

Understory Community Changes Associated with English Ivy Invasions in Seattle's Urban Parks

Abstract

English ivy has become a common invader in Seattle's urban parks and in forests throughout the Pacific Northwest. Despite a great deal of concern over the potential impacts of this species, no studies have investigated ivy's effects on native vegetation in this region. In this study, paired comparisons between ivy-invaded and adjacent non-invaded plots in three Seattle parks were used to quantify changes associated with ivy invasion in the forest understory. Species diversity, percent cover, and tree regeneration were surveyed. Differences in species diversity, calculated as both richness and evenness, were not significantly different between invaded and non-invaded plots. Ivy-invaded plots did have significantly higher total cover, and significantly lower non-ivy cover, than non-invaded plots. The reduction of percent cover in invaded plots was primarily due to the loss of native shrubs. A plot where ivy had been removed over five years was also surveyed, and percent cover in this plot showed intermediate values relative to invaded and non-invaded plots, for both total cover and cover of native shrubs. The number of trees regenerating in the understory was higher in invaded plots, though this difference was not significant. These results suggest that English ivy invasions have substantial impacts on understory cover, and may influence the species composition and diversity of forest communities over the long-term by increasing vegetative cover and suppressing dominant native shrubs.

Introduction

English ivy (*Hedera helix*), a ubiquitous species in North American landscaping, is now an increasingly common component of Pacific Northwest forests (PNW-EPPC 1997, Bell et al. 2003). The establishment of this non-native species in natural areas, particularly urban parks, is causing a great deal of concern over its potential impacts (Miller 1994, Reichard 2000, Baskin 2002). Specifically, English ivy forms patches of continuous cover, which appear to exclude other understory species (Reichard 2000). However, there is almost no quantitative information regarding the effects of ivy invasions on existing vegetation. Here I examine changes in understory vegetation associated with ivy infestations of urban parks in Seattle, WA.

First introduced to North America during colonial times as an ornamental ground cover (Wyman 1969), English ivy remains a staple of the horticultural industry. The features that make ivy a reliable choice for landscaping are also those that make it a troublesome invader: aggressive vegetative spread and tolerance of a variety of light conditions (Thomas 1980). In addition, ivy's fruits are attractive to dispersers (primarily

birds), facilitating its spread from residential to wilderness areas (Reichard 2000). In its native forests, ivy proliferates in light gaps (Beekman 1980, Schnitzler 1995), and this may be why communities with deciduous or mixed canopies appear to be particularly susceptible to ivy invasions (Papanikolas 1996, Reichard 2000).

To date, there are no published studies of the effects of English ivy on forest communities in the Pacific Northwest. Thomas (1980, 1998) has examined ivy invasions in eastern deciduous forests, where native vines were already a prominent feature of these communities (Teramura et al. 1991). Despite a history of interacting with native vines, herbaceous vegetation cover, tree seedling survival and tree longevity showed marked declines in the presence of English ivy (Thomas 1980). Identifying these sorts of impacts will be critical for determining both whether an invader such as ivy warrants difficult and costly control efforts (Parker et al. 1999, D'Antonio and Meerson 2002), and whether its commercial sale should be limited (Baskin 2002).

The purpose of this study is to document understory plant community changes associated with English ivy invasions of natural areas in Seattle, WA. Park managers in these areas are already trying to assign priority to controlling large infestations of this species (Miller 1994, Papanikolas 1996). To quantify the potential impacts of ivy invasion on

¹ Current Address: Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064.
E-mail: dlugosch@biology.ucsc.edu

understory communities, I compared ivy-invaded and non-invaded vegetation at several sites across three parks. At each site, I examined 1) species diversity, including both richness and evenness, 2) percent cover, differentiating between native and non-native vegetation as well as between herbs and shrubs, and 3) the number of tree seedlings persisting in the understory. I also quantified these same community attributes at an ivy removal site, in order to assess the recovery of this site from the impacts of English ivy invasion.

Methods

Study Sites

In order to investigate community changes associated with ivy invasions in Seattle’s urban parks, understory vegetation was sampled at 11 pairs of ivy-invaded and non-invaded sites during July 1997. These sites were distributed among three nature reserves within the city of Seattle: Carkeek Park, Discovery Park and Schmitz Park (Figure 1). Vegetation is similar among all of these parks,

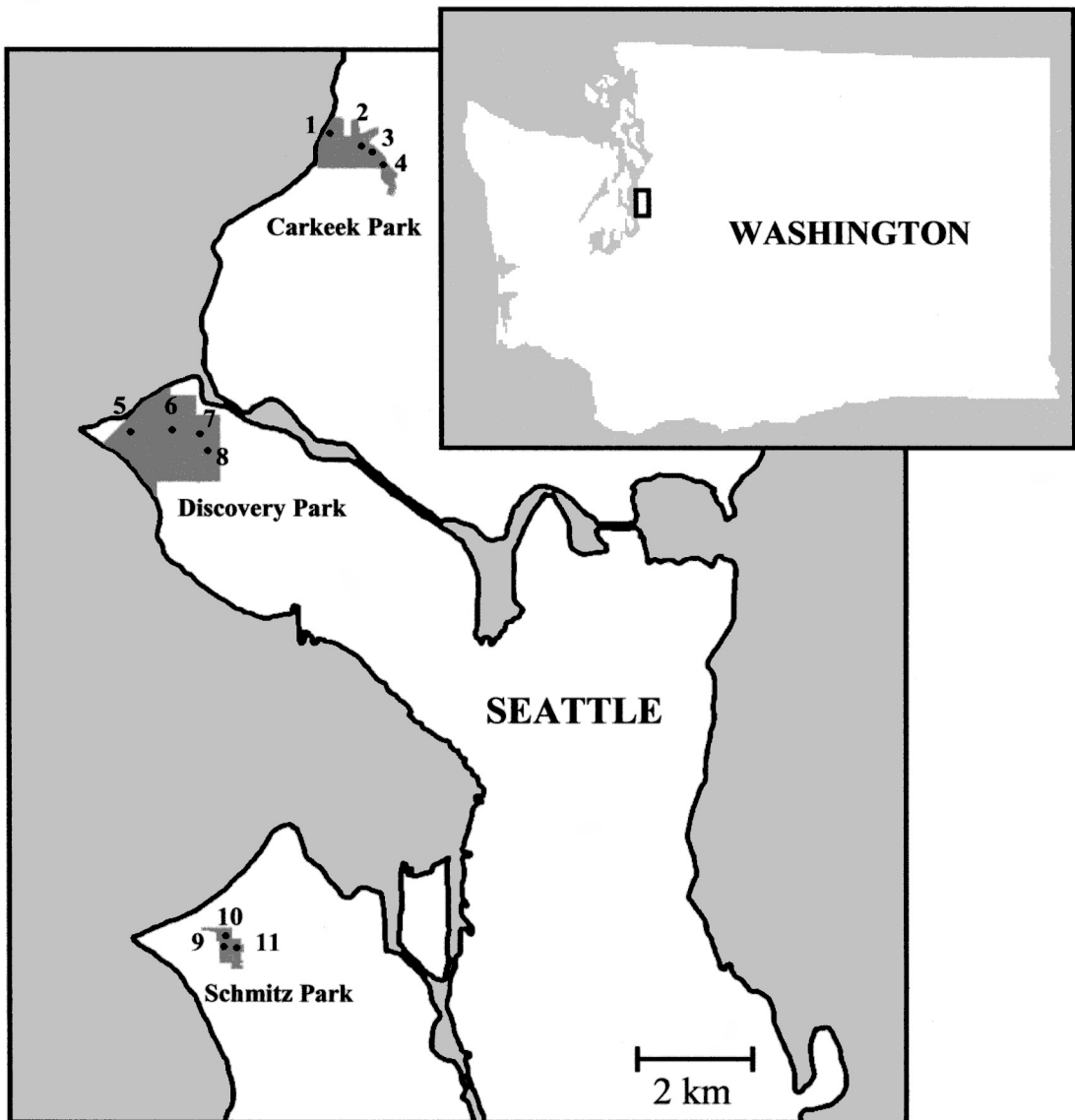


Figure 1. Map showing location of study sites. Pairs of plots (dots) were located in three parks in Seattle, WA.

which lie within the western hemlock (*Tsuga heterophylla*) vegetation zone common to the Pacific Northwest United States (Franklin and Dyness 1988). Vegetation in this region was historically dominated by conifers, principally western hemlock and Douglas-fir (*Pseudotsuga menziesii*); however, each of these parks has experienced logging activity in the past 100 years, and bigleaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*) are currently among the canopy dominants (Miller 1994, Papanikolas 1996).

At each site, a pair of 5m radius circular plots were established in adjacent ivy-invaded and non-invaded areas. All invaded plots were located within areas of apparently continuous and uniform understory ivy cover. In order to avoid possible canopy effects from ivy growing on trees, all invaded plots were placed where no ivy had extended into living tree foliage. Non-invaded plots were located either directly adjacent to the invaded plot or as close as possible to the invaded area, with slope, aspect, canopy species, and canopy cover matching (within 5%) those of the invaded plot. Occasionally, small amounts of ivy were detected in 'non-invaded' plots upon sampling (see Table 1).

The presence of an area where ivy has been hand-pulled at Discovery Park afforded an opportunity to note potential vegetation recovery after ivy removal. Volunteers and park staff had removed the ivy during the previous five winters, when roots and vines could be successfully extracted by hand-pulling from moist soils. This site was located adjacent to an existing pair of invaded/non-invaded plots. A sampling plot was placed at this removal site for qualitative comparison to any patterns seen in the invaded vs. non-invaded contrasts.

Vegetation Sampling

Percent cover values for understory species at each site were estimated using five, 1 m radius, circular quadrats within each plot. One sampling quadrat was located at the center of each plot, and four additional quadrats were placed at random distances between two and four meters in each cardinal direction from the center of the first quadrat. Absolute percent cover of all herb and shrub species was visually estimated in each quadrat, allowing total cover to exceed 100% where the cover of different species overlapped one another.

Nonzero cover values of one percent or less were recorded as 1%. In the case of both mosses and grasses, individual species were not distinguished from one another and were instead surveyed as groups. The abundance of tree seedlings was also assessed by counting all seedlings present within the plot (5 m radius). Tree seedlings were defined as those trees having a diameter of 5 cm or less.

Data Analysis

In order to investigate community changes associated with ivy invasions, differences in species diversity, vegetation cover, and tree seedling counts were compared between paired invaded and non-invaded sites. Because multiple plots were placed within each of three parks, Analysis of Variance (ANOVA) was used first to test for a park effect on differences between paired invaded and non-invaded plots for any particular response variable. Because park effects were non-significant in all cases (see details in Results), all sites were pooled for subsequent analyses.

Species diversity was quantified both by species richness and by an index of cover evenness. Ivy cover was excluded from both the richness and the evenness variables. Understory species evenness (E) was calculated using the following equation (Smith and Wilson 1996):

$$E = 1 - 2 \left[\frac{1}{S} \sum \arctan \left\{ \frac{[\ln(x_i) - \sum \ln(x_i)/S]^2 / S}{S} \right\} \right],$$

where x_i = percent cover of the i^{th} species and S = the total number of species. An evenness of 1 represents complete evenness (where all species have equal cover values) and 0 indicates complete dominance by a single species. Two-tailed paired t-tests were used to compare richness and evenness in invaded and non-invaded plots.

Vegetation cover data were analyzed for associations between ivy invasion and both the total absolute cover and the absolute cover of particular groups of species, specifically native and non-native herbs and shrubs. All subplot data were averaged by species to arrive at a plot value before analysis. Differences in total cover (both including and excluding ivy cover) were assessed using two-tailed paired t-tests. Wilcoxon sign rank tests were used to compare the total cover of a given species group (i.e. native herb, native shrub, non-native herb, non-native shrub) in an invaded plot with the total cover of that group in the paired non-invaded plot. When a species

TABLE 1. Percent cover and tree seedling counts for non-invaded / invaded (/ removal) plots at all sites.

	CARKEEK PARK SITES			DISCOVERY PARK SITES			SCHMITZ PARK SITES				
	1	2	3	4	5	6	7	8	9	10	11
<i>Hedera helix</i>	0.0/83.2	5.6/95.6	2.6/83.4	0.0/98.2	0.0/99.8	9.6/97.4	0.0/64.6	0.0/62.4/4.6	0.0/95.2	4.0/44.8	1.6/82.0
NATIVE SHRUBS											
<i>Amelanchier alnifolia</i>	-	2.0/0.0	-	-	-	-	-	-	-	-	-
western serviceberry	-	2.0/0.0	-	-	-	-	-	-	-	-	-
beaked hazelnut	23.8/3.0	0.0/7.4	22.4/8.0	-	0.0/0.2	1.0/0.0	-	5.4/3.8/0.0	-	-	3.0/0.0
<i>Corylus cornuta</i>	-	1.4/17.4	-	-	-	-	-	0.0/0.0/13.0	-	-	-
<i>Gaultheria shallon</i>	-	-	-	-	-	-	-	0.8/0.8	-	-	-
<i>Holodiscus discolor</i>	0.6/16.0	-	-	-	-	-	0.8/0.8	5.6/0.0/0.0	-	-	-
ocean-spray	-	-	-	-	-	8.8/1.2	0.4/0.0	0.0/0.2/0.0	-	-	-
dull Oregon grape	18.2/2.0	-	1.2/0.0	-	-	1.2/0.0	12.4/0.0	2.0/4.8/12.6	84.2/0.0	77.0/45.4	18.0/8.6
<i>Mahonia nervosa</i>	33.2/5.8	2.8/5.0	9.4/26.2	2.8/5.2	-	2.0/0.0	0.2/0.0	0.0/0.8/0.2	-	7.4/7.8	0.0/7.6
<i>Polystichum munitum</i>	-	2.4/0.0	-	0.0/2.0	-	-	-	-	-	-	-
bracken-fern	-	2.4/0.0	-	0.0/2.0	-	8.0/10.0	-	-	-	-	-
<i>Pteridium aquilinum</i>	-	-	-	-	-	-	-	-	-	-	-
<i>Rosa gymnocarpa</i>	-	-	-	-	-	-	-	-	-	-	-
baldhip rose	-	-	0.4/0.0	-	-	-	-	-	-	-	-
<i>Rubus parviflorus</i>	-	-	13/4.0	13.8/15.8	51.6/8.6	5.8/0.6	34.6/16.0	38.0/11.6/7.4	-	-	2.8/0.0
<i>Rubus ursinus</i>	1.2/5.2	18.2/15.2	13/4.0	13.8/15.8	51.6/8.6	5.8/0.6	34.6/16.0	38.0/11.6/7.4	-	-	2.8/0.0
Pacific blackberry	-	-	-	-	-	-	-	-	-	0.0/6.3	65.0/39.0
<i>Sambucus racemosa</i>	-	-	-	-	-	-	-	0.0/3.0/5.0	-	-	-
elderberry	-	-	-	-	-	-	-	-	-	-	-
<i>Symphoricarpos albus</i>	-	-	-	-	-	-	-	-	-	-	-
common snowberry	-	-	-	-	-	-	-	-	-	-	-
NATIVE HERBS											
<i>Dicentra formosa</i>	-	-	3.0/0.0	-	-	0.2/0.0	-	-	-	-	-
Pacific bleedingheart	-	-	3.0/0.0	-	-	0.2/0.0	-	-	-	-	-
<i>Equisetum hyemale</i>	-	-	-	8.0/1.0	-	-	-	-	0.0/0.4	-	-
common horsetail	-	-	-	8.0/1.0	-	-	0.4/0.0	-	-	-	-
<i>Gallium aparine</i>	-	0.6/0.2	0.4/0.2	-	-	-	-	0.0/3.0/5.0	-	-	-
cleavers	-	0.6/0.2	0.4/0.2	-	-	-	-	0.0/2.0/0.0	-	-	-
<i>Smilacina racemosa</i>	0.0/1.2	0.0/0.4	-	-	-	-	-	0.0/0.0/0.2	-	0.2/0.2	-
false Solomon's seal	-	-	1.0/0.0	49.2/0.0	-	-	-	-	-	-	-
<i>Tolmiea menziesii</i>	-	-	1.0/0.0	49.2/0.0	-	-	-	-	-	-	-
youth-on-age	-	-	3.0/0.8	0.2/0.0	-	17.2/0.0	-	-	4.2/21.0	0.0/0.4	0.6/1.8
<i>Urtica dioica</i>	-	-	3.0/0.8	0.2/0.0	-	17.2/0.0	-	-	-	-	-
stinging nettle	-	-	3.0/0.8	0.2/0.0	-	17.2/0.0	-	-	-	-	-
NON-NATIVE SHRUBS											
<i>Cytisus scoparius</i>	-	-	-	-	-	-	-	1.6/0.0/0.0	-	-	-
Scotch broom	-	-	-	-	-	-	-	1.6/0.0/0.0	-	-	-
<i>Ilex aquifolium</i>	0.0/1.2	0.0/0.2	-	-	0.0/3.2	0.0/10.2	0.0/5.0	0.2/5.6/10.6	1.0/0.0	0.0/0.4	-
English holly	-	-	-	-	-	-	-	0.0/0.0/0.6	-	-	-
<i>Rubus discolor</i>	-	-	-	19.2/0.0	-	-	-	-	-	4.8/0.0	-
Himalayan blackberry	-	-	-	19.2/0.0	-	-	-	-	-	-	-
NON-NATIVE HERBS											
<i>Cirsium arvense</i>	-	-	-	-	9.4/0.0	-	-	-	-	-	-
Canadian thistle	-	-	-	-	9.4/0.0	-	-	-	-	-	-
<i>Daucus carota</i>	-	-	-	-	-	-	-	0.0/0.6/0.0	-	-	-
Queen Anne's lace	-	-	-	-	-	-	-	0.0/0.6/0.0	-	-	-
<i>Geranium robertianum</i>	-	-	-	-	-	-	-	23.4/0.0/0.4	-	-	0.0/0.4
herb Robert	-	-	-	-	-	-	-	23.4/0.0/0.4	-	-	-
<i>Vicia sativa</i>	-	-	-	-	1.6/0.0	-	-	-	-	-	-
common vetch	-	-	-	-	1.6/0.0	-	-	-	-	-	-
OTHER SPECIES											
<i>Geum</i> sp.	-	-	-	-	-	-	-	0.2/0.0/0.0	-	-	-
avens	-	-	-	-	-	-	-	0.2/0.0/0.0	-	-	-
<i>Lonicera</i> sp.	-	-	-	-	-	1.2/0.0	-	-	-	-	-
honeysuckle	-	-	-	-	-	1.2/0.0	-	-	-	-	-
<i>Rubus</i> sp.	-	-	-	-	-	0.2/0.0	-	-	-	12.4/0.2	-
blackberry	-	-	-	-	-	0.2/0.0	-	-	-	12.4/0.2	-
<i>Bryophyta</i>	1.4/1.4	-	5.2/0.4	2.0/0.4	-	1.0/0.0	0.4/2.8	0.6/1.6/8.2	-	1.6/2.6	4.4/1.2
mosses	-	-	5.2/0.4	2.0/0.4	-	1.0/0.0	0.4/2.8	0.6/1.6/8.2	-	1.6/2.6	4.4/1.2
<i>Poaceae</i>	-	0.2/0.0	-	-	11.8/0.0	0.8/0.0	1.6/0.0	1.0/0.2/1.0	0.2/0.0	-	0.0/0.2
grasses	-	0.2/0.0	-	-	11.8/0.0	0.8/0.0	1.6/0.0	1.0/0.2/1.0	0.2/0.0	-	0.0/0.2
TREE SEEDLINGS	9/21	3/6	0/12	0/1	1/5	10/25	21/20	7/0	0/0	0/5	0/1

could not be identified confidently, that species was excluded from the analysis. To explore the effect of ivy cover on tree regeneration, the total number of tree seedlings was compared between invaded and non-invaded plots using a two-tailed paired t-test.

The level of significance was set at $P = 0.05$ for all statistical tests. Tests were performed using the statistical software JMP v. 5.1 (SAS Institute, Inc 2004).

Results

Understory Species Diversity

Thirty species were encountered across all 11 sites (Table 1). An ANOVA detected no park effect on either species richness ($F_{2,20} = 0.61$, $P = 0.571$) or evenness ($F_{2,20} = 0.15$, $P = 0.865$). There was no significant difference between invaded and non-invaded plots in total species richness, total species evenness, native species richness or native species evenness (Table 2).

TABLE 2. Results of paired t-tests comparing richness and evenness in non-invaded and invaded plots, based both on the total number of species and on native species in particular.

	Non-Invaded	Invaded	t_{10}	P
Total Richness	7.4	6.0	1.574	0.147
Total Evenness	0.24	0.30	1.305	0.221
Native Richness	4.9	4.3	0.763	0.463
Native Evenness	0.30	0.38	1.517	0.160

Understory Cover

Total cover of all understory species was significantly higher in invaded plots ($t_{10} = 5.974$, $P < 0.001$), averaging 77.4% in non-invaded plots and 117.2% in invaded plots (Figure 2). This relationship was reversed when ivy cover was excluded from the total cover ($t_{10} = 6.755$, $P < 0.001$), with non-invaded plots averaging 75.3% and invaded plots 34.8% cover (Figure 2). There were no significant park effects on total cover (ANOVA), either including ($F_{2,20} = 1.65$, $P = 0.251$) or excluding ($F_{2,20} = 0.33$, $P = 0.731$) ivy cover.

Native shrubs were the primary source of the decline in total cover with ivy invasion, showing significantly lower cover in ivy-invaded plots ($\chi^2_1 = 32$, $P = 0.002$). Both native and non-native herbs also declined in invaded plots, but these dif-

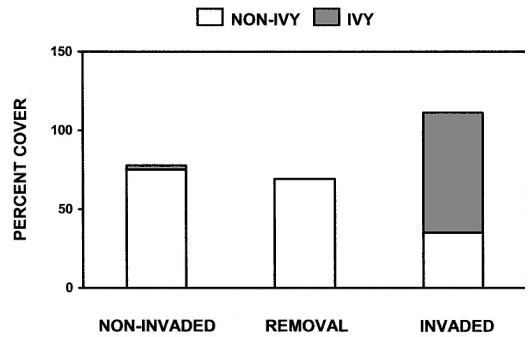


Figure 2. Mean percent cover of ivy and non-ivy species for all non-invaded plots, the single 5 yr ivy-removal plot, and all ivy-invaded plots.

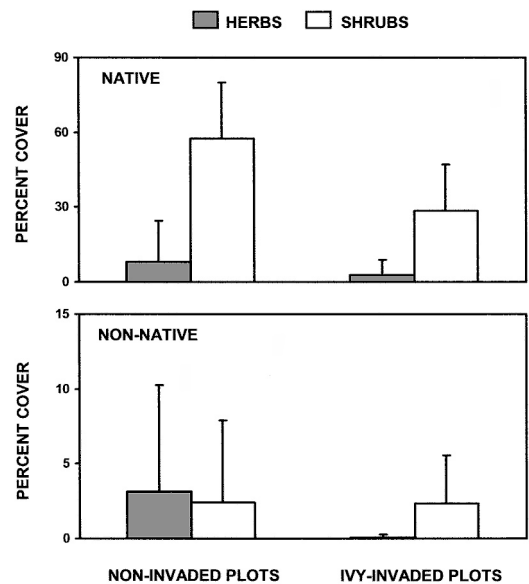


Figure 3. Percent cover of native and non-native herbs and shrubs in non-invaded and ivy-invaded plots. Error bars indicate +/- one standard deviation.

ferences were not significant (respectively: $\chi^2_1 = 2.5$, $P = 0.82$ and $\chi^2_1 = 2.0$, $P = 0.50$). Non-native shrubs appeared unaffected by ivy-invasion status ($\chi^2_1 = 5.5$, $P = 0.57$) (Figure 3). Species groupings are listed in Table 1. Large ferns were included as shrubs due to their similarly large and robust perennial habit.

Tree Regeneration

An average of 4.6 tree seedlings were encountered in non-invaded plots, versus 8.7 in invaded plots. A one-way ANOVA found no effect of park on

the number of tree seedlings ($F_{2,20} = 0.58$, $P = 0.584$). The increase in tree seedling number in invaded plots was not significant ($t_{10} = 2.067$, $P = 0.066$).

Removal Plot

For cover variables that were significantly different between invaded and non-invaded plots, the 5 yr removal plot at Discovery Park showed intermediate values. Total cover in this plot was 68.8%, falling between average values for total non-ivy cover in non-invaded and invaded plots (Figure 2) and between absolute values for the adjacent non-invaded (78.0%) and invaded (37.2%) plots. While cover values of all species groups were greater in the removal plot than in the invaded plot, the cover of native shrubs showed the largest response to ivy removal (Figure 4).

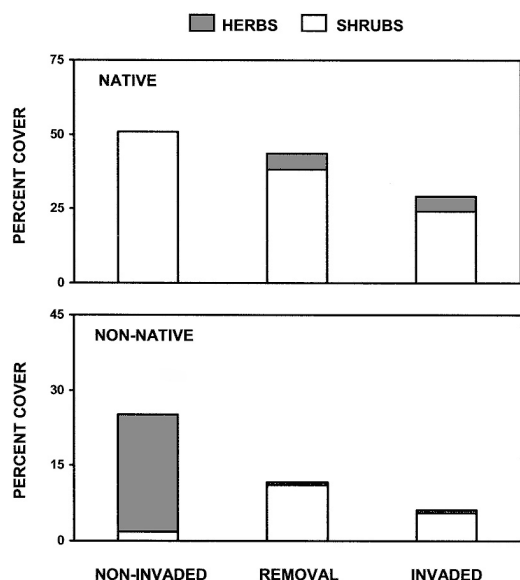


Figure 4. Percent cover of native and non-native herbs and shrubs at the invaded, removal, and non-invaded plots at site 8 in Discovery Park.

Discussion

One of the primary concerns for natural area managers is the loss of native diversity that might be caused by invading species (Randall 1996, Gurevitch and Padilla 2004). Research has shown species diversity to be both positively and negatively associated with invasions (Parker et al. 1999), but poor comparability of scale and methods among

studies impedes generalizations (D'Antonio and Kark 2002). There was no change in either total species diversity or diversity of native species (richness or evenness) in ivy-invaded plots in this study. A similar study of invasions of the woody vine *Vinca minor* in Illinois also did not reveal an effect of the invasion on native diversity (Schulz and Thelen 2000). While it is possible that ivy invasions do not have substantive consequences for native species composition, experimental manipulations of ivy cover and long-term surveys of ivy introductions are necessary to address this question rigorously. In particular, because this study focused on areas where ivy had not established in tree canopies, the observations reported here may reflect the early stages of an ivy invasion. The conclusion from this study is only that ivy invasion is not currently having dramatic effects on species diversity in these parks. The impacts of ivy invasions on native diversity may accumulate through time, both directly through effects on regeneration of native species and indirectly through effects on abiotic conditions (e.g. nitrogen addition, see Trémolières et al. 1988).

In contrast to overall diversity measures, ivy invasion in this study was associated with significant changes in percent cover of understory species. Overall, total cover increased from approximately 75% in non-invaded plots to over 100% in ivy-invaded plots. Ivy has created an additional layer of vegetation at these sites, potentially reducing light availability below. Thomas (1980) observed a similar pattern on upland sites at Theodore Roosevelt Island (Virginia), though at floodplain sites ivy cover merely replaced cover of existing species. Future work in the Pacific Northwest should compare ground-level light incidence directly between non-invaded and ivy-invaded areas. If ivy does decrease light availability at the forest floor, an important subsequent issue will be whether changes in light availability have consequences for germination or growth of native species.

Regardless of mechanism, the cover of the other species in ivy-invaded plots was less than half of its value in non-invaded sites. The magnitude of this effect is similar to generalizations from manipulative removal or addition experiments of invaders (D'Antonio and Kark 2002). Indeed, the total cover in the ivy removal plot in this study was nearly equal to cover in non-invaded plots. While the paired comparisons in this study are

purely observational, and differences could be due to undetected changes in site characteristics, the response of the removal plot suggests that ivy presence is the primary causal agent of the large declines in cover of resident species. Such striking changes in abundance seem likely to impact the structure, function, and ultimately diversity of ivy-invaded communities.

A closer inspection of the cover data revealed that most of the difference between invaded and non-invaded plots was due to declines in the cover of native shrubs. Non-native herbs and shrubs were not significantly different between the two plot types. These results are consistent with the observation that invaders often have neutral or even positive effects on other non-native species (Simberloff and Von Holle 1999). However, these results in particular should be interpreted with care, as the absolute cover of non-native species was low or zero in many plots, impeding accurate quantification of cover values.

Native shrubs also showed the greatest apparent increase in the ivy removal plot, suggesting that this group of species is particularly sensitive to any impacts of ivy. These patterns contrast directly with Thomas's findings that herb suppression by ivy was greater than either shrub or tree suppression (Thomas 1980 p.60). These contrary results raise interesting and important questions about the specific consequences of ivy invasions in the Pacific Northwest. First, competition experiments between ivy and both native shrubs and native herbs will be necessary to establish whether shrubs are indeed most sensitive to inhibition by ivy. Shrubs are a more dominant life form in Pacific Northwest forests than in eastern forests (Franklin and Dyness 1988), and so they may simply have proportionately more cover to lose to a newly-dominant invader (e.g. Thomas (1980) frequently encountered less than one woody individual per square meter). If the impacts of ivy on shrubs are more severe than on other species, then what are the mechanisms responsible for this? Is mechanical damage or competition for particular resources (e.g. light or water) more important? Which life stages of shrubs are most sensitive? Experimental work that address these questions will help to suggest which species are most likely to be impacted by ivy and to predict the community consequences of ivy invasions.

Perhaps surprisingly, tree seedlings were not significantly less abundant in understory habitats invaded by ivy, and showed a trend toward more seedlings in invaded sites. This pattern again runs contrary to that seen by Thomas (1980), and to reports of other vines that appear to arrest overstory succession (Hegarty and Caballe 1991). A common perception in the Pacific Northwest is that shrubs of any kind inhibit forest tree regeneration (e.g. Hibbs and Giordano 1996, but see Beach and Halpern 2001). The relative inhibitory effects of native shrubs versus ivy on both germination and growth of trees is unclear and a ripe area for study. The tree seedlings in this study may have germinated before ivy established, and their persistence might be insensitive to, or even positively affected by ivy. Initial germination and establishment of trees seedlings should be more sensitive to the changes in understory cover that ivy invasion induces, and assessing this directly should be a high priority for future research. If ivy invasions do prove to alter patterns of forest regeneration, the importance of ivy removal will be especially high (D'Antonio and Meerson 2002).

The results of this study suggest that English ivy is having an impact on the cover of native species in Seattle's urban parks, although these changes have not resulted in substantial reductions in species diversity at present. Experimental manipulations, competition experiments, and long-term surveys will be critical to confirming these results and understanding the mechanisms responsible for the patterns observed here. The associations between ivy and both shrubs and tree seedlings in this study run counter to previous observations of ivy-invaded habitats in eastern forests, highlighting the need for more local investigations of the impacts of this aggressive invader.

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