AoB PLANTS http://aobplants.oxfordjournals.org/

Open access – Research article

Long-term population demography of *Trillium recurvatum* on loess bluffs in western Tennessee, USA

James E. Moore[1,2*], Scott B. Franklin[2,3], Gary Wein[2,4] and Beverly S. Collins[2,5]

[1] Department of Biology, Christian Brothers University, Memphis, TN 38104, USA
[2] Edward J. Meeman Biological Field Station, The University of Memphis, Millington, TN 38058, USA
[3] School of Biological Sciences, The University of Northern Colorado, Greeley, CO 80639, USA
[4] Highlands-Cashiers Land Trust, Highlands, NC 28723, USA
[5] Department of Biology, Western Carolina University, Cullowhee, NC 28723, USA

Received: 8 February 2012; **Returned for revision:** 26 March 2012; **Accepted:** 14 April 2012; **Published:** 18 April 2012

Citation details: Moore JE, Franklin SB, Wein G, Collins BS. 2012. Long-term population demography of *Trillium recurvatum* on loess bluffs in western Tennessee, USA. *AoB PLANTS* **2012**: pls015; doi:10.1093/aobpla/pls015

Abstract

Background and aims Understanding the demography of long-lived clonal herbs, with their extreme modularity, requires knowledge of both their short- and long-term survival and ramet growth patterns. The primary objective of this study was to understand the dynamics of a clonal forest herb, *Trillium recurvatum*, by examining temporal and small-scale demographic patterns. We hypothesized: (i) there would be more variability in the juvenile age class compared with non-flowering adult and flowering adult classes due to year-to-year fluctuations in recruitment; (ii) rates of population growth (λ) and increase (r) would be highest in non-flowering ramets due to a combination of transitions from the juvenile stage and reversions from flowering adults; and (iii) inter-ramet distances would be most variable between flowering and juvenile ramets due to a combination of clonal growth, seed dispersal by ants and ramet death over time.

Methodology Census data were collected on the total number of stems in the population from 1990 to 2007, and placed within one of three life stages (juvenile, three-leaf non-flowering and three-leaf flowering). Modified population viability equations were used to assess temporal population viability, and spatial structure was assessed using block krigging. Correlations were performed using current and prior season weather to current population demography.

Principal results The first hypothesis was rejected. The second hypothesis was supported: population increase (r) and growth rate (λ) were highest in non-flowering ramets. Finally, the third hypothesis was rejected: there was no apparent density dependence within this population of *Trillium* and no apparent spatial structure among life stages.

Conclusions Overall population density fluctuated over time, possibly due to storms that move soil, and prior year's temperature and precipitation. However, density remained at some dynamic stable level. The juvenile age class had greater variability for the duration of this study and population growth rate was greatest for non-flowering ramets.

Introduction

Clonal plants make up ~40 % of our planet's flora (Tiffney and Niklas 1985) and dominate many harsh environments (Billings and Mooney 1968). Their extreme modularity allows these plants to forage more broadly, integrate larger plant bodies and forgo sexual

* Corresponding author's e-mail address: jmoore25@cbu.edu

reproduction. Understanding the demography of long-lived clonal herbs requires knowledge of both their short- and long-term survival and ramet growth responses. Over the short term, population size and age structure can vary due to year-to-year differences in numbers of flowering plants and ramet growth rates. Over the long term, population growth rates may be density dependent (Tomimatsu and Ohara 2010), vary spatially in response to factors such as forest fragmentation (Jules 1998) or vary greatly in response to abiotic factors, e.g. precipitation (Klimešová and Klimeš 2008).

Among clonal forest understorey herbs, such as *Trillium* species, demography and population demographic structure reflect the pools and rates of transition from young (juvenile) through adult non-flowering to flowering life history stages. These life history transitions can be affected by biotic factors such as deer herbivory, which can decrease relative leaf area and the transition from non-flowering to flowering plants, cause ramets to regress in stage and have lower fecundity, and increase the probability of non-emergence (i.e. decrease new ramet production) (Knight 2004; Leege *et al.* 2010). Distance to edge, fragmentation or disturbance can also affect recruitment and demography of *Trillium* species, and there is some evidence for density-dependent growth rates (Tomimatsu and Ohara 2010). For example, *Trillium ovatum* plants within 65 m of the edge in small remnants of uncut forest showed lower recruitment than plants in interior populations (Jules 1998). However, non-clonal *Trillium camschatcense* across a range of forest fragment sizes showed wide variation in fecundity; population growth rates (λ) were affected both by density and year-to-year climate variation (Ohara 1989; Ohara *et al.* 2006).

Variation in transitions between life history stages, seed production, recruitment and clonal growth creates wide variation in short- and long-term population age structure among clonal forest understorey herb species. In a short-term (2-year) study of *Trillium maculatum* population demographic and spatial genetic structure, Walker *et al.* (2009) found that the number of seedlings and the proportion of one-leaf (juvenile) plants differed between years, but the proportions of three-leaf non-flowering and flowering plants remained the same. Over the longer term, marked individuals of *Trillium apetalon* (a non-clonal species) were followed over 12 years. At steady state, frequencies of three-leaved and flowering plants were low, but consistent flowering over years yielded relatively high frequencies of seedlings (Ohara *et al.* 2001). As a result of this variation, both short- and long-term studies of marked individuals may be needed to elucidate the effects of clonal growth on *Trillium* demography and demographic structure.

The objectives of our research were to monitor a population of a clonal *Trillium* species (*T. recurvatum* Beck) over time and examine temporal population dynamics. We hypothesized that the number of ramets in each age class would differ significantly from year to year (probably the result of no seedling recruitment). We examined dynamics of each age class (juveniles, non-flowering adults and flowering adults) separately. We hypothesized that this population would have greater variability in the juvenile age class due to year-to-year fluctuations in recruitment, and the rate of population increase (r) and population growth rates would be highest in non-flowering ramets due to a combination of transitions from the juvenile stage and reversions from flowering adults. We also examined the potential effects of prior- and current-season temperature and precipitation on ramet production and demographic transitions. Finally, we expected the spatial co-pattern to be greater for flowering vs. non-flowering and non-flowering vs. juvenile age classes, when compared with flowering vs. juvenile ramets due to seed dispersal (away from the parent) by ants.

Materials and methods

Trillium recurvatum Beck is a clonal perennial understorey herb that reaches the northern limits of its range in southern Michigan and Wisconsin; it ranges west to eastern Iowa and Missouri, east to Pennsylvania, and south through the heart of its range in Indiana and Illinois, extending into northern Louisiana and Alabama (O'Connor 2007). In Tennessee, *T. recurvatum* occurs from the Cumberland Plateau region westward. Plants emerge in late January and February, flower in April–June and senesce in late July–September (Strausbaugh and Core 1978). When reproduction from seed occurs, *T. recurvatum* has double dormancy; ants collect the seeds and feed upon the elaiosomes, discarding the seeds in tunnels until germination occurs (Case and Case 1997). Breeding system studies suggest that *T. recurvatum* is strongly outcrossing (Sawyer 2010). It is considered rare in Alabama, Iowa, Louisiana, North Carolina, Ohio, Texas and Wisconsin (NatureServe 2006).

This research is part of an ongoing, long-term analysis of *T. recurvatum* population demographics at Meeman Biological Field Station (MBFS), which is owned and operated by the University of Memphis, Memphis, TN, USA. Meeman Biological Field Station is a 252-ha site ~40 km north of Memphis, TN, and 3 km east of the Mississippi River on a Chickasaw Bluff. Meeman Biological Field Station is found in the narrow transition zone

between the Mississippi River Valley and West Tennessee Coastal Plain ecotypes (Fenneman 1938), and is composed of loess soil. These soils, specifically Memphis silt loams, are fine-silty, mixed, Typic Hapludalfs (Alfisols), which have high erodability on slopes in this region (McCarthy 1990). The yearly average temperature is 16 °C. July is the warmest month, averaging 26.6 °C, and January is the coldest month, averaging 4 °C (Fig. 1A). Average yearly precipitation is 132 cm with a majority of precipitation occurring during the winter and spring months (Fig. 1A). Average growing season at this site is 230 days. The overstorey of this site is primarily mature oaks and hickories. The early spring ground layer is rather sparse, with *Podophyllum peltatum* L. found upslope in relation to the study plots.

Vegetation sampling

In 1990, a five-by-five array of (2 m × 2 m) plots was established along a west-facing slope under an overstorey forest. Within each plot, *T. recurvatum* plants were counted and their demographic stage was recorded as flowering, non-flowering (three-leaf) or juvenile (one-leaf). The cotyledon stage recognized by some researchers (Kahmen and Jules 2005; Webster and Jenkins 2008) was grouped with the one-leaf stage in this study.

In 2004 and 2007, several ramets from each life stage were examined for relative age and reproductive mode (seed vs. rhizome). These ramets were a part of the population but outside of the plot array. Each ramet was extracted to determine whether the ramet originated that year from a seed or rhizome and the constriction rings on each rhizome were counted to approximate age (Hanzawa and Kalisz 1993; Kahmen and Jules 2005). Although older rhizomes are known to lose older portions (due to rot), we did not attempt to add years in this study. Thus, our data represent minimum plant ages.

Data analysis

Abundance data were analysed using parametric paired *t*-tests to compare flowering to non-flowering, flowering to juvenile, and non-flowering to juvenile cohorts for each year separately. As a measure of cohort variability among years (i.e. temporal variability), we used coefficients of variation following Sokal and Rohlf (1981), which incorporate corrections for small sample sizes. To address how climatic variables influenced ramet production and demographic transitions, we ran Pearson correlation analyses on demographic data with prior and current year's growing season (March–June) precipitation and temperature, respectively. All analyses were conducted in SAS v9 (SAS Institute, Cary, NC, USA).

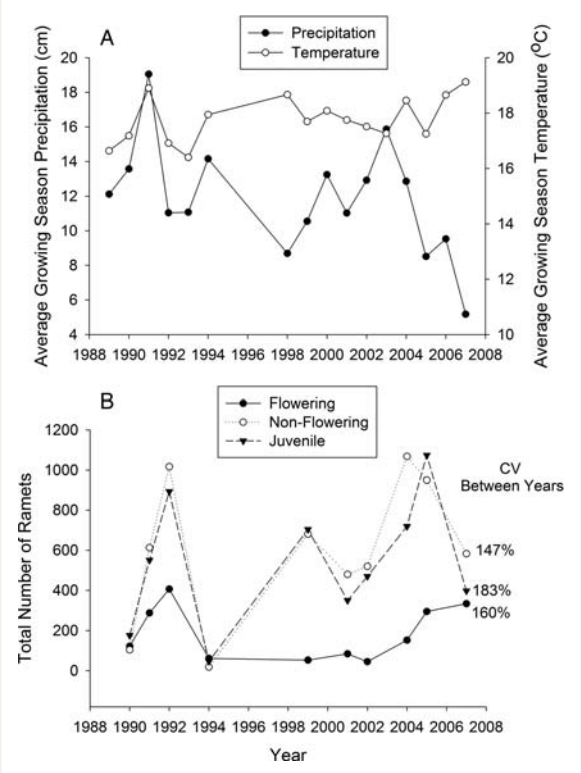

Fig. 1 (A) Average growing season precipitation (cm) and temperature (°C) for MBFS for the study period. (B) Patterns of demography of *T. recurvatum* over a 10-year period for flowering (closed circles), non-flowering (open circles) and juvenile (closed triangles) individuals. Total numbers of individuals in each age class were summed over all 25 plots for the collection period. Coefficients of variation (CV) for each plot over the 10 years of the study are listed down the right-hand side of the panel and refer to the temporal variability of each age class.

We assessed population viability (PVA) using count data according to Morris *et al.* (1999). Methods described within Morris *et al.* (1999) did not address clonal plants, where researchers find it difficult (unless destructive sampling is used) to determine whether a particular ramet is an individual or a part of the clone. We followed the minimum recommendations of Morris *et al.* (1999) by having at least 10 censuses for population viability assessments. We used simple parameter estimates of μ and σ^2 to determine whether the population distribution changed among age classes from year to year. This method, which follows Dennis *et al.* (1991), involves two steps: (i) calculating simple transformations of the counts and years in which the counts were taken; and (ii) performing linear regression, setting the regression intercept to zero and obtaining estimates of μ and σ^2

(Morris *et al.* 1999). Once estimates of μ and σ^2 were obtained, we then described trajectories of each age class across the study duration. The parameter μ determines how quickly the mean population increases. The second parameter, σ^2, determines how quickly the variance of the normal distribution increases. If $\mu < 0$ extinction is certain, but if $\mu > 0$ the population is expected to grow, although some unforeseen factor (e.g. windfall, herbivory, etc.) may cause σ^2 to increase (Morris *et al.* 1999). These estimates were calculated in Microsoft Excel following Morris *et al.* (1999).

To address how demographic patterns fluctuated spatially, we used block krigging with flowering individuals as the *z* variable and non-flowering ramets as the covariate to compare how related cohorts were in space. *X* and *Y* variables were obtained from the spatial arrangement of plots within the array. This analysis was conducted for each possible cohort combination (flowering × non-flowering; flowering × juvenile; non-flowering × juvenile) ($N = 3$) across all years except 2002, for which we had only total numbers for each age group ($N = 9$) rather than the plot-level data. The best-fit model was used to interpret the model selection: the model that explained the greatest spatial variation was used (i.e. spherical, Gaussian, exponential and linear).

Results

Paired *t*-tests showed that the mean number of flowering vs. non-flowering ramets varied greatly and significantly from year to year for eight of the nine years (Table 1). The number of flowering ramets differed from juveniles for five of the nine years, and the number of non-flowering to juvenile ramets differed for four of the nine years (Table 1). Raw abundance counts indicate similar demographic patterns for non-flowering and juvenile ramets: flowering ramets were less abundant than juveniles or non-flowering ramets each year except 1990 and 1994 (Fig. 1B). The proportion of flowering ramets in this population was also lower than that of juveniles or non-flowering plants each year except 1994, when the proportion of non-flowering ramets was low (Fig. 2). On average, non-flowering ramets dominated population proportions throughout this study (Fig. 2). Correlation analyses indicated that non-flowering and juvenile age classes were significantly positively correlated with prior year's growing season temperature (non-flowering $P = 0.042$, $r = 0.648$; juvenile $P = 0.032$, $r = 0.674$; flowering $P = 0.169$, $r = 0.472$) and all age classes were non-significantly positively correlated with prior year's growing season precipitation. Unlike prior year's growing season, the current year's growing season precipitation showed negative non-significant correlations for all age classes, and temperature showed a non-significant positive correlation for flowering individuals (flowering $P = 0.730$, $r = 0.127$). Non-flowering and juvenile individuals were non-significantly negatively correlated with current-season temperature.

Observations of rhizome rings in 2004 revealed four juveniles (24 %) and one non-flowering three-leaved individual (7 %) appeared to establish from seed, while all flowering ramets established from rhizomes (Table 2). None of the 63 ramets examined in 2007 established from seed: all were from rhizomes. The age of juveniles

Table 1 Paired *t*-test results for different stages of growth for *T. recurvatum* across the study years. Bold numbers indicate significance at $P < 0.05$.

Year	Flowering/juvenile		Flowering/non-flowering		Non-flowering/juvenile	
	t	*P*	*t*	*P*	*t*	*P*
1990	−1.24	0.23	0.69	0.495	−1.23	0.232
1991	−2.68	**0.013**	−0.37	**0.001**	1.39	0.176
1992	−1.94	0.065	−2.92	**0.008**	1.32	0.201
1994	0.78	0.444	2.65	**0.014**	−2.44	**0.023**
1999	−3.13	**0.005**	5.2	**<0.0001**	−0.15	0.885
2001	−3.09	**0.005**	−4.67	**<0.0001**	2.12	**0.045**
2004	−2.93	**0.007**	−3.64	**0.001**	2.78	**0.011**
2005	−2.97	**0.007**	−3.74	**0.001**	−1.08	0.289
2007	−0.92	0.367	−2.85	**0.009**	2.88	**0.008**

ranged from 2 to 17 years, averaging 4 years in 2004 and 7 years in 2007. The three-leaved non-flowering stage ranged from 4 to 20 years and flowering ramets ranged from 5 to 27 years. Flowering ramets were, on average, older than three-leaved ramets (Table 2): 85 % of flowering ramets were at least 10 years old and the majority were in the mid-teens.

Trillium PVA estimates indicate that this population increased over the study duration (Table 3). Non-flowering ramets, which could include transitions from juveniles or reversions from flowering ramets, had the greatest rate of increase. The average population growth rate (λ) and continuous rate of increase (r) were highest for the non-flowering stage class (Table 3). Population fluctuations (or variability) (σ^2) were also highest for non-flowering and juvenile ramets (Table 3).

Spatial co-patterns among cohorts were generally strong, but varied among years (Table 4). In 1990 and 1994, little pattern was found among cohorts. For 1999, 2001 and 2004, strong spatial co-variation occurred among flowering and non-flowering, and flowering and juvenile cohorts at fairly large scales (30–50 m), and much smaller spatial patterning occurred among non-flowering and juvenile cohorts (7–8 m). In 2005, all cohort co-patterns were small (4–6 m), but increased again (9–13 m) in 2007. The co-pattern between non-flowering individuals and juveniles tended to have the smallest spatial scale.

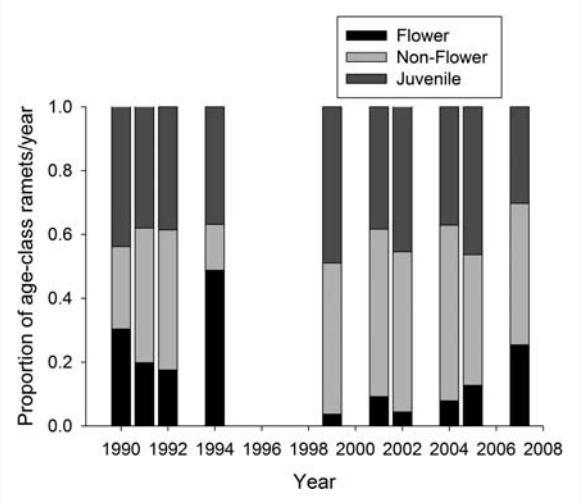

Fig. 2 Proportion of total population for each age class/year for *T. recurvatum*. Total numbers of individuals in each age class were summed over all 25 plots for the collection period and the proportion of each age class out of the total number of ramets was determined.

Discussion

This *T. recurvatum* population has primarily vegetative reproduction, as only 11 % of observed stems originated from a seed. Other forest herbs, such as *Uvularia perfoliata*, have a 'waiting' strategy, in which vegetative ramet production maintains populations under closed canopy, and seed production is associated with canopy gaps (Kudoh *et al.* 1999). Alternatively, a high degree of vegetative reproduction in North American *Trillium* species has been linked to the degree of habitat instability, such as in floodplains (Ohara 1989). The unstable soils of the loess bluffs (Miller and Neiswender 1987; McCarthy 1990) may combine with a relatively closed forest canopy over the *T. recurvatum* population to promote vegetative reproduction.

Although the number of ramets in each life history stage and the proportion of each stage fluctuated from year to year, juvenile and non-flowering plants made up the greatest proportion of the *T. recurvatum* population over the nine observed years between 1990 and 2007. Collectively, juveniles and non-flowering plants averaged 82 % of the population over all years, although

Table 2 Life history reproduction of a population of *T. recurvatum* at Edward J. Meeman Biological Station, western Tennessee, in spring of 2002 and 2007. Individuals were selected in an effort to pose the least damage to the long-term health of the population. A minimal sample was collected. Average (mode in parentheses) rings refer to annual constriction rings of the rhizome and are expected to correlate with age (Hanzawa and Kalisz 1993).

	Total stems		Average rings		Stems from seed		Stems from rhizome		% Rhizome	
Age structure	**2002**	**2007**	**2002**	**2007**	**2002**	**2007**	**2002**	**2007**	**2002**	**2007**
Juvenile (1 leaf)	17	21	4	7 (2)	4	0	13	21	76	100
Non-flowering (3 leaf)	15	21	12	10 (7)	1	0	14	21	93	100
Flowering adult	4	21	16	14 (16)	6	0	4	21	100	100

Table 3 **Measures of population viability for age classes of clonal *T. recurvatum* in western Tennessee.**

	Flowering	Non-flowering	Juvenile
Estimated μ	0.059	0.101	0.048
Estimated σ^2	0.536	1.808	1.057
Continuous rate of increase (r)	0.327	1.005	0.577
Lower 95 % confidence limit for r	−0.109	−0.087	−0.136
Upper 95 % confidence limit for r	0.763	2.098	1.278
Average finite rate of increase (λ)	1.387	2.733	1.780
Approximate lower 95 % confidence limit for λ	0.897	0.917	0.873
Approximate upper 95 % confidence limit for λ	2.145	8.150	3.589

Table 4 **Spatial covariate analysis of *T. recurvatum* stage classes.** Best-fit model illustrates the model which gives the highest r^2.

Covariate comparison	Year	Best-fit model	Range (A)	Proportion	r^2
Flower × non-flower	1990	Linear	18.90	0.00	0.37
	1991	Spherical	7.09	0.56	0.02
	1992	Spherical	6.95	0.60	0.01
	1994	Linear	18.90	0.00	0.45
	1999	Gaussian	33.80	0.88	0.78
	2001	Gaussian	38.70	0.80	0.69
	2004	Gaussian	51.80	0.77	0.27
	2005	Exponential	5.43	0.53	0.01
	2007	Spherical	12.30	1.00	0.72
Flower × juvenile	1990	Spherical	6.16	0.60	0.00
	1991	Spherical	6.47	0.57	0.01
	1992	Spherical	6.96	0.64	0.01
	1994	Linear	18.90	0.00	0.78
	1999	Gaussian	7.40	1.00	0.01
	2001	Gaussian	38.90	0.92	0.59
	2004	Gaussian	40.70	0.99	0.36
	2005	Gaussian	4.82	0.56	0.01
	2007	Spherical	13.40	0.76	0.61
Non-flower × juvenile	1990	Linear	18.90	0.00	0.42
	1991	Spherical	6.90	0.99	0.09
	1992	Spherical	5.77	0.91	0.00
	1994	Spherical	39.14	0.62	0.72
	1999	Gaussian	7.69	1.00	0.34
	2001	Gaussian	7.36	1.00	0.30
	2004	Gaussian	8.14	1.00	0.22
	2005	Spherical	6.16	0.77	0.01
	2007	Gaussian	9.28	1.00	0.52

there was proportionally greater representation of flowering plants in 1994 and 2007, and the number of flowering plants increased from 2002 to the end of collections in 2007. Among clonal herbs of temperate forests, ramet growth rates and the proportion of flowering plants can be positively correlated with a 'favourable' growing season (Charron and Gagnon 1991), higher light availability or time since canopy disturbance (Bierzychudek 1982; Levine and Feller 2004; Patsias and Bruelheide 2011), or lower plant density (Levine and Feller 2004). A weak (non-significant) positive correlation of flowering plants with growing season temperature and corresponding increase in flowering plants with growing season temperature between 2004 and 2008 suggest that *T. recurvatum* may increase growth and flowering under favourable growing conditions, although it does not show strong developmental canalization through organ pre-formation as reported in other species (Heidrun *et al.* 2004).

Contrary to our hypothesis, the number of juvenile ramets did not vary the most over years; rather, non-flowering ramets showed the highest variability. Possibly, primarily clonal reproduction led to more consistent recruitment and stability of the juvenile class, while reversion rates from flowering ramets and the maturation of juvenile ramets created variability in the non-flowering class. The broad age range of juveniles (2–17 years) suggests wide variation in time spent in that age class, and overlap in age between the oldest non-flowering (10–14 years) and flowering (14-year average) ramets suggests that reversions could have occurred. In addition, significantly positive correlations with prior year's growing season temperature and weak (non-significant) positive correlations with prior year's growing season precipitation suggest year-to-year variation in growing conditions affect plant growth and transitions. Overall, time spent in the juvenile class and reversion rates may reflect climate variation and localized variation in less seasonal environmental factors, such as light, soil resources or soil stability (ramet disturbance) (Jacquemyn *et al.* 2005), or environmental or demographic stochasticity (Damman and Cain 1998).

Our results for *T. recurvatum* support those of populations of other clonal *Trillium* species, which also can have a high proportion of non-flowering plants. For example, over a 2-year period, the proportion of flowering and non-flowering plants in a *T. maculatum* population remained similar, with non-flowering plants making up 66–67 % of the population (Walker *et al.* 2009). Populations of non-clonal *Trillium* species have also been shown to maintain a relatively high frequency of juvenile plants (Ohara *et al.* 2001, 2006). Ohara *et al.* (2001) showed that frequencies of one-leaf *T. apetalon* plants were high, with only 3.2 % transitioning to three-leaf plants from one year to the next, suggesting that plants could remain, and possibly accumulate, in the one-leaf stage up to 31 years. Similarly, only 1.6 % of surviving one-leaf *T. camschatcense* (also non-clonal) plants transited to the three-leaf stage over a year; however, 16.3 % of flowering plants regressed to three-leaf non-flowering plants (Ohara *et al.* 2006).

Although PVA revealed that all three life history stages of *T. recurvatum* increased over the study period, non-flowering plants showed the greatest rate of increase. Their increase potentially reflects both transitions out of the juvenile class and reversion of flowering plants to non-flowering plants. This trend contrasts with non-clonal *Trillium* species, which have a low rate of transition from the juvenile class (1.6–3.2 %) and can spend decades as a juvenile plant (Ohara *et al.* 2001, 2006). If the youngest and oldest observed *T. recurvatum* ages are considered, plants could transition out of the juvenile stage in as little as 2 years (to become 4-year-old non-flowering plants) or remain as juveniles for 17 years. Rates of reversion from flowering to non-flowering plants could not be directly assessed for *T. recurvatum*, although, as noted above, the age overlap between older non-flowering and flowering ramets suggests that reversions could have occurred.

Spatial patterns between life history stages of *T. recurvatum* did not follow those shown in relatively dense populations of other *Trillium* species. For example, fine-scale spatial structure in a dense (55–63 plants m^{-2}) population of the clonal species *T. maculatum* was due to clumping of juveniles, which grow in the spaces between older individuals (Walker *et al.* 2009). We found no evidence for density effects on growth or spatial pattern within the *T. recurvatum* population, although life history stages co-varied in some years through distances up to 39 m. Nor were there greater distances between flowering plants and juveniles, as hypothesized if ants carry seeds away from parent plants. In many clonal herbs, spatial patterns among ramets are a function of both recruitment patterns and clonal growth architecture (e.g. Angevine and Handel 1986). As ramets of *T. recurvatum* are not inter-connected by rigid rhizomes, characteristics of the loess bluffs may have contributed to changing spatial patterns among individuals. In particular, soil movement on the upper slopes, where the *T. recurvatum* population is located, could easily move individual plant positions from year to year.

Conclusions and forward look

Overall, this *T. recurvatum* population is not constrained spatially and is expanding. Evidence for this view includes a relatively high proportion of juvenile and non-flowering adult ramets; the highest population growth in the non-flowering adult class; lack of evidence for density dependence and increasing proportion of flowering plants. Clonal growth has probably increased the rate of spatial spread and may allow the rate of spread to match microsite conditions (Alpert and Stuefer 1997). Further work is needed to elucidate the relative contributions of clonal vs. seed recruitment to *T. recurvatum* population genetic structure and demography.

Contributions by the authors

This research was initiated by G.W. and B.S.C. All authors contributed equally to writing this manuscript.

Acknowledgements

The authors thank the University of Memphis for permitting the use of the MBFS. We also thank Dennis Whigham and two anonymous reviewers for helpful suggestions on a previous version of this manuscript. J.E.M. also thanks students of the fall 2011 Botany 216 Course at Christian Brothers University, Memphis, for helpful comments and suggestions.

Conflict of interest statement

None declared.

References

Alpert P, **Stuefer JF**. **1997**. Division of labour in clonal plants. In: de Kroon H, van Groenendael J, eds. *The ecology and evolution of clonal plants*. Leiden: Backhuys, 137–154.

Angevine MW, **Handel SN**. **1986**. Invasion of forest floor space, clonal architecture, and population growth in the perennial herb *Clintonia borealis*. *Journal of Ecology* **74**: 547–560.

Bierzychudek P. **1982**. The demography of jack-in-the-pulpit, a forest perennial that changes sex. *Ecological Monographs* **52**: 336–351.

Billings WD, **Mooney HA**. **1968**. The ecology of arctic and alpine plants. *Biological Reviews* **43**: 481–529.

Case FW, **Case RB**. **1997**. *Trilliums*. Portland, OR: Timber Press, 285 pp.

Charron D, **Gagnon D**. **1991**. The demography of northern populations of *Panax quinquefolium* (American ginseng). *Journal of Ecology* **79**: 431–445.

Damman H, **Cain ML**. **1998**. Population growth and viability analyses of the clonal woodland herb, *Asarum canadense*. *Journal of Ecology* **86**: 13–26.

Dennis B, **Munholland PL**, **Scott JM**. **1991**. Estimation of growth and extinction parameters for endangered species. *Ecological Monographs* **61**: 115–143.

Fenneman NM. **1938**. *Physiography of the Eastern United States*. New York: McGraw-Hill.

Hanzawa FM, **Kalisz S**. **1993**. The relationship between age, size, and reproduction in *Trillium grandiflorum* (Liliaceae). *American Journal of Botany* **80**: 405–410.

Heidrun H, **Dennis FW**, **O'Neill J**. **2004**. Timing of disturbance changes the balance between growth and survival of parent and offspring ramets in the clonal forest understory herb *Uvularia perfoliata*. *Evolutionary Ecology* **18**: 521–539.

Jacquemyn H, **Brys R**, **Honnay O**, **Hermy M**, **Roldán-Ruiz I**. **2005**. Local forest environment largely affects below-ground growth, clonal diversity and fine-scale spatial genetic structure in the temperate deciduous forest herb *Paris quadrifolia*. *Molecular Ecology* **14**: 4479–4488.

Jules ES. **1998**. Habitat fragmentation and demographic change for a common plant: *Trillium* in old-growth forest. *Ecology* **79**: 1645–1656.

Kahmen A, **Jules ES**. **2005**. Assessing the recovery of a long-lived herb following logging: *Trillium ovatum* across a 424-year chronosequence. *Forest Ecology and Management* **210**: 107–116.

Klimešová J, **Klimeš L**. **2008**. Clonal growth diversity and bud banks of plants in the Czech flora: an evaluation using the CLO-PLA3 database. *Preslia* **80**: 255–275.

Knight TM. **2004**. The effects of herbivory and pollen limitation on a declining population of *Trillium grandiflorum*. *Ecological Applications* **14**: 915–928.

Kudoh H, **Shibaike H**, **Takasu H**, **Whigham DF**, **Kawano S**. **1999**. Genet structure and determinants of clonal structure in a temperate deciduous woodland herb, *Uvularia perfoliata*. *Journal of Ecology* **87**: 244–257.

Leege LM, **Thompson JS**, **Parris DJ**. **2010**. The responses of rare and common trilliums (*Trillium reliquum*, *T. cuneatum*, and *T. maculatum*) to deer herbivory and invasive honeysuckle removal. *Castanea* **75**: 433–443.

Levine MT, **Feller IC**. **2004**. Effects of forest age and disturbance on population persistence in the understory herb, *Arisaema triphyllum* (Araceae). *Plant Ecology* **172**: 73–82.

McCarthy KP. **1990**. *An analysis of gully development in Meeman-Shelby Forest State Park, Tennessee*. Master's Thesis, The University of Memphis, Memphis, TN.

Miller NA, **Neiswender J**. **1987**. A vegetational comparison study of the third Chickasaw Loess Bluff, Shelby County, Tennessee. *Castanea* **52**: 151–156.

Morris WF, **Groom M**, **Doak D**, **Karieva P**, **Fieberg J**, **Gerber L**, **Murphy P**, **Thompson D**. **1999**. *A practical handbook for population viability analysis*. Washington, DC: The Nature Conservancy.

NatureServe. **2006**. *NatureServe Explorer: An online encyclopedia of life*. Version 6.1. NatureServe, Arlington, Virginia. **www.natureserve.org/explorer**.

O'Connor RP. **2007**. *Special Plant Abstract for Trillium recurvatum (prairie trillium)*. Lansing, MI: Michigan Natural Features Inventory, 3 pp.

Ohara M. **1989**. Life history evolution of the genus *Trillium*. *Plant Species Biology* **4**: 1–28.

Ohara M, **Takada T**, **Kawano S**. **2001**. Demography and reproductive strategies of a polycarpic perennial, *Trillium apetalon* (Trilliaceae). *Plant Species Biology* **16**: 209–217.

Ohara M, **Tomimatsu H**, **Takada T**, **Kawano S**. **2006**. Importance of life history studies for conservation of fragmented populations: a case study of the understory herb, *Trillium camschatcense*. *Plant Species Biology* **21**: 1–12.

Patsias K, **Bruelheide H**. **2011**. Is the degree of clonality of forest herbs dependent on gap age? Using fingerprinting approaches to assess optimum successional stages for montane forest herbs. *Ecology and Evolution* **1**: 290–305.

Sawyer NW. **2010**. Reproductive ecology of *Trillium recurvatum* (Trilliaceae) in Wisconsin. *American Midland Naturalist* **163**: 146–160.

Sokal RR, **Rohlf FJ**. **1981**. *Biometry: the principles and practice of statistics in biological research*. San Francisco: W.H. Freeman, 776 pp.

Strausbaugh PD, **Core EL**. **1978**. *Flora of West Virginia*. Morgantown, WV: Seneca Books.

Tiffney BH, **Niklas KJ**. **1985**. Clonal growth in land plants: a paleobotanical perspective. In: Jackson JBC, Buss LW, Cook RE, eds. *Population biology and evolution of clonal organisms*. New Haven, CT: Yale University Press, 35–66.

Tomimatsu H, **Ohara M**. **2010**. Demographic response of plant populations to habitat fragmentation and temporal environmental variability. *Oecologia* **162**: 903–911.

Walker AN, **Foré SA**, **Collins BS**. **2009**. Fine-scale structure within a *Trillium maculatum* (Liliaceae) population. *Botany* **87**: 223–230.

Webster CR, **Jenkins MA**. **2008**. Age structure and spatial patterning of *Trillium* populations in old-growth forests. *Plant Ecology* **199**: 43–54.