Effects of *Ehrharta erecta* on the redwood understory and implications for restoration

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ABSTRACT

Biological invasions, particularly by exotic grasses, have the potential to reduce biodiversity and to alter ecosystem functions and disturbance regimes in native communities. *Ehrharta erecta* Lam. (panic veldt grass) is an evergreen perennial grass with life history traits that makes it an aggressive competitor against native species. It spread extensively beyond the sites of its experimental introduction around the central coast region of Northern California in the 1930s, and it has invaded the redwood understory on the UCSC campus. In my study, I compared photosynthetic rates of native species with and without the surrounding invader removed in order to gain insight into the physiological effect of *E. erecta* on native species. In a separate experiment, I compared the effectiveness of herbicide application and manual removal in controlling *E. erecta* on the UCSC campus. I evaluated how each treatment influences the recovery of natural communities by planting native redwood understory herb *Clinopodium douglasii (*Benthe.) Kuntze into treated plots, alongside unplanted controls, in order to examine 1) the effect of *E. erecta* removal treatments on native survival and growth rate 2) the effectiveness of native vegetation restoration in reducing reinvasion of *E. erecta*. A better understanding of the degree and mechanisms of impact of *E. erecta* on native species will serve to guide restoration priorities for invasive species management.

INTRODUCTION

Biotic invasions are occurring at a higher rate than ever before, and are contributing to human-driven ecological changes on scale with other major drivers such as habitat conversion and climate change (Vitousek et al. 1996, Parker et al. 1999, Mack et al. 2000, Butchart et al. 2010). The impact of invasive species is second only to human population growth and associated habitat degradation in reducing world biodiversity (Soulé 1999, Pimentel 2010). Although most exotic species that become established outside their native ranges are harmless (Davis 2003), the exceptions can be disastrous to native communities by reducing biodiversity and altering ecosystem processes, often at a large cost to humans (Vitousek et al. 1996, Pimentel et al. 2000). Many weedy natives spreading from Eurasia and Africa to the grasslands and favorable climates of the Americas, Australia, and Oceania have altered the composition of native communities, and changed the frequency and intensity of natural disturbance regimes (D'Antonio & Vitousek 1992, Rejmanek et al. 2005). There is still much to be understood about the context and mechanisms of invasive dominance and how invasions should be addressed.

The 'panic' or 'erect' veldt grass, *Ehrharta erecta* Lam. was reported in Northern California in the 1930s, and was planted throughout the central coast region, including two 25-m^2 plots on the UCSC campus, by UC Berkeley researcher G. L. Stebbins (1985) as part of a study of relationships between chromosome number and invasive ability. At the end of the 40-year study, the "green monster" (Gluesenkamp 2004) had spread extensively beyond the experimental sites, with an unusually high capacity for colonization (Stebbins 1985). *Ehrharta erecta* is native to South Africa's Cape region, which, like California, is one of five regions in the world with a Mediterranean climate, characterized by mild wet winters and dry summers. This similarity in climate may in part explain its rapid establishment. It is currently invasive in the San Francisco Bay Area and South Coast California Floristic Provinces (Baldwin et al. 2012). Even after 80 years of proliferation in these regions, there is little quantitative information about the ecological impacts of *E. erecta* and methods for controlling its invasion (Pickart 2000).

Ehrharta erecta has proliferated into a wide variety of habitats including dunes, shrubland, forest, and urban areas, where it tolerates a broad range of climatic and edaphic conditions, from arid to moist and shady habitats, including sandy, waterlogged, and rocky soils (Sigg 1996). *Ehrharta erecta* has the largest introduced geographic range of all species in the genus (Gluesenkamp 2004). Because of its ability to establish in a broad range of habitats, *E. erecta* may pose a threat to California's sensitive plant communities. It is particularly well adapted to shady habitats and areas of heightened moisture levels such as irrigated areas, and under shrubs and trees, including the redwood understory on the UC Santa Cruz campus (McIntyre 2005, Sherman 2012). During summer months, the *E. erecta* dries and creates a dense thatch (Pickart 2000). The increased organic matter in the understory produced by *E. erecta* (living grass and last year's growth) is thought to inhibit native germination and increase the fuel load for potential fires (Frey 2005). The life history of *E. erecta* makes it an aggressive competitor against both natives and other exotics, which raises the possibility of shifts in species composition to *E. erecta* monocultures, and loss of micro- and macro-biotas associated with native vegetation (Cal-IPC 1999).

This invasive is considered a species of concern because of its rapid rate of spread and ability to survive in a variety of habitats and suppress natural diversity (Gluesenkamp 2004). On heavily invaded sand dunes, increased ground cover of *E. erecta* reduced the cover of native species (Gluesenkamp 2004). In a small pilot experiment, *E. erecta* removal had a significant positive effect on the photosynthetic rate of native herb *Stachys bullata* (I.M. Parker 2011, unpublished data), suggesting that *E. erecta* may compete with other understory species. No other studies have documented the physiological responses of native species challenged with *E. erecta* invasion.

Several control treatments have been tested for their effectiveness of eliminating *Ehrharta* species. Nearly all control techniques have been limited to the other two *Ehrharta* species, and there has been little information quantifying the impacts on *E. erecta* (Pickart 2000). Broad-spectrum herbicides have been shown to effectively reduce *E. erecta* abundance, although grow-back is significant in following years without repeated applications (Gluesenkamp 2004, Pickart 2000). The “scorched-earth” approach that includes one to several applications of herbicide to remove all above-ground vegetation is often considered the most effective in *E. erecta* removal (Frey 2005). The effect of herbicide use on native vegetation has not been documented. Frey (2005) proposed that manual removal actually stimulates seed germination and increases abundance of *E. erecta,* and repetition of this treatment is usually suggested (Pickart 2000, Gluesenkamp 2000). Tarping or solarization was not shown to effectively eliminate *E. erecta*, as the plants survived under the tarp and the seeds remained dormant until uncovered (Gluesenkamp 2004). Fire was shown to increase *E. calycina* in an invaded region in Australia (Milberg & Lamont 1995). A fungal pathogen has been tested on *E. calycina* in its native South African range, but this biological control has not been tested in the invasive Californian range (Pickart 2000). The Land Conservancy of San Luis Obispo employed a management program to control sister species *Ehrharta calycina,* that included a regime of mowing, monocot-specific herbicide application, followed by a broad-spectrum herbicide application (Pickart 2000). Additionally, the US Air Force (1999) reported the use of broad-spectrum herbicide to control *E. calycina,* and native seeding and outplanting to restore dune scrub communities (Pickart 2000).

Planting nursery-propagated native seedlings or plants after the removal of exotic species often enhances restoration success by reducing reinvasion of the exotic and increasing native cover, an important step in restoring a native community (Stromberg & Kephart 1996, Cal-IPC 1999, Pickart 2000, Corbin & D'Antonio 2004). Outplanting propagules can be used to supplement "passive restoration" in cases where the native plants are dispersal limited or the seed bank is absent due to long time dominance of an exotic (Steven & Sharitz 2007, Young et al. 2005). Natives may be dispersal- and seed-limited due to long term dominance of a non-native, or the accumulation of non-native thatch that prevents the germination and growth of natives (Erskine Ogden & Rejmánek 2005). Strategies that reduce competitiveness of exotics while increasing the establishment of native species can lead to successful restoration of natives that may not recover without supplemental plantings (Corbin et al. 2004).

In this study, I compared photosynthetic rates of two native redwood understory species, *Clinopodium douglasii* and *Stachys bullata*, with and without manual removal of the surrounding *E. erecta*. I predicted that removal of the invader would lead to increased photosynthesis (and transpiration). I also compared the effectiveness of herbicide and manual removal in controlling *E. erecta*, and then evaluated how each treatment influenced the restoration success of planting *C. douglasii*, a native species.

MATERIALS AND METHODS

Study site

All sites were on the UCSC campus, in Santa Cruz County, CA. For the photosynthesis measurements, I selected a site on a previously unstudied yet perhaps the most highly invaded region of the UCSC campus, at the north-eastern corner of campus near Crown College (37.00073°N, -122.05441°W).

Ehrharta erecta populations and study sites were mapped by UCSC student Joel Sherman for an undergraduate thesis in 2012 (Sherman 2012, Figure 1). He observed *E. erecta* along walkways, roads, streambeds, and around rock swales below drainage outputs, and established 12 study sites in mixed evergreen forest and bay laurel/oak woodland. I selected five of

Sherman's sites (sites 3, 4, 5, 6 and 9) that experienced the least pedestrian traffic for the removal and transplant study.

Study Species

Ehrharta erecta

Ehrharta erecta is a sprawling perennial grass with semi-erect stems 30-60 cm tall (Baldwin et al. 2012). The leaf blades are broad, green, flat, 5-12 cm long, and 4-9 mm wide. It is shade-tolerant and capable of low-light photosynthesis, and prefers high soil moisture and dense canopy cover (McIntyre & Ladiges 1985, Sherman 2012).

Ehrharta erecta has two different methods of reproduction. *Ehrharta erecta* has ascending stems that can drop seed >50 cm away from the parent (Baldwin et al. 2012). *Ehrharta erecta* can also spread vegetatively via underground stems, which are thick-matted and can crowd out neighboring plants (Sigg 1996, Frey 2005). *Ehrharta erecta* flowers and produces large quantities of seed year-round, but may have a dormant period during summer droughts (Cal-IPC 1999, Brown & Brooks 2002, Frey 2005). Seeds fall from the grass as the flowers dehisce, and are thought to be dispersed either by wind or by water (Frey 2005, Sherman 2012), although more research is necessary to confirm the primary dispersal mechanism. Seeds are presumed to have a low initial germination rate, but an extremely high germination rate after one year (McIntyre & Ladiges 1985).

Clinopodium douglasii and *Stachys bullata*

Yerba buena, *Clinopodium douglasii* Benth. (Kuntze), is a perennial, decumbent herb native to the redwood understory and other shady woodland and chaparral habitats. The stems can be woody, crawling, and can send roots down. Leaves are opposite, ovate to spade- or triangle-shaped, often shallowly dentate, hairy, 10-35 mm long, and 5-25 mm wide (Baldwin et al. 2012).

Hedge nettle, *Stachys bullata* Benth., is an annual herb with erect stems, 40-80 cm tall, with stiff, sharp, reflexed hairs (Baldwin et al. 2012). Leaves are ovate with cordate bases and obtuse tips, 3-18 cm long, and covered in soft-stiff glandular hairs. It is abundant in mixed-evergreen forest understory communities in coastal California.

Both *S. bullata* and *C. douglasii* leaves have a citrus-mint aroma when crushed due to volatile oils containing terpenes that can have anti-herbivory, antimicrobial, allelopathic, pesticidal, and antioxidant properties (Hay & Waterman 1993). The amount and potency of terpenes produced by these plants may be influenced by environmental conditions experienced by the plant, including water or nutrient stress (Gershenzon et al. 1978).

Experimental Design

Experiment 1: Effect of E. erecta *removal on photosynthesis of two native species*

At the Crown study site, I selected ten naturally growing *S. bullata* and six *C. douglasii* individuals and marked them with numbered flags. All plants were more or less erect, without visible herbivory, surrounded by *E. erecta, and were* at least three meters apart.

Half of the individuals of each species were randomly assigned to *E. erecta* removal treatment and half to control. Treatment consisted of manual removal of all *E. erecta* within a 25 cm radius from the lower stem of the plant. I measured fresh biomass (shoots and roots) of *E. erecta* after removal (Table 1). One week after removal, I measured transpiration with a Decagon SC-1 Leaf Porometer, chlorophyll content with Apogee Chlorophyll meter, and chlorophyll fluorescence with an Opti-Sciences OS-1p fluorometer. Photosynthetic data were collected one week after removal with the intention of allowing individuals to recover from trauma from soil and root disturbance due to pulling. All data were collected from treatment and control plants within a two-hour time block (1100-1300) with the purpose of controlling for time-of-day effects on photosynthesis.

Because the photosynthetic rates of only five individuals could be completed in two hours, each treatment group was split in half, with five individuals measured on the first day, and the remaining five individuals on the next. Both days included an even mix of control and treatment individuals (2:3 control:treatment on day one, 3:2: control:treatment on day two). The removal treatment was also applied over two days, one week before data collection to give a constant time from pulling to measurement.

Experiment 2: Comparison of E. erecta *control methods*

I used a split-plot design to investigate the effects of *E. erecta* control and the transplanting of native *C. douglasii* on the restoration of invaded plots. At each of the five sites, three rectangular plots (1.0×0.5 m each) were randomly assigned to one of three treatments; herbicide application, manual removal of *E. erecta*, and control. Post-treatment, half of each plot was planted with nine evenly spaced *C. douglasii* transplants in three rows of three, 12.5 cm apart with a 12.5 cm border around the edge of plots to reduce any border effects (Figure 2).

Treatments were applied to the research plots in February 2013. In removal plots, the living grass was removed by hand as completely as possible while trying not to disturb the native plants. Herbicide plots were sprayed with Round-up, a broad-spectrum herbicide with the active ingredient glyphosate, using a backpack sprayer containing a diluted solution of 22.25 mL glyphosate per 1 L of water. This solution contained a blue dye, and plots were sprayed until visibly covered with the dye.

The *C. douglasii* seedlings were planted in half of the plots in May 2013. The plants were started from cuttings collected on the UCSC campus in October 2012 and propagated in conetainers (3.8 cm diameter, 14 cm tall) at the UCSC greenhouses with temperatures ranging from 65-45F from day to night, and a twice daily misting regime, then grown outdoors in natural conditions for four months prior to planting. I tagged individuals using numbered bird bands, and measured the length of tagged branch (in cm) and number of stems of each individual after transplanting. The transplants were monitored and watered in to ensure successful establishment, receiving 0.75 gallons of water per plot every two days for the first two weeks after planting.

In October 2013, I quantified survival of *C. douglasii* in each plot, marking plants as either "survived" or "not-survived". I measured the change in stem height (in cm) and number of stems of each surviving individual to determine the growth rate over the six-month growth period.

I measured pre-treatment percent cover of plots in February 2013, and post-treatment percent cover of plots in October 2013 using the point-intercept method and a 0.5×0.5 m quadrat with 100 points. There was no significant difference in pre-treatment percent cover among the treatments ($F_{2,2}$=0.31, p=0.74, Figure 3).

Statistical Analysis

I used a nested ANOVA to test for differences between *E. erecta* removal treatments for transpiration, chlorophyll content, and chlorophyll fluorescence of *C. douglasii* and *S. bullata*. For each response species, individuals were nested within treatment and five replicate measures were nested within each individual.

I used an ANOVA to test for a difference in the percent cover of *E. erecta* in herbicide, removal, and control plots before treatments were applied.

I used an ANOVA to test for the effect of herbicide, removal, and control treatments on percent cover of *E. erecta* after 6 months of growth. I used a post-hoc Tukey's test with α=0.05 to determine which treatments were significantly different from each other.

I used a logistic regression to test for a difference in survival of *C. douglasii* plants among treatments. To test for a difference in proportional growth and number of stems of *C. douglasii* plants among treatments, I used an ANOVA with site as a blocking factor. I log transformed (+1) proportional growth to improve normality.

RESULTS

Experiment 1: Effect of E. erecta *removal on photosynthesis of two native species*

Both transpiration rate and chlorophyll content in *S. bullata* were significantly higher in treatment individuals than control individuals ($F_{1,9}$=11.9, p=0.0013, Figure 4, $F_{1,9}$=450.6, p<.0001, Figure 5). The opposite trend than expected occurred in *C. douglasii*, with transpiration rate being lower in treatment individuals than control individuals ($F_{1,5}$=12.1, p=0.0019, Figure 6), and there was no difference in chlorophyll content between control and treatment individuals ($F_{1,5}$=0.49, p=0.49). There was no difference in chlorophyll fluorescence between treatments in *S. bullata* ($F_{1,9}$=1.41, p=0.24), however in *C. douglasii*, there was higher chlorophyll fluorescence in control than treatment individuals ($F_{1,5}$=17.4, p=0.0003, Figure 7).

Experiment 2: Comparison of E. erecta *control methods*

There was a significant effect of treatment on final percent cover of *E. erecta* ($F_{2,20}$=11.9, p=0.0004, Figure 8**).** There was no significant effect of planting and no significant interaction among treatment and planting on final percent cover or *E. erecta* ($F_{1,20}$=0.17, p=0.68, $F_{2,20}$=0.17, p=0.84).

There was significant difference in survival of *C. douglasii* among treatments, with herbicide having the lowest survival, removal having the highest survival, and control having an intermediate survival (Table 2, Figure 9.).

There was a significant difference in proportional growth of *C. douglasii* among treatments, with proportional growth being lowest in herbicide treatment, highest in removal treatment, and intermediate in the control treatment ($F_{10,77}$=2.17, p=0.029, Figure 10).

There was no difference at the end of the experiment in number of stems of *C. douglasii* among treatments ($F_{10,91}$=1.79, p=0.072), and all three treatments had a net loss of stems over the course of the experiment (Figure 11).

DISCUSSION

Experiment 1: Effect of E. erecta *removal on photosynthesis of two native species*

There was higher transpiration rate and chlorophyll content in *S. bullata* when the surrounding *E. erecta* was removed, suggesting that the control individuals were under the stress of competition with *E. erecta.* Transpiration rate drops when a plant closes its stomata to prevent water loss during times of water stress, subsequently reducing the rate of photosynthesis due to a decrease in carbon uptake. Lower transpiration rates therefore may indicate more water stress in *S. bullata* individuals surrounded by invasive grass. Transpiration also allows the plant to cool itself, and so a reduction in transpiration rates of *S. bullata* control individuals may leave them vulnerable to heat stress and potential damage to the photosynthetic apparatus. Under water and heat stress, a plant will begin to show signs of senescence and suffer from a loss or breakdown of chlorophyll content in the leaves (Blum 2011). Environmental stresses that affect the photosynthesis of a plant result in a decline in chlorophyll fluorescence, reflecting damage to the photosynthetic apparatus (Blum 2011). It is important to note that transpiration rate can also be affected by other environmental parameters including air temperature, relative humidity, light intensity, and air speed, which were not controlled for in this study.

Water is a limiting resource in most terrestrial ecosystems (McAlpine et al. 2008). In June 2013, sites invaded by *E. erecta* on the UC Santa Cruz campus had a lower moisture content than un-invaded sites, which could suggest that either *E. erecta* preferentially invades sites with lower moisture, or that it effectively extracts water from the soil, perhaps more rapidly than native species (Winfield 2013). McIntyre & Ladiges (1985) found that *E. erecta* might be a severe competitor for soil moisture, reducing the amount available to natives and therefore restricting native growth and photosynthesis. The availability of nitrogen and other nutrients is linked to soil water, and may be an additional limiting factor to native plants if *E. erecta* can uptake water at a higher rate or is tolerant to lower moisture conditions than the natives (Everard et al. 2010).

In Mediterranean regions, plants are often water-limited during the summer drought, and competition between species is often for water (Clary et al.

2004). The outcome of competition will be correlated with both the ability to utilize available water and phenology, or timing of plant growth (Clary et al. 2004). Many common California invaders are annual grasses, which avoid the detrimental effects of the summer drought by setting seed quickly and then senescing, shifting the competitive advantage away from the native perennial vegetation that must allocate resources toward surviving year-round (Clary et al. 2004). A study comparing native and invasive species in a Mediterranean region found invasives to have better responses to water stress, allowing for continued photosynthesis for longer during drought conditions and subsequent higher leaf temperature, a trait associated with "invasiveness" (Godoya et al. 2011). *Ehrharta erecta* remains green year-round although it does slow its growth during increased summer temperatures. It is unusual to see perennial invasives with the ability to outcompete perennial natives with a similar life history. Perhaps even more unusual is that *E. erecta* is a drought-tolerant grass that can grow in the shade, an additional advantage against natives that differs from most invasive grasses in California.

I found the opposite trend in the effect of invader removal on *C. douglasii* transpiration and chlorophyll fluorescence than in *S. bullata*. This may be a result of soil disturbance during removal of *E. erecta*. McLellan et al. (1995) examined the design of removal experiments and found that pulling up the roots of standing vegetation can have an adverse effect on the remaining plants by disrupting the mycelium interactions, soil aggregation and water holding capacity, and plant rooting patterns and growth. It is possible that *C. douglasii* was adversely affected by the removal because it is a crawling plant that resprouts from underground stems and is therefore in more direct contact with the soil than *S. bullata,* which is more or less erect. McLellan et al. (1995) recommended clipping above-ground biomass instead of total removal, however that strategy would be ineffective against *E. erecta* considering its ability to resprout from root masses. Additionally, it is inevitable that removing plants from a site will alter other important environmental factors, and these side-effects can confound the results of removal experiments if they significantly affect plant performance (McLellan, Fitter & Law 1995). Manual removal of invasives is a time-consuming control method that is not practically applied on a large scale, but this alternative to herbicide can be used to preserve native vegetation. However, if the process of manual removal is destructive to natives, this may facilitate further invasion. Before applying a manual removal treatment, it may be beneficial to consider the physical attributes of native plants in an area, such as belowground stem and root sensitivity.

Future studies could repeat this experiment by comparing invaded and non-invaded sites, therefore eliminating the potential for measurements to be affected by soil disturbance from removal. However, in such comparative experiments, it is hard to control for other factors. It may also be beneficial in further studies to remove both native and invasive plants around treatment individuals in order to eliminate the confounding factor of above- and below-ground competition with other native plants (Vidra et al. 2007).

Experiment 2: Comparison of E. erecta *control methods*

Six months after the application of control methods, herbicide plots showed a nearly 100% reduction in *E. erecta,* and manual removal plots showed an 89% percent reduction in *E. erecta*, and they were both significantly lower than control plots, which had a 24% reduction in cover. These results suggest that either treatment is much better than no treatment. As evaluated by post-hoc comparisons, there was no significant difference in cover between removal and herbicide treatment plots. My results are not exactly consistent with previous studies that favored a “scorched earth” approach to eliminating *E. erecta* over manual removal, which showed mixed success (Pickart 2000, Gluesenkamp 2004, Frey 2005). There was low cover of *E. erecta* in removal plots, suggesting that if seed germination was stimulated by manual removal as in previous studies (Pickart 2000, Frey 2005), it was at a low rate. It may be that after more time, significant differences between herbicide and manual removal plots will develop.

Planting *C. douglasii* did not result in a reduction in *E. erecta* cover in comparison to no planting. This was unexpected, because outplanting natives in other studies helped resist further invasion by occupying space and resources and gaining a competitive edge over aggressive exotics (Stromberg & Kephart 1996, Cal-IPC 1999, Pickart 2000, Corbin & D’Antonio 2004, Vidra et al. 2007). This suggests that “passive restoration” is just as sufficient as outplanting without spending the time, money, and resources. However, this study was limited to six months, and it may take longer to see the effect of outplanting natives on *E. erecta* cover.

Contrary to expectation, survival and proportional growth of outplanted *C. douglasii* was the lowest in herbicide treatment. The herbicide treatment was predicted to have the highest outplanting success because *E. erecta* as well as other herbaceous vegetation was eliminated, therefore increasing the availability of soil water and resources to *C. douglasii* compared to plots with competing vegetation intact (Newton & Preest 1988). In other studies, reestablishment of natives is a critical next step after eliminating exotics, and often follows an herbicide treatment with success (Stromberg & Kephart 1996, Seabloom et al. 2003, Greygiel et al. 2009, Stanley et al. 2011).

Herbicides can be beneficial or detrimental depending on the frequency of spraying and how long the herbicide persists in the soil (Crone et al. 2009). Application of a broad-spectrum herbicide such as glyphosate eliminates non-target native species due to limited selectivity and can have unknown impacts on native species (Crone et al. 2009, Stacy et al. 2005). Glyphosate is applied to the foliage, and is translocated to the shoots and roots of the treated plant and then broken down in the soil (Fletcher & Freedman 1986). The amount of time in which it persists is dependent on soil microorganisms and microconditions, but in most cases is reported to break-down 10-30 days after application (Fletcher & Freedman 1986). However, studies have shown a variety of lengths of decomposition time of glyphosate, from 60 days (Newton et al. 1984) to eight months (Fletcher & Freedman 1992), to continued persistence after one year (Levesque & Rahe 1992). In this experiment, there were two months between the application of the herbicide and the outplanting of *C. douglasii,* which may or may not have been enough time for the herbicide residue to be eliminated.

The impact of glyphosate on soil fertility has been studied with mixed results. Some studies have found that glyphosate is not harmful in concentrations used in the field, but can have detrimental effects on soil organic matter at high, undiluted concentrations, including toxicity to the soil microorganisms that contribute to decomposition of organic matter and availability of nutrients (Fletcher & Freedman 1986, Thompson et al. 2000, Carlisle & Trevors 1988). Another study found glyphosate in field concentrations to be detrimental to many fungal species that form symbioses with plants in the rhizosphere (Levesque & Rahe 1992). Glyphosate has also shown decreased prey consumption and fertility in arthropod predators due to toxicity and changes in vegetation structure (Benamu et al. 2010).

The unexpected results of the low outplanting success in herbicide treatments could be due to direct toxicity of herbicide residue, but it could also reflect indirect effects such as a loss or change in soil organic matter, or increased herbivory due to a decrease in arthropod predation. Continued monitoring of these plots with a focus on percent cover and density of natives will determine if herbicide has an effect on native reestablishment in subsequent years. It may be the case that *C. douglasii* is particularly sensitive to glyphosate, either due to direct or indirect effects. Studying the reintroduction of another native, or with another herbicide may be beneficial. Additionally, there could be other reasons that have nothing to do with the herbicide itself, such as the bare ground resulting in increased soil temperature and dryness.

According to the stem count results, there was a tendency of *C. douglasii* to shrink over time, and some shrank less than others. However, there was no difference between treatments despite the difference in survival and growth, suggesting that measuring the number of stems of each *C. douglasii* individual was not an effective measure of establishment success.

Much remains unknown about the seed bank of *E. erecta,* and whether control efforts will be challenged with a long-lasting, resilient seed bank. Because of the high production of seed by *E. erecta,* it is suggested that both removal and herbicide treatments will have to be repeated (Brey 1996, Pickart 2000). This shows that long-term restoration projects It will be important to continue monitoring these plots over time to examine both the regrowth of *E. erecta* and the interaction between *E. erecta* and *C. douglasii.* In a previous restoration study, the negative effect of exotic annual grasses on native perennial productivity became diminished over time (Corbin & D'Antonio 2004). The competitive interactions favored the exotics after the first growing season, but the natives were able to establish and reduce the productivity of the exotics over the four-year study period (Corbin & D'Antonio 2004), suggesting the value in long-term restoration projects.

In summary, *E. erecta* showed a negative impact on the physiology of one native species, *S. bullata*, while the impact on *C. douglasii wa*s unclear due to other effects of the treatment. More studies are needed to quantify the impacts of E. erecta on individual plants as well as ecosystems. Herbicide and manual removal were effective at dramatically reducing *E. erecta* over a 6-month period. My study showed the potential for negative effects of herbicide on native species (as shown in the outplant), but also the potential for negative effects of hand-pulling on native species (as shown by the physiology experiment). These effects could limit the ability for the native community to return to its pre-invaded state after treatment. Both treatments appear to have the ability to alter the soil environment, and therefore it could be valuable to assess and manage soil conditions before outplanting. Herbicide is generally more cost-effective and less labor-intensive than manual removal, and is more realistic for land managers to apply on a large scale. A longer term and larger scale study is needed to extend my results and provide clear guidelines for the management of this aggressive invasive plant.

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Table 1: Biomass of Ehrharta erecta removed around treatment individuals of *Clinopodium douglasii* and *Stachys bullata*.

Species	**Individual**	**Biomass (g)**
C. douglasii	4	39.48
C. douglasii	3	78.24
C. douglasii	5	45.98
C. douglasii	6	108.55
C. douglasii	10	40.43
S. bullata	6	47.72
S. bullata	8	53.19
S. bullata	3	22.66
S. bullata	7	43.75
S. bullata	5	45.47

Table 2: Effect of site and treatment on survival of C. douglasii transplants.

Source	**Nparm**	**DF**	**L-R ChiSq**	**Prob>CHiSq**	**Other DF?**
Site	4	4	9.94321248	0.0414	
Treatment	2	2	9.97156844	0.0068	

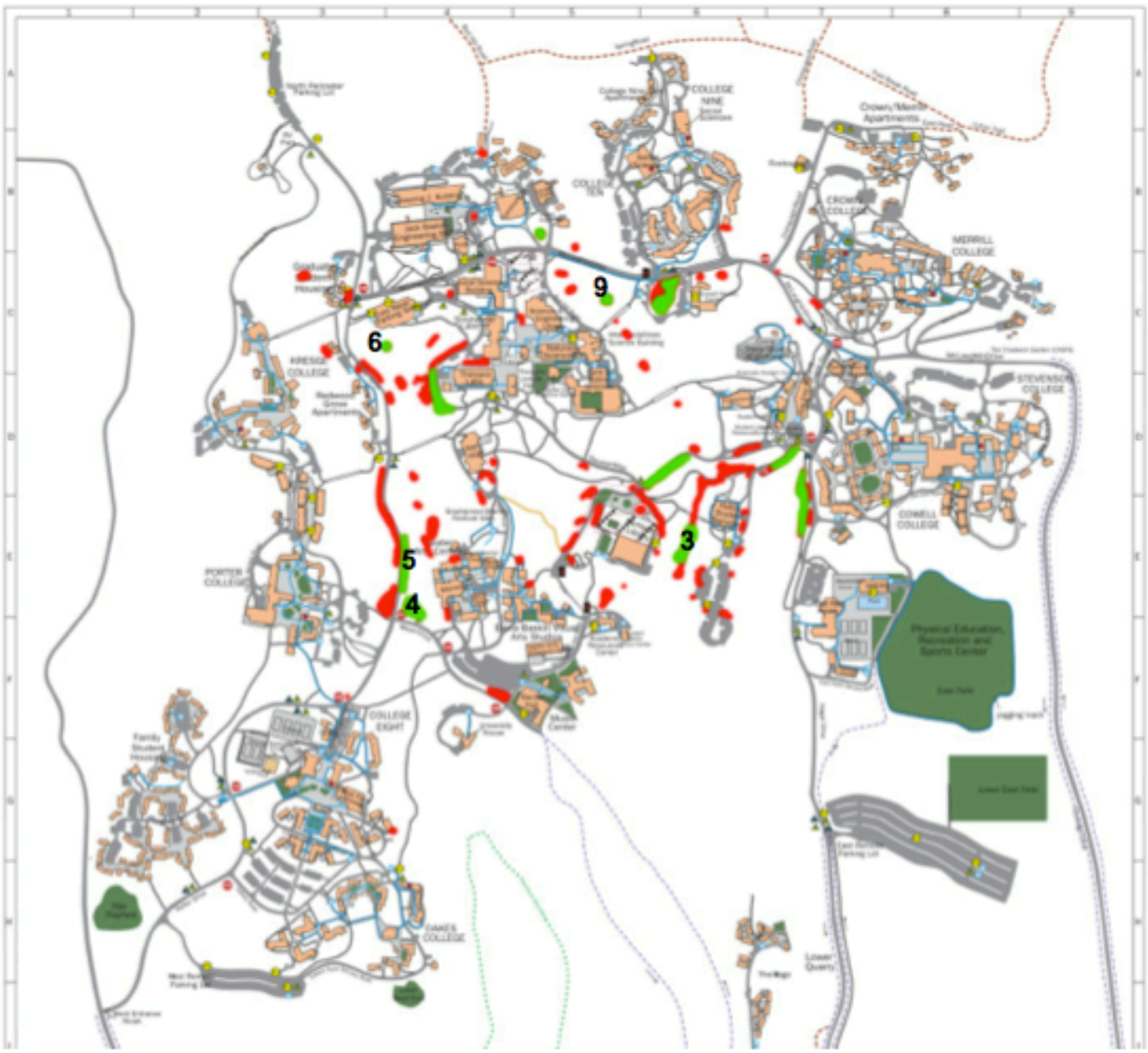

Figure 1: Populations of *Ehrharta erecta* (red) on the UC Santa Cruz campus as of fall 2012, with locations of study sites in green. My study sites are marked with associated site number. Map provided by UCSC, *E. erecta* populations and study sites labeled by Joel Sherman.

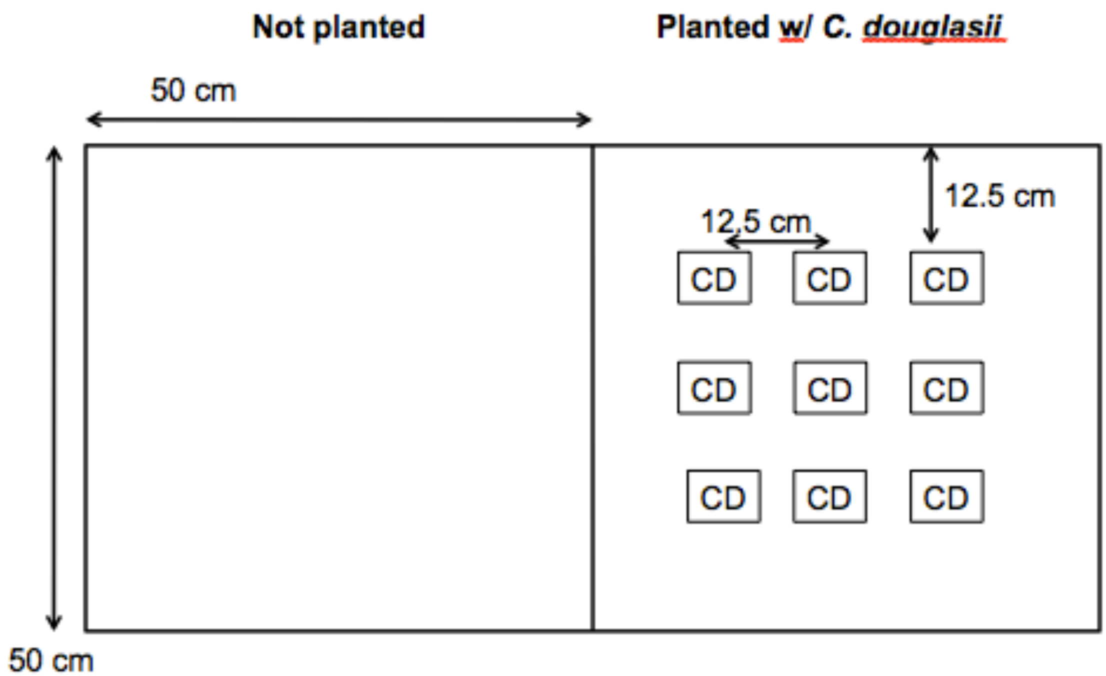

Figure 2: Layout of split-plot design. *Clinopodium douglasii* (CD) was outplanted into half of each treatment plot, while the other half remained unplanted.

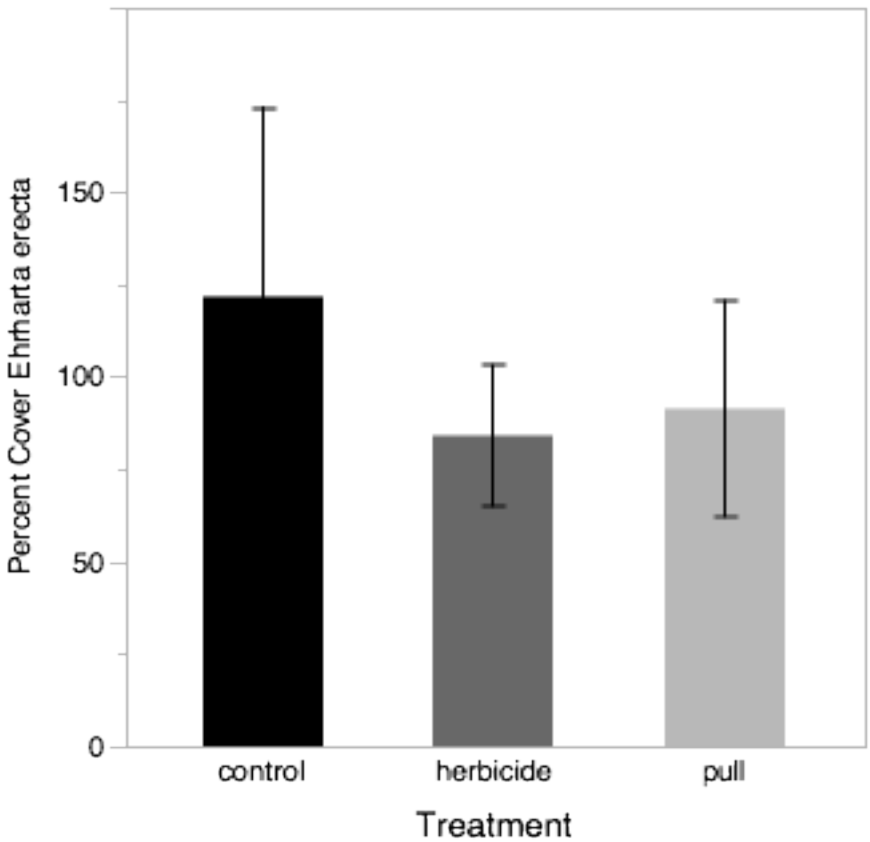

Figure 3: Percent cover of *Ehrharta erecta* as baseline data measured before treatments were applied. Error bars represent ± 1 SE from the mean.

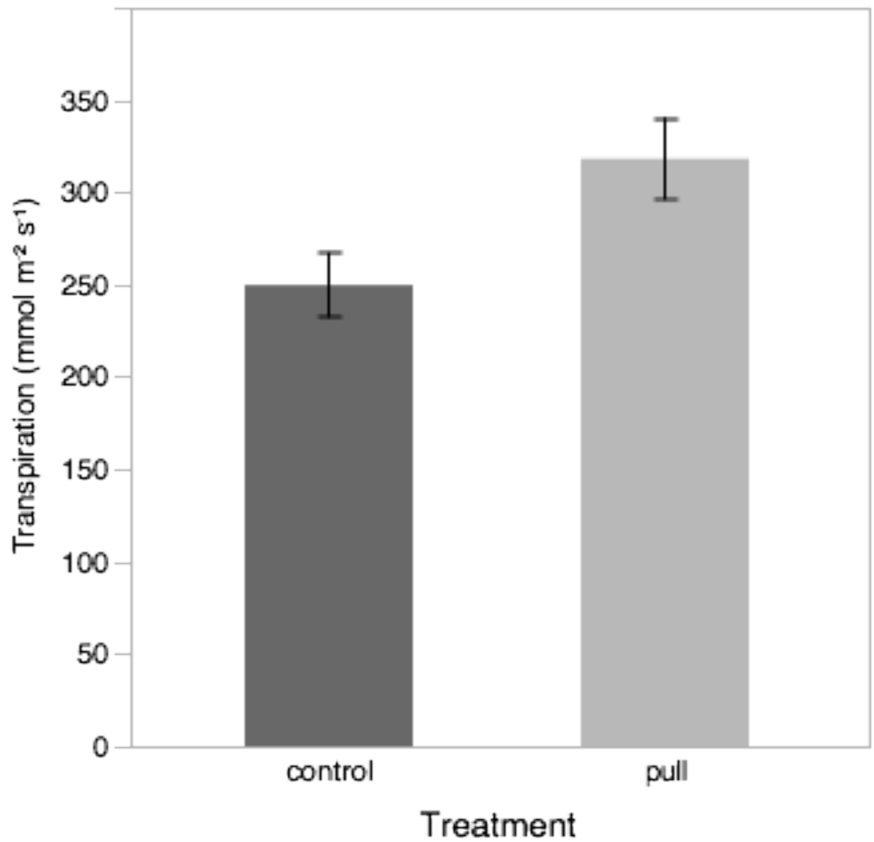

Figure 4: Transpiration rate in *Stachys bullata* with the surrounding *Ehrharta erecta* removed (pull), and not removed (control). Error bars represent ± 1 SE from the mean.

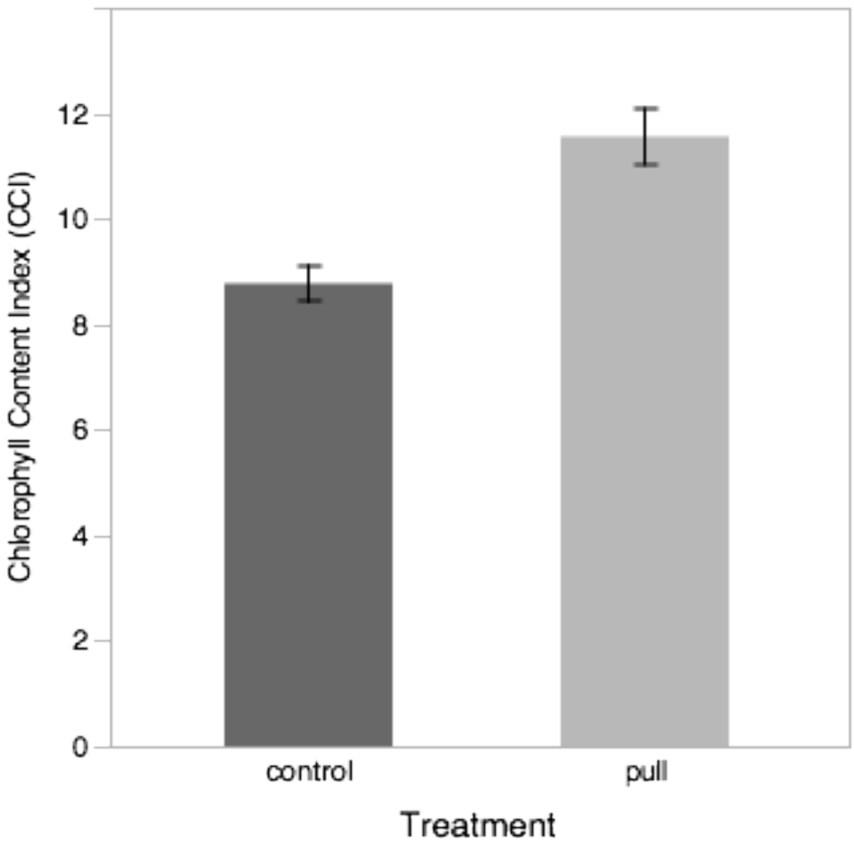

Figure 5: Chlorophyll content in *Stachys bullata* with the surrounding *Ehrharta erecta* removed (pull), and not removed (control). Error bars represent ± 1 SE from the mean.

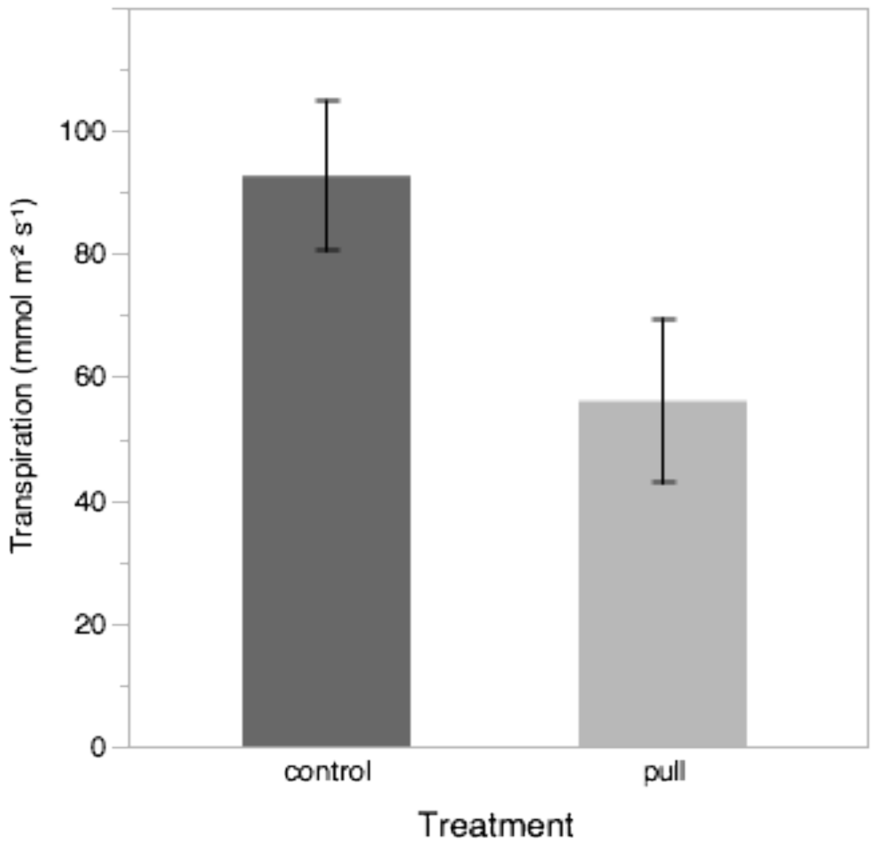

Figure 6: Transpiration rate in *Clinopodium douglasii* with the surrounding *Ehrharta erecta* removed (pull), and not removed (control). Error bars represent ± 1 SE from the mean.

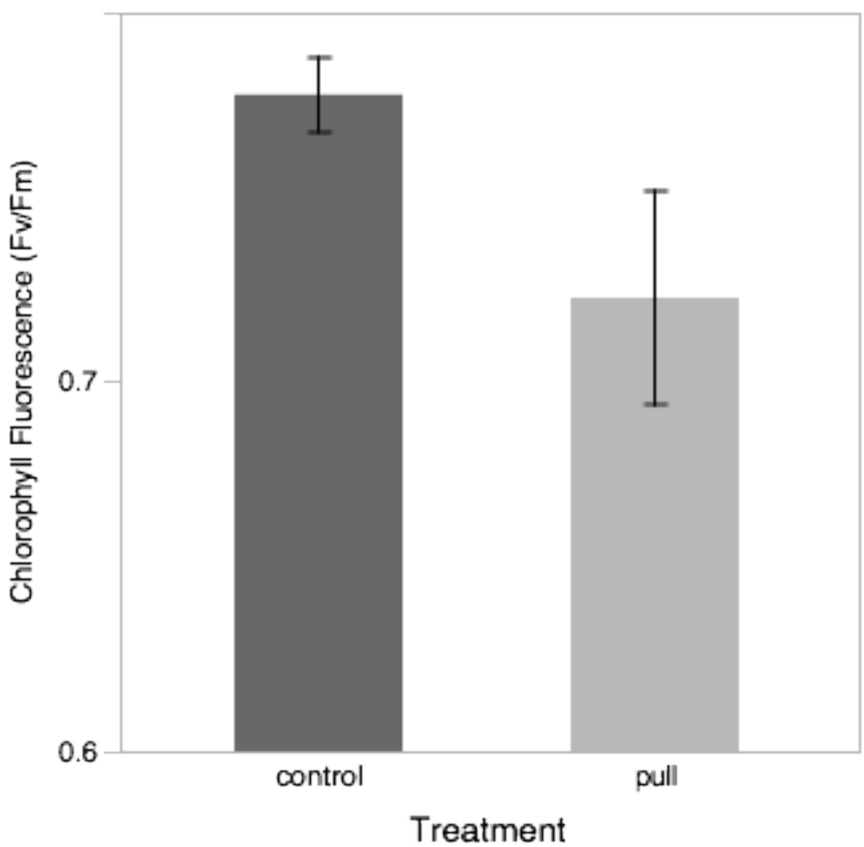

Figure 7: Chlorophyll fluorescence in *Clinopodium douglasii* with the surrounding *Ehrharta erecta* removed (pull), and not removed (control). Error bars represent ± 1 SE from the mean.

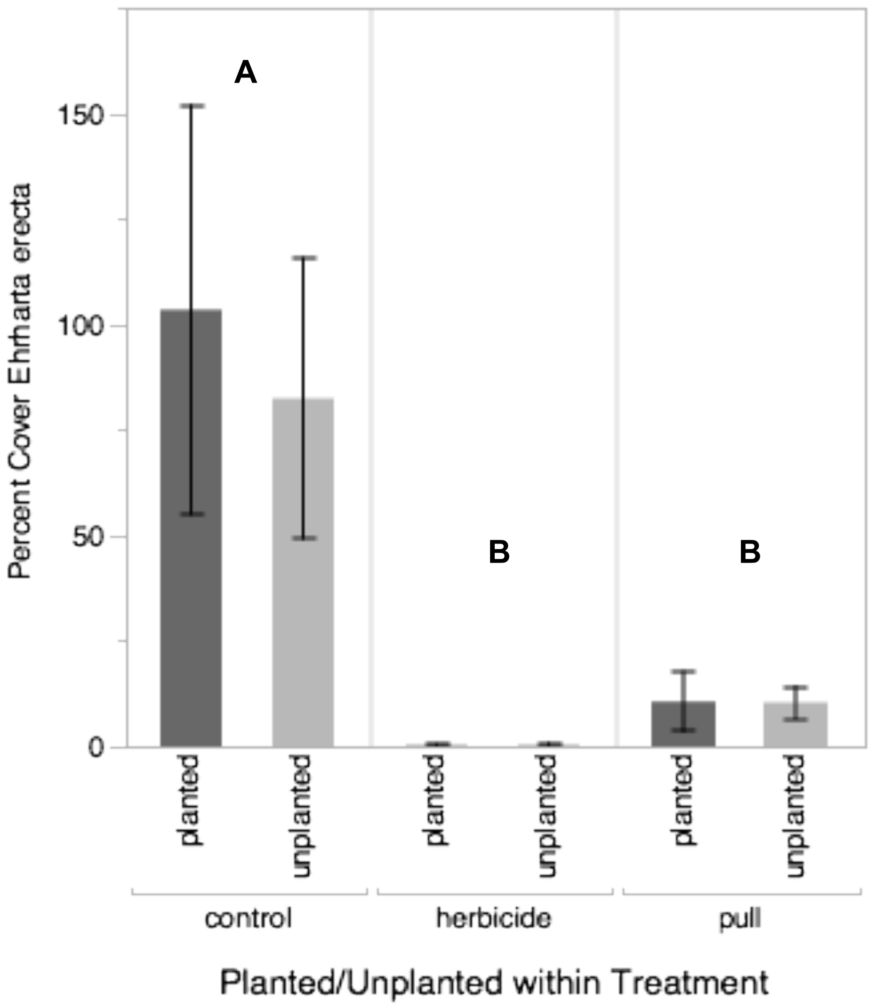

Figure 8: Percent cover of *Ehrharta erecta* in plots with control, herbicide, and pull treatments, either planted with *C. douglasii* or unplanted. Error bars represent ± 1 SE from the mean. The different letters represent treatments that were significantly different from one another, based on the post-hoc Tukey's HSD test.

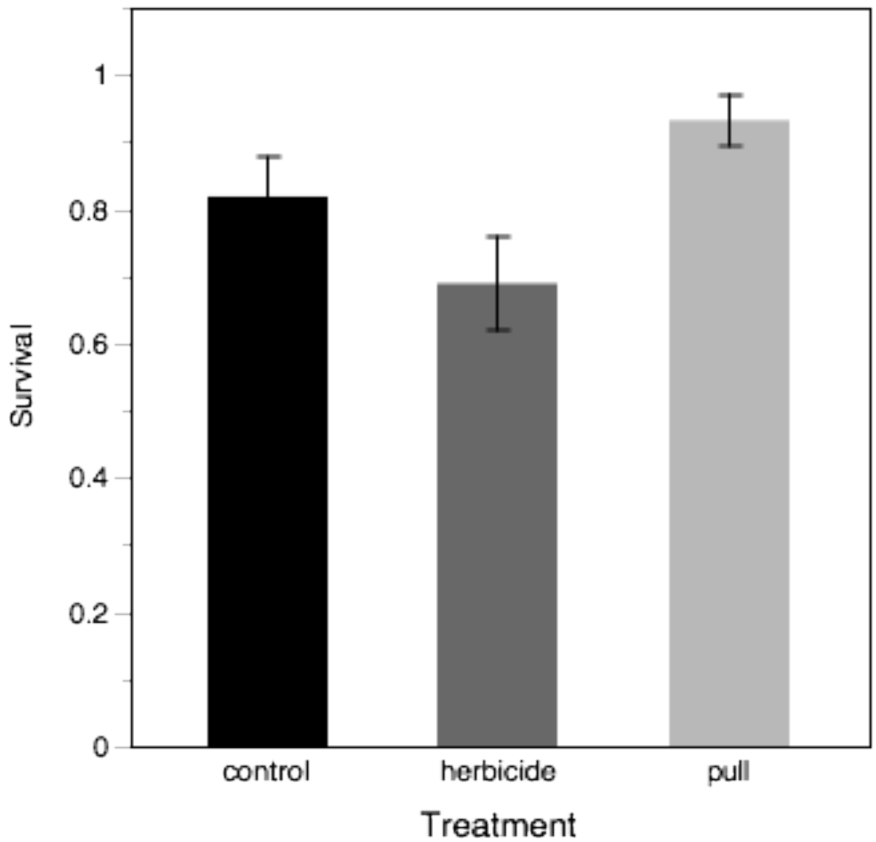

Figure 9: Survival after six months of *C. douglasii* planted in control, herbicide, and pull treatment plots. Error bars represent ± 1 SE from the mean.

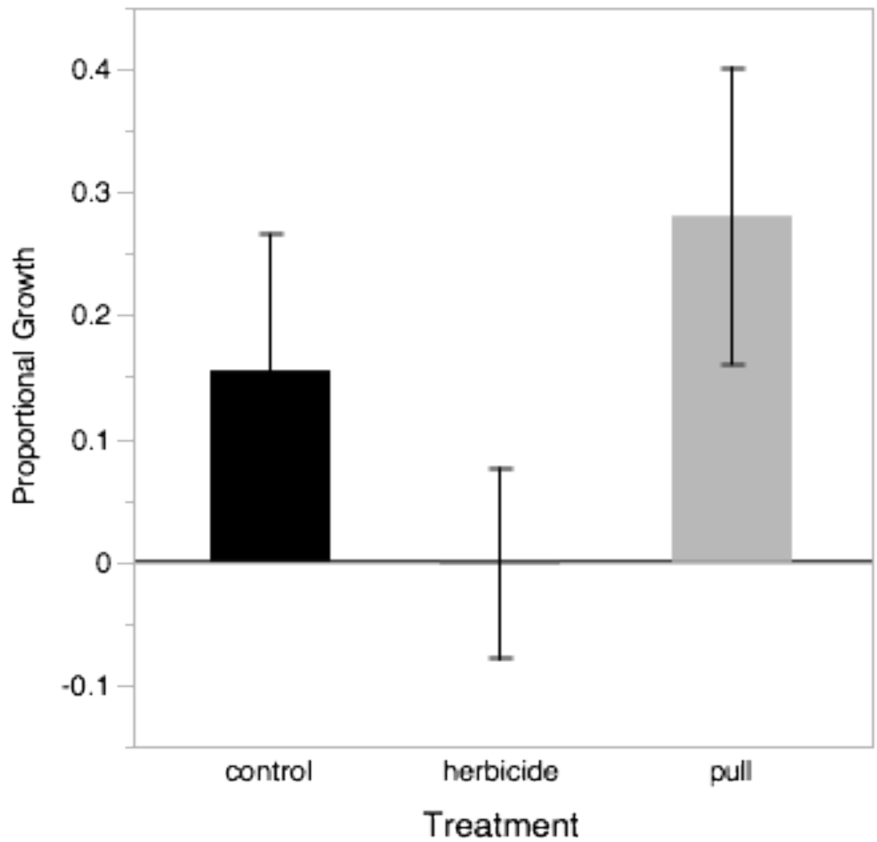

Figure 10: Proportional growth after six months of *Clinopodium douglasii* planted in control, herbicide and pull treatments. Error bars represent ± 1 SE from the mean.

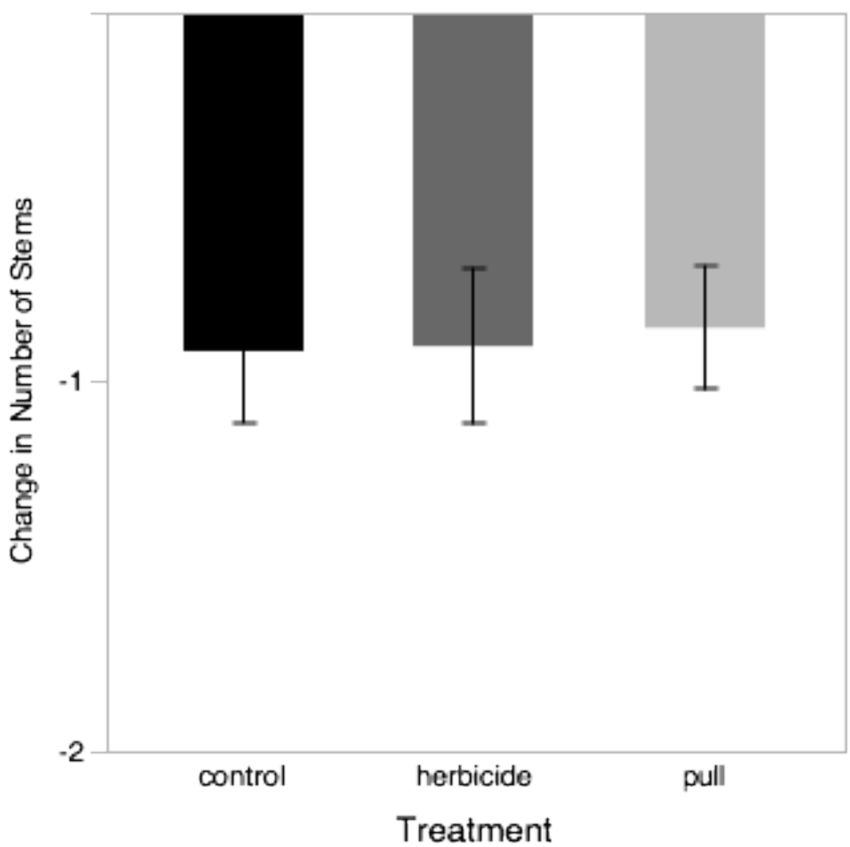

Figure 11: Change in number of stems after six months in *Clinopodium douglasii* planted in control, herbicide, and pull treatments. Error bars represent ± 1 SE from the mean.