

VARIATION IN RESPONSES OF LATE-SERIAL HERBS TO DISTURBANCE AND ENVIRONMENTAL STRESS

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Abstract. Clonal herbs that attain maximum development in late-seral forest are often assumed to have similar responses to disturbance and to be functionally equivalent. However, little is known about the demographic or physiological responses of these plants to disturbance or to the altered conditions of the post-disturbance environment. Following harvest of a mature coniferous forest, we compared abundance, demographic changes, and physiological acclimation of three clonal herbs (*Asarum caudatum*, *Clintonia uniflora*, and *Pyrola picta*) that differ in belowground morphology and leaf longevity. We measured ramet density, leaf area, and demographic variables (survival, clonal growth, flowering, and seedling establishment) before and for two years after harvest, and in adjacent undisturbed forest. Acclimation to increased solar radiation was assessed two years after harvest by measuring leaf mass per unit area (LMA) and chlorophyll *a:b* ratios of leaves produced in the current year. Although initial declines in abundance were similar, demographic responses indicate that patterns of recovery varied greatly among species. Two years after logging, ramet survival and clonal growth (production of new ramets) of *Clintonia* were greater in the harvest area than in the forest. *Asarum* had lower survival in the harvest area, but greater clonal growth, and *Pyrola* showed no difference in either survival or growth between environments. Only *Asarum* produced seedlings, although their survival was low in the harvest area. All species had higher LMA in the harvest area, but only *Clintonia* (with annual leaves) had a higher chlorophyll *a:b* ratio, suggesting the greatest potential for acclimation to increased light. Our results demonstrate that forest herbs with greater rhizome plasticity and shorter leaf duration have greater potential to acclimate after disturbance than those with rigid architectures and persistent leaves. Thus, species with comparable successional roles can vary substantially in their demographic and physiological responses to disturbance, with potential consequences for long-term recovery.

Key words: *Asarum caudatum*; chlorophyll content; *Clintonia uniflora*; forest herbs; light acclimation; plant demography; *Pyrola picta*; timber harvest.

INTRODUCTION

One explanation for the associations of some plant species with late-seral forests is that they respond similarly to disturbance and environmental stress. Although these species commonly show dramatic declines in abundance after stand-replacing disturbance (Schoonmaker and McKee 1988, Halpern 1989, Halpern and Spies 1995, Nelson and Halpern 2005), little is known about their demographic responses or abilities to acclimate to the environmental stresses of the post-disturbance forest. Most forest herbs are clonal (e.g., Sobey and Barkhouse 1977, Antos and Zobel 1984, 1985a) and fitness generally is limited by growth and survival rather than fecundity (Fagerström 1992, Silver-town et al. 1993, Salomonson et al. 1994). Once

extirpated, these species have limited ability to recolonize: most lack a seed bank (Archibold 1989, Halpern et al. 1999), flower infrequently (Geber et al. 1997, Lindh 2005), and have limited dispersal ability (Bierzzychudek 1982, Cain and Damman 1997, Matlack 2005). Thus, persistence through early succession is dependent on successful morphological and physiological acclimation to sudden changes in environment. Conservation of forest herbs in managed landscapes necessitates an understanding of the interplay among life history traits, effects of disturbance on population dynamics, and potential for physiological acclimation to environmental stress.

The wide range of architectures and growth strategies present among clonal forest herbs (Sobey and Barkhouse 1977, Antos and Zobel 1984, Antos 1988) could lead to different responses to disturbance or associated changes in environment. For instance, variation in belowground morphology, including rhizome thickness and depth or distance between ramets, may shape responses to mechanical disturbances that destroy or bury plants, or sever their rhizomes (Sobey and Bark-

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house 1977, Antos and Zobel 1984, 1985a, b). Phenotypic variation in rhizome growth can facilitate escape from adverse conditions, movement into new environments, or acquisition of resources from multiple locations (Slade and Hutchings 1987, Hutchings 1988, van Groenendael et al. 1996). In addition, some species produce dimorphic rhizome segments (long and short shoots) that confer flexibility in rhizome-system development, permitting ramets to remain in favorable environments or to move to new locations if conditions are unfavorable (e.g., de Kroon et al. 1994, Lezberg et al. 2001).

Leaf morphology and physiology can also influence ability to acclimate to changes in environment. Species adapted to shade differ in their abilities to acclimate to high-light environments by adjusting leaf morphology or biochemistry (Björkman 1981, Osborne et al. 1994). In the forest understory, shade plants allocate more resources to light capture and production of chlorophyll *b* (chl *b*) than to maintenance of photosynthetic reaction centers and associated production of chlorophyll *a* (chl *a*) (Pearcy and Sims 1994). However, abrupt increases in light associated with forest canopy removal can cause light, temperature, and water-deficit stress in shade-adapted species (Osmond 1983). These stresses may lead to photoinhibition, photorespiration, and destruction of chlorophyll (photooxidation) (Powles 1984, Pearcy et al. 1989). Plants have evolved numerous forms of photosynthetic acclimation to high-light conditions. These include adjusting the ratio of leaf mass to surface area (LMA) through production of thicker leaves with taller or more layers of palisade cells (Gamon and Pearcy 1989) or increasing chl *a:b* ratios (Lambers et al. 1998). Without these or other modifications, plants may sustain damage to their photosynthetic apparatus (Powles 1984).

Another factor that may influence acclimation is leaf lifespan, which varies inversely with net photosynthetic capacity (Reich et al. 1991). Short leaf duration can facilitate rapid acclimation to changes in light availability because the sun or shade character of a leaf is largely determined during leaf development (Lambers et al. 1998). Thus, whole-plant acclimation may be delayed until shade leaves are replaced with leaves formed in high light. However, some plants can change LMA in mature leaves by producing an additional layer of palisade parenchyma upon exposure to increased irradiance (Bauer and Thöni 1988).

Initial survival and performance in the post-disturbance environment are also shaped by microsite variation; soil disturbance, logging slash, and residual plant cover can be highly patchy after timber harvest, resulting in considerable variation in soil-surface radiation and temperature (e.g., McInnis and Roberts 1995, Heithecker and Halpern 2006). Shading by taller vegetation or woody debris can be beneficial, but burial beneath dense accumulations of slash can prevent meristem emergence and survival. Quantifying relation-

ships between these factors and plant response contribute to understanding initial declines in abundance and the mechanisms that shape early responses to stress.

In this study, we compare demographic and physiological responses to timber harvest of three clonal forest herbs: *Asarum caudatum*, *Clintonia uniflora*, and *Pyrola picta*. These species were selected because they are broadly distributed, reach maximum abundance in late-seral forests, and differ in below-ground morphology and leaf duration. We hypothesized that different sets of traits could lead to differences in patterns of abundance, demographic response, or acclimation to environmental change. We posed the following questions: Do species respond differently to disturbance and environmental stress? Specifically, how does timber harvest affect species abundance (ramet density and leaf area) or demographic trends (rates of ramet survival, clonal growth, flowering, and seedling establishment)? Do initial declines in abundance or demographic responses vary with post-harvest ground conditions (disturbed soil or logging slash) or shading by herbs or shrubs? Are LMA and chl *a:b* ratios greater for plants in logged areas than in undisturbed forest, suggesting acclimation to high-light conditions?

METHODS

Study site: physical environment and vegetation

This study was conducted in the Gifford Pinchot National Forest in southwestern Washington (46°22'07" N, 121°34'40" W). The site occurs on a steep (40%) southeast-facing slope at an elevation of 1012–1122 m in the *Tsuga heterophylla* zone (Franklin and Dyrness 1973). Soils are well drained, but fairly shallow, consisting of loamy sands derived from residuum and colluvium with a shallow surface layer of volcanic ash originating from the 1980 eruption of Mount St. Helens (Wade et al. 1992). The regional climate is characterized by warm, dry summers and cool, wet winters with most precipitation falling between October and April (Franklin and Dyrness 1973).

At the time of harvest, forests were 70–80 years old and dominated by *Pseudotsuga menziesii*, with occasional *Tsuga heterophylla* and *Thuja plicata*. Canopy height averaged 36 m; tree density, 1150 trees/ha; and basal area, 56 m²/ha. Common understory species included *Acer circinatum*, *Berberis nervosa*, *Pteridium aquilinum*, *Achlys triphylla*, and *Chimaphila umbellata*.

Sampling occurred within the logged portion of a 13-ha aggregated-retention harvest unit (part of the DEMO experiment; Halpern et al. [2005]), and in adjacent undisturbed forest (hereafter "forest"). In September 1997 all merchantable trees (>18 cm dbh) were felled and removed, leaving residual slash in place. Total slash cover averaged 77%; slash depth averaged 14 cm, but exceeded 30 cm at some locations. Cover of exposed mineral soil was low, averaging 4% (Halpern and McKenzie 2001). Microclimatic measurements taken seven years after harvest showed strong contrasts in

radiation and temperature between logged and forested areas (Heithecker and Halpern 2006). Photosynthetic photon flux density (PPFD) over the growing season averaged $36.4 \text{ mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ in the harvest area, but only $8.6 \text{ mol} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ in the forest. Mid-summer air and soil temperatures were much higher in the harvest area: mean daily values by 3.3°C and mean maxima by as much as 5.6°C . These differences were likely to have been even greater at the time of our study, when mineral soil was first exposed and plant cover was much reduced (Halpern and McKenzie 2001). Strong contrasts in microclimate between logged areas and residual forest are typical in this region (Chen et al. 1993), which underscores the idea that herbs present before disturbance are exposed to sudden environmental stress.

Study species

The study species (*Asarum caudatum*, *Clintonia uniflora*, and *Pyrola picta*) are perennial forest herbs that spread via rhizomes to form clones and are common from the west coast of North America inland to the Rocky Mountains (Hitchcock and Cronquist 1973). All three reach maximum abundance in mature or old-growth forests and are adversely affected by logging (Halpern 1989, Halpern and Spies 1995, Nelson and Halpern 2005). However, they differ in leaf duration, belowground morphology, rates of flowering and seedling establishment. *Asarum caudatum* (Aristolochiaceae) has ramets with one or two cordate to reniform leaves that persist for up to three years. It is mat-forming via stout rhizomes with short internode segments that are distributed mainly in the litter layer. Flowers are purple to dark brown and solitary. This species has received little study compared to its northeastern relative, *A. canadense*. The latter produces new leaves, ramets, and flowers only after plants are several years old, and exhibits higher rates of seedling establishment than other rhizomatous forest herbs (Cain and Damman 1997, Damman and Cain 1998).

Clintonia uniflora (Liliaceae) has ramets with one to three basal leaves that are short-lived, typically surviving one growing season. Rhizomes are thin, shallowly buried, and vary markedly in length (Antos 1988). *Clintonia* can produce a solitary white flower that yields a metallic-blue fruit; however, most plants do not flower in undisturbed forest (Antos 1988), and seedling establishment is uncommon (C. R. Nelson, *personal observation*). *Clintonia borealis*, which has been intensively studied in forests of eastern North America (Pitelka et al. 1985), exhibits similar characteristics: current-year ramets produce one or two rhizomes that yield next year's ramets, and plants do not flower until they are ~ 10 years old.

Pyrola picta (Ericaceae) has a basal rosette of evergreen leaves that are long lived (>3 yr). Leaf morphology varies with environment: in dry sites, leaves have more epicuticular waxes, smooth margins, more stomata on the lower surface, and two layers of palisade

cells (Copeland 1947, Haber 1987). In contrast to *Asarum* and *Clintonia*, *Pyrola* has deeply buried rhizomes that are branching, with root systems that have strong associations with both ericoid and arbutoid mycorrhizae (Largent et al. 1980, Haber 1987). Inflorescences contain up to 25 flowers (Haber 1987) and, although plants flower frequently, seedling establishment is rare (C. R. Nelson, *personal observation*).

Sampling design

Pre-harvest sampling was conducted from 21 July to 5 September 1997. In a 6-ha area of a planned harvest unit and a 7-ha area of adjacent forest, we identified for each study species groups of ramets ("patches") based on four criteria: (1) ≥ 15 ramets in a patch, (2) >15 m from neighboring patches of the same species, (3) >60 m from the harvest-unit edge, and (4) all ramets in a patch fit within a 1×4 m plot (to facilitate access to all ramets with minimal disturbance). From these patches, nine were randomly selected for each species in each environment. Maximum distances between patches were ~ 240 m in the harvest area and ~ 275 m in the forest.

All ramets within each plot were numbered with aluminum tags to monitor survival. For each ramet, leaf length and width were measured and multiplied to estimate leaf area, then summed for all ramets in a plot (total leaf area). The number of ramets with flowers was counted. All measurements taken during the initial sampling were repeated during the first and second summers after harvest (1998 and 1999; years 1 and 2, respectively). Tagged ramets that survived were remeasured; new ramets (produced through clonal growth) and seedlings (germinants with cotyledon leaves) were tagged and measured. To relocate ramets, slash was carefully lifted and replaced, as necessary; almost all tags were successfully relocated (3.5% loss). Seedlings were treated as ramets in subsequent years.

To quantify ground conditions and shading by residual vegetation in the harvest area, additional measurements were made in year 1. Cover (%) of disturbed soil and logging slash was visually estimated in each plot. Slash was characterized by three density classes: light (non- or minimally overlapping wood or foliage); moderate (multiple overlapping pieces); or heavy (entirely overlapping pieces). Cover in each class was estimated independently (i.e., the total of the three classes was not constrained to 100%). In addition, total cover (%) of associated herbs (<1 m tall, including subshrubs) and shrubs (≥ 1 m tall) was estimated in each plot.

Leaf mass per unit area (LMA) and chlorophyll content were determined in year 2 (24–25 July 1999). For each species, one leaf produced during the current growing season was collected from randomly selected ramets in the harvest area and adjacent forest ($n = 20$ in each environment for *Clintonia* and *Pyrola*; $n = 18$ for *Asarum*); sampled ramets within each environment were >30 m apart. Leaves were placed on ice in the dark until processed. Within 12 hours of collection, two disks (each

1.13 cm²) were cut from each leaf and placed in light-proof glass vials with 6 mL of N, N-dimethylformamide. Vials were stored in the dark at 2°C for seven days, after which absorbance of chl *a* ($A_{664.5}$) and chl *b* (A_{647}) was read in 1.00 cm cuvettes using a Beckman DU-64 spectrophotometer (Beckman Coulter, Fullerton, California, USA; following methods of Brown [2000]). Chlorophyll content (chl *a* and chl *b*) was calculated using the extinction coefficients provided in Inskeep and Bloom (1985). Leaf dry weight was determined with a Mettler balance (Mettler-Toledo, Columbus, Ohio, USA) after drying for 48 h at 70°C. LMA was calculated as dry weight divided by area (mean of three readings from a LI-COR 3100 leaf area meter [LI-COR, Lincoln, Nebraska, USA]).

Statistical analyses

To account for local variation in abundance before treatment, effects of harvest on ramet density and leaf area were expressed as the difference between pre- and post-treatment measurements (year 1 = 1998–1997; year 2 = 1999–1997). Demographic responses were quantified as follows: ramet survival as the percentage of previous-year ramets present in the current year; clonal growth as the number of new, vegetatively produced ramets divided by the total number of ramets present in the previous year; flowering as the percentage of ramets with flowers; and seedling density as the number of germinants per square meter.

To test for variation in species' abundance and demographic responses to timber harvest, we conducted repeated-measures analysis of variance (Underwood 1997), with species and environment (forest vs. harvest area) as fixed effects. Replication of abundance and demographic variables was at the patch level. Response variables were square-root transformed to correct for unequal variance between environments. Where significant time $\times$ environment or species $\times$ time $\times$ environment interactions were detected, post hoc comparisons were made to compare group means: between environments at each time interval (for two-way interactions), or between environments at each time interval for each species (for three-way interactions). Given our focus on the responses of species to environment (forest vs. harvest area), we report, but do not discuss, the relevance of significant main effects of species (which were chosen to differ in their traits) or of species $\times$ time interactions.

Linear regression was used to test whether first-year changes in abundance or demographic traits in the harvest area were influenced by post-harvest ground conditions or shading by residual vegetation. Separate regression models were developed for each of the five response variables (see above) as a function of each predictor (cover of disturbed soil; light, medium, or heavy slash; herbs; and shrubs). For each model, we tested for homogeneity of slopes among species (Sokal and Rohlf 1981); where slopes differed, separate

regression models are reported ($n = 9$ for species-specific models; $n = 27$ for combined models). Response variables did not require transformation.

Two-factor ANOVA (Sokal and Rohlf 1981) was used to test whether leaf mass per unit area (LMA) or Chl *a:b* ratio differed between environments (suggesting morphological or physiological responses to increased light) and whether the nature of these responses differed among species. Each model included species and environment as fixed effects and their interaction. If a significant interaction was detected, *t* tests were used to compare mean values between environments for each species. Response variables were square-root transformed to correct for unequal variance between environments.

All statistical analyses were conducted using Systat 10.0 (SPSS 2001). An alpha level of 0.05 was used as the criterion for statistical significance.

RESULTS

Prior to timber harvest, ramet density, total leaf area, and flowering were similar for all species between plots in the area to be logged and plots in the area to remain undisturbed (Table 1). Only *Asarum* had seedlings, which did not differ between plot groups.

Changes in ramet density and total leaf area

Timber harvest resulted in significant, short-term declines in ramet density in all species (significant time $\times$ environment interaction, Table 2; Fig. 1a–c). The absence of a three-way interaction in the full model (Table 2) suggests that species showed similar recovery in year 2. However, trends for *Pyrola* clearly indicate that ramet density remained depressed in the harvest area (Fig. 1c). A separate repeated-measures ANOVA for *Pyrola* yielded a highly significant main effect of environment ($F_{1,16} = 13.894$, $P = 0.002$), but no time $\times$ environment interaction (confirming that loss of degrees of freedom to additional terms in the full model limited our ability to detect this effect).

Timber harvest also induced significant, short-term declines in leaf area (significant time $\times$ environment interaction, Table 2; Fig. 1d–f). As with the test for ramet density, absence of a three-way interaction suggests similar performance among species (i.e., a decline in year 1 and recovery in year 2; Fig. 1). However, as with ramet density, trends for *Pyrola* suggested that leaf area remained depressed in the harvest area: this was confirmed by a separate repeated-measures ANOVA for *Pyrola* (significant main effect of environment [$F_{1,16} = 6.578$, $P = 0.021$], but no time $\times$ environment interaction).

Post-treatment demographic trends

Species differed in ramet survival in response to timber harvest (significant species $\times$ time $\times$ environment interaction; Table 2). For all species, first-year ramet survival was significantly reduced in the harvest area:

TABLE 1. Abundance and demographic traits for *Asarum caudatum*, *Clintonia uniflora*, and *Pyrola picta* prior to logging in plots in areas to remain undisturbed forest (forest) and to be harvested (harvest area).

Variable	Forest		Harvest area		<i>t</i>	<i>P</i>
	Mean	SE	Mean	SE		
<i>Asarum caudatum</i>						
Ramet density (no./m ²)	9	2	10	3	−0.3	0.768
Total leaf area (cm ² /m ²)	588	248	478	172	0.4	0.720
Flowering (% of ramets)	2.1	1.1	6.7	3.0	−1.4	0.180
Seedling density (no./m ²)	0.3	0.2	0.5	0.2	−0.5	0.642
<i>Clintonia uniflora</i>						
Ramet density (no./m ²)	5	1	6	1	−0.4	0.703
Total leaf area (cm ² /m ²)	310	66	342	60	−0.4	0.722
Flowering (% of ramets)	<0.1	<0.1	0.1	0.1	−0.1	0.933
<i>Pyrola picta</i>						
Ramet density (no./m ²)	10	1	10	2	−0.1	0.957
Total leaf area (cm ² /m ²)	257	28	253	34	0.1	0.941
Flowering (% of ramets)	7.0	1.2	17.0	5.4	−1.8	0.107

Notes: No seedlings of *Clintonia* or *Pyrola* were observed. Test statistic (*t*) and *P* values are from *t* tests (*n* = 9 patches per environment).

survival rates were ca. 30% of those in the forest (year 1; Fig. 2a–c). In year 2, however, species diverged in their responses. For *Asarum*, ramet survival remained depressed in the harvest area (Fig. 2a), but for *Clintonia* it was significantly greater (Fig. 2b). For *Pyrola*, ramet survival was comparable between environments (Fig. 2c).

Species also differed in patterns of clonal growth (ramet production) in response to harvest (significant species $\times$ time $\times$ environment interaction; Table 2). For *Asarum*, growth rates were initially lower in the harvest area, but in year 2 they were markedly higher (Fig. 2d). For *Clintonia*, rates were initially similar between environments, but in year 2 they were significantly higher in the harvest area (Fig. 2e). In contrast, clonal growth of *Pyrola* was not affected by harvest (Fig. 2f).

Flowering occurred infrequently in all species (<4% of ramets; data not shown) and was virtually absent in *Clintonia* (thus *Clintonia* was not included in the full ANOVA model; Table 2). For *Asarum* and *Pyrola*,

flowering was consistently much lower in the harvest area than in the forest (significant main effect of environment; Table 2). Neither *Clintonia* nor *Pyrola* produced seedlings in either environment. Presence and density of *Asarum* seedlings was highly variable within environments and over time; seedlings were observed in four to six of the nine patches per environment. Mean densities of *Asarum* seedlings were higher in the harvest area than in the forest (1.2 vs. 0.4/m² in year 1, and 4.9 vs. 0.7/m² in year 2), but not significantly so. However, survival in the harvest area was lower (7% vs. 56% in year 1 and 28% vs. 34% in year 2).

Relationships with post-harvest ground conditions and residual understory vegetation

Initial changes in species abundance and demographic performance showed strong relationships with post-harvest ground conditions (type and cover of slash) and residual vegetation. Cover of heavy-density slash was negatively associated with change in leaf area of *Pyrola*

TABLE 2. Effects of time (1 and 2 years after disturbance), species (*Asarum*, *Clintonia*, and *Pyrola*), and environment (forest vs. harvest area) on plant abundance and demographic traits from repeated-measures ANOVA (see Figs. 1 and 2).

Source of variation	df	Change in ramet density (no./m ²)		Change in leaf area (cm ² /m ²)		Ramet survival (%)		Clonal growth (%)		Flowering† (%)	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Time	1	5.479	0.023	6.620	0.013	2.218	0.143	41.795	< 0.001	0.060	0.808
Species	2	5.497	0.007	360.094	< 0.001	140.866	< 0.001	82.737	< 0.001	0.101	0.753
Environment	1	5.744	0.020	3.100	0.085	39.876	< 0.001	4.598	0.037	14.793	0.001
Time $\times$ species	2	5.230	0.009	1.975	0.150	17.364	< 0.001	15.456	< 0.001	2.484	0.125
Time $\times$ environment	1	9.546	0.003	9.877	0.003	4.041	0.050	28.478	< 0.001	0.409	0.527
Species $\times$ environment	2	1.804	0.176	1.376	0.262	6.232	0.004	2.203	0.122	0.001	0.973
Time $\times$ species $\times$ environment	2	1.892	0.162	1.475	0.239	7.791	0.001	6.554	0.003	0.143	0.708

Notes: *P* values are in boldface for significant ($P \leq 0.05$) main effects and interactions. Error degrees of freedom (df) = 48 for between-subject analysis of main effects (species and environment) and their interaction, and error df = 48 for within-subject analysis of time and its interaction with main effects.

† The model for flowering does not include *Clintonia* because of insufficient numbers of flowering individuals; thus, df = 1 for all sources of variation except error, for which df = 32 for both within- and between-subjects analysis.

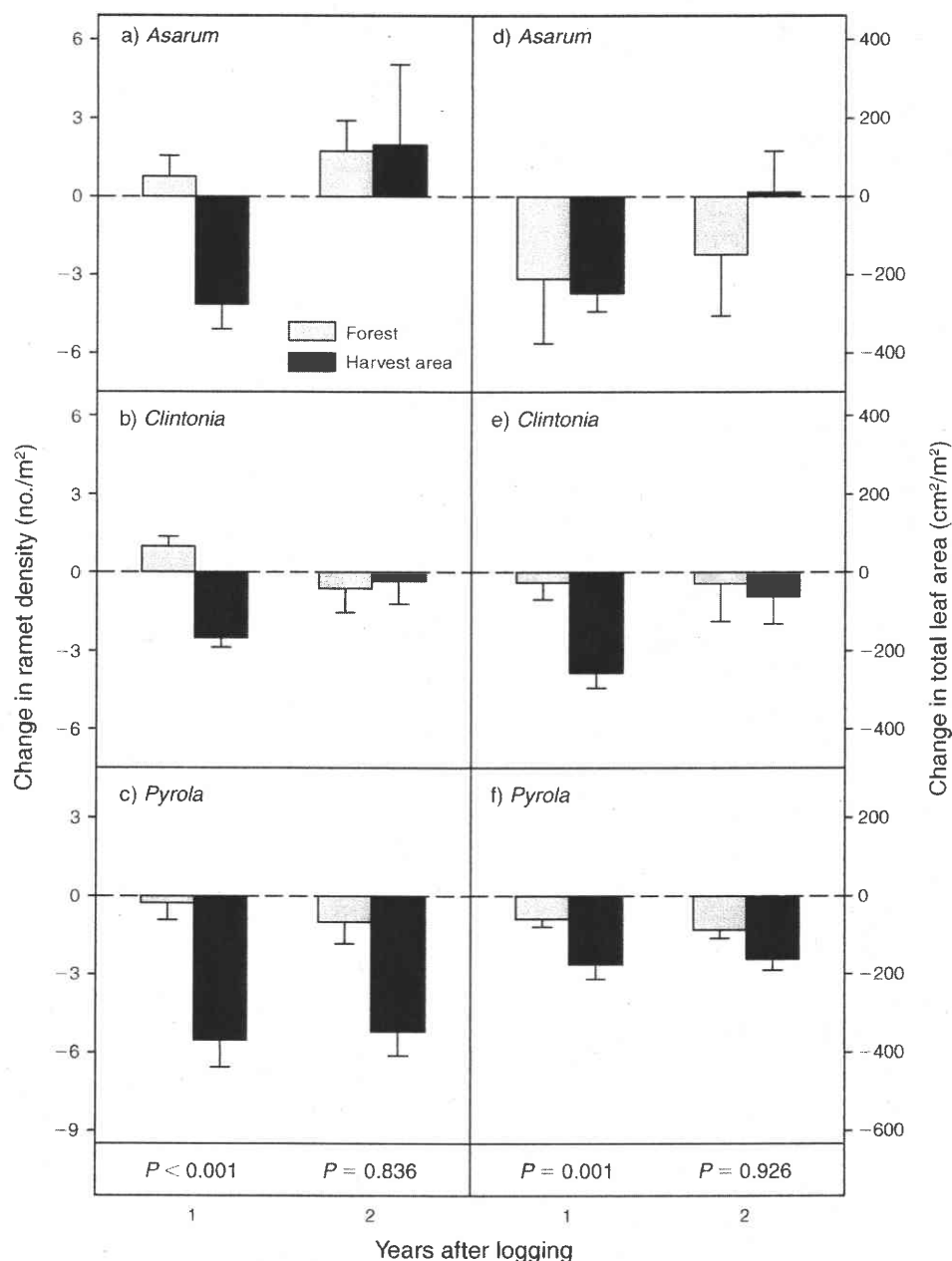


FIG. 1. Changes (mean + SE) in (a–c) ramet density and (d–f) total leaf area for *Asarum caudatum*, *Clintonia uniflora*, and *Pyrola picta* in undisturbed forest and adjacent harvest area, one and two years after logging. *P* values below the lower panels are the results of post hoc comparisons between environments for each year ($df = 1$), following significant time $\times$ environment interactions from repeated-measures ANOVA (Table 2).

and ramet survival of all species (Table 3). In contrast, cover of light- and moderate-density slash was positively associated with ramet survival and clonal growth of *Asarum* (Table 3). Cover of disturbed soil was not significantly related to any measure of species response. Relationships with residual vegetation were consistently positive: greater cover of herbs and/or shrubs was associated with smaller declines in ramet density (*Asarum* and *Clintonia*) and with greater rates of ramet survival (*Pyrola*) or clonal growth (*Clintonia*) (Table 3).

Leaf mass per unit area and chlorophyll content

All species had significantly higher leaf mass per unit area (LMA) in the harvest unit than in the forest, although the magnitude of response differed among species (significant species $\times$ environment interaction; Table 4, Fig. 3a). In contrast, the response of leaf chlorophyll (chl *a:b* ratio) to environment differed among species in both direction and magnitude (significant species $\times$ environment interaction; Table 4, Fig.

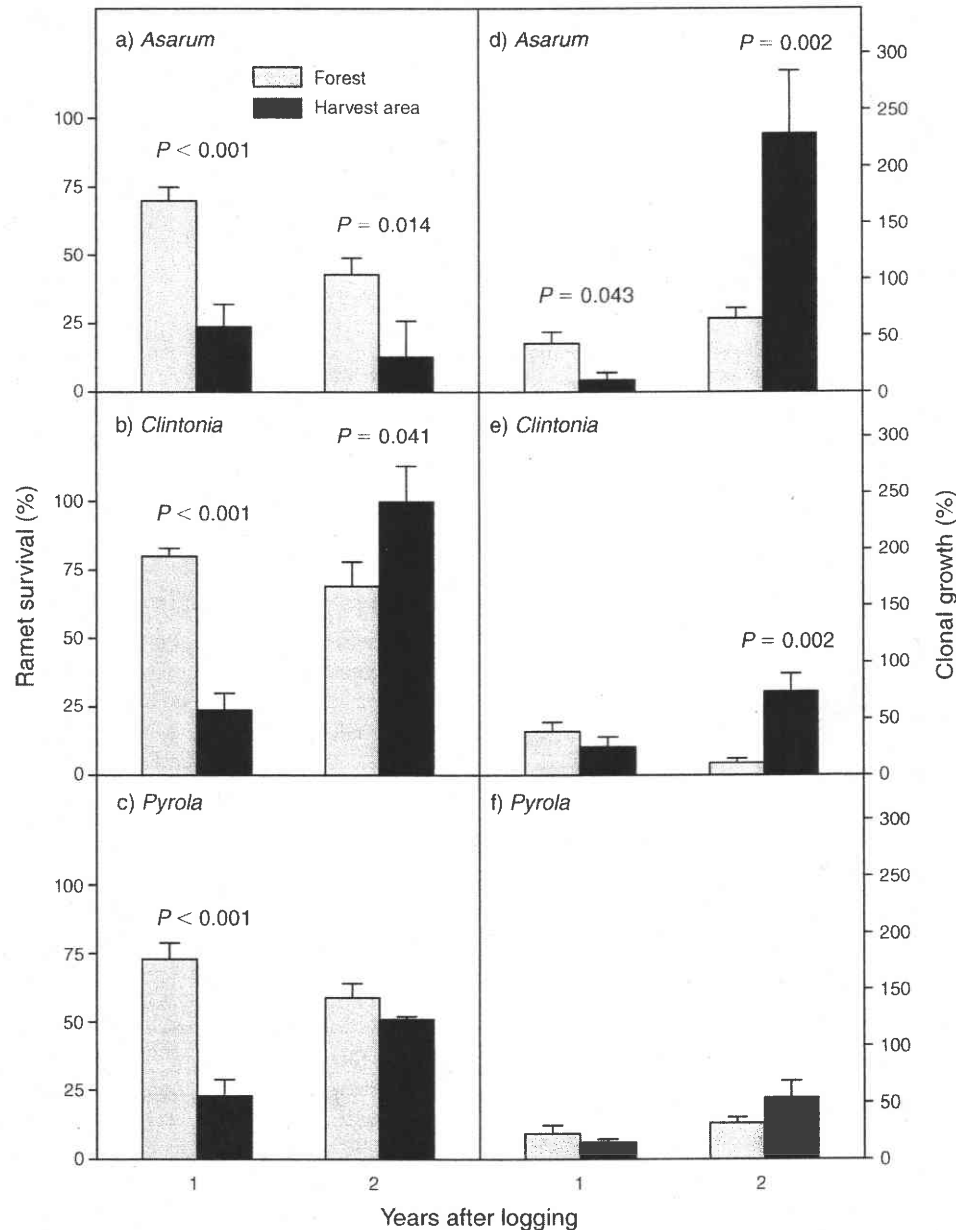


FIG. 2. Mean ($\pm$ SE) (a–c) ramet survival and (d–f) clonal growth for *Asarum caudatum*, *Clintonia uniflora*, and *Pyrola picta* in undisturbed forest and adjacent harvest area, one and two years after logging. P values are the results of t tests between environments for each year ($df = 16$), following significant time $\times$ species $\times$ environment interactions from repeated-measures ANOVA (Table 2); only significant P values ($P \leq 0.05$) are shown.

3b). For *Asarum*, chl $a:b$ was significantly lower in the harvest area, for *Clintonia* it was significantly greater, and for *Pyrola* it did not differ between environments.

DISCUSSION

Initial responses to timber harvest

Plant species that reach maximal development in late-seral forests show dramatic declines after stand-replacing disturbance and require long periods of time for populations to recover (MacLean and Wein 1977,

Schoonmaker and McKee 1998, Halpern 1989, Halpern and Spies 1995). Initial declines may reflect the direct effects of disturbance or adverse conditions in the post-disturbance environment. In this study, we observed immediate and substantial reductions in ramet density and leaf area in all three species. We expected the magnitude of decline to differ among species with different rhizome traits (thickness or depth in the soil) due to differential susceptibility to mechanical damage. However, we found no evidence of this, perhaps because of limited soil disturbance. Instead, declines appear to

TABLE 3. Significant regressions between first-year responses of species in the harvest area and post-harvest ground conditions (cover of logging slash [by density class], herbs, and shrubs).

Response variable	Predictor	Species	Model		
			Coefficient	P	R ²
Change in ramet density	herbs	<i>Asarum caudatum</i>	0.703	0.035	0.49
	shrubs	<i>Clintonia uniflora</i>	0.225	0.009	0.64
Change in leaf area	heavy slash	<i>Pyrola picta</i>	-8.310	0.013	0.61
Ramet survival	herbs	<i>Pyrola picta</i>	0.008	0.042	0.47
	shrubs	<i>Pyrola picta</i>	0.003	0.008	0.66
	light slash	<i>Asarum caudatum</i>	0.005	0.031	0.51
	heavy slash	all species	-0.004	<0.001	0.56
Clonal growth	shrubs	<i>Clintonia uniflora</i>	0.016	0.001	0.81
	moderate slash	<i>Asarum caudatum</i>	0.005	0.032	0.50

Notes: Only significant relationships are reported; where regression coefficients did not differ among species, a combined model is shown. Cover of disturbed soil was not a significant predictor in any model. See *Methods: Study site and species* for descriptions of slash-density classes.

have resulted from burial during logging. We found strong negative relationships between cover of heavy slash (dense accumulations of foliage and woody debris) and ramet survival of all three species. Although forest herbs vary in their abilities to survive shallow burial, deep burial (>15 cm) typically results in ramet mortality (Antos and Zobel 1985a, b). Regression analyses also suggest that environmental stress contributed to initial plant declines. The poorer performance on average in the harvest area was partly ameliorated in patches with greater surviving vegetation or light- or moderate-density slash. In the absence of overstory cover, solar radiation and temperature can be greatly reduced in these microsites, benefiting species adapted to shade (Hungerford and Babbitt 1987, Breshears et al. 1998, Heithecker and Halpern 2006).

Measurements in undisturbed forest illustrate the potential for plant abundance to vary annually in the absence of obvious disturbance (Økland 1995, Damman and Cain 1998, Nelson and Halpern 2005). Total leaf area showed particularly large variation: an average difference of 24% between years. Annual variability in temperature, resource availability (e.g., soil moisture), or other factors that affect plant productivity may contribute to this variation. This underscores the importance of control data in interpreting responses to disturbance: large declines in leaf area of *Asarum* in the harvest area in year 1 were matched by similarly large declines in the forest. In comparison to leaf area, ramet density showed

less variability in the forest and thus may be a better indicator of population response to disturbance.

Responses to post-harvest environmental conditions

Do species that respond similarly to the direct effects of disturbance vary in their demographic and physiological responses to changes in environment? Two years after harvest, ramet densities of *Asarum* and *Clintonia* were similar to densities in undisturbed forest. However, recovery was not achieved by similar means. For *Asarum*, ramet survival remained very low, but clonal growth increased dramatically; more than three times as many new ramets were produced in the harvest area as in the forest. For *Clintonia*, however, both survival and growth were greater in the harvest area, consistent with its ability to produce dimorphic rhizomes (long and short shoots). This allows *Clintonia* to respond to spatial and temporal variation in environment by retaining ramets on short rhizomes in favorable microsites and placing ramets in new locations through growth of long rhizomes (Antos and Zobel 1984, Antos 1988). This flexibility may be a successful strategy in forests in which resource or environmental conditions vary, or after disturbance (Lezberg et al. 1999, 2001). In contrast to *Asarum* and *Clintonia*, ramet density and leaf area of *Pyrola* remained depressed in the harvest area and demographic traits (rates of survival and clonal growth) suggest poorer potential for recovery, at least in the short term.

Recruitment by seed is uncommon in clonal forest herbs (Cain et al. 1997) and can be highly variable both

TABLE 4. Effects of species and environment (forest vs. harvest area) on leaf mass per unit area and chl *a:b* ratios (see Fig 3).

Source of variation	df	Leaf mass per unit area (mg/cm ²)		Chlorophyll <i>a:b</i> ratio	
		F	P	F	P
Species	2	189.240	<0.001	8.615	<0.001
Environment	1	124.195	<0.001	0.000	0.997
Species × environment	2	12.141	<0.001	5.153	0.007

Notes: Significant ($P \leq 0.05$) main effects and interactions are in boldface. Error degrees of freedom (df) = 110.

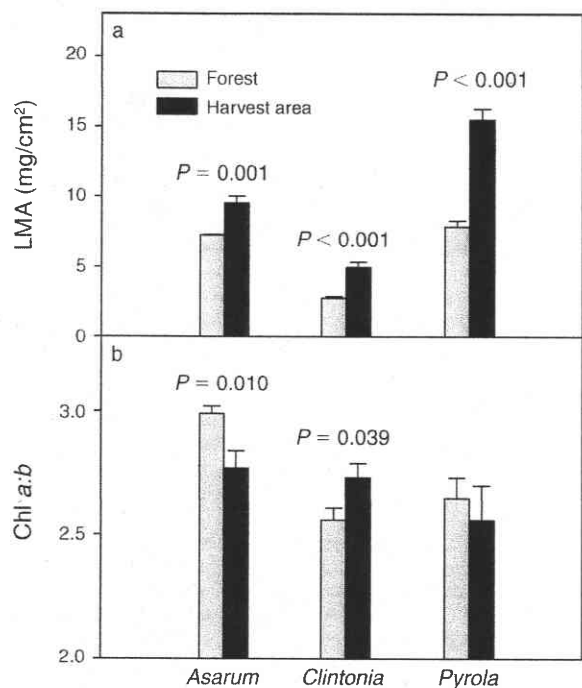


FIG. 3. Mean ($\pm$ SE) (a) leaf mass per unit area (LMA) and (b) chl *a:b* ratios of leaves produced in the current growing season for *Asarum caudatum*, *Clintonia uniflora*, and *Pyrola picta* in undisturbed forest and adjacent harvest area, two years after logging. P values are the results of *t* tests between environments ($df = 34$ for *Asarum*; $df = 38$ for *Clintonia* and *Pyrola*), following significant species $\times$ environment interactions from two-factor ANOVA (Table 4). Only significant P values ($P \leq 0.05$) are shown.

in time and space (Barkham 1980, Damman and Cain 1998). Thus, it was not surprising that only *Asarum* produced seedlings, and these were distributed unevenly among existing clones. Mean densities in the harvest area reached ~ 5 seedlings/m² despite very low rates of flowering. Although rates of seedling survival were low, they were comparable to those of vegetative ramets, suggesting potential for sexual reproduction to contribute to population growth in the harvest area for this species (see also Damman and Cain 1998). Similar potential was not evident, at least in the short term, for *Clintonia* or *Pyrola*.

Comparisons of leaf morphology and biochemistry between environments suggest that species also differ in their abilities to adjust to abrupt changes in light. All three species showed large and significant differences in leaf morphology between environments: LMA was 31–97% greater in the harvest area, consistent with the response expected under higher light (Gamon and Pearcy 1989). However, only *Clintonia* exhibited a significantly higher chl *a:b* ratio in the harvest area, suggesting physiological acclimation (Anderson et al. 1988, Lambers et al. 1998). High phenotypic plasticity in response to changes in light availability—also observed in *C. borealis* (Pitelka et al. 1985)—may be achieved by

complete, annual turnover of leaves, which allows for rapid adjustment of leaf morphology and biochemistry. Greater leaf retention in *Asarum* (up to three years) and *Pyrola* (>3 yr) may limit physiological plasticity. In contrast to the expected direction of adjustment, *Asarum* had a lower chl *a:b* ratio in the harvest area, which could substantially compromise photosynthetic rates and may explain its much lower rate of ramet survival. *Pyrola* showed no difference in chl *a:b* between environments, but this lack of adjustment did not appear to affect survival or growth. One possible explanation is that *Pyrola* employs novel strategies to acclimate to increased irradiance, such as adjusting electron transport or photophosphorylation and carbon assimilation, as has been observed in some shade-adapted species (Chow et al. 1991). Clearly, additional research is needed to understand the physiology of *Pyrola* in high-light environments and how this affects survival and growth.

Implications for rates of recovery

What do these responses suggest for future recovery of these species? Caution must be taken in extrapolating from initial trends, but distinct differences in early demographic and physiological performance suggest that the pace of recovery is likely to differ among species. Recovery of *Pyrola* and *Asarum* are likely to lag behind that of *Clintonia*. *Pyrola* showed large, persistent reductions in density and leaf area, no adjustment of chl *a:b* ratio, and no sexual reproduction in the harvest area. However, rates of ramet survival and clonal growth were no lower than in the forest. This suggests short-term reliance of surviving ramets on subsidies from below-ground reserves. If photosynthesis is reduced by lack of adjustment in pigments, reserves are likely to be depleted over time leading to population decline.

Rapid production of new ramets of *Asarum* supported its short-term recovery in the harvest area. However, the high rate of initial growth that we observed—possibly supported by carbohydrate reserves in rhizomes—is unlikely to be sustained for several reasons: ramet survival is very low, physiological acclimation is poor, and a rigid rhizome architecture coupled with short annual segments restricts movement into more favorable microsites. Future declines in *Asarum* would be consistent with long-term observations and demographic simulations of *A. canadense* in high- and low-light environments (early- and late-successional forest [Cain and Damman 1997, Damman and Cain 1998]): low ramet survival in high-light environments resulted in gradual population decline. Moreover, simulations indicated that population growth was more sensitive to survival (which was very low in our species) than to sexual or clonal reproduction (which were comparatively high). *Clintonia* may not face similar constraints on recovery: abundance, demographic patterns, and physiological acclimation were either similar between environments or greater in the harvest area.

Plant functional types are used as a basis for generalization (Smith et al. 1997). Clonal herbs that attain maximum development in late-seral forest are often assumed to have similar responses to stand-replacing disturbance and to the ensuing changes in environment. As a result, they are often treated as functional equivalents in community-level studies (e.g., McKenzie et al. 2000, Battles et al. 2001, Halpern et al. 2005). Our comparative analyses of populations of a small number of species demonstrate considerable variation in demographic and physiological response, variation that can be associated with differences in belowground morphology, leaf duration, and leaf biochemistry. *Clintonia* showed the greatest potential for recovery, a function of its dimorphic rhizomes, annual turnover of leaves, and capacity to adjust chl *a:b*. By contrast, high ramet mortality, relatively inflexible architecture, and perennial leaves may limit the ability of *Asarum* to adjust to this new environment. Flexibility in clonal growth (Lezberg et al. 2001) and annual turnover of leaves may be critical to coping with disturbance and abrupt environmental change. Understanding the variation in these traits may be a key to predicting differences in response among plant species that have been viewed as ecologically similar. Our study represents an initial attempt to explore this variation for a small group of species in a single forest. Additional studies of a greater diversity of species and forests are needed to improve our understanding of the physiological and demographic responses to disturbance of late-seral forest herbs.

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