

# Assessing the recovery of a long-lived herb following logging: *Trillium ovatum* across a 424-year chronosequence

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## Abstract

We investigated the long-term recovery of *Trillium ovatum* (Liliaceae) following clear-cut logging by assessing demographic trends across a forest chronosequence that ranged in age from 2 to 424 years. In each of 20 sites across the chronosequence, we used 50 × 50 m plots to assess the population size, age and stage structure, seed production, and the spatial distribution of seedlings relative to reproductive plants. We found that *Trillium* populations were significantly reduced in younger sites and a significant positive relationship of population size and stand age, suggesting that population recovery following stand-replacement disturbances may take centuries. Slow recovery rates of *Trillium* can partly be explained by short seed dispersal distances. We found 67% of new *Trillium* recruits within only one meter of potential parent plants. Despite the general trend of slow recovery, a few recently disturbed populations showed fast population growth. In these cases, high rates of post-disturbance recruitment were related to the number of individuals surviving the disturbance event. We found that local, within-site seed production can most likely mitigate limited dispersal abilities of *Trillium*. The rate of *Trillium* recovery following disturbance, therefore, depends on the number of plants that have persisted through the disturbance event and serve as within-site seed sources. Our study suggests that the nature of the stand-replacement disturbance (i.e., magnitude and intensity) may be critical in determining the recovery of understory plants in managed forests.

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## 1. Introduction

Human disturbances and management for timber production have modified forested landscapes world-

wide (UNEP, 2001). Regions that were once continuously covered by unmanaged forest ecosystems now appear as mosaics of forest remnants surrounded by agriculture, urban development, clear-cuts, or even-aged tree plantations (Saunders et al., 1991). The conversion of old-growth or primary forest to younger, secondary forests through stand-replacement disturbances such as clear-cut logging has raised considerable concern about the loss of biodiversity,

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since herbaceous understory species characteristic of old-growth forests are absent from recovering forests, even centuries after disturbance (Alaback, 1982; Whitney and Foster, 1988; Halpern and Spies, 1995; Dupouey et al., 2002; Moola and Vasseur, 2004). While most research regarding the effects of clear-cut logging on species diversity has focused on trees and wildlife, the effects on understory herb diversity in secondary forests remain poorly understood (Peterken and Game, 1984; Dzwonko and Loster, 1992; Honnay et al., 1999).

Several mechanisms have been proposed as influential in the slow recovery process of understory plant communities following clear-cut logging. For instance, Duffy and Meier (1992) proposed that slow growth and low reproductive rates and logging-induced changes in the microhabitat of the forest floor result in reduced diversity of vernal herbs. Meier et al. (1995) suggested that populations of understory plants had established under climate regimes different from current ones. Once eradicated from a site, some species are unable to re-establish under present conditions. Long-term successional trends that promote niche diversification and further resource availability for a number of different understory species have also been suggested as an explanation for the positive relationship between forest age and understory diversity (Dzwonko and Loster, 1989; Scheller and Mladenoff, 2002). Most importantly, however, seed dispersal has been described as a mechanism limiting the recovery of several understory herbs in various secondary forests (Matlack, 1994; Brunet and von Oheimb, 1998; Bossuyt et al., 1999; Verheyen and Hermy, 2001).

To mitigate limited seed dispersal from outside sources by within-site reproduction, survival of some individuals through disturbance is likely to be of high importance for population recovery in secondary forests. Unfortunately, determining survival rates of understory herbs through the process of clear-cut timber harvest and evaluating the importance of survival for population recovery is difficult. Following disturbance, understory herbs can persist in the ground as rhizomes or bulbs for several years and are thus difficult to detect (Hughes and Fahey, 1991). Consequently, it remains unclear how frequently understory plants can persist through stand-replacement disturbances and what the role of the residual plants is in the re-establishment of new populations in secondary forests.

In this study, we assessed *Trillium* populations along a chronosequence of forest stands in the Pacific Northwest, USA, ranging in age between 2 and 424 years. *Trillium* produces a single stem each season, which leaves an annual constriction ring on the rhizome. By counting the rings on the rhizome, the age of each individual plant within a population can be determined (Jules, 1998). Further, because the date of all timber harvesting in our study area is known, the age of individual plants can be used to determine whether the plant had persisted through disturbance or had been recruited after disturbance (Jules, 1998). This feature of *Trillium*, combined with its longevity and non-clonal habit, makes *Trillium* an ideal organism for investigating the importance of residual plants for population recovery following stand-replacement disturbances. Specifically, this study addressed the following three questions: (1) What is the effect of stand-replacement disturbances such as clear-cut harvesting on *Trillium* population sizes? (2) Do trillium populations recover after harvest, and if so, how long does it take for recovery? (3) How important is survival through disturbance and local reproductive output relative to recolonisation from distant populations for the recovery process?

## 2. Materials and methods

### 2.1. Study area

The study was conducted in the Sucker Creek watershed in the central Siskiyou Mountains of southwest Oregon, USA. Climatic conditions in this region include cool, moist winters and warm, dry summers. We studied mid- to high-elevation coniferous forests (1000–2100 m), which are dominated by Douglas-fir (*Pseudotsuga menziesii*) and white fir (*Abies concolor*) in the overstory. Older forests in this area have relatively rich understory herbaceous communities (Whittaker, 1960; Jules and Rathcke, 1999). Forest stands in this region were subject to frequent fires that occurred roughly every 60 years before fire suppression efforts began in the early 1900s (Agee, 1991). The frequency of stand-replacement fires is, however, unknown. In the 1960s, an era of intensive forest management began in the watershed. Over a period of 30 years, approximately, 40% of the

late successional forests were clear-cut for timber. After clear-cutting, most sites were broadcast-burned to reduce both woody debris and remaining vegetation, and were then replanted with Douglas-fir seedlings in subsequent years (U.S. Forest Service, 1995). Thus, the landscape in the Sucker Creek watershed includes a mosaic of remnant forest fragments of various ages and clear-cut plantations, mostly less than 40 years of age.

## 2.2. Study organism

*Trillium ovatum* is a long-lived herbaceous perennial, common throughout forests of western North America. *Trillium* produces several distinct life history stages (Brandt, 1916). The cotyledon stage lasts one growing season, after which the plant produces a single leaf from its rhizome. Eventually, individuals will develop its characteristic three-leaf stage. Three-leaf plants can be reproductive or vegetative. Prior to this study, the oldest *Trillium* found was 72 years of age (Jules, 1998).

## 2.3. Field work

In June 2000, twenty 50 m × 50 m plots were established in separate forest stands that ranged from 2 to 424 years in age. Nine of the 20 plots were situated in forests that had originated after clear-cut timber harvest between 1960 and 1996, and were replanted the year after cutting (2–40 years in age at the time of the study). Because there were no forests clear-cut before 1959 in the watershed we could not use managed stands solely to assess long-term recovery of *Trillium* after clear-cutting. Thus, 11 plots were established in stands, which had originated after natural stand-replacement fires (87–424 years in age at the time of the study) as proxies for the potential long-term development of *Trillium* populations. For the nine clear-cut sites, we used the year of the first planting of Douglas-fir seedlings as the date of stand initiation (data available from U.S. Forest Service). For the 11 unmanaged forests, the age of the stand was determined using increment core samples taken from the oldest generation of trees in a site.

To reduce the effects of non-stand age related factors in the chronosequence, sites were located in a single watershed and only on west to northwest facing

slopes at an elevation between 1295 and 1495 m, where previous studies have shown that *Trillium* reaches its greatest abundance in old-growth forests under these conditions (Whittaker, 1960; Jules, 1998). To ensure the same potential vegetation type for all chronosequence sites under undisturbed conditions, only those younger sites (<100 years of age) were selected where stumps or burned snags of old-growth conifers (>200 years) indicated a similar pre-disturbance overstory vegetation as was observed in the older sites. In addition, all plots were situated at least 60 m away from the nearest forest-clear-cut edge to eliminate edge effects (see Jules and Rathcke, 1999).

Environmental data were collected in each stand to account for potentially confounding factors along the chronosequence. Between 10 and 12 August, 2000, approximately 300 g of soil was collected at a depth of 5 and 25 cm from 10 randomly selected locations per stand. Wet and dry weight was determined and the percent soil moisture was calculated. Canopy cover was estimated using a spherical densiometer (Forest Densiometers, Model-A, Arlington, Virginia). Measurements were taken at 10 randomly selected locations within each plot. Slope and aspect were measured using an inclinometer and a compass, respectively. Elevation was determined using U.S. Geological Service maps (scale 1:24,000).

To assess the differences in size and demographic structure of trillium populations across stands, ten 2 m × 50 m parallel transects, each separated by 3 m from the next, were laid out following topographic contours in each plot. Along all transects, the total number of *Trilliums* was counted and the age of each individual recorded by excavating the rhizomes and counting the annual constrictions (see Section 1). While young rhizomes were usually intact, most rhizomes of older individuals had been previously damaged by herbivory or decay. Burrowing depth and rhizome thickness of *Trillium* increase with the age of the plant. We, therefore, used the size of the scar, thickness and burrowing depth of the rhizome to estimate the proportion of the rhizome that was not available for counting constriction rings and classified the damaged rhizomes into four different damage categories: class E (no damage), class D1 (less than 10 rings lost), class D2 (up to 20 rings lost), class D3 (21

or more rings lost). For data analyses, no years were added to actual number of constrictions for class E, 5 years for class D1, 15 years for class D2 and 25 years for class D3. Estimating rhizome damage adds potential error to the demographic data. In the work presented here, however, we are mainly interested in survival through disturbance and post-disturbance recruitment. Surviving individuals in the younger sites were in many cases more than 25 years older than the disturbance event, confidently indicating survival. Most of the younger *Trilliums* (<10 years of age) showed no damage and thus served as precise estimates of recent recruitment.

In addition to age, each individual within a population was classified into one of the different stage-classes: cotyledon, one-leaf vegetative, three-leaf vegetative and reproductive. To compare the distributions of stage-classes of *Trillium* between populations, we used the percentage of each stage-class in a given population.

To test whether seed production influences the recovery of *Trillium* populations, the number of seeds produced by reproductive plants along each transect was recorded in the same season as the demographic structure of *Trillium* populations was determined. In addition to the absolute number of seeds produced in a population, the average number of seeds produced per reproductive plant in a population, and the number of seeds produced in relation to population size, were used to further assess the factors that are influencing *Trillium* seed production.

To estimate the role of dispersal for recovery of *Trillium* populations, the position of each recorded *Trillium* was determined by measuring its *x*, *y* coordinates within our 50 × 50 m plot. These coordinates were used to calculate the distance of juvenile plants to the closest potential parent plant. All plants 11 years and younger were considered juveniles, since the youngest reproductive plant found in this study was 12 years old and all plants 12 years and older were defined as potential parent plants. Plants were considered potential parent plants independently of their stage-class in 2000, since plants can alternate between vegetative and reproductive status frequently (Jules, 1998). The analysis of dispersal was limited to the 13 sites that had initiated 100 years ago or earlier. In these sites population densities of *Trillium* are generally low and the distance between potential parent plants is large

enough to clearly show the proximity of juveniles to adult plants. In older sites with higher population densities, the distance between potential parent plants is often small, such that juveniles always grow in close proximity to adult plants. These sites were omitted from the analysis of dispersal to avoid a bias towards short dispersal distances that probably do not represent actual dispersal events.

#### 2.4. Data analysis

Regression analyses (simple and multiple stepwise) were used to test for effects of site characteristics (stand age, slope, elevation, aspect, canopy openings) on *Trillium* population size, stage-class distribution and seed production. Standardized partial correlation coefficients were calculated for the multiple regressions to compare the influence of all the significant site characteristics on dependent variables. When tested for multicollinearity, soil moisture was significantly correlated with stand age ( $p < 0.001$ ,  $R^2 = 0.540$ ). Thus, since soil moisture is most likely dependent on stand age, it was excluded from our analyses. All data were normally distributed except for percent canopy openings, which was log-transformed. The criteria for an independent variable to be accepted in the model was set at  $p < 0.05$ , and the variables were rejected if  $p > 0.05$ . All analyses were performed using SPSS, Version 11.0 (SPSS Inc., 2001).

### 3. Results

Along the chronosequence *Trillium* populations increased in size from 0 to 456 plants per plot (Table 1, Figs. 1 and 2). Stand age and aspect explained 80.4% of the variation in population size, indicating that stand-replacement disturbances highly reduced *Trillium* populations in size (Table 2). Within the recently disturbed sites, however, population sizes varied greatly, with some populations being near extinction and others with intermediate levels of abundance (Fig. 1, Site 1–9). In these recently disturbed sites, recruitment after disturbance was highest in those populations that had high numbers of individuals surviving the disturbance event (Fig. 1). However, it was not possible to statistically test for this relationship, because the number of plants that had initially

Table 1

Stand age, *Trillium* population size, stage class distribution (%) and seed production for the 20 different forest stands in chronosequence

Site	Stand age in 2000 (years)	<i>Trillium</i> population size (number of individuals)	Stage class distribution (%)				Total number of seeds	Seeds per reproductive plant	Seeds per total number of plants
			Cot	OL	Veg	Repro			
1	2	23	0	0	43.5	56.5	0	0	–
2	11	137	0.7	11.7	35.0	52.6	1271	17.7	9.3
3	18	11	0	27.3	45.5	27.3	62	20.7	5.6
4	19	127	0	39.4	40.9	19.7	277	11.1	2.2
5	21	0	–	–	–	–	–	–	–
6	21	6	0	16.7	66.7	16.7	5	5.0	0.8
7	34	2	0	0	100	0	0	0	0
8	38	226	3.5	33.6	51.8	10.6	149	6.2	0.7
9	40	42	0	14.3	78.6	7.1	11	3.7	0.3
10	87	22	0	0	100	0	0	–	0
11	95	29	3.5	27.6	69.0	0	0	–	0
12	95	48	0	33.3	56.3	10.4	33	6.6	0.7
13	98	88	0	2.3	91.0	6.8	80	13.3	0.9
14	116	234	0.4	6.0	80.3	13.3	119	3.8	0.5
15	125	85	2.4	27.0	55.3	14.1	101	8.4	1.2
16	176	220	3.2	28.2	63.2	2.7	152	25.3	0.7
17	249	284	2.8	8.5	61.3	26.8	808	10.6	2.8
18	270	322	0	8.7	86.3	4.4	138	9.9	0.4
19	295	92	0	14.1	57.6	27.2	n.a. <sup>a</sup>	n.a. <sup>a</sup>	n.a. <sup>a</sup>
20	424	456	1.1	12.7	71.3	14.3	481	7.4	1.0

Cot, cotyledons; OL, one-leaf vegetatives; Veg, three-leaf vegetatives; Repro, reproductives.

<sup>a</sup> Seed production was not measured in this site.

survived the disturbance event, but died before our study, was unknown. Since these plants most likely have contributed to the recovery process, we could not estimate the correlation between initial survival and post-disturbance recruitment.

The proportions of each population comprised of any stage-class were not correlated with stand age (Table 2). The proportion of cotyledons in a

population was, however, negatively correlated with slope. The proportion of one-leaf vegetatives was not significantly correlated with any of the independent variables (Table 2). The proportion of three-leaf vegetatives showed a negative correlation with canopy openings, whereas the proportion of reproductives showed a strongly positive correlation with percent open canopy (Table 2). When tested in a simple linear

Table 2

Partial correlation coefficients and  $R^2$  from multiple stepwise regression models with *Trillium* demographic variables as dependent variables and independent site characteristics as explanatory variables for 20 different forest stands

	Stand age	% Open canopy	Slope	Elevation	Aspect	$R^2$
Total number of <i>Trillium</i>	0.64***	–	–	–	0.49***	0.804
Percentage of cotyledons	–	–	–0.50*	–	–	0.251
Percentage of one-leaves	–	–	–	–	–	–
Percentage of vegetatives	–	–0.55*	–	–	–	0.304
Percentage of reproductives	–	0.76***	–	–	–	0.582
Total number of seeds	–	0.53*	–	–	–	0.279
Seeds per reproductive plant	–	–	–	–	–	–
Seeds per total number of plants	–	0.68**	–	–	–	0.460

A (–) indicates a non-significant partial regression coefficient.

\*  $0.05 > p > 0.01$ .\*\*  $0.01 > p > 0.001$ .\*\*\*  $p < 0.001$ .

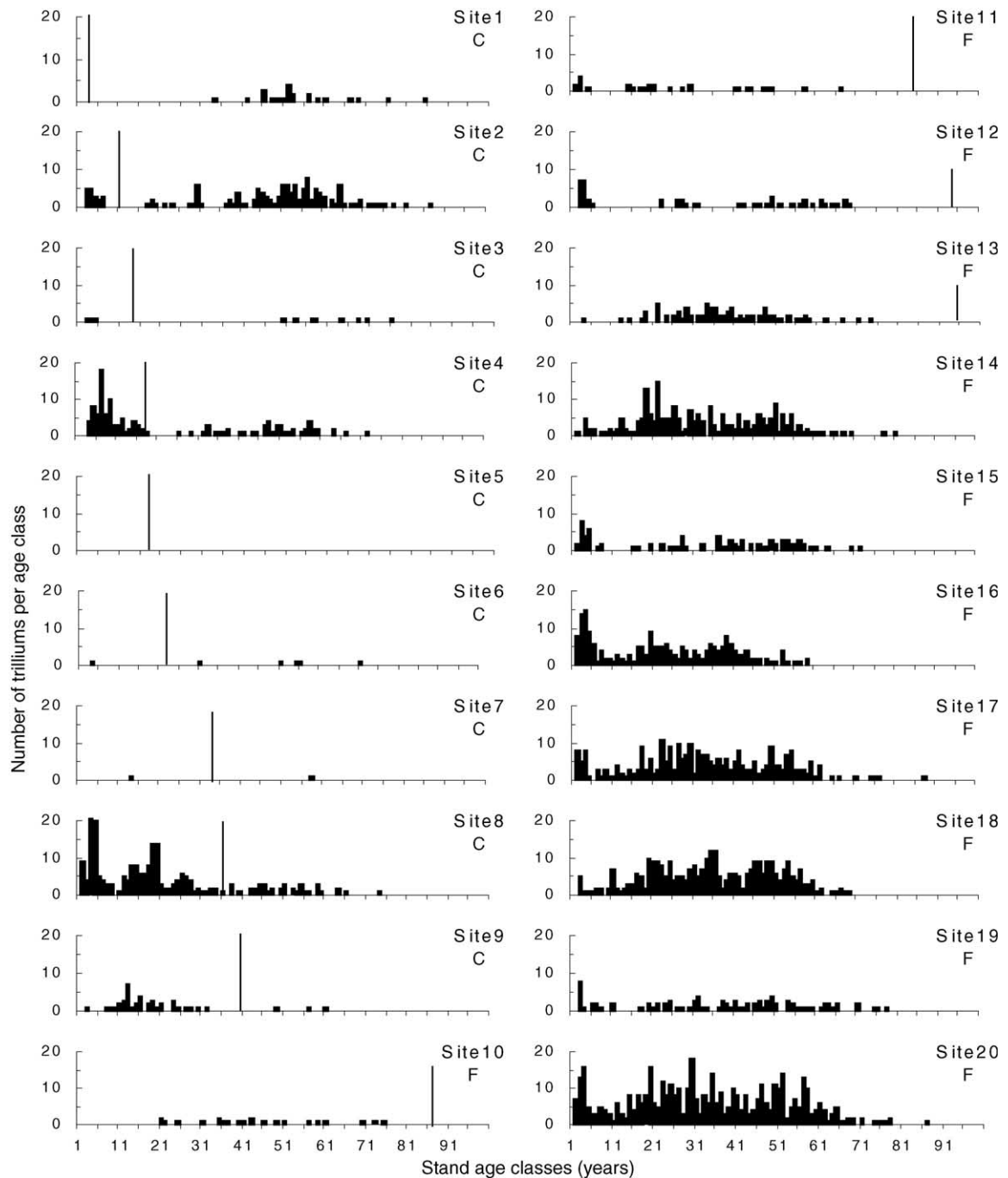


Fig. 1. Demographic structure of *Trillium* populations in 20 different forest stands ranging from 2 to 424 years in age. The vertical line indicates time of disturbance (Site 1–13). For older sites (Site 14–20) the disturbance event was more than 100 years ago and is not shown on the graph. Plants to the right of the line have persisted disturbance and were still alive in the year 2000. Plants to the left have recruited into the population since the disturbance event. Sites 1–9 established after clear-cut logging (C) whereas Site 10–20 established after natural stand-replacement fire (F).

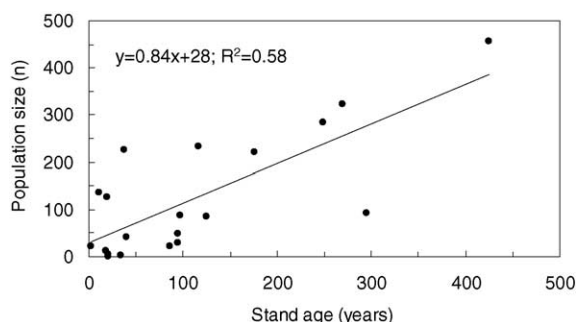


Fig. 2. Relationship of *Trillium* population sizes and stand age for forests in the Sucker Creek watershed, southwestern Oregon, USA.

regression, percent open canopy alone explained 81% of the variation in percent reproductives in a population (Fig. 3).

In multiple stepwise regression analysis, no correlation was found between total number of seeds produced in a population and stand age (Table 2). The number of seeds produced in a population was, however, correlated with percent open canopies (Table 2). The number of seeds produced per reproductive plant was also not correlated with stand age or any other site attributes (Table 2). However, the number of seeds produced in relation to population size was positively correlated with percent canopy openings (Table 2, Fig. 3). In a linear regression, percent canopy openings alone explained 77% of the variation of seeds produced in relation to population size (Fig. 3).

Sixty-seven percent of juvenile trilliums that had recruited into the populations in Sites 1–13 during the last 11 years were found within 1 m of potential parent

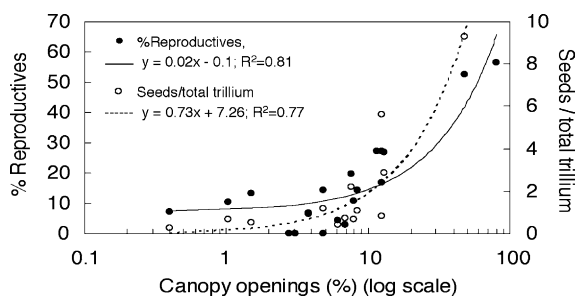


Fig. 3. Percent reproductives and number of seeds produced per total number of trilliums in a population plotted as a function of percent open canopy (log scale). Site 1 was excluded from the analysis (see text).

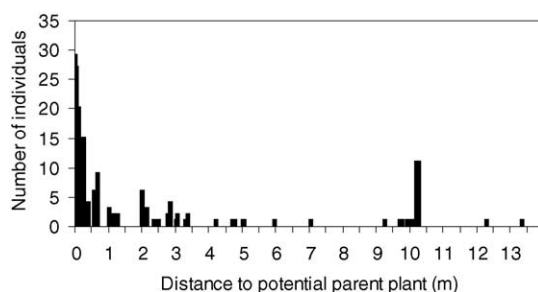


Fig. 4. Distances of juvenile *Trilliums* (all plants 11 years or younger) to potential parent plants (all plants 12 years and older) for Sites 1–13.

plants (Fig. 4). However, few plants had distances to potential parent plants of more than 10 m.

#### 4. Discussion

The generally low abundance of *Trillium* in younger sites suggests that disturbance events reduced the size of *Trillium* populations under study. The rate of recovery for *Trillium* populations after a stand-replacement event was slow so that populations appear to be increasing in size even centuries after disturbance (Figs. 1 and 2). Understory plant recovery following clear-cut logging is generally assessed using chronosequences of forest stands of 0 to <100 years in age, since secondary forests having originated after clear-cut logging more than 100 years ago are rare in many regions (MacLean and Wein, 1977; Brakenhielm and Liu, 1998; Reich et al., 2001). The data presented here indicate, however, that there is a clear need to investigate the effects of clear-cutting over longer time scales than those used in many previous studies. While our use of stands originating from both clear-cuts and natural stand-replacing fires provides valuable information, it presents limitations that should be noted. Clear-cutting and natural fires that created our younger and older stands, respectively, are not identical disturbances. Thus, *Trillium* populations found in younger forests may not confidently reflect the result of a natural stand-replacing fire, nor can current *Trillium* populations in older forests surely reflect the projected future of *Trillium* found in the young stands, recovering from clear-cutting. On the other hand, the impacts affecting vegetation are



comparable in both disturbance scenarios; both clear-cutting and stand-replacement fires result in canopy removal and significant shifts in abiotic factors (Chen et al., 1995). In addition, prescribed fires following clear-cutting, where woody debris is removed, are quite similar to natural fire events. Consequently, because clear-cutting in our study area began in the 1960s, the older stands that are recovering from natural stand-replacing fires are the best and only proxy for use in a long-term chronosequence.

In our study, recovery of *Trillium* populations among the younger sites alone was not strongly related to age. Sites 2, 4 and 8, for example, have much higher *Trillium* abundances than sites of comparable or even greater age. The demographic structure of *Trillium* populations in these younger sites reveal many recruitment events during the last decade, indicating that in these recently clear-cut sites conditions are appropriate for recruitment and fast population recovery (Fig. 1). Further, our study has shown that those populations that have considerably high recruitment rates have persisted through disturbance in high numbers, while those populations where recruitment was limited survival was low or absent (Fig. 1). Population recovery of the non-clonal plant *Trillium* depends on seed production and dispersal. However, the spatial distribution of young and old *Trilliums* in our study sites (Fig. 4), and the limited seed dispersal by ants described in the literature (Mesler and Lu, 1983), suggest that dispersal distances for *Trilliums* are limited. Consequently, we conclude that the *Trillium* plants that have persisted through disturbance seem to facilitate within-site reproduction and thus foster population recovery.

To test if survived *Trillium* individuals were in fact facilitating within-site reproduction, we monitored seed production of these plants. We found that *Trilliums* in recently disturbed sites produced large quantities of seeds and that percent canopy openings showed a strongly positive correlation with the proportion of plants in a population that were reproductive and with the number of seeds that were produced in relation to population size (Fig. 3). Disturbances in forests are typically related to canopy openings, indicating a likely cause–effect relationship, where increased seed production following disturbance may compensate disturbance-related reductions in population size. The effect of increased seed production was even stronger when the youngest site

(Site 1) was excluded from the analysis. This site showed an unusually high percentage of reproductive plants with no seeds produced, which may be a result of the extreme environmental conditions found in very recently clear-cut sites.

In summary, population recovery of *Trillium* populations following clear-cut logging depends on a sufficient number of individuals surviving the disturbance event. Since survival rates are, however, generally low, the recovery process of *Trillium* populations is slow and might last centuries. While the design of our study supports this interpretation only indirectly, three key points in our data support our conclusion: (i) the relationship of individuals persisting through disturbance and recruitment; (ii) the limited dispersal ability of *trillium*; and (iii) the sufficient within-site seed production and recruitment in recently disturbed sites.

Our results support a number of studies that have investigated changes in understory plant composition through secondary succession following clear-cut logging (Dyrness, 1973; Schoonmaker and McKee, 1988; Elliott et al., 1997). In general, most understory plant species have been shown to be largely resilient to disturbances associated with clear-cut logging. Halpern and Spies (1995), for example, demonstrated that 70–90% of understory species in Pacific Northwest forests survived logging and burning and that most species lost through disturbance eventually recolonized the sites. In contrast to species presence, however, the abundance of understory plant populations generally remained depressed compared to pre-disturbance levels, even in the oldest secondary forests investigated (Halpern, 1989; Duffy and Meier, 1992).

The effects of stand replacing disturbances on understory plant species and the slow recovery rates have largely been explained by the life history traits of most species (Halpern, 1989). Slow growth rates, slow reproductive rates, limited seed dispersal and limited colonization ability are traits often associated with many herbaceous woodland species (Beattie and Culver, 1981; Hughes and Fahey, 1991; Matlack, 1994; Brunet and von Oheimb, 1998; Hermy et al., 1999; Bossuyt and Hermy, 2001; Singleton et al., 2001). *Trillium* shares many of these life history traits and can be regarded as a useful model organism for studying the mechanisms of population recovery of forest species after disturbance.



The work presented here has important implications for forest management if the maintenance of understory species diversity is desired. Because of potential future timber harvesting and natural stand-replacement fires in our study area, the few remaining old-growth fragments have a finite longevity. Thus, persistence of understory plant species like *Trillium* across large landscapes, which include plantations of various ages, will not be solely a function of the amount of the old-growth habitat patches remaining, but rather will also depend strongly on habitat in managed matrix. However, stand rotation rates in forests of the Pacific Northwest have traditionally been between 60 and 120 years (U.S. Forest Service, 1995). Our work indicates that in the majority of the managed sites in the Sucker Creek watershed, *Trillium* populations will not have recovered to pre-disturbance levels within this time period. Thus, repeated logging events, coupled with natural stochastic disturbances, will lead to further reduction of *Trillium* and other understory plant populations, unless fast recovery of populations in between extinction events is fostered, for example by ensuring within-site survival of few individual through disturbance that serve as founder plants of the regeneration of populations as shown in this study. Consequently, biological diversity in a forested landscape may depend on management practices, which are designed in such a way that either the frequency or intensity of timber harvesting is greatly reduced to permit the recovery of plants in managed forests.

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