Growth and clonal integration of sweetgrass (Hierochloe odorata) in western Montana

Dawn M. White

The University of Montana

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Growth and clonal integration of Sweetgrass (Hierochloe odorata) in western Montana

by

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B.S., The University of Great Falls, Great Falls, Montana, 1996

Presented as partial fulfillment of the requirements for the degree of

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Hierochloe odorata, commonly known as Sweetgrass, is regarded as a spiritual medicine used by native people throughout North America. This cool season grass reproduces primarily via rhizomes, giving rise to interconnected clones from the same parent plant. Clonal integration has been shown to be beneficial in many plant species. In western Montana H. odorata is restricted to wet meadows; however, very little ecological information is known on the environmental conditions required to sustain healthy populations and on the potential benefits of clonal integration. The objectives of this study were to (1) evaluate the growth and physiological performance of H. odorata in different microhabitats, and (2) to determine whether clonal integration is advantageous for the growth of this species.

Growth and physiology of H. odorata was monitored during 2001 in six different microenvironments selected within a wet meadow in western Montana: ‘Dry Open’, ‘Closed Canopy’, ‘Forest Edge’, ‘Open Canopy’, ‘Under Shrub’ and ‘Wet Open’. Clonal dependency in each environment was determined by comparing growth and physiology of H. odorata in intact and severed ramets (disconnected from their sister ramets) arranged in paired plots. Photosynthesis rates, water potential and height of H. odorata ramets were compared across treatments and microenvironments throughout the season. Ramet biomass and nitrogen were measured at the end of the season.

H. odorata was present in all microenvironments examined except in Dry Open and Closed Canopy plots, where low moisture and excessive shade may limit its distribution. Growth and physiology of intact ramets was similar across all microenvironments where H. odorata was present. Severing did not result in significant differences in leaf water status and photosynthetic rates in any of the environments. However, severing ramets resulted in decreased plant height in Wet Open plots and to a lesser extent in Forest Edge plots. Similar trends were observed for ramet biomass.

My results suggest that H. odorata is sensitive to water deficit and that clonal growth is important in wet open environments, where the species is commonly found. Maintaining rhizomatous connections may increase restoration success when transplanting this species into the open meadow habitat that H. odorata prefers.
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INTRODUCTION

Increasing population pressure and human activities over the last century (i.e., development, irrigation, livestock grazing) have resulted in land use changes that have altered the structure and function of many ecosystems (Woodwell 1977, Wilcox and Murphy 1985, Vitousek et al. 1997). The resulting habitat loss and fragmentation have decreased biodiversity (Frankel and Soulé 1981, Barbier et al. 1994), which may result in further changes in ecosystem function (Chapin et al. 1997).

Besides impacts on ecosystem function, biodiversity loss can be especially important when it involves plants that are culturally significant. The loss of culturally significant plant species threatens the traditions of indigenous peoples (Grinde and Johansen 1995). The conservation and restoration of these species requires not only a solid understanding of their ecology, but communication with tribal people and tribal authorities to combine scientific ecological knowledge with traditional ecological knowledge.

My research addresses the ecology of *Hierochloe odorata*, a wetland species in Montana, which is culturally significant to many Native American tribes throughout North America. *Hierochloe odorata* (L.) Beauv. commonly known as Sweetgrass, Vanilla Grass or Holy Grass is highly regarded by indigenous people throughout North America as a spiritual medicine. Besides its use as numerous medicines, it is used in perfumes, baskets, sachets and tonics (Densmore 1974, Hart 1976, Moerman 1998, Winslow 2000).

*Hierochloe odorata* is a cool season grass, and is native to the temperate and cooler regions Eurasia and North America, but also exists south in mountainous regions.
of the Northern Hemisphere (Gould and Shaw 1983, Gray 1950). *Hierochloe odorata* is typical of open, wet areas (USFW 1998, Hitchcock 1971) that are relatively undisturbed. These wetland areas are highly productive, diverse and dynamic systems in both time and space (Hansen et al. 1995).

Although *H. odorata* is secure globally, its distribution is restricted in parts of its range, including Montana (MTNHP 1997-2000). Such limited distribution has raised the concern of Native American people of western Montana (Bigcrane pers. comm.). This fragrant, cool season rhizomatous perennial has been traditionally harvested for centuries and more recently has spiked in demand by non-indigenous people (i.e. new age uses, soaps). The distinctively sweet and appealing aroma of *H. odorata* is due to the presence of coumarin in the leaves and rhizomes (Ueyama et al. 1991, Lewis and Elvin-Lewis 1977). Coumarin is a phenolic-type secondary metabolite produced by *H. odorata* that also serves to deter herbivores.

In spite of the cultural significance and potential management needs, little is known about the ecology of *H. odorata* in western Montana. Given its increasing harvest pressures and the concern of native people about the conservation status of *H. odorata*, management is necessary. The management of populations of native species requires basic ecological knowledge of habitat preference and reproductive strategies. My primary research objective is to increase our knowledge of the autecology of *H. odorata* across a moisture gradient in a natural wetland habitat.

As with other common wetlands graminoids (e.g., *Carex*), *H. odorata* reproduces primarily vegetatively by rhizomes (Norstlag 1960). This clonal reproduction is an important life history trait of *H. odorata* that might increase its fitness in temporally and

Resource transfer within and between plants is apparently driven by source-sink relationships. Research using stable and radioactive isotopes has shown that clonal plants can transfer carbon, water and nitrogen between connected ramets (Williams 1964; de Kroon et al. 1996; D’hertefeldt and Jónsdóttir 1999; Alpert 1996). For example, the graminoids Carex flacca and C. hirta have been shown to translocate water from wetter ramets to drier ramets (de Kroon et al. 1996). In addition to water, Carex arenaria, has also been shown to transfer carbon (D’hertefeldt and Jónsdóttir 1999). Nitrogen transfer from source ramets to sink ramets has been demonstrated in Carex flacca but only when associated with water transfer (de Kroon et al. 1998). The importance of functional integration in clonal plants has been demonstrated with severing experiments whereby sister ramets are disconnected. For instance, Harnett and Bazzaz (1983) showed that severed ramets of Solidago canadensis suffered decreased growth and severe mortality relative to intact ramets.

Hierochloe odorata has very low seed viability, ranging from 2% (Norstog 1960) to 36% (Weimarck 1967, USDA NRCS 2001). Such low seed viability could restrict the long-range dispersal via seeds. This and the fact that H. odorata is often apomictic (Norstog 1963, Weimarck 1967) suggest that adaptation to local conditions may be particularly important for H. odorata populations. Functional integration via resource sharing between H. odorata ramets may explain why in some instances H. odorata can
occupy areas that are less suitable for other species (Goldsmith and Murphy 1980, Norstog 1960).

While *Hierochloe odorata* in Montana is most common in open wet meadows, it also occurs underneath open canopies, and shaded stream banks (Dorn 1984). However microhabitat preferences of *H. odorata* in western Montana have never been documented. Similarly, the potential benefits of the clonal nature of *H. odorata* in its natural microhabitats have never been investigated.

The objectives of this study were 1) to determine whether *H. odorata* growth differs across microenvironments and 2) to assess the level of clonal dependency on the growth and physiology of a rhizomatous cool season grass. These objectives were addressed by measuring growth in different local microenvironments and by comparing the growth of intact and severed ramets in these environments. Specifically, I tested the following hypothesis:

1) *Hierochloe odorata* height and biomass is greatest in moist, open microenvironments relative to dry, shaded environments.

2) *H. odorata* benefits from its clonal nature: severed ramets exhibit reduced growth relative to intact ramets.

2.1 The benefits of clonal growth vary depending on the microenvironment.

Observations of growth patterns across microenvironments will provide information on suitable sites appropriate for relocation purposes, and will enhance our ability to restore existing populations of *H. odorata*. Understanding the degree of clonal dependence in *H. odorata*...
odorata may increase our ability to propagate this species. For example, if the benefits of clonal integration are environment-specific removal of genets for subsequent restoration purposes may be appropriate in some environments but not in others.

METHODS

Site

The effects of microhabitat and clonal dependency on the growth of *H. odorata* were examined in a wet meadow at 1400 m elevation located near Lolo Hot Springs (46°43'N; 114°31'W) in Missoula County, Lolo National Forest, Montana, USA. The microtopography of the meadow is variable, resulting in drier areas slightly elevated from the water table and depressed areas closer to the water table. Overall, the meadow is dominated by graminoids such as *Carex* sp. and *Poa* sp. with some forbs (*Solidago missouriensis*, *Senecio integerrimus*, and *Fragaria virginiana*). The meadow is intersected by shallow water courses where riparian shrubs such as *Salix* and *Betula* are common. The meadow is surrounded by a mixed conifer forest dominated by *Pinus contorta*, with some *Abies lasiocarpa*.

Clonal Dependency

Clonal dependency was examined, by comparing the growth of plants with intact rhizomes to that of plants where the rhizomes had been “severed” or cut from their sister ramets. In early May 2001, six microenvironments within the meadow and adjacent forest were identified to assess the influence of microhabitat on *H. odorata* growth throughout the summer of 2001. These environments included: Dry Open (DO), Wet Open (WO), Shrub (SHR), Open Canopy (OC), Forest Edge (FE) and Closed Canopy
(CC). DO plots were located in elevated, dry areas in the middle of the meadow. Open plots were located in the middle of the meadow well away from trees. SHR plots were located immediately under *Salix* sp. shrubs. OC plots were underneath open canopies at the periphery of the meadow except for one plot that was within a cluster of *Pinus contorta* in the middle of the meadow. FE plots were located within the wet meadow, but were no more than 5 m from the dense closed canopy forest. CC plots were within the dense canopy of the adjacent forest. These microenvironments represented distinct apparent microhabitats due to the influence of adjacent vegetation, and availability of light (highest in WO and lowest in CC) and moisture (highest in WO and lowest in DO). However, as the spring advanced, we were unable to find *Hierochloe odorata* in any of the CC and DO plots. *Hierochloe odorata* was found in all of the four remaining microenvironments (FE, OC, SHR, WO) where growth was monitored during the rest of the summer. However light and soil moisture availability was monitored for all plots.

**Experimental Design**

Effects of microhabitat and clonal dependency on plant performance were examined with a field experiment utilizing a split-plot design. Micro-environmental effects were assessed at four levels corresponding to the four microhabitats selected: Forest Edge (FE), Open Canopy (OC), Under Shrubs (SHR) and Wet Open (WO). A minimum of five paired plots were identified for each environment. Placement of the plots was randomized to the extent that it was possible. However, spatial bias in the placement of FE and OC plots was unavoidable, as these environments were found at the periphery of the meadow (with some exceptions). Severing treatments (intact and severed) were randomly assigned to one of each paired plot, which were between one and
2 meters apart. Plots were circular, with an outside radius of 25 cm. Approximately ten ramets were tagged within an inside circle with a radius of 15 cm (area = 0.71 m²), and monitored monthly from June to September 2001. These ramets were marked by inserting a thin steel wire approximately 4 cm into the ground with an aluminum label next to the ramet. All treatments had 5 replicates except for WO, which had six replicates. Therefore, the design resulted in a total of 21 sets of paired plots, each set consisting of 21 “intact” plots and 21 “severed”.

Severing occurred in late April and early June, by inserting a tree-planting spade throughout the entire external perimeter of each plot (25 cm radius from the center of the plot) at a depth of at least 20 cm into the soil surface. Preliminary observations confirmed that rhizomes are located above this depth. Re-compacting the soil into the cuts minimized potential for air and water entry through the thin trenches made with the spade. Ramets in the “severed” plots were within 15 cm of the severing line and were presumed to be mostly isolated from sister ramets outside the center plots. Plots severed in late April included: 5 WO plots, 2 OC plots, and 2 SHR plots. All FE, 3 OC, 3 SHR and 2 WO plots were severed in early June. The differences in severing time were due to difficulties in identifying *H. odorata* before flowering.

**Measurements of Abiotic Factors**

Photosynthetic active radiation (PAR) was measured between 10:00 and 16:30 hours on June 22, 2001 to assess differences in maximum light intensity between environments. Measurements were taken with a LI-250 light meter (Li-Cor, Inc., Lincoln, NE) at 5 positions within each plot 20 cm above the ground surface, at the center of the plot and at the four cardinal positions 15 cm from the center.
Soil moisture was measured monthly in each microenvironment using a Troxler Sentry 200 AP moisture monitor (Troxler Electronic Laboratories, NC). PVC pipes (5.1 cm inner diameter) were inserted to a depth of approximately 50 cm between the severed and intact plots in each environment (n = 5 per environment). We recorded the relative water content (% volume) at 15, 30 and 40 cm depths from the ground surface monthly, from mid-May through late August.

Plant Response Measurements

Hierochloe odorata leaf water status in intact and severed plots for each environment was measured using the pressure chamber technique described by Scholander et al. (1965) with a pressure chamber (PMS instrument company, Corvallis, Oregon) in June, August and September. An aboveground ramet stem was collected from each plot between 13:00 and 16:00 hours (the hottest part of the day) and immediately sealed in a plastic bag then stored in a humid cooler no longer than 20 minutes. This resulted in 5 replicates per microenvironment and clonal dependency treatment. Sampled ramets were adjacent to those tagged for seasonal monitoring of height.

Photosynthesis measurements were conducted monthly from June to September between 10:00 and 13:00 hours, using a Portable Photosynthesis System (LI-6200 Li-Cor, Inc., Lincoln, NE). Net photosynthesis rates (A μmol CO₂ m⁻²s⁻¹), stomatal conductance (gₛ mmol m⁻²s⁻¹), transpiration (Ε mmol m⁻²s⁻¹) and water use efficiency (WUE) measurements were measured from one unlabeled ramet from each treatment and environment for a total of 5 replicates for each “severed” and “intact” plot. Measured ramets were adjacent to tagged ramets for growth monitoring. Photosynthesis rates on a
leaf area basis were calculated based on Li-Cor measurements and leaf areas calculated from blade length and width. Transpiration rates were calculated from $g_s$ and leaf to air vapor pressure difference calculated from leaf and air-temperature and relative humidity measurements taken with the open cuvette.

Height of tagged ramets in each treatment and environment was measured periodically through the summer of 2001, as the distance from the ground surface to the apex of the tallest non-senescing leaf blade of green tissue. Only green tissue was included in height measurements. Monthly measurements also included total number of senescing and non-senescing leaves, number of stems, and number of flowers.

At the end of the season (August for WO, FE, OC plots and September for SHR plots), the total number of *H. odorata* ramets per plot was recorded (including labeled and unlabeled ramets) and their total aboveground biomass was measured by harvesting all ramets and oven drying them at 65°C for 48 hours. For each plot the number and biomass of labeled and unlabelled ramets were recorded separately. Aboveground biomass of all vegetation was separated by functional groups: graminoids, forbs and shrubs. Oven-dried foliage from each treatment and environment was finely ground and analyzed for total nitrogen in the Stable Isotope Laboratory of the University of California, Davis.

Statistical Analysis

All variables measured in “intact” and “severed” plots within each environment were analyzed using a split-plot design per date with environment as the main plot and clonal dependency as the split plot. Ramet height and individual aboveground ramet biomass values per plot were the average of the individual ramets within each plot (i.e., $n$
Soil moisture data at 15 and 30 cm depths were averaged and graphed. Soil moisture was measured one time per environment between intact and severed plots, and data was analyzed using a 1-way ANOVA to test the null hypothesis that soil moisture does not vary between environments. For all variables for which clonal dependency was not significant, differences at any given date between environments were analyzed by pooling data for intact and severed plots using a one-way ANOVA.

Within each environment, height changes over time between intact and severed were analyzed using a 2-way ANOVA with severing treatment as one factor and date as a repeated factor. Differences in individual ramet biomass, biomass of other graminoids present per plot, ramet density, and leaf nitrogen content (% weight) between intact and severed plots at the end of the season were analyzed with a 2-way ANOVA (environment and treatment). Tukey/HSD were used for post hoc tests to detect differences between environments. Additional tests to detect whether responses to severing treatment varied between environments were performed with a one-way ANOVA, using the difference of severed and intact biomass values per paired plot. The relationship between *H. odorata* ramet biomass and total biomass of other graminoids was analyzed by linear regression analysis. Contrasts were considered significant at $\alpha \leq 0.05$ and marginally significant at $\alpha$ between 0.05 and 0.1.

RESULTS

Maximum PAR was similar in intact and severed plots, and data for the two plots were pooled for subsequent analyses. While there were some differences between
morning (10:00-13:00 hours) and afternoon (1:30-16:30 hours) measurements, maximum PAR tended to be greatest in WO and DO plots, intermediate in FE and OC plots and lower in CC and SHR plots (Figure 1).

Soil moisture was highly variable, but generally high early in the season, and tended to decline as the summer progressed (Figure 2). In general soil moisture tended to be lower in CC, OC and DO plots throughout the season. During mid-May, soil moisture was highest in WO plots, lowest in CC and OC plots, and intermediate in DO and SHR plots (Figure 2). Differences were statistically significant between WO and CC, DO, FE and OC (P<0.05; Tukey HSD test). SHR plots showed intermediate soil moisture levels, but did not differ statistically than other plots, possibly because ice was still present in some of the SHR plots, resulting in highly variable soil moisture measurements. As soil moisture decreased in July and August, DO plots were significantly drier than SHR plots in July and drier than SHR and WO plots in August. As in July, OC and CC plots in August tended to be drier than FE and WO plots although differences were lower than in July.

Leaf xylem water potential ($\psi_{\text{leaf}}$) did not differ between plants in intact and severed plots at any given date or environment. For all environments $\psi_{\text{leaf}}$ was highest in June and declined sharply by August and September (Figure 3). Differences in $\psi_{\text{leaf}}$ between environments were only apparent in August ($F_{\text{environment}} = 4.14; \ P_{\text{environment}} = 0.016$), when ramets in the WO exhibited lower (more negative) $\psi_{\text{leaf}}$ relative to OC ramets, with intermediate values for the FE and SHR.

Photosynthetic rates declined from early July to early September with the greatest decline from early to late July (Figure 4). Photosynthetic rates did not differ between
plants in intact versus severed plots within each environment ($P_{\text{treatment}} > 0.05$), nor between environments ($P_{\text{environment}} > 0.05$). However, values from late July to September tended to be greater in the FE plots (Figure 4). Stomatal conductance ($g_s$) and transpiration rates ($E$) followed similar patterns as those for photosynthesis (not shown).

Height of intact ramets increased from June to maximum values in mid July for OC, WO, and FE and in late August for SHR (Figure 5; $F_{\text{time}} = 17.3$, $P_{\text{time}} < 0.0001$). Height declined in late September for OC, WO, and FE (indicating senescence) but remained near to maximum in SHR (Figure 5). Overall, ramet height did not differ between environments ($F_{\text{environment}} = 0.64$, $P_{\text{environment}} = 0.60$) and significant changes over time ($F_{\text{time}} = 17.30$, $P_{\text{time}} < 0.0001$) were similar for all environments ($F_{\text{time} \times \text{environment}} = 1.52$, $P_{\text{time} \times \text{environment}} = 0.14$). One way ANOVA per date also revealed no significant differences in ramet height between environments ($0.15 < F_{\text{environment}} < 2.0$, $0.16 < P_{\text{environment}} < 0.92$). ‘Maximum’ height (in August) of intact ramets was not significantly different between environments ($P > 0.05$, Figure 6).

For each environment, changes in height over time were similar for intact and severed ramets (Figure 7; $P_{\text{time} \times \text{treatment}} > 0.05$). Overall, “intact” ramets were significantly taller than “severed” in WO ($P = 0.02$), and tended to be taller in FE ($P = 0.09$), but not in OC and SHR environments ($P = 0.4475$ and $0.7704$ respectively; Figure 7). At the FE there was a marginal treatment $\times$ time interaction ($P = 0.07$) due to significant differences between intact and severed in late July and late August, but not at other sampling times.

Biomass of “intact” ramets was similar to that of severed ramets and did not differ across environments ($F_{\text{environment}} = 1.26$, $P_{\text{environment}} = 0.30$; $F_{\text{treatment}} = 1.16$, $P_{\text{treatment}} = 0.29$;
Figure 8a). However, the difference Intact-Severed biomass varied marginally between environments ($F_{\text{environment}} = 2.82, P_{\text{environment}} = 0.07$) with the greatest differences in FE and WO (Figure 9). These results suggest that severing is likely to have a negative effect on *H. odorata* individual biomass, but only in certain environments (FE, WO). Total biomass of other graminoids was greater in WO and lower in FE although differences between environments were only marginally significant ($F_{\text{environment}} = 2.43, P_{\text{environment}} = 0.09$). Biomass of other graminoids did not differ between severing treatments ($F_{\text{treatment}} = 0.03, P_{\text{treatment}} = 0.86$). There was a negative relationship between total biomass of graminoids within a given environment and biomass of individual *H. odorata* ramets (Figure 10). Ramet density (Figure 8c) was similar across environments ($F_{\text{environment}} = 1.07, P_{\text{environment}} = 0.37$) and was not affected by severing ($F_{\text{treatment}} = 0.28, P_{\text{treatment}} = 0.60$), although there was a tendency for higher density in “severed” relative to “intact” plots.

Nitrogen content was consistently higher in severed relative to intact ramets, however differences were not statistically significant (Figure 11; $F_{\text{treatment}} = 3.27, P_{\text{treatment}} = 0.0798$). Leaf N content did not differ between environments ($F_{\text{environment}} = 0.25, P_{\text{environment}} = 0.86$).

**DISCUSSION**

The first objective of this study was to document whether *H. odorata* growth differed across microhabitats. My results show that, overall, *H. odorata* grew similarly in all microenvironments where it was present. However, we did not find *H. odorata* in CC
or DO plots, suggesting that reduced soil water availability and perhaps light availability limit the distribution of *H. odorata* in certain environments.

The results reported here are consistent with the fact that *H. odorata* is a cool season grass native to the temperate regions of Eurasia and North America (Gould and Shaw 1983). The cool season nature was evident from the strong decline in photosynthesis (Figure 4) from early to late July, which corresponded with a strong decrease in soil moisture and leaf water potential from June to July. Therefore, *H. odorata* appeared to be very sensitive to the declines in soil moisture and the subsequent water stress. Most likely, high photosynthesis rates in early July, when soil moisture was high and temperatures were favorable, were preceded by high rates in June. Subsequent decreases of photosynthesis in late July, suggest that photosynthesis is sensitive to reduced soil moisture and, perhaps, high temperatures typical of July in Montana. Similar seasonal patterns have been demonstrated in other wet meadow species such as *Carex nebrascensis*, *C. rostrata*, *C. lanuginosa*, *Juncus balticus*, *Poa pratensis* and *Festuca arundinaceae* (Svejcar and Trent 1995, Huang and Fu 2000, Sala and Nowak 1997).

The absence of *H. odorata* in DO and CC plots is not surprising, because *H. odorata* is a grass typical of open wet areas known to require constant and high moisture availability (Norstog 1960). Soil moisture during July and August was significantly lower in DO plots, while in July soil moisture tended to be lower in CC plots perhaps as a result of tree water uptake. These results are consistent with the fact that in Montana, *H. odorata* is commonly found in wetlands and is considered a Facultative Wetland species by the USFW (MTNHP 1997-2000). Consistent with this, the limited current distribution
of *H. odorata* in Ohio has been attributed to wetland draining and consequential decreases in soil moisture (Norstog 1960). In addition to low soil moisture early in the season, the absence of *H. odorata* in CC plots may be due to limited light availability and competition by trees and under-story species.

Overall, physiology and growth of *H. odorata* from June to September was very similar in all microhabitats where it was present. This is consistent with the fact that soil moisture was similar and that PAR was not excessively low in any of these environments. In addition, growth in the greenhouse (data not shown) was significantly reduced at extremely low light intensities (18-76 µmol m\(^{-2}\)s\(^{-1}\)).

*Hierochloe odorata* ramets in WO plots in August exhibited significantly greater water stress than ramets in the other environments. The increased water stress was not a response to decreases in soil moisture availability, because overall soil moisture between microenvironment where *H. odorata* were present did not differ greatly. Over the course of the day, WO plots offer little protection against high radiation and associated high temperatures. Stress in WO plots is likely due to high transpiration rates that increase water stress in response to increased temperatures (Lambers et al. 1998). Ramets in OC plots exhibited the least amount of water stress in August, which likely corresponds to the protection of over-story species, rather than increases in soil moisture. On the contrary, OC plots tended to have lower soil moisture, which might reflect tree water use over time (as in CC), although differences were only significant in May. The presence of some over-story cover might facilitate *H. odorata* responses to high irradiance and associated high temperatures. Because FE plots were placed at the southwest of the forest boundary, FE plots were generally more shaded at the beginning of the day, resulting in frost
present on the leaves for a longer period relative to other plots. This cooler microhabitat may have been more conducive to lower early transpiration in the morning; however in the late afternoon, conditions dramatically change to much greater light intensities and associated higher temperatures. This daily temporal shift in somewhat extreme abiotic conditions is likely to increase stress by *Hierochloe odorata* in FE plots, whereas constant exposure to high radiation is likely to increase stress in WO plots.

Differences in ramet photosynthetic rates across environments were only apparent at the end of the growing season, when photosynthetic rates were significantly higher in FE over OC ramets (Figure 4). The inclination for higher photosynthetic rates in FE might be attributed to notable differences observed between FE and other environments. Because I measured photosynthesis rates during mid-morning hours at maximum light intensity (during sun flecks at FE plots), measurements at the FE, but not in the other plots, were preceded by a favorable period of cool temperatures. The tendency of higher photosynthesis in FE ramets did not correspond to similar increases in height or biomass, indicating that overall growth depends on integrated photosynthesis (during the entire day) and respiration losses.

While average *Hierochloe odorata* ramet biomass and total biomass of other graminoids at the end of the season did not differ significantly between environments, the two variables were negatively correlated, suggesting that the presence of graminoids (mostly *Carex* sp) has a negative influence on *Hierochloe odorata* ramet biomass. *Hierochloe odorata* does not develop dense growth as in turf grasses (personal observations, Klebesadel 1974). The low total biomass of *Hierochloe odorata* combined with substantial variation in this variable might explain why only average ramet *Hierochloe odorata* biomass rather than total biomass
correlated with total biomass of other graminoids. The observation that \textit{H. odorata} might be a poor competitor relative to other dominant wetland species is consistent with observations by Goldsmith and Murphy (1980) suggesting that \textit{H. odorata} occupies areas with highly variable water tables and salinity concentrations, where competition from neighboring species is much reduced.

The second objective of this research was to determine whether clonal growth is beneficial for \textit{H. odorata}. When ramets were severed, some differences were observed. Density of \textit{H. odorata} ramets in severed plots was similar to that of intact plots (Figure 10), indicating that disturbance to rhizomes does not stimulate ramet proliferation. The tendency for a slight, but consistent increase in leaf nitrogen concentration in ramets of severed plots, could be due to the fact that severing prevents allocation of N to interconnected below ground rhizomes, where some nitrogen may be stored for potential transfer to neighboring ramets upon demand.

Overall, my results suggest that severing had negative effects in WO and to a lesser degree in FE, but not in OC and SHR plots. In FE plots, however, differences were only significant for some dates. In contrast to height results, data for total biomass did not show treatment differences for any of the environments. However, trends were consistent with height results, with lower biomass in severed WO and FE plots, than in intact plots. Furthermore, when the difference between intact and severed plot biomass was compared between environments, there was a marginally significant treatment effect (\(P = 0.07\)) with higher differences in WO and FE plots.

The negative effect of severing rhizomes during late May on height and biomass in FE and WO indicates that clonality (i.e., belowground rhizome connection) throughout
the growing season may be particularly beneficial in these environments. These findings are consistent with other research that suggests that ramets of clonal plants share diverse resources and function as a physiologically integrated unit (Hartnett and Bazzaz 1983, Pitelka and Ashum 1985, Alpert and Mooney 1986, de Kroon et al. 1996, D'Hertefeldt and Jónsdóttir 1999).

The degree of physiological integration varies between species and environmental conditions. For example, Hartnett and Bazzaz (1983) determined that *Solidago canadensis* genets were physiologically interdependent and suffered severe mortality and decreased growth when connections were severed, especially when severing occurred early in the season. Their results also suggested a strong source-sink relationship between connected *S. canadensis* ramets, where illuminated ramets connected to shaded siblings photosynthesized 20% more relative to those connected to illuminated siblings. Alpert and Mooney (1986) showed that resource translocation between connected rosettes in *Fragaria chiloensis* support rosettes in unfavorable conditions, preventing death by drought in dry sites and shade stress in shaded sites. Resource sharing among clonal plants has been shown to be particularly beneficial in heterogeneous environments where overall genet resource acquisition is maximized by the exploitation and subsequent sharing of resources by individual ramets where these resources are abundant (Harnett and Bazzaz 1983, Alpert and Mooney 1986, de Kroon et al. 1996, D'Hertefeldt and Jónsdóttir 1999). Salzman and Parker (1985) showed that rhizomes in *Ambrosia psilostachya* clones transport both water and photosynthates to ramets subjected to salinity stress. Assimilate translocation among intraclonal tillers has also been shown to
occur in *Lolium perenne* (Forde 1966) and this integration allows the support of individual tillers under shaded stress (Ong and Marshall 1979).

A key advantage of clonal integration is the alleviation of stress, where individuals do not suffer independent fates (Pitelka and Ashum 1985). My results suggest that resource sharing within a genet during June or July is likely to be more important in WO and FE plots than in OC and SHR plots. While I did not measure detailed small-scale differences in resource availability between paired plots and within each environment, severed and intact plots were randomly located within each environment (i.e. microhabitat was presumably similar for severed and intact plots). Light availability in WO plots was consistently high, while soil water availability was abundant early in the season with subsequent declines similar to those in other environments. Therefore, WO plots were placed in the apparently most constant environment. In contrast, in OC plots light availability was variable in time and space due to shade by adjacent trees (i.e. ramets where not consistently subjected to low and high light). The fact that in this experiment clonality was detected to be most important in the apparently most constant environment and not significant in the apparently most variable (OC) suggests that clonal growth in *H. odorata* is not necessarily related to spatial heterogeneity.

Why is clonality apparently important in WO and FE but not in OC and SHR? Two explanations are possible for the observed negative effects of severing in some, but not all, environments. First, WO and FE may be the most stressful environments for *H. odorata* where redistribution of below ground resources stored in rhizomes may be important. Severing may greatly restrict the amount of resources that sister ramets would
share via rhizomatous connections, which may explain decreased plant height and biomass. High continuous exposure to sunlight throughout the day in WO plots and the afternoon in FE plots could significantly increase heat stress in these plots relative to more protected OC and SHR plots. Heat-induced increases in respiration and decreases in photosynthesis (Larcher 1995) could increase carbon demand and clonal dependency. Intact ramets in WO and FE might experience less overall respiration costs due to lack of rhizome disturbance and may be better able to cope with heat-induced respiration due to increased access to a larger carbon storage provided by the genet via rhizomatous connections.

Some degree of clonal integration might also occur in SHR plots, where intact ramets tended to have lower biomass than severed ones (although differences were not significant). Better growth in severed ramets suggests that these ramets 'save' some resources that would otherwise be donated to other sister ramets in adjacent open areas (away from the Shrub) via long rhizomatous connections. The tendency for decreased biomass in donor ramets was also observed in *Ambrosia psilostachya* by Salzman and Parker (1985) and in *C. flacca* by de Kroon et al. (1998) in greenhouse studies. Their evidence suggests that donor ramets endure costs rather than benefits, as a result of resource sharing within genets. Ramets under isolated shrubs within the meadow might actually be considered a source for resources to ramets in the adjacent open meadow. This is supported by the observations that ramets in SHR plots tended to grow tallest and over a longer period of time compared to those in other environments, although these differences were not significant.
Clonality might be important in all environments but due to the time severing occurred, differences were only detected in some environments. The largest differences due to severing were observed in WO plots, which overall (5 of 7 plots) were severed earlier in the season (late April; see methods). Young ramets severed from their genet, may have experienced a larger deficit in resources due to lack of clonal integration. However, height and biomass in FE plots were marginally affected by severing. In contrast to WO plots, FE plots were all severed in early June. Therefore if severing had occurred earlier in the season in FE plots, differences might likely be more significant.

Hartnett and Bazzaz (1983) demonstrated that when young ramets of *Solidago canadensis* were severed early in the season, ramets experienced significantly greater mortality and reduced growth compared to those severed later in the season. Delayed severing of 3 out of 5 plots of the OC and SHR treatments until early June could have contributed to the lack of differences due to severing in these environments.

The benefits of clonal growth of *H. odorata* may relate to its habitat preferences such as open wet areas that undergo a strong seasonal fluctuation in water table (Norstog 1960, Goldsmith and Murphy 1980, Lynch and Lupfer 1995, pers. observations.). These areas are often inundated in early spring but experience substantial temporal and spatial fluctuation of the water table. Areas of shallow water table are typically occupied by *Carex*, while the drier elevated areas are often occupied by less flood tolerant grasses such as *Andropogon* sp. (Norstog 1960). Clonal species are able to exploit these spatially and temporally variable environments. D’Hertefeldt and Jónsdóttir (1999) found *Carex arenaria* to be very clonally dependent while exhibiting little morphological deviations across spatially and temporally variable local environments. *H. odorata* also showed
little difference in height and biomass across environments, which may reflect an averaging effect of clonal integration. In spite of weak or lack of differences in other environments, it is important to emphasize that clonality is important in is the most common environment for \textit{H. odorata} in western Montana: wet and open environments.

Although our study did not examine performance of \textit{H. odorata} along a broad environmental gradient, but rather on a small scale, the work reported here has some implications towards restoration practices. \textit{H. odorata} requires high moisture and light availability, especially early in the growing season. Optimum habitat appears to extend to meadows with some over story vegetation (trees or shrubs) resulting in an open canopy habitat with some protection against excessive heat and desiccation.

The clonal nature of \textit{H. odorata} suggests that restoration success may increase when transplanting entire genets. However, a second year of data would be important to determine whether severing responses last in the long-term. These data suggest that in more extreme and less variable habitats (i.e. completely open) severed ramets suffer decreased growth. In less extreme environments responses to severing were less pronounced and transplanted individuals (or smaller “plugs”) for restoration purposes in these environments may allow further expansion into surrounding harsher environments. These results suggest that transplant survival is likely to increase with genet size, which could result in taller more aesthetically beneficial ramets in appropriate habitats.

Conserving existing local \textit{H. odorata} populations and habitat is vital to traditions of native people. With increasing population and accelerated development pressures on tribal lands there is a greater need to effectively manage these areas. Scientific knowledge can address conservation needs that may result from the loss of, or gaps in
traditional knowledge and traditional cultural resource management. The bridge between scientific and traditional knowledge to manage culturally significant organisms requires a high degree of sensitivity towards culturally significant issues. Consultation with local tribal agencies and their preservation ethno-biologists can mitigate concerns on both scientific and traditional ends of the spectrum.

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Fig. 1. Mean PAR between 10:00 and 13:00 hours (a) and between 13:30 and 16:30 hours (b) on June 22, 2001. Letters represent significant differences ($P < 0.0001$) using one-way ANOVA. N values range from 40-80. Note that data were not normally distributed even after several transformations tried.
Fig. 2. Changes in relative soil moisture content (% vol.) during the season in the different environments. Values are the average of measurements taken at 15 and 30 cm surface depth. P values denote significant differences between environments (one-way ANOVA per time period, \( \alpha = 0.5 \)).
Fig. 3. Mean leaf water potential for *H. odorata* during June (*F*<sub>environment</sub> = 1.86, *P* = 0.1562), August (*F*<sub>environment</sub> = 4.14, *P* = 0.0155) and September (*F*<sub>environment</sub> = 0.49, *P* = 0.6902). Error bars are one standard error of the mean. Differences between microenvironments in August are indicated by lowercase letters (one-way ANOVA, α = 0.05).
Figure 4. Mean photosynthesis rates of *H. odorata* ramets during the 2001 growing season. Error bars are one standard error of the mean. Values are averaged for intact and severed plots (n varied between 6 and 10).
Fig. 5. Mean height of intact *H. odorata* ramets over time. Error bars are one standard error of the mean (n= 6 to 10).
Fig. 6. Mean maximum height of intact ramets across environments in August. Error bars are one standard error of the mean.
Fig. 7. Mean height of *H. odorata* intact (solid symbols) and severed (open symbols) ramets over time within each environment. Error bars are one standard error of the mean. Asterisks denote differences due to severing at that time period.
Fig. 8. (a): Mean biomass of *H. odorata* "individual" ramets across environments. (b): Mean total biomass of other graminoids across environments. (c): Mean number of "individual" *H. odorata* ramets per plot. Gray bars represent intact ramets and hatched bars represent severed ramets. Error bars are one standard error of the mean.
Fig. 9. The change in biomass of “individual” *H. odorata* ramets as a result of severing: $F = 2.82$, $P = 0.07$. Error bars are one standard error of the mean. (One-way ANOVA, $\alpha = 0.5$).
Fig. 10. Relationship between mean biomass of other graminoids and mean biomass of “individual” *H. odorata* ramets for a given environment.

\[ r^2 = 0.91, \ P = 0.03 \]
Fig. 11. Mean leaf nitrogen content (% w/w) of *H. odorata* ramets in severed and intact plots across different environments. Error bars represent one standard error.
APPENDIX: Botany Internship with the Bureau of Land Management, Roseburg District Office, Oregon
The variable geographic and climatic factors in southwest Oregon contribute to
diverse and often rare or endemic plant communities. A significant portion of this area
was acquired by the federal government to manage its resources. The major source of
revenue in this area is the sale of forest products, mainly timber, with some revenues
from grazing allotments and mining. It is the responsibility of these federal land
management agencies to comply with the Endangered Species Act and conserve the rare
and sensitive plant communities, while managing for these resources. In the following, I
will discuss my internship experience as a Botanist with the Department of Interior
Bureau of Land Management (BLM), my objectives and the major challenges that I have
encountered as a botanist interested in the conservation of rare plant species.
Additionally, I will discuss potential solutions for resolving the conflicts of interest
between land managers interested in revenues and ecologists/conservationists.

I completed an internship with the Bureau of Land Management, Roseburg
District Office, Roseburg, Oregon to fulfill the requirements of the Training Within
Environmental Biology program which supported my graduate research at the University
of Montana. This program was funded by the National Science Foundation to the
Division of Biological Sciences of the University of Montana. The objective of this
program is to prepare graduate students to bridge basic environmental research with
environmentally focused private and public agencies. I was involved in a full-time
internship, from June 2002 through September 30, 2002, for a commitment of 640 hours,
which was funded through the Student Career Experience Program (SCEP). The
objectives of my internship were the following:
1. To bring current academic knowledge to natural resource agencies, bridging academic and agency scientists.

2. To obtain experience that will aid in the management and conservation of threatened, endangered and sensitive plant species. This experience will potentially be applicable to managing and conserving culturally significant species on tribal lands.

3. To work with agency personnel to promote the incorporation of ecological concepts into plant management plans.

4. To develop and maintain professional contacts within the BLM, other federal land management agencies, state land management agencies, tribal governments, and academia for the purpose of efficient information transfer, including scientific data, ecological expertise, technical support and public education.

The combining of four separate physiographic regions in southwest Oregon contributes to the convergence of several rare or sensitive species and unique plant communities. These regions include: the Klamath Mountain region, one of the oldest formations in the United States; the Western Cascade region, one of the newest; some Coastal range in the west, and the Willamette Valley in the north (Franklin and Dymess 1973). Many of the rare plants in this region are endemic to the serpentine areas that occur as a broad band stretching across the Roseburg area. The highly variable geomorphology, topography and precipitation combined with mild temperatures contribute to a wide variety of plant communities. Forests are comprised primarily of Douglas-fir and hemlock with some Grand-fir, Ponderosa pine, western redcedar, Port Orford cedar, incense-cedar and a number of hardwoods (i.e. several species of oak, maple, *Rhododendron*, alder and madroño). The numerous varieties of shrub and herb
species contribute to an abundance of forested plant associations. Oak savannah and serpentine meadows are unique communities in this region.

Southwest Oregon is comprised of a significant portion of federal lands, and is managed for its resources, primarily timber. The BLM was created to essentially manage the Oregon and California (O&C) railroad grant lands, which consists of most of the federal land in southwest Oregon. Management staff in the BLM of western Oregon is primarily comprised of foresters, who apply traditional forestry practices that are often in conflict with biological conservation.

Management of forest resources is important to local communities because of the dispersal of timber revenue: 25% to the U.S. Treasury, 25% to the BLM and 50% to the County from which the resources were based. Lands are primarily managed for Douglas fir production. Because Douglas fir can thrive in heterogeneous environments in coastal and mountain areas of the Pacific Northwest (Bames et al. 1998), this species can quickly expand and out-compete many other types of plant communities as a result of fire suppression.

Emphasis on timber production in southern Oregon has lead to fire suppression, increased forest plantations and other disturbances, all of which have impacted biological diversity. Fires suppression has allowed Doug-fir to encroach onto oak-savannah and meadow plant communities with a consequent negative impact on rare and sensitive species. For example, fire suppression has noticeably reduced the habitat for rare endemic Umpqua mariposa lily (Calochortus umpquaensis) occurring on serpentine soils (Holmes and Basham 2002).
Much of the forested lands and plantations are often comprised primarily of Doug-fir. On federal lands, however, such plantations often include a small number of other species (e.g., incense-cedar, Grand-fir). Although these planted units may not vary in species or age as in natural stands, forest age heterogeneity is accomplished by appropriate arrangement of harvest units over time and federal checkerboard ownership by sections. Plantations surrounding federal lands are often aerially sprayed with pesticides to eliminate broadleaf/hardwood cover and promote Doug-fir succession. This practice, however, is restricted to private landowners.

Ground-disturbing activities include clear-cuts and harvesting on steep slopes, timber operations and machinery, road building and maintenance. These activities can negatively impact the land by increasing erosion, landslides and weed invasions. The mild climate of southwest Oregon enhances the invasion of noxious weeds, which are a major problem due to their ability to aggressively dominate native plant communities. For example, the annual yellow starthistle (*Centaurea solstitialis*) is an aggressive invader that can switch to a short-lived perennial in this region. Yellow starthistle is known to encroach into habitat of the rare endemic species *Calochortus coxii* and *C. umpquaensis*. The change in the invader from an annual to short lived perennial further complicates weed control strategies, particularly in areas with rare, threatened or endemic species.

Biologists play an important role towards compliance with the Endangered Species Act, which requires federal agencies to survey for and protect listed species in any federal action (i.e. timber sales, road construction, land exchanges). While an intern as a Student Trainee Botanist, I have become familiar with agency policies, procedures
and regulations. Conducting botanical surveys and recommending the appropriate actions concerning sensitive plant species is the primary duty of the botanist whom I assisted. I have become proficient in identifying plants, particularly threatened, endangered and sensitive (TES) species. I have also gained experience in writing sighting reports and proposals to fund contractors, in addition to recommending appropriate conservation measures involving actions that may affect TES plant species. More important than expertise in plant identification are skills in identifying and effectively communicating concerns to the agency managers, particularly when their final projects do not consider necessary management action to protect TES species. I have provided the agency with effective communication skills, problem solving and willingness to take on new reconciling roles. Essentially, I have taken on the role as a team member to help the agency succeed.

Part of the value of this internship was gaining first-hand experience with natural resource management and decision-making. Because not all recommendations coincide with management objectives, decision outcomes can generate major conflicts between resource management views and species conservation goals. Management decisions based on interpretations that reflect the intent and fundamental nature of the Endangered Species Act should take into account the views from biologists and ecologists in management positions in addition to those of foresters. During this internship it has become clear to me that management practices that support species diversity might be developed through outreach efforts from the academic community and better communication practices, relaying scientific results to broad non-academic audiences effectively.
For example, recent scientific research reveals that management of noxious weeds using biological agents may have unexpected negative outcomes such as negative impacts on non-targeted species. Herbicidal applications may have similar unexpected impacts on native plant communities. Therefore, management protocols may be outdated and overlook the protection of TES species. A clear understanding of plant ecology is integral to both weed management and plant conservation objectives.

Conservation programs under the Northwest Forest Plan were adapted to support species associated with old growth forests and spotted owl habitat. The change in conservation objectives brought about by this plan has resulted in decreased timber harvesting, from an average annual harvest in 1984-1988 for the Roseburg District totaling 254 million board feet to 45 million board feet in 1999 (U.S. Department of the Interior Roseburg District Office 1994). With the large economy in southern Oregon dependent on timber, management plans need to compromise between local economic needs and conservation. With investment to noxious weeds in the millions of dollars (ODA 2000) and the concurrent loss of timber production, there is a need to combine both academic and research expertise to address natural resource management to meet conservation and economic concerns. Additionally, federal agencies like the BLM with changing land management priorities need to work with and educate communities that are faced with economic restructuring.

Southwest Oregon offers many unique botanical resources. The BLM in southern Oregon relies on biologists (including botanists) to survey and make appropriate recommendations that comply with the Endangered Species Act in addition to the management plans that address the conservation of old growth forest and spotted owl
habitat in the Pacific Northwest. My academic training contributes to resource
management from an ecosystem perspective.

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