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Flowering of understory herbs following thinning in the western Cascades, Oregon

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ABSTRACT

Thinning of young forest stands encourages development of the understory layer by increasing the levels of light and belowground resources. High-intensity thinning, with associated ground disturbance and high light levels, can lead to dominance by early seral species or by a few species of shrubs, while low-intensity thinning may not increase resource levels enough to encourage forest herbs. Changes in herb-layer abundance can be hard to detect because forest-floor herbs are often slow growing, but flowering increases rapidly in response to high resource levels. This study examined flowering of the understory herb community before and 5 years after low-intensity thinning. Flowering of 10 herb species was sampled in 62 nine-meter radius plots in six treatment units within the H.J. Andrews Experimental Forest. Thinning proved to be the most important determinant of the composition of the flowering assemblage (that is of which plants were flowering in a given plot). Old-growth species and release species (those specializing in large forest openings) showed higher numbers of flowering ramets following thinning. Release species also showed significant positive linear relationships with the plot-level degree of reduction in Douglas-fir (*Pseudotsuga menziesii*) basal area (BA), while old-growth species showed no significant relationships and forest generalist species showed significant negative linear relationships with reduction in BA. Plot-level reduction in BA explained little of the variation in numbers of flowering ramets per plot for most species except for the release species *Hieracium albiflorum* and the forest generalist *Trillium ovatum*. The overall lack of strong linear relationships between herb flowering and reduction in BA makes it difficult to predict optimal thinning intensities for these species. However, the results of this study suggest that even when low-intensity thinning does not significantly change herb abundance it could still influence the ecology of the understory herb community by increasing carbon allocation to sexual reproduction.

1. Introduction

The effects of thinning on understory herbs depend on the intensity of the thinning and on the degree of ground disturbance. In young (25–80-year old) *Pseudotsuga menziesii* forests in the Pacific Northwest, thinning significantly increases cover of disturbance-responsive release species and of non-natives, while having mixed effects on the abundance of forest-obligate species (Bailey et al., 1998; Thomas et al., 1999; Beggs, 2005; Chan et al., 2006). Even though thinning generally stimulates growth of understory species, ground disturbance and slash from logging operations can damage herb populations, which may or may not recover before the canopy closes again (Thomas et al., 1999; Berger et al., 2004; Wilson and Puettmann, 2007). A few orchids and ericaceous species that rely on mycorrhizal fungi for part or all of their carbon acquisition (myco-heterotrophs; Leake, 1994) disappear after clearcut harvesting (Dyrness, 1973; Nelson and Halpern, 2005) and may decline in abundance following thinning (Bailey et al., 1998; Thomas et al., 1999; Beggs, 2005). Thinning can also allow a low-diversity shrub layer to dominate the understory (He and Barclay, 2000; Thysell and Carey, 2001), despite an initial decline in some shrubs due to ground disturbance (Beggs, 2005).

The current study is part of a larger experiment to explore the effects of converting even-aged young Douglas-fir stands to an uneven-aged condition (Uneven Aged Management Project [UAMP], Anderson, 2007). Although the long-term management of the sites will include multiple thinning entries and under-planting of several tree species, the current study focuses on the effects of the initial thinning entry. This thinning was low-intensity compared to other similarly designed thinning studies (Poage and Anderson, 2007). Ground disturbance was minimized through the use of high-lead cable yarding, except on the flattest areas, and understory shrubs and tree seedlings were left intact wherever possible (Anderson, 2007). No previous study in this region had explored whether low-intensity thinning could increase populations of native forest-floor herbs without precipitating dominance

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of the understory by disturbance-responsive species. Five years after thinning on the UAMP sites, there was no change in understory cover (Anderson, 2007), and there were few significant changes in individual species cover in comparison to pre-thinning values (Anderson, unpublished data). The lack of response by release and non-native species probably reflects their requirements for ground disturbance and high light levels. Among forest-obligate herbs, the lack of response may be explained in part by the fact that many forest herb species employ a strategy of slow growth rates, low energy consumption, and extremely long lifespan of the genet (Eriksson, 1993, 1996). The transient pulse of resources following a low-intensity thinning operation may not be large enough or last long enough for changes in understory abundance (here measured as cover) to occur.

The current study tests the hypothesis that low-intensity thinning may lead to an increase in flowering by understory herbs even when there is no obvious increase in abundance. Flowering should provide a more sensitive index of plant response to resource levels than does abundance because while abundance changes very slowly, and may mostly reflect past stand conditions, flowering in understory herbs generally occurs only when resource levels are high (McCall and Primack, 1987; Hughes et al., 1988; Cunningham, 1997). In these stands, flowering ramets were almost entirely absent prior to thinning, so changes in flowering should be easier to detect than changes in abundance. Flowering is also important to study because flowering in understory herbs usually leads to seed set (McCall and Primack, 1987), so increases in flowering may affect long-term population dynamics.

Previous studies in *Pseudotsuga menziesii* forests have shown that understory herb and shrub flowering relate to stand density, and that this relationship is stronger for flowering than for vegetative abundance. Flower numbers differ more among stands of different management histories than do abundance or frequency of understory herb species (Lindh and Muir, 2004). In a young *Pseudotsuga menziesii* forest, all understory species examined except for *Chimaphila menziesii* flowered more in plots with lower basal area (BA). In contrast, species presence correlated with BA only for *Tiarella trifoliata* and *Chimaphila menziesii* (both positively) and abundance correlated with BA only for *Chimaphila menziesii* (positively) and *Trientalis latifolia* (negatively; Lindh, 2005). At the individual plant level, flowering *Linnaea borealis* individuals were found in higher light microsites than were non-flowering individuals; interestingly, this result was true for *Chimaphila menziesii* as well (Lindh, 2005). Thinning of young stands increased fruit production in most common understory shrub species in most years (Wender et al., 2004). Although old-growth forests have very different stand structure than young forests, the responses of herb species to environmental variables should be the same in old and young forests. A study involving creation of gaps in old-growth forests found a 30-fold increase in fecundity (number of seed capsules per meter squared of plant cover) for *Linnaea borealis*, while abundance increased only 10-fold; for *Tiarella trifoliata*, fecundity increased 230-fold while vegetative growth increased 10-fold (St. Pierre, 2000). Growth of both species, and fecundity of *Tiarella trifoliata*, appeared to respond primarily to increased soil moisture, while *Linnaea borealis* fecundity responded positively to light and soil moisture; interestingly, the response to light occurred only at low moisture levels and *vice versa*. In uncut portions of these same stands, removing belowground competition by severing tree roots with trenches significantly increased herb abundance and (observationally) increased the number of flowering ramets of *Tiarella trifoliata* (Lindh et al., 2003).

The current project examines whether there is a change in the number of flowering ramets of several dominant understory herbs following low-intensity commercial thinning. While all thinning prescriptions were low-intensity, the details of the thinning prescriptions varied among study units and the implementation of the thinning varied among plots within study units. As a result, I was able to ask whether post-thinning flowering in plots correlated with the plot-level change in Douglas-fir BA. I also examined whether the thinning response differed among species known to have different seral associations and disturbance responses.

2. Methods

2.1. Study sites and sampling design

Study sites were in the H.J. Andrews Experimental Forest (44°N, 122°30′W) on the west slope of the Cascade Range in Oregon, USA. This region experiences summer drought, with less than 10% of the total rainfall of about 200 cm falling during the summer months (Bierlmaier and McKee, 1989). Portions of the forest that have not been harvested support 300 to 500-year old stands with a dominant canopy of *Pseudotsuga menziesii* and a sub-canopy of *Tsuga heterophylla*. Second-growth stands examined in this study originated between 1950 and 1960 after clearcut harvest and broadcast burning of old-growth stands and were seeded or planted with *Pseudotsuga menziesii*. The present study was carried out on six of the sixteen treatments units of the larger UAMP study (Anderson, 2007); sampling was not carried out on other units because many of the treatment units had already been thinned at the time that this study was initiated. The design of the current study was constrained by the design of the larger UAMP study and by the availability of unthinned units at the time of sampling.

Treatment units were scattered within an approximately 2 km × 2 km area, ranged from 470 to 890 m in elevation and had NE to NW aspects (Table 1). Each treatment unit provides an independent replicate of the thinning treatment, since most units were not contiguous, and units had different slopes and aspects, independent management histories and different pre-harvest tree-densities (Table 1). At the beginning of this study, median trees per hectare (tph) in treatment units ranged from 650 to 970 (based on sample plots, not complete stand cruises). Average *Pseudotsuga*

Table 1
Characteristics of treatment units, including thinning prescription, harvest year, plant association, elevation range, average slope and median pre- and post-thinning density (tph) and BA (m^2/ha)

UAMP unit	Treatment	Year	Plant association	Elevation (m)	Slope (%)	TPH pre	TPH post	BA pre	BA post (min, max)
4	Light	1956	BENE-GASH[a]	717–774	33	765	480	34	22 (21, 31)
2	Light + gap	1951	BENE	805–853	41	650	460	38	27 (15, 37)
14	Light + gap	1950	BENE	497–601	36	970	560	43	31 (13, 38)
3	Heavy	1951	BENE	846–890	22	750	440	39	27 (19, 37)
7	Heavy	1950	POMU	630–735	26	660	360	37	24 (18, 33)
11	Heavy	1959	BENE-GASH	470–522	21	845	340	33	16 (10, 24)

[a] BENE, *Berberis nervosa*; GASH, *Gaultheria shallon*; POMU, *Polystichum munitum*.

menziesii tree diameter in sample plots was 24 cm. The UAMP study included three thinning prescriptions: a light thin, which aimed to achieve a relative density of 30, a light thin with 10% of the stand area in 0.05–0.1 ha gaps, and a heavy thin to relative density of 20, where relative density is Curtis' Relative Density Index (calculated as basal area over the square root of mean diameter of trees in the stand; see Anderson, 2007 for full study design). I sampled one light thin unit, two light thin with gap units, and three heavy thin units. In actual implementation, residual densities were higher than had been intended (Anderson, 2007), and plot-level thinning intensities varied widely. Median post-harvest densities (360–560 tph) and BA's (range 33–43 m^2/ha) on study plots did not correlate well with thinning prescriptions (see Table 1), leading me to focus on the overall effects of thinning rather than on differences between prescriptions. Overall, all of the treatment units in the current study had high residual densities compared to even the lightest prescription in other similarly designed studies: 250 tph for the Young Stand Thinning and Diversity Study (Davis et al., 2007) and Siuslaw Thinning and Underplanting for Diversity Study (Chan et al., 2006), and 300 tph in the Density Management Study (Fahey, 2006). In terms of BA, the UAMP "light thin" and "light thin with gaps" retained 78% of BA and the "heavy thin" retained 67% (Anderson, 2007), while light thinning treatments in other similar studies retained 50–60% of BA (Poage and Anderson, 2007). In the present study, skyline cables were used for most yarding; tractors were used only where slopes were less than 25%, which occurred only in small portions of the study units. Overall, ground disturbance was minimal and many understory shrubs remained intact. Pre- and post-thinning tree data and vegetation abundance were collected by UAMP crews. Pre-thinning tree data was collected in 1997–1998, thinning operations took place in the fall of 2000, and post-thinning tree data was collected in 2001.

2.2. Data collection

All sampling of flowering was carried out by the author to maintain consistency of the data. Prior to harvest, permanent tree macroplots of 0.10 ha had been laid out covering 7–15% of each treatment area. Plot centers had been randomly chosen from an evenly spaced grid of potential locations. A 9-m radius vegetation plot was established at the center of each macroplot for data collection in this study. Sixty-two plots were sampled across the six treatment units; 27 in "light thin with gap" units, 30 in three "heavy thin" units and five in one "light thin" unit. Aspect (recoded as degrees deviation from NE in either direction), slope and elevation were derived from a digital elevation model (DEM).

In each plot, the presence or absence of all herb and shrub species was recorded. Nomenclature follows Hitchcock and Cronquist (1973). Flowering of 10 focal herb species was visually estimated as the number of flowering events per 9-m radius plot. A flowering event was defined as a flowering ramet for most species, which had distinct ramets, and as the number of inflorescences for *Linnaea borealis*, which lacked distinct ramets. Focal species were chosen because they were abundant, encompassed a range of stand age associations, and maintained evidence of flowering (fruit or spent flowers) that persisted throughout the sampling period. Focal species were classified into three groups based on their response to clearcutting (Dyrness, 1973) and their relative abundance in young, mature and old-growth forests (Spies, 1991). In the following descriptions, species in bold flowered in at least 25% of plots (post-thinning) and were included in all analyses; other species flowered in more than 5% but less than 25% of plots and were included only in ordination analysis.

i. *Release species* (**Hieracium albiflorum, Trientalis latifolia** and *Osmorhiza chilensis*) are subordinate forest herbs and shrubs that are released by overstory removal (Halpern, 1989; McKenzie et al., 2000). They are associated with young or mature rather than old-growth forests, or show no stand-age affiliation (Spies, 1991).
ii. *Forest generalists* (**Trillium ovatum**, **Chimaphila menziesii**, *Anemone* spp.) are also most abundant in younger forests (Spies, 1991), but do not respond positively to clearcutting (Dyrness, 1973).
iii. *Late-seral species* (**Linnaea borealis**, **Coptis laciniata**, *Achlys triphylla*, and *Tiarella trifoliata*) are most abundant in old-growth forests (Spies, 1991). They show mixed responses to clearcutting (Dyrness, 1973), and are often associated with gaps in old-growth forest (Stewart, 1988; St. Pierre, 2000).

Pre-thinning flowering data were collected in mid-August 2000. Post-thinning flowering data were collected in late June 2005, the fifth growing season following thinning treatment. *Anemone deltoidea* and *Anemone lyallii* were considered as one taxon because it was not possible to distinguish between non-flowering individuals of the two species.

2.3. Statistical methods

Non-metric multidimensional scaling (NMS; McCune and Grace, 2002), an ordination technique, was used to evaluate changes in flowering of the herb community in individual plots from before to after thinning. NMS provides a low-dimensional (usually 2 or 3D) diagram in which the distance between sample units reflects their similarity in composition (in this case, their similarity in numbers of flowering ramets for each of the 10 focal species). The number of flowering ramets of each species in each plot was divided by the total number of flowering ramets of that species in all plots. This relativization by species totals equalizes the influence of common and rare species on the resulting ordination. A "dummy species" was included in equal abundance in every plot to allow plots that had no flowering ramets to remain in the analysis (NMS does not allow empty sample units). NMS analyses were conducted using PC-ORD software (Version 4.10, McCune and Mefford, 1999) with the Sørensen distance measure and the "slow and thorough" ordination settings (random starting configurations, 40 runs with real data, a maximum of 400 iterations, step-length = 0.20, and stability criterion = 0.00001).

For formal hypothesis tests on differences in flowering of individual species before and after thinning, I averaged all the plots that were sampled in one treatment unit in year, thus using treatment unit as the experimental unit in the analysis. The plots within each unit were not independent and treating them as such in the context of a hypothesis test would result in pseudoreplication. This averaging produced a dataset with 12 average flowering values for each species: one for each of the six treatment units in each of 2 years. To test for an effect of thinning on flowering in all the plant species considered simultaneously, I used the blocked multi-response permutation procedure (MRPP; McCune and Grace, 2002) in PC-ORD. The pre- and post-thinning data from each treatment unit were considered a "block" to account for the repeated-measures structure of the data. In PC-ORD I chose the Euclidean distance measure, and specified that median alignment should be performed. Before running the analysis I standardized each flowering value by its norm, meaning that I divided each flowering value by the square root of the sum of squares for that species. This relativization was performed to equalize the weighting of common and rare species; I used this particular technique because it is compatible with the Euclidean distance measure used in blocked MRPP.

The effect of thinning on individual species was assessed using the Wilcoxon signed rank test (on paired before/after data) because of non-normality of the data (for most species it yielded results that were not strikingly different from the results of Student's *t*-tests). Analysis was carried out in SPLUS (Version 2000; Mathsoft, 1999). Because of the small sample size (six treatment units in each year), this study has limited statistical power. As a result, I will discuss as "suggestive" differences with *p*-values greater than 0.05 but less than 0.1.

The effect of change in *Pseudotsuga menziesii* BA on flowering of individual species was estimated using general linear models (GLMs) in SPLUS. BA was used rather than canopy cover because it integrates above and belowground effects of trees, it is easy to estimate and therefore reliable, and it has been found to correlate with herb flowering in previous studies (Lindh and Muir, 2004; Lindh, 2005). For old-growth and forest generalist species, I used only those plots in which the species was present prior to thinning, since no flowering ramets ever occurred in previously unoccupied plots. For release species, I also included any plots with post-thinning flowers. I used numbers of flowering ramets rather than increase in flowering because I was interested in potential reproductive output; the results would have been similar either way because the pre-harvest flower numbers were very low. This analysis was carried out on plot-level data and was used to judge relative strength and direction of relationships between tree variables and flowering in plot-level data; the *p*-values cannot be interpreted strictly because the plots were aggregated in treatment units rather than occurring as independent random samples of the study landscape. The response distribution was specified as Poisson but included a term that allowed for over-dispersion (quasi-likelihood approach; Schabenberger and Pierce, 2002; Lindh, 2005 for more details). Model explanatory power was expressed as percent reduction in deviance (PRD) from the null model to the current fitted value. PRD is analogous to the more familiar coefficient of determination (R^2), although since it may not scale the same as R^2, direct comparison of the two measures may not be appropriate (Schabenberger and Pierce, 2002). Significance of terms was assessed using drop-in-deviance *F*-tests. Two species (*Linnaea borealis* and *Trientalis latifolia*) had one or two outlier plots with approximately three times as many flowering ramets as in any other plot; these points were dropped from the analysis.

3. Results

Thinning had a significant effect on the overall composition of the flowering community (blocked MRPP, $A = 0.16$, $p = 0.008$), as assessed by comparing treatment units before and after thinning. Thinned plots also showed flowering assemblages that were distinct from unthinned plots in an NMS ordination (Fig. 1). NMS ordination of plots in terms of the number of flowering ramets of each species provided a three-dimensional solution (stress = 17.57, *p*-value = 0.020 based on Monte-Carlo simulations) that explained 72% of the variation in the data. Axis 1, which explained 32% of the variation in the data, reflected variation in community composition due to thinning; although pre-thinning and post-thinning plots were intermixed, most pre-thinning plots were restricted to the lower half of Axis 1 and most post-thinning plots appeared higher on the axis (Fig. 1). Flowering of all focal herb species except for *Tiarella trifoliata* was positively correlated with position on Axis 1 (Table 2), with *Linnaea borealis*, *Trientalis latifolia*, and *Hieracium albiflorum* showing the largest positive correlations. Plots in the one "light" thinning treatment unit were all low on Axis 1, while plots from the "light thin with gaps" and "heavy thin" treatment units occupied overlapping multivariate space that spanned most of Axis 1. The upper end of Axis 1 was occupied by a few plots from the "heavy thin" treatment units. The position of plots on Axis 1 was correlated with *Pseudotsuga menziesii* BA ($r = -0.34$) and change in *Pseudotsuga menziesii* BA ($r = 0.55$; Fig. 2), as well as with change in total BA and change in tree density ($r = 0.53$, $r = 0.46$, respectively).

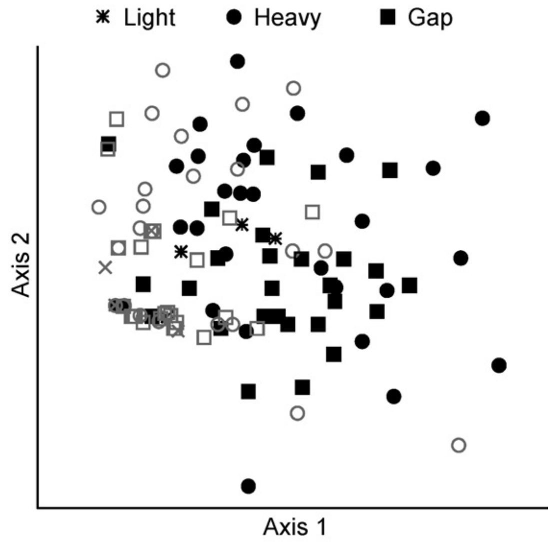

Fig. 1. NMS ordination of pre- and post-thinning plots in terms of their flowering assemblages (data from 10 herb species in 124 plots). Open gray symbols are before thinning, filled black symbols are after. Symbol shape indicates thinning prescription. "Gap" indicates the light thin with gaps treatment; note that no sample plots were located in gap centers.

Axis 2, which explained 22% of the variation in the original data, reflected variation in community composition that was interpreted as being related to soil moisture, with wetter sites getting higher scores (Fig. 1). Position on Axis 2 was positively correlated with the pre-harvest presence of the mesic-site ferns *Adiantum pedatum* and *Blechnum spicant*, and with the mesic herbs *Boykinia elata*, *Mitella* spp., *Streptopus* spp., and *Circaea alpina* ($r > 0.4$ for all). Flowering of *Coptis laciniata*, *Linnaea borealis*, *Trillium ovatum* and *Tiarella trifoliata*, but not of other focal species, were positively correlated with score on Axis 2 (Table 2). Axis 3 (not shown in figure), which explained 18% of the variation in the original data, reflected variation in community composition due to pre-thinning canopy openness, with the relatively few plots that were naturally open or partly open due to rocky soils getting low scores.

Table 2

Correlations of numbers of flowering ramets per plot with positions of plots on the first two axes of the NMS ordination of pre- and post-thinning data together. Interpretations of axes are based on correlations of axes with environmental variables and on patterns of presence/absence of all herb and shrub species

	Axis 1	Axis 2
	Thinning	Moisture
Old-growth		
Coptis laciniata	0.28	0.26
Linnaea borealis	0.41	0.23
Forest generalist		
Trillium ovatum	0.26	0.45
Chimaphila menziesii	0.19	−0.14
Release		
Trientalis latifolia	0.49	−0.10
Hieracium albiflorum	0.44	−0.15

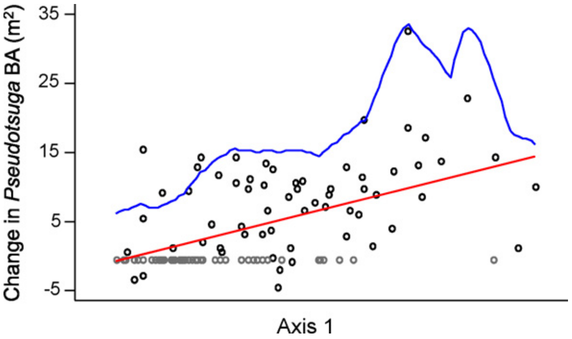

Fig. 2. Change in *Pseudotsuga menziesii* BA vs. position on Axis 1 from NMS ordination of plots in terms of their flowering composition. Black circles are post-thinning plots, gray circles are pre-thinning plots, which by definition have zero change in basal area. Lines generated by PC-ORD; straight line is from simple linear regression, line of maximum response is calculated to include 95% of points.

Of six species surveyed, all showed larger numbers of flowering ramets after thinning (Table 3). The differences were significant ($p < 0.05$) for the release species *Trientalis latifolia* (18 flowering ramets per plot afterwards vs. 2.6 before) and *Hieracium albiflorum* (3.6 vs. 0.14) and for the old growth associated species *Linnaea borealis* (113 vs. 5.3). For the old-growth associated species *Coptis laciniata* the difference (0.83 vs. 0.23) was suggestive of statistical significance ($p = 0.10$). There were no significant effects of thinning on forest generalist species. Forest generalist and old-growth species never flowered in plots in which they had not been present prior to thinning. Among release species, *Trientalis latifolia* flowered in four newly colonized plots and *Hieracium albiflorum* flowered in 11 newly colonized plots.

Linear regression showed a significant effect of post-thinning change in BA on flowering for some species (Table 4). Numbers of flowering ramets of the forest generalists *Trillium ovatum* and *Chimaphila menziesii* showed negative linear relationships with reduction in BA, while numbers of flowering ramets of the release species *Trientalis latifolia* and *Hieracium albiflorum* (Fig. 3) showed positive linear relationships with BA reduction. Models had little explanatory power except for the release species *Hieracium albiflorum*, which showed a 34% reduction in deviance, and the forest generalist *Trillium ovatum*, which showed a 25% reduction in deviance.

Table 3
Mean number of flowering ramets per plot before and 5 years after thinning. Probability values from Wilcoxon signed rank tests on plot-level data ($n = 6$ pairs). Values from old-growth are included for comparison only; they are from plots of the same size sampled in a previous study on nearby stands (Lindh and Muir, 2004)

Species	Mean before (S.E.)	Mean after (S.E.)	*p*-value	Old growth
Old-growth				
Coptis laciniata	0.23 (0.13)	0.83 (0.31)	0.10	3.54
Linnaea borealis	5.31 (2.31)	112.84 (72.25)	0.05	97.05
Forest generalist				
Trillium ovatum	0.44 (0.33)	0.68 (0.36)	0.11	1.64
Chimaphila menziesii	0.94 (0.22)	1.39 (0.77)	0.92	0.74
Release				
Trientalis latifolia	2.61 (0.84)	18.36 (3.33)	0.00	4.32
Hieracium albiflorum	0.14 (0.08)	3.57 (1.47)	0.03	0.62

Table 4
Coefficients from regression models of the effect of change in *Pseudotsuga menziesii* BA on the mean number of post-thinning flowering ramets per plot for understory herb species. Coefficients are untransformed Poisson regression coefficients. Terms with asterisks contributed significantly to model fit as judged by drop-in-deviance *F*-tests

	Change in BA (m^2)	dp[a]	PRD[b]
Old-growth			
Coptis laciniata	−0.026	3	1
Linnaea borealis	0.020	258	1
Forest generalist			
Trillium ovatum	−0.145*	4	25
Chimaphila menziesii	−0.053*	6	4
Release			
Trientalis latifolia	0.032*	16	5
Hieracium albiflorum	0.093*	10	34

[a] dp, dispersion parameter, where a value of 1 indicates a Poisson distribution and larger values indicate over-dispersion (in this case, the presence of a few plots with very large numbers of flowers).

[b] PRD, percent reduction in deviance, an approximate metric of explanatory power.

4. Discussion

The most important conclusion of this study is that low-intensity thinning can lead to an increase in flowering of many understory herb species even when there is no significant change in understory herb abundance. Five years after low-intensity thinning in young *Pseudotsuga menziesii* stands, both old-growth associated herb species, which have evolved to respond to canopy gaps, and release species, which specialize in clearcuts, burns, and other large disturbances, showed increased flowering, while forest generalists showed equivocal or negative flowering responses. Ordination analysis of flowering data revealed that thinning was the most important source of variation in flowering composition of the plots, more important even than variation in site moisture status. While the overall thinning prescriptions in this study were low-intensity, plot-level thinning intensities varied widely. Correspondingly, the ordination of flowering data showed a range of post-thinning plot compositions, with some plots having many flowering ramets and other plots having few flowering ramets and remaining close to the flowering composition of pre-thinning plots. Variation within treatment units, both in the degree of reduction in BA and in unmeasured factors such as site history, was more important than differences between thinning prescriptions, since plots from all three treatments were intermixed across the ordination diagram.

Among old growth associated and release species, the largest increases in flowering were in two species with rapid clonal growth, *Linnaea borealis* (20-fold increase) and *Trientalis latifolia* (sevenfold increase); and in a non-clonal member of the Aster family, *Hieracium albiflorum* (25-fold increase). All three species

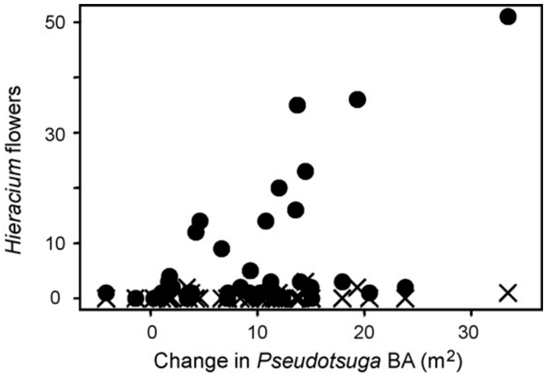

Fig. 3. Number of *Hieracium albiflorum* flowering ramets in occupied plots vs. change in *Pseudotsuga menziesii* BA. Solid dots are post-thinning, crosses are pre-thinning.

have previously been shown to be indicator species for thinned in comparison to unthinned areas (Beggs, 2005). Although *Linnaea borealis* was classified here as old growth associated because it reaches its highest abundance in old-growth stands (Spies, 1991), it is sometimes classified as a release species (McKenzie et al., 2000) because of its ability to respond quickly to new canopy openings. It expands along the ground surface *via* stolons, which grow an average of 0.4 m a year (Antos and Zobel, 1984), and from which frequent side branches extend, bearing flowers only when resource levels are adequate (Eriksson, 1992, 1988). The increase in flowering seen here in thinned plots cannot have occurred without the growth of many new stolons, and high densities were observed in some heavily thinned plots in the field. The fact that this vegetative growth was not evident in the abundance data (Paul Anderson, unpublished data) may reflect much larger noise in the abundance data due to small plot sizes, to difficulty in estimating cover and to turnover in field crew personnel. The release species *Trientalis latifolia* also expands clonally, but in this species ramets extend one or more ephemeral rhizomes each year, at the end of which a new tuber is produced, replacing the old ramet. Rhizome length depends on resource availability and can exceed one meter; large plants may produce more than one new tuber in a year (Anderson and Loucks, 1973). In these young forests, typically only 50% of ramets flower (personal observation), so there is a bank of non-flowering individuals able to begin flowering when resource conditions improve. The third species that responded strongly to thinning in this study, *Hieracium albiflorum,* produces copious seed, which germinates in a variety of young forest conditions (Lindh, in preparation). For *Hieracium albiflorum*, flowering response to thinning probably reflects both the maturation of previously non-reproductive rosettes and the flowering of newly established individuals. All three of these species achieved post-thinning densities of flowering ramets comparable to or higher than in nearby old-growth stands sampled previously (Lindh and Muir, 2004; data shown for comparison in Table 3). For these species, thinning of a young forest creates microsites that are arguably better (and more abundant) than the microsites created by tree fall gaps in old growth. In young forests, even small canopy openings should create high light levels because the surrounding trees are short and there is relatively little competing vegetation.

More shade-tolerant species showed smaller responses to thinning, although the direction of the response depended on the seral association of the species. These smaller responses may reflect the tradeoff in which these species tolerate low resource levels by having intrinsically slow growth rates. Flowering of the old-growth associated species *Coptis laciniata* increased in response to thinning but still remained well below that observed in nearby old-growth stands (Table 3). It is clonal and may have many ramets in a genet, but is limited in its ability to rapidly increase flower numbers because there is only one flowering stalk per ramet. It is unclear whether *Coptis laciniata* would eventually achieve a larger flowering response to thinning if the canopy remained open, or whether it requires other specific aspects of the old-growth environment for optimal growth and reproduction. It is interesting to note that in the field, large numbers of *Coptis laciniata* individuals were sometimes observed flowering in very heavily thinned plots and that these individuals had small, chlorotic leaves, probably due to effects of intense sunlight.

Flowering of the forest generalists *Trillium ovatum* and *Chimaphila menziesii* showed no significant responses to the overall thinning treatments in this study. *Chimaphila menziesii* is clonal and very shade tolerant; its negative relationship with the plot-level degree of BA reduction will be discussed below. *Trillium ovatum* cannot rapidly change vegetative abundance or flower numbers because it is non-clonal and each ramet produces at most one flowering stalk. The lack of flowering response observed here may reflect small pre-thinning populations, loss of individuals as a result of thinning or failure of vegetative individuals that survived thinning to grow enough to flower. *Trillium ovatum* does not flower unless individuals have reached a threshold size, which requires at least 10 years of age (St. Pierre, 2000). Although canopy gaps do stimulate flowering in this species (St. Pierre, 2000), it does not flower as much in full sun as in part sun (St. Pierre, 2000; Lindh, 2005). *Trillium ovatum* populations can decline as a result of more intense harvest, either heavier thinning (Beggs, 2005), or clearcutting (Dyrness, 1973; Jules and Rathcke, 1999), but, at least in the western Cascades, recover within 5 years of clearcutting (Dyrness, 1973).

Because there was very little ground disturbance in this study, and no sample plots experienced total canopy removal, I expected that flowering would respond linearly to BA reduction, with the most heavily thinned plots showing the greatest flowering response for most species. In practice, however, only release species showed the expected significant positive relationships with BA reduction, while old-growth species showed no significant relationships with BA reduction, and forest generalists showed significant negative relationships. Reduction in BA had relatively little explanatory power for most species. The exceptions were *Trillium ovatum* and *Hieracium albiflorum*, for which the percent reduction in deviance exceeded 25%. *Trillium ovatum*'s negative relationship with BA reduction is potentially worrisome given the other documented negative effects of harvest on this species (Jules and Rathcke, 1999; Beggs, 2005). The forest generalist *Chimaphila menziesii* also showed a negative relationship with thinning, but with very little explanatory power. This lukewarm response to thinning is consistent with the idea that this species may be obtaining photosynthate both directly and via mycorrhizal connections with trees (see discussion in Lindh, 2005). Because of *Chimaphila menziesii*'s near-ubiquity in young *Pseudotsuga menziesii* forests in the western Cascades, its negative flowering response to BA reduction is probably not a reason for concern. However, *Chimaphila menziesii* may serve as an indicator for the suitability of the habitat for rarer obligately or facultatively mycotrophic species such as *Pyrola* spp., *Goodyera oblongifolia*, and other orchids. My overall conclusion from these results is that, even under conditions of minimal ground disturbance, it is difficult to determine an optimal thinning intensity for the understory herb community. A spatially variable pattern of BA reduction is most likely to provide at least some patches where the stand density is right for the herb populations that happen to occupy that patch, and should prevent extirpation of any species from the site.

The current study provides an indication of how understory herb flowering may respond to thinning, but the scope of inference is small because the study units were all located within a 2 km × 2 km area of the H.J. Andrews Experimental Forest. Another limitation of this study is that year-to-year variation in flowering, which does occur in understory herbs (Tyler, 2001), is potentially confounded with the effect of thinning. Although in theory inclusion of a control treatment unit would have solved this problem, sampling of the one nearby control treatment unit was abandoned because the understory herb populations in this unit were so sparse that no flowering ramets were found even after harvest. Other evidence, however, provides strong support for the idea that the pre- and post-harvest differences seen here resulted from harvesting and not year-to-year variation. If the increase in flowering had resulted from annual variation, the plot-level increases should not have been correlated with change in BA. Furthermore, ordination of the post-thinning data alone (results not shown) yielded similar gradients to those seen in the ordination of pre- and post-thinning data together, confirming an effect of thinning separate from year-to-year variation. I used the same plot design to study flowering in many young stands of similar age and management history across the H.J. Andrews Experimental Forest in the years 2000–2002 (Lindh and Muir, 2004; Lindh, 2005). One set of plots was sampled in both 2000 and 2001, revealing up to twofold variation in the number of flowering ramets per species from year to year. While noticeable, this degree of variation is small compared to the 4- to 25-fold increases observed in the current study (Lindh unpublished data). Prior to thinning, flowering of old-growth and release species in the current study plots was generally somewhat lower than in comparable unthinned young stands, suggesting, as I observed in the field, that these understory communities were somewhat depauperate. After thinning, numbers of flowering ramets for species in these two groups were higher than in any comparable unthinned stand sampled during these years, which suggests that the thinning effect was much larger than any year-to-year variation. Year-to-year variation in flowering in understory herbs is driven primarily by climate (Tyler, 2001). The 2-year period before each sampling year was made up of a wet year (220 cm of precipitation) followed by a dry year (160–175 cm; McKee, 2005), so rainfall should not account for any differences between sampling years.

The increased flowering observed on these study sites after thinning could lead to establishment of new individuals from seed. In long-lived understory herbs, establishment of a few new individuals from seed may have large effects on the long-term dynamics of the populations. In wild ginger (*Asarum canadense*), a modeling study suggests that although establishment from seed is rare, it is important to population dynamics because it allows the establishment of genets in more suitable locations that can compensate for the occasional loss of genets in the least suitable locations (Damman and Cain, 1998). On average, shade tolerant species ought to be able to survive closed-canopy conditions and thus ought to have longer-lived genets than light-demanding species. In the western Cascades, *Coptis laciniata* is such a species; its abundance is uncorrelated with tree BA even in closed-canopy young forests (Lindh, 2005). As a result of its ability to survive in dense forest patches, *Coptis laciniata* probably loses very few genets over time and its populations should be able to persist without the establishment of new genets. More light-demanding species such as *Linnaea borealis* probably suffer greater genet loss, due either to small-scale events like growth of a hemlock understory layer in an old-growth canopy gap or to larger-scale events like canopy closure in planted young forest stands. One would expect that populations of light-demanding species would thus be more dependent on the establishment of new genets from seed.

Establishment of new genets depends not just on flowering but also on seed set and establishment from seed. A seed sowing experiment has demonstrated that for two of this study's focal species, locally produced seed is viable and can establish successfully in young forests (Lindh, in preparation). Seeds of *Coptis laciniata* and *Hieracium albiflorum* sown in young forest plots not only germinated, but established and survived over a 5-year period, with *Hieracium albiflorum* survival rare and *Coptis laciniata* survival relatively common. Seedlings of some forest-generalist and release species appeared spontaneously in the seedling plots, while old-growth species did not. Informal observation indicates that the forest generalists *Trillium ovatum* and *Anemone* spp. produce observable seedling clumps near sexually reproducing adults in young forests (personal observation). In old growth, *Trillium ovatum* seedlings occur in forest and at gap edges but not within experimentally created gaps (St. Pierre, 2000). The forest generalist *Chimaphila menziesii* has been shown to rapidly colonize young forest plots after canopy closure (C.B. Halpern unpublished data), suggesting establishment from seed. In *Linnaea borealis*, seed set is abundant and at least some seed is viable, but seedlings are uncommon in the wild (Eriksson, 1992); *Linnaea borealis* seedlings were not observed in the current study. *Trientalis latifolia* also produces viable seed, but seedlings have not been observed in the field (Anderson and Loucks, 1973; personal observation). It is interesting that these latter two species, which show the least evidence of ability to reproduce from seed, are the ones that, as argued above, should in theory rely the most on it.

An important implication of this study is that thinning may influence sexual reproduction of understory herbs, and thus plant population dynamics, without having a large effect on vegetative abundance. Changes in plant populations would required that thinning leads not just to increased flowering, but also to increased seed set, which has not been tested. Further work will examine the link between flowering and seed set for these species, in thinned and unthinned young forest and in old growth. Further work will also explore the long-term (10-year) vegetative and flowering response to thinning for these species, as well as their responses to future thinning entries as the treatment units continue to be converted to an uneven-aged condition.

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