the threats facing ecosystems worldwide—
logging, development, mining, disease, invasive nonnative organisms,
overexploitation, predation, etc. Long-lived, rhizomatous species such as *T.
*ovatum* can be initially resistant to disturbance, but long-term monitoring will be
needed to know if populations remain robust over time—this research will clarify the use of this species as an indicator of forest understory health. Baseline data on population structure and dynamics, as well as the environmental requirements of this species are needed for a better understanding and conservation of *T. ovatum* in Montana. Research presented in Chapter 2 addresses the gaps in knowledge of the basic demographic characteristics of *T. ovatum* in Montana, as well as presenting a discussion of specific potential threats to these populations.

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Chapter 2

Life history and demography of a long-lived, herbaceous perennial, *Trillium ovatum* Pursh. (Liliaceae), in Western Montana

ABSTRACT

Long-lived herbaceous plants represent an important element of the biodiversity of many forest ecosystems, yet few long-term studies have followed these populations intensively through time. This study examined the demography of *Trillium ovatum*, a species of interest for conservation in western Montana, to learn: 1) what are the demographic characteristics of *T. ovatum* near its eastern limit of range and; 2) how are these characteristics affected by weather, climate, and site characteristics? Populations in three representative riparian coniferous forest ecosystems were sampled over 9 growing seasons in which stage classes and densities of plants were monitored in each population. In addition, information on age structure, and fecundity were gathered from a subsample of plants. *Trillium* populations were found to have a remarkable demographic pattern in this region, with plants requiring 18-19 years to reach sexual maturity, and an average of 27% of reproductive (flowering) adults periodically retrogressing to a nonflowering (regressive) stage class. Juvenile plants were more abundant than nonflowering regressive and reproductive plants at all three sites. Age and number of seeds produced were positively correlated with individual plant size. Yearly fecundity measures of fruit set, number of seeds produced per flowering plant, and seeds per square meter were highly variable. Dormancy was observed in all adult stage classes, with most plants returning to above ground status in the following year or two, although some plants exhibited dormancy for 3-5 years. This extended dormancy made assessing mortality difficult, but juvenile plants showed an overall average of 2% mortality of plants that had been dormant for more than three years and only one site had incidence of mortality in the reproductive stage class. Tallies of new plants each year showed that far more juvenile plants were ‘recruited’ into the population than died, and these recruits also showed low mortality, but the general relationship of these recruits to population dynamics is unclear due to extreme longevity of *T. ovatum* populations. Generally low fecundity and recruitment may limit the ability of these populations to recover from stress or mortality events, and suggests they may be quite sensitive to climatic changes, and fire disturbances that are likely to occur in this region. Continued long-term monitoring will be invaluable for understanding responses of long-lived forest understory species to the complex interplay of these environmental stresses.

INTRODUCTION

Understory vegetation exhibits the greatest species and structural diversity in temperate forests and plays critical functional roles in forest ecosystems (e.g. Alaback 1996, Gilliam 2007). Historically the significance of this layer has been
underappreciated in forest research, and there remains a plethora of common species of the understory whose basic life history characteristics, community interactions, and ecological roles are not yet known (Gilliam and Roberts 2003, Gilliam 2007, Whigham 2004). Many forest herbs are long lived, yet few long-term data are available to fully appreciate the demography of these species (Bierzychudek 1982, Jolls 2003, Whigham 2004). Plant demographic variation—an accurate representation of survival, recruitment and mortality that includes environmental stochasticity—can only be sufficiently captured when followed for many years (Fiedler 1987, Menges 2000). Long-term baseline studies of iteroparous understory plants are important for understanding population dynamics and the unique adaptations of these species to the forest environment (Ohara and Kawano 2005, Whigham 2004).

Herbaceous understory species, in general, and specifically long-lived perennials, are particularly sensitive to disturbance due to their slow rates of growth, recruitment, and regeneration (Kahmen and Jules 2005, Meier et al. 1995, Nantel et al. 1996, Singleton et al. 2001, Wyatt and Silman 2010). Competition for microsites containing three primary resources—light, soil nutrients, and moisture (which are highly limited in the forest environment) (Gilliam 2007, Muller 2003, Tomimatsu and Ohara 2002, Whigham 2004)—can affect the demography of
forest species, particularly seed establishment and survival of seedlings. Climate change may alter resource availability, as well as temperature and moisture conditions, and thus affect plant population dynamics. Consequently, tracking changes in recruitment, survival, and mortality of plants through long-term studies of understory species may help elucidate broad ecosystem changes.

Natural extinction rates are higher in herbaceous plant species than any other forest layer, thus threats to the understory represent risks to forest biodiversity and ecosystem function as a whole (Gilliam 2007, Jolls 2003, Wyatt and Silman 2010). Key threats to plant populations include habitat destruction (loss, degradation, fragmentation, and pollution), introduction of alien/invasive species (and their corresponding diseases), harvest and overexploitation for human use (medicinal, floral, and horticultural trades), climate change, disease, and predation (Gilliam 2007, Given 1994, Jolls 2003, Whigham 2004, Wilcove et al. 1998).

Research of long-lived plant populations requires an understanding of the dynamic aspects of the population in its environment. Demographic monitoring can be used to assess if populations are maintaining themselves under current conditions (Schemske et al. 1994). The demographic structure of a population—the distribution of individuals in each stage class (seedlings, juvenile, and
reproductive)—can give clues to the status of a population (Oostermeijer et al. 1994, Rabotnov 1969). Survival of any given population depends on its vital rates (plant fecundity, seedling recruitment, and survival) and mortality rates. Other important factors in population dynamics include requirements of size or age to reach reproductive status and factors impeding reproductive effort, germination, and establishment.

Western Trillium (*Trillium ovatum* Pursh.) is a long-lived forest perennial that grows at the eastern limit of its distribution range in the mesic forests of western Montana where it is exposed to increased aridity and highly variable climatic conditions as compared to populations on the west coast of the United States (NOAA 2010). Growth, reproduction, recruitment, and survival rates in plant populations situated at the extreme edges of distribution ranges are often compromised (Charron and Gagnon 1991, Routheir and Lapointe 2002). *T. ovatum* growing in Oregon and California, where *Trillium* habitat is considered ‘optimal,’ take many years to reach sexual maturity, have low recruitment rates, and only reproduce sexually (Jules 1997a and b, Kawano et al. 1992). Studies on forest perennials in general (Charron and Gagnon 1991, Harper 1977, Kawano 1985, Werner and Caswell 1977), and Trillium species in particular (Hanzawa and Kalisz 1993, Kawano et al. 1986), have shown that survivorship and fecundity
schedules are closely linked to plant size, and plants living at the eastern edge of the range potentially have extended growth schedules to reach these size thresholds. Extensive research of *Trillium* species, including *T. ovatum*, has been accomplished, yet no studies have extended to populations in Montana, where it is the only occurring *Trillium* species and has been shown to have distinct chromosomal differences which may reflect the fluctuating climatic conditions of the Rocky Mountain region (Fukuda and Channell 1975, Kawano et al. 1992).

This long-term demographic study of *Trillium ovatum* was initiated to: 1) determine the life history stages, stage class structure, and yearly transitions among stage classes of populations in western Montana; 2) determine age and size of plants and the relationship(s) among age, size, and stage class; 3) determine how many years it takes for plants to reach sexual maturity (age of first reproduction) and fecundity schedules; and 4) determine forest structure and site characteristics, including soil moisture and light penetration, and weather and climate influences at each site.

**METHODS**

**Study species**

*Trillium ovatum* is a long-lived, herbaceous perennial plant found in mesic, forested sites from southern British Columbia, southward through the Cascades in Washington and Oregon, to the California Coast Range as far south as Monterey County on the coast, and east to the northern Rockies from southern Alberta south to Utah and northern Colorado (Case and Case 1997, Hitchcock and Cronquist 1973, Jules 1998, Lackschewitz 1991, UBC Bot. Garden 1977, Renner 1980, Weber and Wittman 1990). Each spring (late April or early May) plants produce one shoot that grows from an underground rhizome and bears one or three leaves and, in reproductive plants, a single pedunculate flower (Goodspeed and Brandt
1916, Jules 1997a, Levkovitz 1984, Mesler and Lu 1983). Stem and floral buds for the next season are laid down during active growth season from February to late July (Brandt 1916). Seeds are released in July, during senescence of all aboveground parts (Kawano et al. 1992).

Life-history stages of *T. ovatum* include: “cotyledon” stage, “one-leaf” vegetative stage, three-leaf “juvenile” vegetative stage, and three-leaf flowering (“reproductive”) stage (Jules 1997b, Kawano et al. 1992). Stage class regression (reverse transition from “flowering” reproductive to a “nonflowering” regressive stage) is exhibited in *T. ovatum*, and dormancy (lack of growth above ground for one or more years) has been observed (Goodspeed and Brandt 1916, Jules 1997b). Plants are not sexually mature until they are at least 15 years old, based on studies conducted in California, Oregon, and British Columbia (Brandt 1916, Jules 1997a and b, University of British Columbia Botanical Garden 1977). Jules (1997a) found that plants in Oregon range up to 72 years old.

Recruitment of offspring in *T. ovatum* is exclusively dependent upon sexual reproduction (no clonal reproduction occurs) (Goodspeed and Brandt 1916, Jules 1997a and b, Kawano et al. 1992), plants are self-incompatible, and cross-pollination by insects is necessary for seed production (Jules 1997b, 1998,
Levkovitz 1984). Each flower produces a single fleshy capsule containing one to more than 150 seeds (in California and Oregon), each bearing an elaiosome that is attractive ants and yellow jackets (*Vespula vulgaris*) (Berg 1958, Jules 1996, Levkovitz 1984, Mesler and Lu 1983). There is no evidence of a persistent seed bank for this species (Jules, *pers. communication*, Mesler and Lu 1983), and seeds require one cold period (winter) for germination, at which time only the root emerges, and another cold period for cotyledon emergence (Deno 1993, Jules 1997b.)

**Study Sites**

Three *Trillium ovatum* populations were sampled near Missoula, in western Montana, along small forested streams or seep habitats on gentle terrain at similar elevations that had no evidence of recent disturbance. Populations were located 80 meters or more from a road, heavily-used (major) trail, or other potential disturbances to decrease potential ‘edge effects’ (Jules 1998, Tomimatsu and Ohara 2002). In the spring of 2001, two representative populations were selected—one in the lower Big Creek drainage of the Bitterroot Valley (Bitterroot National Forest) (46°27.880’ N; 114° 12.674’ W) and one next to Grant Creek in the Missoula Valley (Lolo National Forest) (46°59.331’ N; 113°59.066’ W). During the 2002 field season, another population was selected along Spring Creek (Spring Gulch) in the Rattlesnake drainage (Lolo National Forest) (46°56.496’ N;
113°58.171’ W). Elevations range from 3841 feet at Spring Gulch and 3844 feet at Big Creek to 4304 feet at Grant Creek.

The study area is ecotonal between a semi-arid montane grassland and montane forest (*Pseudotsuga menziesii* and *Pinus ponderosa* dominate). Study sites are west of the continental divide in rain shadow areas, and are dominated by storm tracks from the coastal Pacific Northwest. Weather data from 2001 through 2009 was taken from the Missoula Airport (NOAA 2010) which is located 11, and 9.9 km west of the Grant Creek and Spring Gulch sites respectfully. Annual rainfall is 341 millimeters (including 1052 millimeters of snowfall) and the mean annual temperature is 6.8°C. January temperatures average -5.2°C, July temperatures average 19.3°C. All months except July and August are relatively cloudy with an average of 50% of possible sunshine for the year (NOAA 2010).

**Site history**

While all three sites had no evidence of recent disturbance, some sites had logging disturbances 50 or more years ago, before accurate GIS-verified data were available. Most forest lands in western Montana were subject to selective logging of the largest pine trees before the National Forests were established, and before active management was practiced in the region. There are no records of forest management activity at the Big Creek site (USDA Forest Service, Bitterroot
National Forest, pers. comm. June 2010 Cheri Hartless), and although a few old, large tree stumps were noted in the area indicating past selective logging, no stumps were located in the macroplot. The Lolo National Forest reported that, in general, Spring Gulch underwent "selective harvesting at the turn of the century [that] removed most old-growth ponderosa pine and wildfires in 1919 initiated new second growth stands. Fire suppression since 1919 has allowed an increasingly dense Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) understory to develop on many forested sites and invade the shrub fields" (USFS Lolo National Forest, pers. comm. June 2010 Nora Leetch). Historically the meadow bordering the *T. ovatum* population was homesteaded, and potentially experienced livestock use. No cut stumps were noted in the area of the macroplot, situated in a bottleneck between the stream and a steep mountainside, and the population was considered undisturbed. No historical information was available for Grant Creek, and no cut stumps were present in this field site.

**Macroplot establishment**

*Trillium ovatum* populations at the study sites had aggregated distributions in moist areas. Permanent macroplots were established during the blooming season (May), incorporating 80-90% of the individuals in one population at each site. Each macroplot consisted of a 2-meter-wide belt transect running through the center of the entire length of the population. Each transect contained two adjacent 1-m²
quadrats along the length (see Lesica 1987) and additional perpendicular 1-m² quadrats, creating a “+”-shape (see Figure 1). This design was intended to capture a majority of the population, as well as to maximize microhabitat variation (Heidel and Shelly 2001). Forty 1-m² quadrats were established at Spring Gulch, sixty at Grant Creek, and sixty-five at Big Creek. All four corners of each 1-m² quadrat were marked with 12-inch spike nails to improve precision in relocating plots for annual measurements.

**Fig. 1.** Sample of a permanent macroplot used to sample *Trillium ovatum* plants. Each square represents a 1-m² quadrat.

**Demographic measurements**

Life-history stages of *Trillium ovatum* have not been defined for Montana populations, but were assumed to display typical life history characteristics of *Trillium ovatum* in other regions (Jules 1997b, Kawano et al. 1992). The presence
of the following stages was evaluated at all sites: cotyledon, one-leaf vegetative, three-leaf “juvenile,” and three-leaf “reproductive” (flowering) stage. After the first census year, an additional stage class, “nonflowering” regressive, was recognized for the regression of plants that flowered at least once during a previous year but did not produce flowers in the current year. Once a plant was recorded as “reproductive,” it was subsequently tallied as a reproductive when it flowered or as nonflowering regressive when it did not. Plants not present at time of census were considered dormant (no above-ground growth), and plants dormant for more than three years were considered dead (unless they reappeared after four years, in which case they were considered dormant for all years between disappearance and reappearance).

Population structure was assessed by tallying the numbers of three-leaf individuals in each 1-m$^2$ quadrat by life-history stage. In addition, X,Y-coordinates to the nearest centimeter of all three-leaf plants and their stage class were recorded. Reproductive plants were marked with flagging and plastic identification stakes labeled with plot, individual identification number, and coordinate information. A census was carried out every year, tracking each plant to determine stage class and any changes in reproductive status (e.g. transitions from juvenile to reproductive, or from reproductive to nonflowering regressive, and vice versa), as well as the
appearance of new plants (in 2002, juvenile plants were not censused at Big Creek and Grant Creek). Transitions to and from dormant states by individuals in all three-leaf stage classes were also followed through time. Cotyledons and one-leaf plants were rare and difficult to find and track through time, therefore an intensive tally of total numbers in each 1-m$^2$ quadrat was taken during the 2004 and 2005 field season. In 2004 each plant was marked with a colored plastic toothpick (cotyledons with one specific color to distinguish from one-leaf plants), and in 2005 these plants were tracked to determine transitions to one-leaf or three-leaf stage classes.

**Plant age and leaf size**

Plant age in *Trillium ovatum* can be determined by counting annual leaf scars (constrictions) left on the rhizome from stem production (Brandt 1916, Hanzawa and Kalisz 1993, Jules and Rathke 1999, Kawano et al. 1992). Random samples of individual rhizomes were aged within macroplots at each site after full leaf expansion and before senescence in 2002 and 2003. Plants were classified as “reproductive” if they were flowering when they were aged, and “juvenile” if they were not. “Nonflowering” regressive plants were initially classified as “juvenile” as these populations had not been studied long enough to know if individual plants had bloomed previous to being aged, but were later classified as “nonflowering” if they bloomed within three years of being aged.
Leaf litter and soil were carefully extracted to expose the uppermost portion of the rhizome for counting without disturbing the rootlets that anchor the rhizome. Plants were reburied immediately after completing counts to promote plant survival (Jules 1998 and e.g. Charron and Gagnon 1991). Most plants older than 30 years have lost segments of their rhizome to decay, so age estimates for older plants are most likely underestimates of total age (Brandt 1916, Jules 1997a and b, Kawano et al. 1992, and personal observations for *T. ovatum* in Montana).

Trillium seeds have a 2-year germination cycle (Jules 1997b, UBC Bot. Garden 1977)—with root formation the first year and leaf formation in the next, therefore two years were added to the scar (ring) count to estimate total age (E. Jules, personal communication).

Leaf size of an individual *Trillium* plant has been shown to be a reliable indicator for determining stages in the life history with respect to reproductive potential (Hanzawa and Kalisz 1993, Kawano et al. 1986, Ohara 1989, Ohara and Kawano 1986). During the first season at each site, leaf length and leaf width of one leaf were measured on every three-leaf plant to provide a general index of leaf size. Plants were classified as “reproductive” if they were flowering when leaf measurements were taken, and “juvenile” if they were not flowering. Because
measurements were taken on every individual plant, the data set was too extensive to analyze subsequent bloom events for individual plants, so plants were left in “reproductive” and “juvenile” categories. Additionally, the data subset of plants that were aged was analyzed for comparison with the larger data set, and to look at average size of “nonflowering” plants in this subset. For this category, as above for plant age, “juvenile” plants that bloomed within three years of being measured were reclassified as “nonflowering.”

**Measures of plant survival condition, and fecundity**

Presence/absence of all three-leaf plants, and their reproductive status, in each 1-m² quadrat was recorded each spring after plants emerged. Factors that potentially affect plant survival and fitness were also noted: herbivory of whole plant or plant parts (leaves, flower buds, seed capsule); plant damage or destruction (due to hail, snow, heavy frost, falling branches/trees, wind, etc.); and other factors such as disease, chlorosis, abnormal growth (e.g. meristic variation and/or structural reversions), or aborted flowers. To assess fecundity, seed capsules were collected from every reproductive plant that had a capsule from the first census year through 2005. As a quick field assessment, seeds were deemed viable if they were fully formed, brown, and had an attached elaiosome. The number of viable seeds were counted and noted for individual reproductive plants.
Plant community and forest structure

An expanded plot habitat analysis was conducted to assess plant community and forest structure at each site in the summer of 2003 (July 1 at Spring Gulch), July 2 at Grant Creek, and Aug 6 at Big Creek earlier analysis was not possible because of a fire burning in the area), after plants achieved full leaf expansion. A standard 11-meter radius circle plot (380 m²) centered in each population was established (Pfister et al. 1977) from which the following data were collected: list of all plant species in the plot and respective cover class (percent ground cover); and percent overstory (mature) and understory (seedling/sapling) canopy cover of each tree species and number of canopy layers. These data were used to determine the “habitat type,” or vegetation classification, to assess the general ecological character of each study site (Pfister et al. 1977). All trees larger than 2 centimeters in diameter at breast height were tallied by species and by 5cm-diameter class within the 380 m² plot. These data were used to calculate basal area, to determine relative dominance of trees (percent basal area by species), and stand density (stems/ha). Heights of representative dominant or co-dominant trees of each species were measured with a clinometer (Daubenmire 1968, Pfister et al. 1977). General topography of plot (slope position, aspect, and slope %), GPS location (latitude and longitude), as well as elevation were also noted using a clinometer, compass, and hand-held GPS unit.
Canopy density was also determined by measuring the proportion of solar radiation intercepted by the overstory canopy. This was done by making instantaneous measurements of photon flux density (PPFD) in each 1-m$^2$ quadrat with a Licor 190-SA quantum sensor. A datalogger with a calibrated sensor was also established in a nearby forest opening, making measurements every second and averaging them for each minute. This sensor was used to determine changes in open sky radiation and to allow calculation of light interception by the canopy. Measurements were made between 10 and 12:00 Mountain Standard Time (which is on the average of 1:42 earlier than solar noon) on overcast days. Three readings at *Trillium* plant height were made per 1-m$^2$ quadrat—one reading in the center of the quadrat and one 50cm to each side of center on the outside edge of the macroplot. Percent light interception was then calculated as the ratio of average forest plot PPFD to that of average open sky radiation.

**Soils**

Soil texture class of the surface horizon below the litter layer and within the top 5-10cm (region of plant rhizome growth) was determined in the field at each site (Brady and Weil 1996, DeLuca and O’Herron 1997). Soil series name, taxonomic class, and parent material was found using the Web Soil Survey of the Natural Resources Conservation Service (United States Department of Agriculture).
Gravimetric determination of mass soil water content was assessed at each site in spring (early June) and summer (late July) of 2003. Soil was collected from the center and outside edges (50 cm from center) of nine 1-m² quadrats (six in Spring Gulch) spaced along and at the ends of the main belt transect at each site. A 10-cm diameter soil probe was used to obtain a soil plug 15-cm down from the surface (in some cases less than 15 centimeters was collected due to rocky soil). Plugs were weighed, then placed in a 60°C drying oven for two days, and weighed upon removal from oven. Mass water content ($\Theta_m$) was calculated by dividing the grams of water removed (grams of wet soil minus grams of dry soil) by grams of dry soil.

**Data Analyses**

A life history flow chart was developed and transition probabilities between each of the three-leaf plant stage classes (juvenile, reproductive, and nonflowering regressive), and the corresponding dormant state for each stage class, were computed for each yearly transition at each site to form a transition matrix (Caswell 2001, Lefkovitch 1965, Maschinski et al. 1997, Menges 1990 and 2000). These probabilities were averaged for each transition at each site and at all sites combined. In 2002 three-leaf juvenile plants were not censused in Big Creek and Grant Creek, and transition probabilities for 2002 represent an assumption these
plants were present and nonreproductive, excluding individuals that transitioned to a reproductive (flowering) stage, which were recorded and marked. Nonflowering regressive plants in the first census year were considered juvenile plants until they flowered in subsequent years, as they could not be distinguished from juvenile plants.

Data analyses to detect significant differences among sites for age, leaf size index, seed, and soil variables were carried out, as well as tests for within-site or within-variable differences. P-P and Q-Q plots were graphed to test for normality of data, as well as post-hoc residuals. No transformations of data were necessary. One-way and two-way ANOVAs were used to test for differences among sites and stage classes, and when differences were significant, post-hoc Tukey multiple comparison tests were carried out to test for significant differences between individual sites or stage classes. It was assumed for these and other statistical tests that test results with $P \leq 0.05$ represent statistically significant differences. Boxplot graphs were used for selected data to show the general pattern of variance in the data among sites, and to determine which comparisons warranted further analysis. In each box plot the median value is represented by a line through the box, the box itself represents 66% of the observations, and the error bars represent 95% of the
observations, with outliers plotted beyond these limits as points. All statistical
tests were performed using SPSS Student Version 11.0 (SPSS Inc. 2001).

To assess population structure, plant density, measured as the number of plants per
square meter in each three-leaf stage class, was determined by averaging annual
census counts from 1-m$^2$ quadrat data from each site for 2003 through 2009. Data
from 2001 and 2002 were not used due to the inability to detect nonflowering
regressive plants in the first years of census, and juvenile plants were not censused
in 2002 at Big Creek and Grant Creek. Percentage of reproductive plants, as
measure of the total number of three-leaf plants present in a given year, was
determined by averaging counts from the first census year through 2009. Density
(plants per m$^2$) of cotyledon and one-leaf plants was calculated by averaging
census data from 2004 and 2005. New reproductive and juvenile three-leaf plants
were summed for each year at each site.

Age distribution was assessed by averaging data from each site to determine if
there were differences in age among reproductive, nonflowering, and juvenile
three-leaf plants. Boxplot graphs were used to show the general pattern of
variance in the data among sites, and a one-way ANOVA was used to detect
significant differences in age among sites for each stage class. A two-way
ANOVA was used to determine if significant differences exist in age among reproductive, nonflowering, and juvenile plants, factoring in the affect of site.

Leaf length and leaf width of one leaf from each plant were multiplied to get an index of leaf size. This leaf size index was averaged within juvenile and reproductive stage classes at each site for the entire censused data set, as well as for juvenile, reproductive, and nonflowering regressive stage classes in the subset that was aged. A one-way ANOVA was used on the aged subset to detect significant differences in leaf size index among sites for each stage class, and a two-way ANOVA was used to determine if significant differences exist in leaf size index among reproductive, nonflowering, and juvenile plants, factoring in the affect of site. Additionally, data on plant age and index of leaf size were combined from all sites to assess the relationship of age and size of plants to stage class status using linear regression.

Reproductive success of each population was assessed in three ways. First, fruit set was calculated as the percentage of flowers in the population each year that produced a mature fruit capsule (this measure does not include capsule herbivory by deer, etc.). Second, seed production was calculated as the mean number of viable seeds per mature fruit (Jules 1997b, Tomimatsu and Ohara 2002). A one-
way ANOVA was performed to test for significant differences in mean number of seeds per fruit among sites. Third, the density of seeds produced at each site was calculated as the mean number of seeds per square meter for each year, and averaged for all years. A one-way ANOVA was used to detect significant differences in seed density among sites. The seed density measure, by default, did not count any seeds lost through capsule herbivory, etc., and thus represents the number of seeds that could potentially become seedlings in each plot.

To determine if larger plants had greater reproductive success, plant size (leaf size index) was regressed on the number of seeds produced per plant using simple linear regression (Knight 2003, Hanzawa and Kalisz 1993). Data on seed production are often quite variable due to many localized environmental factors that may limit production on a given site in a particular year. Data from 2002 were used to analyze the affect of site on seed production, as it was a representative ‘good’ seed production year at all sites.

Basal area for each trees species was calculated as the cross sectional area of trees at breast height (1.2 meters) per hectare. Relative dominance was calculated as the proportion of stand basal area by each species. Total overstory density was
calculated by totaling the number of tree stems greater than 2 centimeters in
diameter that were tallied in each plot.

Site differences for seasonal mass soil water content were assessed by running a 1-way ANOVA. A two-sample paired t-test was used to assess differences in soil moisture between spring and summer. To calculate the effects of rainfall on growing conditions for Trillium the monthly rainfall from the wet season of a given year (fall through spring) was summed.

RESULTS

Demographic measurements

Life history stages and population model

*Trillium ovatum* in western Montana exhibit similar life history stages as has been documented for populations elsewhere. Figure 2 shows the life-history stage class diagram including the two three-leaf nonreproductive stages—one represents three-leaf “juvenile” (vegetative) plants that have not yet reached sexual maturity (bloomed) and the other three-leaf nonreproductive stage, the “nonflowering” regressive stage, represented are older plants that have been reproductive at some point during this study, but regressed to a nonflowering state. Transitions between the reproductive stage and nonflowering regressive stage are common—in any
given year an average of 27% of flowering plants regress to a nonflowering stage and an average of 43% of the nonflowering regressive individuals become reproductive again. The majority of plants remain in the same stage class from year to year, particularly juvenile individuals with 83% on average remaining in the juvenile stage class, compared to 71% of reproductive plants remaining reproductive, and 54% of the nonflowering regressive plants staying in the same stage class on average. Generally, only 5% of the juvenile plants transition to the reproductive stage in any given year, and even more (12%) become dormant (Figure 2 and Table 1). Dormancy in every three-leaf stage class has been observed at all three sites, with most plants returning to aboveground status in the following year or two (Figure 2 and Table 1). Many individual plants exhibit repeated dormancy every other year (or so), and there are some plants that reappear after being in a dormant class for 3-5 consecutive years. As a result, mortality rates were difficult to determine, and could only be assessed for four to five transition years. Compared to other stage classes, the overall highest rate of remaining in a dormant state (32%), and highest incidence of mortality (2%) were observed in the juvenile stage class (Figure 2 and Table 1). Average transition probabilities for cotyledons and one-leaf plants were computed from only 1 transition year, and show very low recruitment into the adult three-leaf juvenile stage class (transition probability 0.4%, Figure 2).
Fig. 2. Life history stages and transition probabilities (averaged for all years and sites) of *Trillium ovatum* in western Montana. ‘*’ cotyledon and one-leaf transition probabilities represent only 1 transition year, ‘**’ average number of seeds produced per flowering plant, ‘?’ transitions that are known to happen with no available data.

Big Creek has the highest consistency in flower production, with an average of 82% of reproductive plants producing flowers the next year (range 66 to 92%) (Table 1a). Grant Creek and Spring Gulch have much lower flowering consistency with averages of 62% (range 34 to 86%) and 68% (range 53 to 88%) overall (Table 1b and c). Interestingly, Big Creek also has the highest incidence of dormancy for both reproductive (2.6%) and nonflowering regressive (5.2%) plants, versus plants in Grant Creek (1.4 and 3.0%, respectively) and Spring Gulch (1.6 and 1.2%),
respectively) (Table 1). The highest rate of mortality of reproductive plants was also measured at the Big Creek site, where 2%, on average, of the individuals that exhibited dormancy for 3 years did not reappear and were considered dead (Table 1a). No mortality has been observed in reproductive plants at Grant Creek and Spring Gulch thus far. The average mortality of juvenile plants was fairly consistent at all sites with 2.5% at Big Creek, 1.3% at Grant Creek, and 1.0% at Spring Gulch (Table 1).

Table 1. Transition probabilities for each study site for each year and an average for all years of study. (*in 2002 juvenile plants were not censused in Big Creek and Grant Creek and are not included in the average). “Dormant(R)” are plants that were in the “reproductive” stage class one transition prior to dormancy. “Dormant(NF)” were in the “nonflowering” regressive stage class, and “Dormant(Juv)” were in the “Juvenile” stage class one transition prior to dormancy.

a. Big Creek (N=293)
### Nonflowering

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<th>Dormant(Juv)</th>
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### Dormant(R)

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### Dormant(Juv)

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b. Grant Ck (N=352)

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<td>Dormant(Juv)</td>
<td>Dormant(Juv)</td>
<td>N/A</td>
<td>N/A</td>
<td>0.326</td>
<td>0.314</td>
<td>0.207</td>
<td>0.267</td>
<td>0.441</td>
<td>0.400</td>
<td>0.326</td>
</tr>
</tbody>
</table>

60
Population structure

The density (plants per m²) of juvenile, reproductive, and nonflowering regressive three-leaf plants varied significantly among all sites for all three stage classes.

Juvenile plants were more abundant than nonflowering regressive and reproductive plants (3-11 plants/m² vs. 1-6 plants/m²) at all three sites (Figure 3). Plant densities of the three stage classes were significantly different at Big Creek and...
Spring Gulch, whereas Grant Creek reproductive and nonflowering regressive stage class densities were significantly lower than the juvenile stage class density.

![Graph showing average density (plants/m²) and standard error (bars) of juvenile, reproductive, and nonflowering regressive three-leaf plants at all sites from 2003 through 2009.]

**Fig. 3.** Average density (plants/m²) and standard error (bars) of juvenile, reproductive, and nonflowering regressive three-leaf plants at all sites from 2003 through 2009.

Reproductive plants on average represent 36% (SE± 3%), 20% (SE± 2%), and 28% (SE± 2.5%) of the population at the Big Creek, Grant Creek, and Spring Gulch macroplots, respectively (Figure 4).
Fig. 4. Proportion (and standard error) of the three-leaf *Trillium* population comprised of reproductive plants at each site.

The 2-year census of one-leaf and cotyledon plants showed that there were far more one-leaf plants than cotyledons in populations at all sites in both the 2004 and 2005 census with average densities of 6.10, 6.88, and 23.05 plants/m² (SE±1.61, 0.33, 1.90, respectively) at the Big Creek, Grant Creek, and Spring Gulch sites, respectively. Cotyledons were quite rare with densities at each site ranging from 0.32, 0.61, to 3.75 plants/m² (SE± 0.17, 0.14, 1.73, respectively) at
the Big Creek, Grant Creek, and Spring Gulch sites, respectively (Table 2). There were significant site differences in densities of both cotyledon and one-leaf plants at Spring Gulch, with approximately 4 times more plants, as compared to Big Creek and Grant Creek. In the two years of cotyledon and one-leaf plant census there was extreme variation in total plant numbers, particularly for cotyledons, at all sites. For example in 2004 there were only 10 cotyledons total at Big Creek and 32 in 2005. Grant Creek and Spring Gulch exhibited similar patterns with 2004 counts being 28 and 81, respectively, and 2005 counts recording 45 and 219 total cotyledons, respectively. More one-leaf plants were also present in 2005 at Big Creek and Spring Gulch, with 501 and 998 plants, respectively in contrast with 2004 counts of 292 and 846 one-leaf plants. This pattern was not repeated for one-leaf plants at Grant Creek, with 433 and 393 total one-leaf plants counted in 2004 and 2005, respectively.

Table 2. Average density (plants per m$^2$) of cotyledon and one-leaf plants for 2004 and 2005 and average (±SE=standard error) for both years. *Density is significantly different (p<0.001).

<table>
<thead>
<tr>
<th>Site</th>
<th>Plants per m$^2$</th>
<th>Cot 2004</th>
<th>Cot 2005</th>
<th>Ave (±SE)</th>
<th>1-Leaf 2004</th>
<th>1-Leaf 2005</th>
<th>Ave (±SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Creek</td>
<td>0.15</td>
<td>0.49</td>
<td>0.32 (0.17)</td>
<td>4.49</td>
<td>7.71</td>
<td>6.10 (1.61)</td>
<td></td>
</tr>
<tr>
<td>Grant Creek</td>
<td>0.47</td>
<td>0.75</td>
<td>0.61 (0.14)</td>
<td>7.22</td>
<td>6.55</td>
<td>6.88 (0.33)</td>
<td></td>
</tr>
<tr>
<td>Spring Gulch</td>
<td>2.03</td>
<td>5.48</td>
<td>3.75 (1.73)*</td>
<td>21.15</td>
<td>24.95</td>
<td>23.05 (1.90)*</td>
<td></td>
</tr>
</tbody>
</table>
Plants that had not been previously recorded in the population were tallied each year and average densities (plants/m$^2$) are shown in Table 3 for each site. These plants ranged in size from very small juveniles to large reproductive plants. New juvenile plants were documented at every site every year, whereas only a few new reproductive plants were found throughout the years. The mortality rate of these plants was difficult to determine during this study due to the prolonged periods of dormancy of this species. In 2009, 8% (10 plants) of the total ‘new’ juvenile plants detected prior to 2006 (after which mortality cannot be determined) were considered dead at Big Creek, 6% (6 plants) at Grant Creek, and 1.5% (2 plants) at Spring Gulch, and no reproductive plants exhibited mortality in this time.

Table 3. ‘New’ reproductive and juvenile plant (‘recruit’) density (plants/m$^2$) for each year and averaged over years at each site.

<table>
<thead>
<tr>
<th>Site</th>
<th>Stage class</th>
<th>2002</th>
<th>2003</th>
<th>2004</th>
<th>2005</th>
<th>2006</th>
<th>2007</th>
<th>2008</th>
<th>2009</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Creek</td>
<td>Reproductive</td>
<td>0.02</td>
<td>0.03</td>
<td>0.00</td>
<td>0.03</td>
<td>0.00</td>
<td>0.02</td>
<td>0.00</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Juvenile</td>
<td>0.05</td>
<td>0.31</td>
<td>0.60</td>
<td>0.85</td>
<td>0.11</td>
<td>0.48</td>
<td>0.28</td>
<td>0.43</td>
<td>0.39</td>
</tr>
<tr>
<td>Grant Creek</td>
<td>Reproductive</td>
<td>0.13</td>
<td>0.00</td>
<td>0.00</td>
<td>0.02</td>
<td>0.02</td>
<td>0.02</td>
<td>0.05</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Juvenile</td>
<td>0.07</td>
<td>0.60</td>
<td>0.63</td>
<td>0.30</td>
<td>0.22</td>
<td>0.38</td>
<td>0.10</td>
<td>0.38</td>
<td>0.34</td>
</tr>
<tr>
<td>Spring Gulch</td>
<td>Reproductive</td>
<td>N/A</td>
<td>0.00</td>
<td>0.03</td>
<td>0.00</td>
<td>0.10</td>
<td>0.00</td>
<td>0.03</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Juvenile</td>
<td>N/A</td>
<td>0.50</td>
<td>1.68</td>
<td>1.10</td>
<td>0.48</td>
<td>1.33</td>
<td>0.93</td>
<td>0.65</td>
<td>0.95</td>
</tr>
</tbody>
</table>

Patterns of “birth” and “death” were difficult to assess in these populations. While it is important to understand all demographic aspects, caution should be exercised when using the seedling stages (cotyledon and one-leaf plants) in models for *T. ovatum* due to large annual variations in cotyledon and 1-leaf plant counts,
cotyledons requiring 2 years before above-ground counts can be accomplished, and difficulty locating these small plants, as well as recognizing them as individuals. Each year “new” 3-leaf plants were found at all of the sites and considered “recruits” to the population—an average of 26, 22, and 39 “new” plants per year at Big Creek, Grant Creek, and Spring Gulch, respectively and the mortality of these “recruit” plants is low—Big Creek and Grant Creek each had about two plants per year die and Spring Gulch had less than one plant die per year. This data is from only four years (three at Spring Gulch), due to the inability to determine the fate of dormant plants for recent years. Dormancy also made it difficult to assess mortality in the general populations that were tracked through time. Big Creek, with the smallest population at 293 plants, lost about 13 plants per year, Grant Creek, with 352 plants, had about five plants die per year, and Spring Gulch, where the population is very dense at 763 plants, had about eight plants die per year. The balance of these plant counts indicate that all populations are growing, Big Creek at a rate of about 11 plants per year (3.8% growth), Grant Creek at 15 plants per year (4.3% growth), and Spring Gulch at 28 plants per year (3.7% growth), and the population growth primarily consists of juvenile three-leaf plants.
**Plant age and leaf size**

Ages of sampled reproductive plants ranged from 18 to 58 years (mean 30.1 years, median 28, n=127), 12 to 38 years for juvenile plants (mean 22.7 years, median 22.5, n=60), and 20 to 53 years for nonflowering regressive plants (mean 30.3, median 28, n=28). The age distribution of juvenile, reproductive, and nonflowering plants at each site is shown in Figure 5. There were significant differences in age between the Big Creek and Spring Gulch sites for reproductive plants (p<0.001, Tukey p<0.001), and no significant differences in age among sites for juvenile and nonflowering plants. Reproductive and nonflowering regressive plants were significantly older than juvenile plants (p<0.001), and there was no significant difference in age between reproductive and nonflowering regressive plants (p=0.996). There was a clumping of all stage classes between 25-35 years of age. Plants were assigned to reproductive or juvenile stage classes based on their status at the time of aging, because it was early in the study and no data was available for whether a plant had previously bloomed. Therefore “juvenile” plants that subsequently bloomed within three years of aging were moved to the “nonflowering” regressive category, and plants that bloomed 4 years after aging (9 total plants) were left in the “juvenile” stage class.
Fig. 5. Age distribution of three-leaf *Trillium* plants at each site derived from rhizome sampling (N=number of plants sampled at each site).

Overall leaf size index was significantly greater for reproductive plants than three-leaf juvenile plants, with Big Creek exhibiting the greatest spread in size (Table 4). There were differences in leaf size index among sites, particularly between Big Creek and Grant Creek, as well as between Big Creek and Spring Gulch, with larger reproductive plants in Big Creek, which also had smaller juvenile plants. There were no significant differences in leaf size index between Grant Creek and Spring Gulch for reproductive or juvenile plants (Table 4).
Table 4. Average leaf size index (leaf length times leaf width of one leaf) for reproductive and juvenile *Trillium* plants at each site (±SE) for the entire data set.

<table>
<thead>
<tr>
<th>Site</th>
<th>Leaf Size Index</th>
<th>Repro (cm²) (±SE)</th>
<th>Juv (cm²) (±SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Creek</td>
<td>106.2 (3.88)</td>
<td>13.4 (1.2)</td>
<td></td>
</tr>
<tr>
<td>Grant Creek</td>
<td>76.0 (2.5)</td>
<td>19.7 (1.1)</td>
<td></td>
</tr>
<tr>
<td>Spring Gulch</td>
<td>72.4 (1.5)</td>
<td>16.5 (0.8)</td>
<td></td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td><strong>84.9 (2.6)</strong></td>
<td><strong>16.5 (1.0)</strong></td>
<td></td>
</tr>
</tbody>
</table>

Average leaf size index for the aged subset of plants is shown in Table 5. There were significant differences in leaf size index among each of the three stage classes (p<0.001). There were no significant differences in leaf size index for juvenile plants and nonflowering regressive plants at all three sites (p=0.98 and 0.50, respectively), but there were significant differences in leaf size index for reproductive plants (p<0.001). Again Big Creek had significantly larger reproductive plants than both Grant Creek and Spring Gulch (Tukey=0.001 and 0.01 respectively) with no significant differences in leaf size index of reproductive plants between Grant Creek and Spring Gulch.

Table 5. Average leaf size index (leaf length times leaf width of one leaf) for reproductive, juvenile, and nonflowering *Trillium* plants in the subset of plants that were aged (N=number of plants in each stage class at each site) (±SE).

<table>
<thead>
<tr>
<th>Site</th>
<th>Leaf Size Index</th>
<th>Repro (cm²) (±SE)</th>
<th>Juv (cm²) (±SE)</th>
<th>Nonflow (cm²) (±SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Creek (N=38,18,9)</td>
<td>104.0 (8.3)</td>
<td>21.3 (4.6)</td>
<td>45.9 (5.7)</td>
<td></td>
</tr>
<tr>
<td>Grant Creek (N=44,21,13)</td>
<td>75.2 (3.4)</td>
<td>20.3 (4.0)</td>
<td>55.1 (5.2)</td>
<td></td>
</tr>
<tr>
<td>Spring Gulch (N=45,21,6)</td>
<td>80.8 (4.5)</td>
<td>21.4 (4.2)</td>
<td>48.7 (8.4)</td>
<td></td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td><strong>86.7 (5.4)</strong></td>
<td><strong>21.0 (4.3)</strong></td>
<td><strong>49.9 (6.4)</strong></td>
<td></td>
</tr>
</tbody>
</table>
**Relationship of leaf size, age, and stage class**

Figure 6 shows that the relationship between age and leaf size index was similar for reproductive and juvenile stage classes. Older plants exhibited larger leaf sizes than younger plants, and reproductive plants were both older and had greater leaf area than juvenile plants (p<0.001). Leaf size index is not dependent on age for nonflowering regressive plants (p=0.31).

![Graph showing relationship between leaf size index and age for juvenile, reproductive, and adult nonflowering regressive plants.](image)

**Fig. 6.** Relationship of index of leaf size (cm\(^2\)) and age for juvenile, reproductive, and nonflowering regressive plants (combined for all sites).
**Measures of plant fecundity**

Seed production was highly variable from year to year and dependent on a small fraction of reproductive plants producing fruit in any given year. Fruit set (percentage of flowers that produced mature fruit) averaged 27% (SE±5.7%) at Big Creek, 42% (SE±8.0%) at Grant Creek and 21% (SE±4.1%) at Spring Gulch (Figure 7).

![Graph showing fruit set percentages for each site](image)

**Fig. 7.** Fruit set (percentage of flowers that produce mature fruit) at each site for each year and averaged for all years.

The number of seeds produced per flowering plant (per capsule) was also highly variable among sites and years. For all years that capsules were collected the average number of seeds per capsule was 20.28 (SE± 2.64), 14.35 (SE± 1.89), and 13.37 (SE± 1.42) seeds at Big Creek, Grant Creek, and Spring Gulch respectively (Table 6). The lowest number of
seeds collected from one capsule was one seed at all sites and the greatest number was 74, 49, and 71 seeds at Big Creek, Grant Creek, and Spring Gulch respectively (Table 6).

There were significant differences in the number of seeds per capsule between the Big Creek and Grant Creek, as well as Big Creek and Spring Gulch sites (p=0.001, Tukey p=0.014 and 0.001, respectively), and no significant difference between Grant Creek and Spring Gulch sites (Tukey p=0.73).

**Table 6.** Mean (±SE) and range in number of viable seeds produced per flowering plant (=per capsule) in each year at each site.

<table>
<thead>
<tr>
<th>Site</th>
<th>2001</th>
<th>2002</th>
<th>2003</th>
<th>2004</th>
<th>2005</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Creek</td>
<td>9.00 (2.58)</td>
<td>30.71 (2.77)</td>
<td>21.00 (2.76)</td>
<td>24.00 (2.60)</td>
<td>16.74 (2.48)</td>
<td>20.28 (2.64)</td>
</tr>
<tr>
<td></td>
<td>(1-26)</td>
<td>(1-73)</td>
<td>(1-60)</td>
<td>(2-74)</td>
<td>(1-55)</td>
<td></td>
</tr>
<tr>
<td>Grant Creek</td>
<td>10.89 (2.22)</td>
<td>16.52 (1.15)</td>
<td>14.42 (1.36)</td>
<td>16.36 (2.69)</td>
<td>13.56 (2.04)</td>
<td>14.35 (1.89)</td>
</tr>
<tr>
<td></td>
<td>(1-41)</td>
<td>(1-39)</td>
<td>(2-44)</td>
<td>(1-49)</td>
<td>(1-46)</td>
<td></td>
</tr>
<tr>
<td>Spring Gulch</td>
<td>N/A</td>
<td>20.84 (1.53)</td>
<td>13.18 (1.34)</td>
<td>9.65 (1.38)</td>
<td>9.81 (1.45)</td>
<td>13.37 (1.42)</td>
</tr>
<tr>
<td></td>
<td>N/A</td>
<td>(2-71)</td>
<td>(1-53)</td>
<td>(1-33)</td>
<td>(1-32)</td>
<td></td>
</tr>
</tbody>
</table>

The average number of viable seeds produced per square meter at Big Creek was 11.24 (SE±2.18), 9.49 (SE±1.65) at Grant Creek, and 20.91 (SE±2.94) at Spring Gulch (Table 7). There were no significant differences in seed density among sites (p=0.09).

**Table 7.** Average number (±SE) of viable seeds per square meter for each year and for all years combined at each site.

<table>
<thead>
<tr>
<th>Site</th>
<th>2001</th>
<th>2002</th>
<th>2003</th>
<th>2004</th>
<th>2005</th>
<th>All Years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Creek</td>
<td>1.66</td>
<td>21.26</td>
<td>8.08</td>
<td>14.40</td>
<td>10.82</td>
<td>11.24</td>
</tr>
<tr>
<td>(SE)</td>
<td>(0.63)</td>
<td>(5.23)</td>
<td>(2.12)</td>
<td>(3.99)</td>
<td>(2.45)</td>
<td>(2.18)</td>
</tr>
<tr>
<td>Grant Creek</td>
<td>3.27</td>
<td>18.45</td>
<td>12.50</td>
<td>6.00</td>
<td>7.23</td>
<td>9.49</td>
</tr>
<tr>
<td>(SE)</td>
<td>(1.04)</td>
<td>(3.35)</td>
<td>(2.63)</td>
<td>(2.15)</td>
<td>(1.96)</td>
<td>(1.65)</td>
</tr>
<tr>
<td>Spring Gulch</td>
<td>N/A</td>
<td>43.05</td>
<td>24.05</td>
<td>8.93</td>
<td>7.60</td>
<td>20.91</td>
</tr>
<tr>
<td>(SE)</td>
<td>N/A</td>
<td>(8.63)</td>
<td>(4.14)</td>
<td>(2.48)</td>
<td>(2.14)</td>
<td>(2.94)</td>
</tr>
</tbody>
</table>
The number of viable seeds produced per plant in 2002 (a high seed production year) was significantly correlated to the size of the plant ($R^2=0.55$, $p<0.001$) (Figure 8).

**Fig. 8.** The relationship of leaf size index regressed on number of viable seeds produced per plant for all sites in a high seed production year (2002).

Figure 9 presents an overall view of seed production at each site showing yearly density (per square meter) averages of total plants, reproductive plants, capsules formed, and viable seeds produced in these populations. Reproductive plants are underrepresented and produce about one capsule and few viable seeds per square meter per year on average in each population.
Fig. 9. The average yearly density (per square meter) of total plants, reproductive plants, capsules formed, and viable seeds produced at each site for 2001 through 2005.

**Plant community and forest structure**

All study areas were located in cool, moist sites, which was reflected in both the structure and composition of the plant species. Characterization of all sites is
shown in Table 8 and Table 9. Big Creek and Grant Creek belong to the *Abies grandis/Clintonia uniflora* habitat types, *Clintonia uniflora* series, and Spring Gulch to the *Picea engelmannii/Clintonia uniflora* habitat type, *Clintonia uniflora* series (Pfister et al. 1977). The total basal area of all overstory tree species was 16.5, 22.4, and 39.4 m²/ha at Big Creek, Grant Creek, and Spring Gulch, respectively (Table 8). *Picea engelmannii* dominated the forest overstory at Big Creek, whereas the other two sites had mixed canopies of *Larix occidentalis, Picea engelmannii,* and *Pseudotsuga menziesii* (Table 9). Tree height of representative dominant or co-dominant trees of each species were similar among sites, ranging from 41.45 at Big Creek to 48.77 at Grant Creek. Big Creek had the most open forest canopy with 27.84% solar radiation transmission, as contrasted with 22.98%, and 20.77% at Grant Creek and Spring Gulch, respectively (Table 8).

**Table 8.** Site characterization at Big Creek, Grant Creek, and Spring Gulch.

<table>
<thead>
<tr>
<th>Site</th>
<th>Big Creek</th>
<th>Grant Creek</th>
<th>Spring Gulch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation (meters)</td>
<td>1172</td>
<td>1312</td>
<td>1171</td>
</tr>
<tr>
<td>Slope (%)</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Habitat type: Series</td>
<td><em>Abies grandis</em></td>
<td><em>Abies grandis</em></td>
<td><em>Picea engelmannii</em></td>
</tr>
<tr>
<td>Habitat type: Habitat type</td>
<td><em>Clintonia uniflora</em></td>
<td><em>Clintonia uniflora</em></td>
<td><em>Clintonia uniflora</em></td>
</tr>
<tr>
<td>Habitat type: Phase</td>
<td><em>Clintonia uniflora</em></td>
<td><em>Clintonia uniflora</em></td>
<td><em>Clintonia uniflora</em></td>
</tr>
<tr>
<td>Tree basal area (BA) (m²/ha)</td>
<td>16.5</td>
<td>22.4</td>
<td>39.4</td>
</tr>
<tr>
<td>Tree height of dominant species (meters)</td>
<td>41.45</td>
<td>48.77</td>
<td>44.20</td>
</tr>
<tr>
<td>Average % light</td>
<td>27.84%</td>
<td>22.98%</td>
<td>20.77%</td>
</tr>
</tbody>
</table>
Table 9. Percent basal area occupied by major tree species and percent cover of major understory species at all sites. Understory cover classes are: T=<1%; 1=1-5%; 2=5-25%; 3=25-50%; 4=50-75%; 5=75-95%; and 6=>95% ground cover.

<table>
<thead>
<tr>
<th>Site</th>
<th>Big Creek</th>
<th>Grant Creek</th>
<th>Spring Gulch</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>% BA occupied by major tree species</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abies grandis</td>
<td>18%</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>Larix occidentalis</td>
<td>0%</td>
<td>35%</td>
<td>34%</td>
</tr>
<tr>
<td>Picea engelmannii</td>
<td>82%</td>
<td>17%</td>
<td>23%</td>
</tr>
<tr>
<td>Pseudotsuga menziesii</td>
<td>0%</td>
<td>33%</td>
<td>24%</td>
</tr>
<tr>
<td><strong>Understory Species</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acer glabrum</td>
<td>4</td>
<td>N/A</td>
<td>3</td>
</tr>
<tr>
<td>Amelanchier alnifolia</td>
<td>N/A</td>
<td>2</td>
<td>T</td>
</tr>
<tr>
<td>Arnica cordifolia</td>
<td>1</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Calamagrostis rubescens</td>
<td>N/A</td>
<td>N/A</td>
<td>2</td>
</tr>
<tr>
<td>Clintonia uniflora</td>
<td>2</td>
<td>2</td>
<td>T</td>
</tr>
<tr>
<td>Coptis occidentalis</td>
<td>2</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>Cornus sericea</td>
<td>2</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>Crataegus douglasii</td>
<td>N/A</td>
<td>N/A</td>
<td>2</td>
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<tr>
<td>Viola glabella</td>
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</table>

Soils

Soil at Grant Creek and Spring Gulch is Totelake gravelly loam, in the sandy-skeletal, mixed, frigid Udic Ustochrepts taxonomic class (Web Soil Survey of the Natural Resources Conservation Service, USDA website). The parent material at these sites is sandy and gravelly alluvium. Big Creek soil is Roman family, extreme boulder, in the sandy-skeletal, mixed, Andic Dystrocryepts taxonomic
class (Web Soil Survey of the Natural Resources Conservation Service, USDA website). The parent material of this soil is volcanic ash over till derived from granite and gneiss.

Soil water content was similar among sites. Average mass soil water content ($\Theta_m$) in the spring was 0.34 (SE± 0.02) at Big Creek, 0.37 (SE± 0.02) at Grant Creek, and 0.29 (SE± 0.02) at Spring Gulch (Figure 10), with only Grant Creek and Spring Gulch exhibiting significant differences (p=0.02, Tukey p=0.01) between sites. For summer soil samples the $\Theta_m$ was 0.19, 0.17, and 0.15 at Big Creek, Grant Creek, and Spring Gulch, respectively (SE± 0.01 at all sites), with no significant differences among sites (p=0.22). Not surprisingly, average mass soil water content is significantly different between spring and summer (p<0.001), with spring soils containing about twice as much water (Figure 10).
**Fig. 10.** Mass water content ($(\Theta_m)$=kilograms of water removed per kilogram of dry soil for spring and summer of 2003 at all sites.

**Climatic trends**

There was significant year-to-year variation in precipitation and temperature during the time frame of this study (Fig. 11). Little variation in demography measures (e.g. floral density, fruit production, or plant density, Fig. 12) could be precisely explained with simple linear regression models.
**Fig. 11.** Climatic trends for 2001 through 2008 at the Missoula County airport (1=the eight-year mean).
**Fig. 12.** A comparison of the number of reproductive plants (per square meter) at each site for each year with the nine-year mean density (1=the nine-year mean).

**DISCUSSION**

This demographic study of *Trillium ovatum* in Western Montana demonstrates the value of having multiple years of monitoring at multiple sites for this long-lived species. Significant year-to-year variation is exhibited for many of the demographic measures used in this study that would not have been accurately estimated in a short-term study. While juvenile plants dominate populations and maintain fairly constant transition probabilities at all sites, reproductive plants represent the lowest proportion of plants and, in some populations, exhibit frequent
transitions to a nonflowering regressive state (Table 1 and Fig. 3 and 4).

Inconsistent flower production, coupled with an average range of 21 to 42% of the flowers producing fruit (fruit set), creates dramatic variations in actual seed production each year, and overall low seed counts when considering the total plant population size (Table 7 and Fig. 7 and 9). This variation in seed production and low seed count is reflected in the extreme variation in counts of cotyledons and one-leaf plants in the 2 years they were censused, as well as low recruitment of juvenile 3-leaf plants into all three populations over the entire study (less than 1 plant per square meter per year) (Tables 2 and 3). Thus far, only populations in Big Creek have exhibited mortality of the reproductive stage class, and it is very low on average (1.7%). Mortality of juveniles is low (1.6% average), but occurs consistently each year (Table 1 and Fig. 2). It is highly possible that this is an underestimate of mortality, as juvenile plants are not labeled, and as such, certainty of censusing the yearly reappearance of the exact same individual is diminished, especially with smaller plants that are more cryptic and difficult to distinguish.

This life-history profile is similar to other herbaceous forest perennials that depend on survival, slow individual growth, and low mortality of mature plants, rather than fecundity and recruitment, to maintain stable population sizes (Bierzychudek 1982, Charron and Gagnon 1991, Fiedler 1987, Fredricks 1992, Kawano 1985,
Silvertown 1993). Kawano (1985) describes this pattern of survivorship for *Erythronium japonicum* as “characteristic of those woodland perennials which occupy environments with high environmental predictability” and lists *Trillium* as a similar species. Both Kawano (1985) and Charron and Gagnon (1991) (for *Panax quinquefolium*) ascribe the equilibrium state of populations in “stable” forest habitats to high seedling and juvenile mortality and a long pre-reproductive period (for a “critical” size or biomass for reproduction to be reached), and longevity of established plants. High mortality in juvenile stages for *Trillium* and other temperate forest perennials can be caused by fungal attack, competition, animal or invertebrate predation, heat, desiccation, or damage by direct solar radiation before canopy closure (Kawano 1985, Kawano et al. 1986).

The cotyledon and one-leaf vegetative plants in this study were only censused for two years, and there was enormous variation between years in the total plant numbers at all sites. These plants are very small and difficult to find and identify in many cases, as well as being very delicate, therefore I feel that counts are potentially underestimates of the total number of cotyledons and one-leaf vegetative plants present, but perhaps not an underestimate of their role in the population. Ohara and Kawano (2006) found that the number of plants in the juvenile stage classes of *Trillium tschonoskii* fluctuates drastically due to
competition, environmental constraints, and high mortality, as found in other *Trillium* species. The 1-year average transition probabilities (for all sites combined) from cotyledon to one-leaf stage (0.53) and one-leaf remaining in one leaf stage (0.61) are much higher than would be expected when compared to other studies and also contrast with the low number of “new” three-leaf plants recruited into the population each year, indicating that this might have been an exceptional year for seedlings. It is important to note the transition probability from one-leaf stage to three-leaf juvenile plants is only 0.004, indicating very low recruitment into the three-leaf stage. Long-term data for these stage classes is needed to account for year-to-year variability and make more accurate estimates of survival and mortality of these young plants.

Interestingly, one-leaf vegetative plants at these Montana sites were all approximately the same size and very small (averaging 2.2cm long and 1.5cm wide), in sharp contrast to other studies of *T. ovatum* (and *Trillium* species in general) that define the one-leaf stage as having a range of size classes (Kawano et al. 1986, Kawano et al. 1992, Ohara and Kawano 2005, Ohara and Kawano 2006, Ohara et al. 2006). For example, Kawano et al. (1986) defined five to seven one-leaf vegetative plant size classes with the leaf area of individuals ranging from 0 to 2.51cm$^2$ for the first class, 2.52 to 3.98 cm$^2$ for the second class, etc. on up to about
25 cm². This size variation may be a reflection of environmental differences between coastal populations and populations at the distributional limit. It was also noted that marked one-leaf plants, after transitioning to a small three-leaf juvenile stage, would occasionally revert to a one-leaf stage (personal observation for *T. ovatum* in Montana), a transition that was also noted for *T. camschatcense* in Japan (Ohara and Kawano 2005).

“New” three-leaf plants were recorded during each yearly survey, ranging from very small three-leaf juveniles to very large, presumably older, three-leaf juveniles, as well as a few reproductive plants that had never been documented. It is possible that the larger plants were dormant, or had not been found during the previous census due to the cryptic nature of this species, so this data may not be an accurate reflection of actual recruitment. Heidel and Shelly (2001) discuss recruitment as a better measure of population performance than fecundity measures when it is calculated as the sum of all new, established plants. They map and tally seedlings, but do not count them until they are established, which is similar, but perhaps more exact, to methods used in Elzinga (1998), where the percentage of plants transitioning to next stage class is the number of “new” plants divided by the total number of seedlings counted the year (or transition phase) before. While this study did not encompass this amount of detail, it is reasonable to assume that many of
the “new” three-leaf plants censused have persisted long enough to be considered recruits. The overall mortality rates of these “new” plants can only be determined for a few years of this study, and averaged 5.2% for juvenile “recruits” averaged for all sites, with no incidence mortality in the reproductive stage class “recruits,” indicating overall low mortality of ‘recruits.’ There were far more juvenile plants “recruited” into the population, than died in the general population, and occasionally reproductive plants were recruited, but in very low numbers, and in the case of Big Creek, not enough to replace reproductive plants considered dead.

Mortality in adult stages is difficult to determine as some plants have reappeared after three to five years of dormancy (in both adult and juvenile stages). It is possible that, in some cases, plants were eaten by deer (or another herbivore) before census or some other below ground factor prevented emergence, but the fact remains that these particular plants were not able to gain valuable resources from photosynthesis in the years they did not display above-ground structures, nor reproduce. Dormancy in these populations involves a low proportion of individuals that generally return to normal growth in the following year or two, and does not appear to be synchronous. Prolonged dormancy begs research into potential rhizomatous symbiotic relationships in *Trillium ovatum* that would allow long-term, subterranean survival. Extensive vesicular-arbuscular mycorrhizal
(VAM) relationships have been found in the rhizomes of *T. flexipes*, *T. erectum*, and *T. grandiflorum* (Brundrett and Kendrick 1988, DeMars and Boerner 1995), and DeMars and Boerner (1995) noted that the coarse, magnolioid rhizomes found in *T. flexipes* are characteristic of root types that are generally highly dependent upon endomycorrhizal symbionts.

*Trillium ovatum* rhizomes in this study were also coarse and gnarled, and many exhibited a scorioid shape. Annual leaf scars were tightly compacted to the point of overlapping in many plants. Older rhizomes had very large diameters and lengths, as compared to younger ones, and the older part of the tip was generally missing (broken off or rotted away), which made aging these plants difficult. Because juvenile plants with the smallest leaves were around 20 years old (and their rhizomes were also very small), it is possible that the larger rhizomes, with ends broken off, were anywhere from 20 to 50 (or more) years older than the actual number of counted rings. The clumping of reproductive, juvenile, and nonflowering regressive plants between 25-35 years of age—which is the age range that many of these rhizomes have a broken-off tip, indicates that ages of plants should be considered a minimum age (Fig. 5 and 6). The representation of juvenile plants in this clumping of age may be remnant of not aging enough really small juvenile plants. The additional necessity of modifying stage class
designation for plants that were in a nonflowering regressive stage when they were aged adds to the general lack of clarity about aging these plants, but it is interesting to note that the size (leaf area index) stays fairly consistent across all ages in this stage class, possibly suggesting a threshold of size for reproduction. Trillium in western Montana require at least 18 years to sexually reproduce, suggesting a slow reproductive rate of these plants and particular sensitivity of Montana populations as compared to Oregon, California, and British Columbia where plants are known to become reproductive at 10-15 years of age (Brandt 1916, Jules 1997a and b, University of British Columbia Botanical Garden 1977).

While aging plants is interesting for relative human time frames, a far more important factor in population dynamics of many herbaceous perennials is the size of a plant, or its perennating organ (Bierzychudek 1982, Bierzychudek 1984, Davis 1981, Fiedler 1987, Harper 1977, Rabotnov 1969). Hanzawa and Kalisz (1993), while studying *Trillium grandiflorum*, a close relative of *Trillium ovatum*, found that reproductive plants were significantly older (mean=22.8 years) than juvenile plants (mean=13.3 years), and that reproductive plants also had significantly larger rhizome volumes and total leaf areas. Reproduction in the population they studied occurred once plants reached a threshold of rhizome volume or leaf area. They found that the two measures of plant size--total leaf area and rhizome volume,
were better predictors of plant reproductive status than was the plant age. Four species of *Trillium* (*T. grandiflorum, T. erectum, T. undulatum,* and *T. sessile*) examined by Kawano et al. (1986) showed that the number of propagules produced per plant was dependent on individual biomass. In this study of *T. ovatum* in Montana, the average leaf size index was significantly greater for reproductive plants than three-leaf juvenile plants at each of the three sites (p<0.001)--the overall average size of reproductive plants was 84.9 cm$^2$ (±18.6) and 16.5 cm$^2$ (±3.1) for juvenile plants (Table 4). The number of viable seeds produced per plant in 2002 is strongly positively correlated to plant size ($R^2$=0.55, p<0.001) (Figure 8). Modified data collection for plants transitioning from juvenile to reproductive stages will likely unveil threshold size for reproduction for plants at these sites.

Random events can have a large impact on the reproductive effort of *Trillium*—these events vary in timing, causal agent, and magnitude among and within plots. *Trillium* in Montana are often the first plants to emerge once the snowpack melts, which increases the risk of predation and exposure to extreme weather conditions, and, simultaneously, there are fewer potential pollinators available. Deer or invertebrate herbivory and late snowfall and/or hailstorms play major roles in damage to flowering plants in Montana. Once the plant makes it to the blooming
phase, it still needs to be pollinated and set fruit. Plants that experience disease, aborting flowers, and early senescence (due to unknown environmental and/or biotic factors) will not form capsules or not produce viable seed. Of the capsules that do form there is also a suite of factors that can disturb seed release or dispersal, such as disease, elaiosome robbers, and seed herbivory by mice (which kills the seed) (Jules and Rathcke 1999, Tallmon et al. 2003). Herbivory by deer plays a large role in the reproductive cycle of *Trillium* in western Montana—which is harmful to short-term and long-term reproductive effort when the flower, along with the rest of the plant, is snipped in the spring, but when the seed capsules are eaten, deer can act as important long-distance dispersers of seeds.

recedes, and are often the first aboveground plants where they grow—reproductive plants are first, then large plants, and the smallest plants are last. Deer appear to prefer reproductive plants, although will often eat other large plants in their line of travel, creating a random pattern of herbivory (personal observation). Spring Gulch had the highest rates of flower herbivory, with 34.7% average herbivory of blooming plants for the 2002 through 2005 seasons (unpublished data), which may explain the lower percent fruit set (average 21%) at that site (Fig. 6). When capsule herbivory (4.1%) is added to account for total herbivory by deer of reproductive plants, Spring Gulch also had the highest total rate of herbivory—38.8% of all blooming plants were eaten—but the large population size must have buffered the total number of seeds produced at this site, as there was no significant difference in seed density among sites (Table 7). Big Creek had lower average flower herbivory for the 2001 through 2005 seasons (11.7%), but much higher capsule herbivory (22.4%), for a total of 34.1% herbivory on all reproductive plants (unpublished data). Grant Creek experiences very little herbivory—only 5.3%, on average, of the flowering plants were eaten by deer during the 2001 through 2005 season, potentially accounting for the highest percent fruit set (average 42%) of all sites (Fig. 6). Capsule herbivory at this site is also low (3.4% average), adding to an average 8.7% of the total reproductive plant population being consumed by deer in a given year (unpublished data). While deer population
density is likely lower in Montana than eastern North America, it will be interesting to analyze the effects of deer herbivory on *T. ovatum* population dynamics in these sites.

Sites in this study experienced significant year-to-year variation in precipitation and temperature during the time frame of this study (Fig. 10), but little variation in demographic measures could be explained with simple linear regression models. Many studies confirm formation of reproductive structures and seeds are correlated with precipitation during certain seasons (e.g. Fredricks 1992). Because *T. ovatum* stem and floral buds for the next season are laid down during active growth season from February to late July (Brandt 1916), it is likely that more years of study will bring greater clarity to these relationships.

The forests of western Montana experience disturbance in many forms—beetle kills, logging, fire, and roadbuilding, in addition to the looming threat of climate change. Studies of long-lived species have shown shifts (or eliminations) in distributional range due to climatic disturbance (Hutchings 1987, Crimmins et al. 2011), and a species living at the edge of its distributional range likely has a greater extinction risk. Fire has become more frequent and more intense (Westerling et al. 2006), and is likely to become a major part of forest dynamics,
even in mesic forests where *Trillium* grow. Peter Stickney (USFS, Intermountain Research Station, Fire Sciences Laboratory, Missoula, MT, pers. comm.) has documented *T. ovatum* growing up out of the ashes of recent fires, but it is likely that more intense fires would kill the rhizome along with the duff layer. Survival of the rhizome in this species is essential to population stability, as it is for many long-lived species that exhibit low or sporadic fecundity and recruitment. Fires open the overstory canopy and create forest fragments, which can lead to shifts in herbivore interactions (e.g. mice eating seeds) and changes in microsite conditions (e.g. decreased soil moisture), ultimately causing lower seedling recruitment and establishment and stress to surviving adult plants.

Climate change models predict early loss of snowpack (e.g. Westerling et al. 2006), which can affect the phenology of many plant species. Reproductive *T. ovatum* plants in Montana emerge immediately as the snow melts (personal observation), indicating that the snow plays a large role in the phenology of this species. Shifts in the timing and amounts of snow melt can profoundly alter microsite conditions (soil temperature, soil moisture, etc.), and will likely create stress to plants that are adapted to snowpack. Comparative studies of *T. ovatum* populations in Montana and the Pacific Northwest, where plants are adapted to a
winter rain climate, would be interesting to undertake as changes in climate play out over time.

Stability of understory herb populations is determined by environmental as well as demographic parameters, and long-lived species are particularly sensitive to disturbance due to slow rates of growth, recruitment, and regeneration. While the three undisturbed populations of *T. ovatum* studied in Montana seem stable (~4% population growth rate at each site), the low recruitment rate, slow growth rate, and specialized habitat niche, in the relatively rare and fragmented riparian and seep habitats of montane forests, would suggest limited ability to adapt to new stresses. Additionally, *Trillium* in Montana take longer (18 years) to reach sexual maturity than plants in moist coastal habitats (10-15 years). Continued monitoring will be valuable in assessing population responses to predicted changes in the environment, such as climate change—with associated changes in fire regime, snowpack, temperature, etc.—and possible changes in forest land use, such as medicinal harvesting, development, or logging. There are many special challenges to conserving populations at their range limit, as access for valuable resources (water, soil nutrients) can be limited and disturbance regimes that vary in type, size, intensity, duration, frequency and pattern can have detrimental outcomes. Further work is needed to identify the most fragile populations to monitor, and to
determine the ecological thresholds beyond which local populations may not be able to persist. Documenting the demographic structure and population dynamics of *Trillium ovatum* in Western Montana will provide critical information for conservation planning and sustainable use of this species.

**Literature cited**


