

Seed limitation and lack of downed wood, not invasive species, threaten conifer regeneration in an urban forest

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Abstract Urban forests provide valuable ecosystem services, but their long-term viability is often threatened by low tree recruitment due to seed and/or microsite limitation. Distinguishing between these two causes of low recruitment has important management implications, but has been little studied in urban environments. We tested for seed and microsite limitation in an urban forested park in Seattle, Washington, USA by adding conifer tree seeds and seedlings to experimental plots in which we manipulated microsite conditions by removing invasive ivy (*Hedera* spp.) and adding deadwood. We found that natural seed production was low, and adding seeds increased the number of observed seedlings. Furthermore, adding deadwood increased seedling survival, whereas removing *Hedera* did not have strong effects. Seed limitation is frequently addressed through management actions such as sowing seeds and transplanting seedlings, and our results suggest that such actions address a critical barrier to

tree recruitment in urban forests. However, we also observed strong microsite limitation. At our study site, microsite limitation can be addressed primarily by adding deadwood and retaining coarse woody debris on site. Addressing microsite limitation may be a critical component of successful management efforts to improve tree recruitment in urban forests, and should not be overlooked. Furthermore, our study highlights the need for active monitoring and data analysis alongside management, since the most apparent threat (widespread cover of an invasive plant in this case) may not be the primary limit on suitable microsite conditions.

Keywords Seed limitation · Microsite limitation · *Abies grandis* · *Thuja plicata* · *Tsuga heterophylla* · *Hedera* · Pacific Northwest · Seattle

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Introduction

Urban forests provide critical ecosystem services to large and increasing numbers of people. More than half of the world's population lives in urban areas, and by 2050 the proportion is likely to reach 66% (United Nations, Department of Economic and Social Affairs, Population Division 2014). In the U.S., this proportion is even greater, as nearly 80% of the population lives in urban areas (Nowak et al. 2010). The economic worth of urban forests is great: across the U.S., they are estimated to contain 3.8 billion trees and have been valued at over \$2.4 trillion (Nowak et al. 2002). Urban forests benefit people by filtering air, reducing urban heat island effects, storing carbon, decreasing noise, improving rainwater drainage and soil quality, increasing real estate values, and providing recreational opportunities and habitat (Bolund and Hunhammar 1999; Hutyra et al. 2011; Nowak et al. 2010; Tenneson 2013).

Urban forests experience a broad range of challenges, many of which may threaten regeneration and therefore long-term viability of urban tree populations. Forests can be negatively affected by air pollution in urban areas, especially from ozone, nitrogen, sulfur, and hydrogen deposition, as well as from heavy metals and other toxins that can accumulate in urban soils (Pye 1988; Stolte 1996; Beckett et al. 1998). In addition, urban ecosystems often contain high densities of invasive species that can modify forests and negatively impact native plants (Biggerstaff and Beck 2007). Perhaps because of these challenging conditions, native tree recruitment can be low in urban forests (Broshot 2007; O'Brien et al. 2012).

Tree recruitment may be limited by seed or microsite availability, but the importance of these limitations in urban forests is not known. Seed availability may be low due to reduced seed production in urban forests and due to dispersal limitation, which is common in small, fragmented forests, such as those typically found in urban areas (Matlack 1994; Dalling et al. 1998; Butaye et al. 2002; Condit et al. 2002; Nagamitsu et al. 2014). Seed predation could also reduce the number of seeds available for germination, although the few studies examining seed predation in urban and rural areas have found no difference in predation levels in urban versus rural sites (Lomov et al. 2010; Pufal and Klein 2015; Bode and Gilbert 2016). It is also possible that, even if urban canopy trees produce sufficient seed to overcome losses from seed predation or other post-dispersal destructive events, microsite conditions are poor and do not support tree seedling establishment. Two of the most important constraints on the availability of suitable microsites in urban forests may be competition from invasive species and inadequate soil surface conditions (e.g., a lack of nurse logs, Harmon and Franklin 1989; Biggerstaff and Beck 2007; Elman and Salisbury 2009).

Distinguishing between seed and microsite limitation is important for planning effective management and restoration practices. Addressing the former requires adding seeds or seedlings, whereas addressing the latter requires modifying site conditions. Studies that simultaneously evaluate the importance of seed and microsite limitation for plant establishment are rare, however, particularly in disturbed environments (Uriarte et al. 2010). Many urban ecological studies rely solely on observational approaches, making it difficult to determine the specific mechanisms that lead to poor recruitment in urban environments (Broshot 2007; Carreiro 2008; Elman and Salisbury 2009; O'Brien et al. 2012).

In the Pacific Northwestern United States, management practices have focused on increasing tree recruitment through planting efforts to address the decline in conifer forests in urbanizing areas (Elman and Salisbury 2009). Conifer forests dominated the Pacific Northwest prior to the arrival of European settlers in the 1850s (Kruckeberg 1991). Widespread logging of conifer trees over the past 150 years has altered the successional stage of forests in much of the

region from forests composed of long-lived conifers to forests composed of short-lived deciduous trees (Elman and Salisbury 2009). Improving conifer recruitment has become a high priority for managers of urban public forests because of concerns that the shift to deciduous forest leads to declines in ecosystem functioning and services (Hutyra et al. 2011; Tenneson 2013). For example, the longer life spans and evergreen nature of conifer trees in the region mean that they may provide better long-term carbon sequestration and more effective stormwater retention than deciduous trees (Elman and Salisbury 2009).

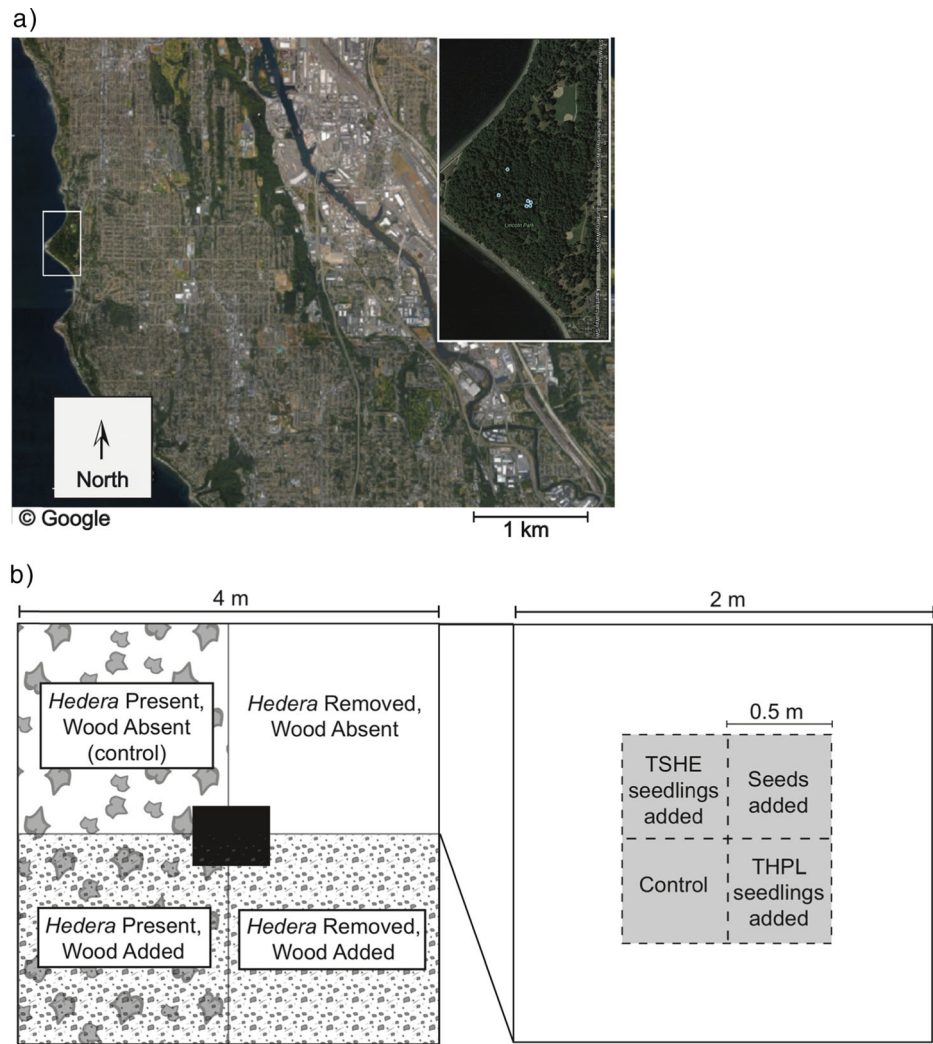
We used an experimental approach to test for seed and microsite limitation in an urban forest in Seattle, Washington, USA. Specifically, we asked: is conifer tree recruitment limited by seed availability and/or by microsite conditions? To address this question, we quantified natural conifer regeneration and conducted a factorial experiment to test for effects of 1) seed limitation, and 2) microsite limitation, including a) presence of the invasive plant English ivy (*Hedera helix* and *H. hibernica*), and b) presence of deadwood, on conifer seed germination, establishment, and growth. We focus on conifer recruitment because conifers make up the dominant climax canopy in forests of the Pacific Northwest, where our study site is located. For microsite conditions, we focus on *Hedera* spp. because this genus frequently creates dense mats on the forest floor in the Pacific Northwest, and is a commonly proposed cause of low tree recruitment in Seattle's forests (Elman and Salisbury 2009). We focus on deadwood because many Pacific Northwest conifer species regenerate at higher rates on rotting wood and nurse logs than on the soil surface (Harmon and Franklin 1989). The majority of Seattle's urban forests are second growth and have low amounts of downed wood, so this lack of deadwood may limit conifer seedling establishment. We found strong effects of both seed and microsite limitation, and we apply our results to make management recommendations for improving conifer recruitment.

Methods

Study site and focal species

This study took place at Lincoln Park, a 135-acre park managed by the City of Seattle, and surrounded largely by residential development with a population density of 5,485 people per square mile (Fig. 1a, U.S. Census Bureau 2012a, b). Approximately 64% of this urban park is forested natural area, including coniferous forest and mixed deciduous-coniferous forest (Earthcorps 2015). The forest overstory consists primarily of bigleaf maple (*Acer macrophyllum*), red alder (*Alnus rubrus*), madrona (*Arbutus menziesii*), and Douglas-fir (*Pseudotsuga menziesii*), with other common conifers including grand fir (*Abies grandis*), western hemlock (*Tsuga*

Fig. 1 Study site and experimental design. We established seven replicate blocks in Lincoln Park, Seattle, Washington (**a**, park is outlined in white; locations of the six blocks used in our analysis are shown by blue dots in inset). Each block was divided into four quadrants, with a different treatment in each quadrant, assigned using a coin toss (**b**). The black rectangle represents the seed trap, located in the center of each block. Each quadrant contained four plots. Into each plot, we added seeds of three focal species, transplanted seedlings of western hemlock (*Tsuga heterophylla*, TSHE) or western red-cedar (*Thuja plicata*, THPL), or established a control plot to monitor natural conifer germination



heterophylla), and western red-cedar (*Thuja plicata*). The ages of overstory trees are unknown, but most conifers were logged from this area to supply masts for the shipbuilding industry in the early 1900s (SDPR-UFP 2002). Significant restoration planting and invasive species removal have occurred and are ongoing in portions of Lincoln Park; however, little or no restoration had occurred in our specific study area, prior to this research (Baker pers. com., SDPR-UFP 2002). At the time of the study, the study area contained dense mats of *Hedera* on the forest floor, under coniferous or mixed forest over story. Here, we focus on the conifer species *Abies grandis* (hereafter *Abies*), *Thuja plicata* (hereafter *Thuja*), and *Tsuga heterophylla* (hereafter *Tsuga*), because they are common coniferous trees in the Puget Sound area, represent dominant climax species in this ecosystem, and are present at the study site. *Pseudotsuga menziesii* is another common conifer in Seattle forests; we chose not to focus on this species because its regeneration is known to rely heavily on canopy disturbance and it is considered a seral species

rather than a climax species in this ecoregion (Burns and Honkala 1990).

Study design

In 2011, we established seven 16-m² blocks in Lincoln Park (Fig. 1). To identify locations for our experimental blocks, we first selected sites with consistent *Hedera* cover over at least 16-m². Of these sites, we tried to select areas that were hidden from view of the trail to limit interference from dogs, hikers, and other users of the park, but this was not always possible. The distance from walking trails to our experimental blocks ranged from 2 to 5 m. Prior to imposing treatments, we conducted surveys to quantify *Hedera* cover, amount of coarse woody debris, and number of naturally occurring conifer seedlings that may have germinated in previous years (Table S1).

Each block was divided into four 4-m² quadrants, which corresponded to our four treatments: control (corresponding to *Hedera* present and deadwood absent), deadwood added,

Hedera removed, and deadwood added + *Hedera* removed (Fig. 1b). To test for the importance of decaying wood, we added decaying woodchips (i.e., deadwood, acquired from a nearby Seattle forest, which was chipped offsite) to half the block (i.e., two quadrants, Fig. 1b). The deadwood was obtained from the City of Seattle, and the identities of its tree species and age of death are unknown. The size of an individual woodchip was approximately one to five square centimeters in area, and they were spread to a depth of approximately 12–15 cm uniformly across the treated quadrants. To test the effect of competition with *Hedera*, we removed all *Hedera* from two quadrants (by hand-pulling), one of which overlapped with the deadwood treatment. This allowed us to investigate the interactive effect of these two potential limitations on regeneration. The two treatments were assigned to each half of the block, using a coin toss. During the course of the study, we observed very little regrowth of *Hedera* in our plots, but when shoots were observed, they were removed.

Each quadrant contained four 0.25-m² plots, with a one meter buffer surrounding plots (Fig. 1b). In February 2011, after *Hedera* and deadwood treatments were established, we planted each plot with one of the following: seeds of all three focal species, *Thuja* seedling transplants, *Tsuga* seedling transplants, or nothing (control) to monitor natural seed germination and seedling establishment. We were unable to acquire enough *Abies* seedlings to include them in the transplant portion of this study. We quantified natural ambient conifer seed production in the first year by establishing a seed trap in the center of each block. Seed traps were monitored and emptied monthly, from September 2011 through March 2012. We compared our measured seed production to 2011 seed trap data from three stands in low-elevation old growth conifer forests at Mount Rainier National Park (stands TA01, TO04, and TO11 at 630, 642 and 564 m above sea level, respectively, Kroiss and HilleRisLambers 2015). These stands may not be perfectly analogous to the forests at Lincoln Park, because they differ in multiple ways beyond urbanization (e.g., the elevation of Lincoln Park is much lower, at 38 m above sea level; the trees are much younger, on average, and conifer abundance is lower at Lincoln Park versus Mount Rainier). Nonetheless, we thought it would be useful to compare the seed abundance at Lincoln Park to seed abundance in a forest, relatively nearby, that does not experience urban pressures, and this was the closest forest for which we could find analogous seed trap data.

Seed addition plots

In February 2011 and January 2012, we planted *Abies*, *Thuja*, and *Tsuga* seeds in seed addition plots (Fig. 1b). Each species' seeds were distributed across approximately 1/3 of the plot. In 2011, we sowed 20 seeds per species per plot by placing seeds on the ground surface. Because 2011

germination and survival rates were quite low (2.5 and 6.7%, respectively, across all species and plots), we sowed more seeds in 2012: 51 *Abies*, 57 *Thuja*, and 64 *Tsuga* seeds, respectively, per plot. Seeds were donated from SilvaSeed in 2011 and from the Washington Department of Natural Resources in 2012; seed viability tests were conducted by these groups, and germination rates were reported as 60–80%. We quantified seed germination and seedling survival in the field every 2 weeks from June through October in 2011 and 2012. Our observed seed germination rates should be interpreted as net post-dispersal seed germination success, because our methods do not allow us to separate effects of microsite conditions on the physiology of germination versus on rates of seed predation or other factors that may alter observed germination.

Transplants plots

In February 2011, we planted 16 *Tsuga* seedlings and five *Thuja* seedlings per plot (Fig. 1). *Tsuga* seedlings were about 1 year old and 3.95 cm tall, on average, and *Thuja* seedlings were 54.93 cm tall, on average, at the time of transplanting. We measured height of all seedlings at the time of transplant, and watered all seedlings on the day they were transplanted only. Height and survival were measured every 3 months. Height was measured from ground level to the apical bud. Seedlings were considered dead when they possessed no green foliage.

Other environmental conditions

To quantify environmental differences between blocks, we estimated initial ground cover, including cover of *Hedera* and coarse woody debris (Woodall et al. 2008). We also measured soil characteristics, light availability, and adult tree identity and size within 10 m for each block. Soil characteristics (pH, depth to O-horizon, soil moisture, organic content) were measured in February 2011, prior to installing treatments. In October 2011, we also measured pH, total carbon and nitrogen, percent organic content, and soil particle size. In addition, every month in each plot throughout the study, we monitored soil moisture (using a Decagon Devices EC-5 soil moisture sensor) and photosynthetic active radiation (PAR, using a quantum light meter, Fieldscout model, made by Spectrum® Technologies, Inc). To quantify differences in local tree neighborhood between blocks, we identified and measured the diameter at breast height (dbh) of all adult trees (>10 cm dbh) within 10 m of the center of each block. We also quantified canopy cover over each block with a densiometer at full leaf-out during the 2011 growing season.

Statistical analyses

To assess differences in seedfall between our study site and old-growth forests at Mount Rainier National Park, we fit a generalized linear mixed effects model (family = negative binomial) with an explanatory variable of forest type and a random effect of block (intercept-only structure). To assess the effects of seed addition and *Hedera* presence, deadwood presence, and their interaction on seed germination, we fit generalized linear mixed effects models, with Poisson distributed response variables, and random effects of year and block (intercept-only structure). To assess the effects on survival of germinated seeds, we fit generalized linear mixed effects models, with binomially distributed response variables (the number of surviving seeds out of the total number of germinated seeds), and random effects of year and block (intercept-only structure).

To assess the effects of seed addition and *Hedera* presence, deadwood presence, and their interaction on survival of transplants, we used generalized linear mixed effects models, fit with binomially distributed response variables. To assess the effects on transplant growth at the end of the study, we used linear mixed effects models with normally distributed response variables and a random effect of block (intercept-only structure). To assess pretreatment differences among blocks for environmental conditions (soils, light, tree neighborhood), we used linear models, with normally distributed response variables. All analyses were completed using R version 3.1.3 (R Core Team 2016).

Results

Our experiment was affected by vandalism on several occasions, including the complete destruction of one block, where large piles of *Hedera* were placed on top and directly adjacent to the block (Block #3). Many transplants were also dug up and moved. For these reasons, we completely abandoned Block #3 and it is not included in our results. In addition, one quadrant of Block #5 was also tampered with: *Thuja* transplants were dug up and moved, and wood was moved to cover many *Tsuga* transplants. We therefore did not include transplant data from this quadrant, but the other three quadrants in this block remained intact and were included in our analysis. Thus, the sample size analyzed here includes a total of 115 *Thuja* transplants (5 transplants per plot X 4 treatments X 6 blocks, minus the 5 transplants lost in one treatment/plot of Block #5) and a total of 368 *Tsuga* transplants (16 transplants per plot X 4 treatments X 6 blocks, minus the 16 transplants lost in one treatment/plot of Block #5). We only have seed trap data in five blocks because, in addition to completely abandoning Block #3 due to destruction, the seed trap from a

second block was repeatedly stolen. Germination plots were unharmed, other than the loss of those in Block #3.

Natural seed production and seedling abundance

We observed low amounts of natural conifer seed production at Lincoln Park, especially in comparison to observations in old growth forests at Mt. Rainier National Park (Fig. 2, Type II Wald χ^2 test: $\chi^2 = 10.35$, $df = 1$, $p < 0.001$). From August 2011 to February 2012, 83 tree seeds fell into five seed traps. Only 29 of these were conifer seeds: 17 *Pseudotsuga* seeds, 6 *Thuja* seeds, 8 *Tsuga* seeds, and no *Abies* seeds. The average number of conifer seeds per trap was 6.2 (SE = 2.6) across all 6 months of monitoring.

Natural seedling abundance was also low. In our initial, pre-treatment surveys of the study area, we observed no conifer seedlings present in any of the seven experimental blocks, nor in their seven paired non-*Hedera* blocks. In control plots, in which seeds were not added, we observed 19 conifer germinants in 2011 (11 *Pseudotsuga*, which was not a focal species for this study, and 8 *Tsuga*) and 19 in 2012 (3 *Abies*, 11 *Pseudotsuga*, 5 *Tsuga*). None of these survived beyond one growing season.

Germination

Germination was low overall and varied by conifer species. For example, in 2012 (when germination rates were highest) 20.5% of added seeds germinated, on average, for *Abies* (SE = 0.6%), 1.0% for *Thuja* (SE = 0.06%), and 1.7% for *Tsuga* (SE = 0.09%), across all treatments. Seed addition

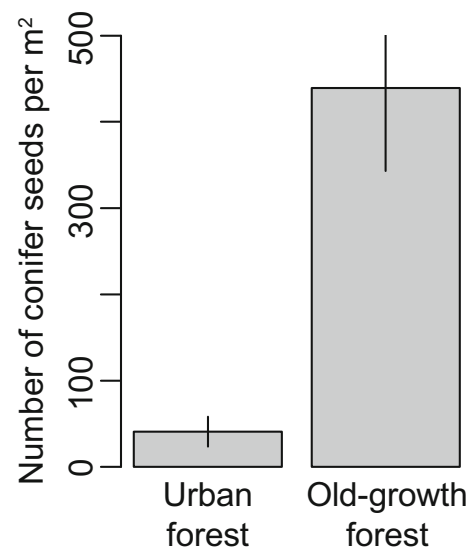


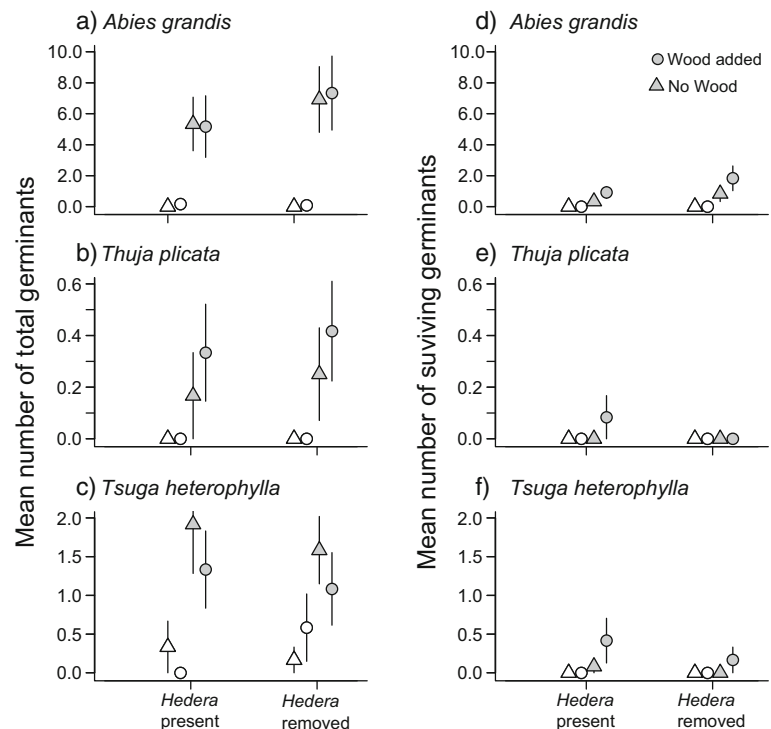
Fig. 2 Seed density was reduced at our urban forest study site, compared with old growth forest sites in the region (Mt. Rainier National Park, Kroiss and HilleRisLambers 2015), based on 2011–2012 seed trap data. Means with standard errors are shown

significantly increased total germination for *Abies* and *Tsuga*, but not for *Thuja* nor for surviving germination of any species (Fig. 3, Table 1). For *Abies*, total germination was lower with *Hedera* present (i.e., *Hedera* had a negative estimate, Table 1). However, the number of surviving *Abies* germinants was higher in plots with wood present (i.e., wood had a positive estimate, Table 1), with a negative but nonsignificant effect of *Hedera* presence (Fig. 3a and d, Table 1). For *Tsuga*, microsite treatment effects were not significant for total germination (i.e., even though the estimate for wood was negative and the estimate for *Hedera* was positive, their standard errors were large enough to suggest that these effects were no different than zero) but the highest surviving germination was observed with wood added (i.e., wood had a positive estimate, Fig. 3c and f, Table 1). For *Thuja*, total germination did not vary significantly by any treatment, and surviving germination was so low that no model could be reliably fit (Fig. 3b and e, Table 1).

Transplant survival and growth

Survival of transplanted *Thuja* and *Tsuga* was highest with the addition of deadwood, and *Hedera* presence had weak negative effects on survival for *Tsuga* (Fig. 4, Table 2). Wood presence also positively affected growth of *Tsuga* (Fig. 4, Table 2). There were no significant treatment effects on growth of *Thuja* (Fig. 4, Table 2).

Fig. 3 Seed addition (gray symbols) increased both total germination (a-c) and surviving germinants after one season (d-f), compared with control plots where no seeds were added (white symbols), for all three focal species. Presence of deadwood did not significantly affect total germination, but positively influenced the number of surviving germinants for *Abies* and *Tsuga*. *Hedera* presence did not strongly influence total germination or surviving germinants. Means with standard error are shown for 2012 data



Other environmental conditions

Initial *Hedera* cover ranged from 36 to 69% within each of our experimental blocks (Table S1). One block had lower *Hedera* cover, on average, than the other blocks, which did not differ from one another (Table S1). Average percent cover for initial coarse woody debris ranged from 0 to 12%, with no significant differences among plots. Most soil characteristics did not differ between plots prior to the installation of our experiment: no significant differences were found across the seven blocks in organic matter content ($F = 0.5179$, $p = 0.4805$), soil moisture ($F = 0.004$, $p = 0.95$), or pH ($F = 0.6643$, $p = 0.4252$).

The mean depth of the organic horizon in each of the seven blocks ranges from 1.4 to 4 cm, with a mean of 2.4 cm. Organic matter content ranged from 7.4 to 27.5% in the seven blocks, with an overall mean of 14.2% (Table S1). Total carbon ranged from 4.2 to 7.6%, with a mean across all blocks of 6.0%; nitrogen ranged from 0.2 to 0.4% with a mean of 0.3%; and hydrogen ranged from 0.6 to 1.0% with a mean of 0.9% (Table S2). The mean water-holding capacity for each of the seven blocks ranged from 38.9 to 63.6%, with a mean of 51.2% and no significant differences between blocks ($F = 0.10$, $p = 0.75$). Moisture content ranged from 23.1 to 71.7%, with a mean of 41.6%, and pH ranged from 4.3 to 6.6, with a mean of 5.5 (Table S1). There were no significant differences between blocks for moisture content or

Table 1 Germination model summaries for generalized linear mixed models for total germination (the total number of seeds germinated) and surviving germination (the number of germinants surviving at the end of one growing season, out of the total number of germinated seeds)

		Total Germinants					Surviving Germinants				
		Estimate	SE	χ^2	df	<i>P</i>	Estimate	SE	χ^2	df	<i>P</i>
<i>Abies grandis</i>	Intercept	-3.23	0.93				-17.93	NA			
	Seeds Added	4.6	0.58	63.41	1	<0.001	15.39	NA	0	1	0.98
	Wood Added	0.07	0.15	0.12	1	0.73	0.92	0.43	8.62	1	0.003
	<i>Hedera</i> Present	-0.26	0.17	6.47	1	0.01	-0.77	0.63	1.79	1	0.18
	Wood* <i>Hedera</i>	-0.07	0.23	0.09	1	0.76	0.42	0.77	0.3	1	0.58
	Residual				89					89	
	Random effects	σ					σ				
	Block (<i>n</i> = 6)	0.84					1.008				
	Year (<i>n</i> = 2)	0.9					0				
		Estimate	SE	χ^2	df	<i>P</i>	Estimate	SE	χ^2	df	<i>P</i>
<i>Thuja plicata</i>	Intercept	-22.57	NA								
	Seeds Added	20.64	NA	0	1	0.99					
	Wood Added	0.51	0.71	1.18	1	0.28					
	<i>Hedera</i> Present	-0.41	0.88	0.3	1	0.58					
	Wood* <i>Hedera</i>	0.18	1.1	0.03	1	0.87					
	Residual				89						
	Random effects	σ					σ				
	Block (<i>n</i> = 6)	0.24									
	Year (<i>n</i> = 2)	1.15									
		Estimate	SE	χ^2	df	<i>P</i>	Estimate	SE	χ^2	df	<i>P</i>
<i>Tsuga heterophylla</i>	Intercept	-1.46	0.45				-41.49	NA			
	Seeds Added	1.7	0.3	32.58	1	<0.001	19.80	NA	0	1	0.99
	Wood Added	-0.05	0.31	1.68	1	0.19	19.98	NA	3.97	1	0.05
	<i>Hedera</i> Present	0.25	0.29	0.05	1	0.83	18.6	NA	0.95	1	0.33
	Wood* <i>Hedera</i>	-0.47	0.44	1.17	1	0.28	-17.68	NA	0	1	0.99
	Residual				89					89	
	Random effects	σ					σ				
	Block (<i>n</i> = 6)	0.56					0				
	Year (<i>n</i> = 2)	0.27					0				

“Wood added” represents the effect of adding decaying woodchips; “*Hedera* present” represents the effect of leaving *Hedera* (i.e., not removing it). *P* values are from Type II Wald χ^2 tests. (Type II tests were used because there were no significant interactions). Standard errors could not be estimated in several cases, due to perfect linear separation (e.g., no *Thuja* seedlings were observed in plots where seeds were not added; these cases are labeled “NA”). Bolded values indicate significant fixed effects ($P < 0.05$). For *Thuja*, survival of germinants was so low that a model could not be fit (see Fig. 3)

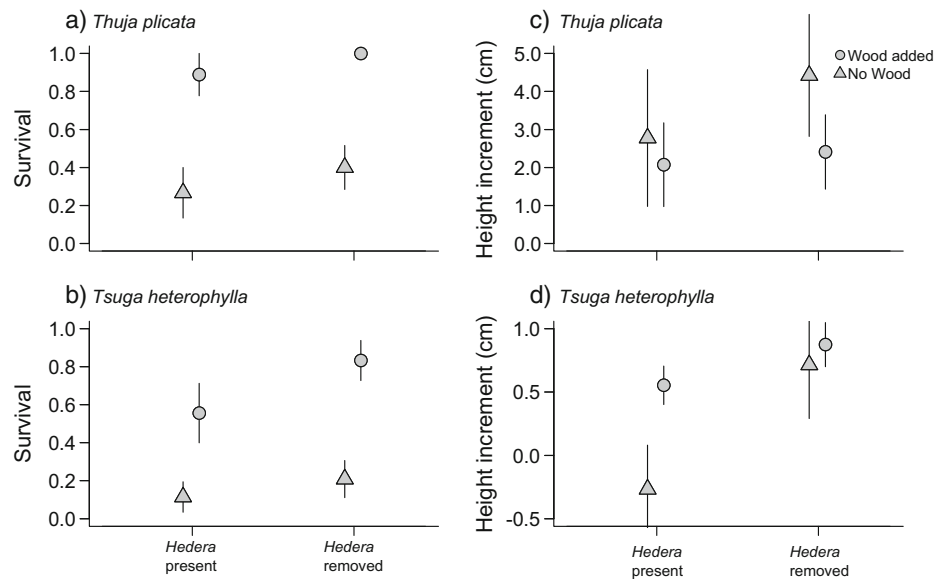
pH (moisture: $F = 0.004$, $p = 0.95$, pH: $F = 0.66$, $p = 0.43$). The only soil variable for which there were significant differences between blocks was average depth of the O-horizon in each block ($F = 7.31$, $p = 0.01$, Table S1).

Our experimental blocks existed under closed-canopy forest, with canopy openness ranging from 2.5 to 11.5% when deciduous leaves were fully emerged. The most common adult trees around our blocks were *Pseudotsuga menziesii* and *Acer macrophyllum*, and they had average diameters ranging from 38.94 to 45.56 cm. No adult trees of our three focal species existed in our blocks, although they did exist in areas near our blocks (personal observation, SDURP-UFP 2002).

Photosynthetic active radiation did not differ by treatment, and did not significantly vary over time (Figure S1a). Soil moisture levels did vary by treatment, but also did not vary significantly over time (Figure S1b). Plots in which *Hedera* was removed had the highest soil moisture throughout the season. During January-February 2011, soil moisture was lowest in plots with woodchips added; however by October 2011, this effect was no longer apparent (Figure S1b).

Because we found minimal differences among blocks in the above environmental conditions, we did not include any of them as covariates in our analyses of germination, survival, and growth.

Fig. 4 Survival (a, b) and growth (c, d) of transplanted conifer seedlings. Adding wood positively influenced survival of both focal species and growth for *Tsuga*. *Hedera* presence had a weak negative effect on survival of *Tsuga*, but did not affect survival of *Thuja* nor growth in either species. Means with standard error are shown



Discussion

Seed limitation appears to be a critical barrier to forest regeneration at our study site, given that germination rates were much higher in seed addition plots than in control plots (Fig. 3). The underlying causes of this seed limitation are uncertain, but likely contributing to the seed limitation is the fact that seed production within the forest patch itself is quite low, at least compared to seed production in old growth forests in the region (Fig. 2). This reduced seed production may be a result of the relatively low abundance and young age of

coniferous overstory trees at our study site. For example, no adult trees of our focal species existed within 10 m of any of our blocks. The seeds of focal species found in our traps likely came from individuals in Lincoln Park located more than 10 m away from our plots (we did observe focal species nearby, SDPR-UFP 2002), since the park is relatively isolated from other forested patches (Fig. 1a) and our focal species commonly disperse only 40–600 m from parent trees (Burns and Honkala 1990). Of course, trees planted in residential yards, which are much closer to our plots than other forested parks, could also act as seed sources. Although two of our focal

Table 2 Transplant survival and growth model summaries for generalized linear mixed models for survival and growth (height increment)

		Survival					Growth				
		Estimate	SE	χ^2	df	P	Estimate	SE	χ^2	df	P
<i>Thuja plicata</i>	Intercept	-0.48	0.60				4.19	1.60			
	Wood Added	19.27	NA	18.83	1	<0.001	-1.78	1.82	0.71	1	0.40
	<i>Hedera</i> Present	-0.75	0.63	1.44	1	0.23	-1.83	2.43	0.39	1	0.53
	Wood* <i>Hedera</i>	-15.10	NA	0.0004	1	0.98	1.43	2.82	0.26	1	0.61
	Residual				113					71	
	Random effects	σ									
	Block (n = 6)	1.04					0.99				
<i>Tsuga heterophylla</i>	Intercept	-1.94	0.74				0.35	0.38			
	Wood Added	4.30	0.55	95.09	1	<0.001	0.47	0.36	6.29	1	0.01
	<i>Hedera</i> Present	-0.87	0.45	8.44	1	<0.001	-1.11	0.53	3.15	1	0.08
	Wood* <i>Hedera</i>	-0.16	0.65	0.06	1	0.81	0.88	0.60	2.15	1	0.14
	Residual				361					163	
	Random effects	σ									
	Block (n = 6)	1.63					0.4792				

P values are from Type II Wald χ^2 tests. Bolded values indicate significant fixed effects ($P < 0.05$)

species are commonly present in residential yards (*Thuja* and *Tsuga*), their density is quite low in these areas in Seattle (i.e., less than one individual per acre, Tenneson 2013). All focal species within this distance were likely relatively small and young. Conifers were logged from the area in the early 20th century (SDPR-UFP 2002), so adult conifer trees are a maximum of 90 to 100 years old, as compared to Mt. Rainier's old-growth forests, where the oldest trees are over 1,000 years old (Franklin et al. 1988). At other sites in the Pacific Northwest, seed limitation has also been observed in areas where large adult conifer trees are sparse (Beach and Halpern 2001; Keeton and Franklin 2005) likely because large, old trees produce more seeds than young, smaller trees (Bonner and Karrfalt 2008).

There are additional factors that may also be contributing to the observed seed limitation. There may be few seeds dispersing into the site from surrounding conifer populations, due to the fragmented forest habitat in this urban setting (Matlack 1994; Dalling et al. 1998; Butaye et al. 2002; Condit et al. 2002). In addition, seeds that do disperse in or are produced at the site may have low viability, perhaps due to pollen limitation (Knight et al. 2005) or they may experience high amounts of seed predation, such as from nonnative earthworms and small mammals (Bowers and Breland 1996; Lobo 2014; Dávalos et al. 2015). For example, it is possible that the greater germination success we observed in the woodchip treatment could be due to seeds being hidden from seed predators, rather than only due to treatment effects on critical abiotic conditions.

Microsite limitation was also an important barrier to establishment in our study. Specifically, addition of deadwood dramatically improved seedling survival. Indeed, no germinants of any species survived beyond one season without the presence of deadwood, and transplant survival increased more than five-fold with deadwood for both *Thuja* and *Tsuga* (Figs. 3 and 4). These findings are similar to studies showing that nurse logs benefit conifer regeneration (Harmon and Franklin 1989; Szweczyk and Szwagrzyk 1996; Simard et al. 1998). Although our deadwood treatment differs from nurselogs and other coarse woody debris in that the size of individual wood pieces was much smaller, it may similarly benefit conifer establishment through reducing competition with understory vegetation, increasing moisture, or altering fungal composition of the substrate (Harmon and Franklin 1989; Simard et al. 1998; Zhong et al. 1999; Elman and Salisbury 2009). Unfortunately, young managed and urban forests often have little coarse woody debris: a survey of Seattle's conifer forests found an average volume of 775 ft³/acre of coarse woody debris, compared with 6400 ft³/acre of coarse woody debris in conifer forests over 250 years old (Elman and Salisbury 2009).

Competition with invasive plants does not appear to pose a great threat to conifer seedling establishment. We observed a

weak negative effect of *Hedera* presence on total germination for *Abies* and on transplant survival for *Tsuga*, with much stronger effects of wood for this species (Fig. 4d, Table 1). We found no negative effects of *Hedera* presence on germination of *Thuja* and *Tsuga*, on survival of *Thuja* transplants, nor on growth for any focal species. Although our results suggest that competition from *Hedera* is not a strong limitation to conifer establishment in Seattle forests, this invasive plant may have a greater impact on other life stages or on other species. For example, *Hedera* can weaken and eventually kill its adult host trees, and adult tree root growth can be suppressed when growing with *Hedera* (Thomas Jr 1980; Shoup and Whitcomb 1981).

Our results have several implications for management of urban forests in the Pacific Northwest and elsewhere. Efforts to improve natural conifer regeneration should focus on adding deadwood, rather than removing *Hedera*, given the much larger effects of wood addition that we observed on seedling survival and growth. We suggest increasing and retaining coarse woody debris (e.g., downed trees) whenever possible in urban parks and forested areas (Elman and Salisbury 2009). If conifer planting is planned, we suggest managers consider adding wood. In addition, we recommend planting tree seedlings, rather than seeds, since we observed extremely low survival rates of seed germinants, even with wood presence. Although transplanting seedlings is more time- and cost-intensive, it is likely to lead to greater establishment (Godefroid et al. 2011). Furthermore, larger seedlings are likely to survive at higher rates; this may explain the higher survival of *Thuja* transplants compared with *Tsuga*, since the latter were much smaller than *Thuja* individuals at the time of transplanting (3.95 cm on average for *Tsuga* versus 54.93 cm on average for *Thuja*).

More broadly, our findings highlight that restoration efforts should include data collection and continual evaluation of management success. At the time of our research, management activities in Seattle's urban forests included planting conifer seedlings and removing *Hedera*, but not adding deadwood (Baker per. comm.). Transplanting is often conducted by volunteers and is not systematically monitored afterwards, making it difficult to evaluate the success of these efforts. Conducting research alongside management will help ensure that the most effective strategies are used to accomplish specific goals. With careful planning and monitoring, this approach can also improve basic understanding of urban forest ecology, about which many questions remain. For example, we found that conifer regeneration was limited by interactive effects of seed and microsite limitation, but it is unclear if this finding is relevant only for our specific site or is common to urban forests in general. As urban human populations grow, and we continue to depend on the ecosystem services provided by urban forests, it will be increasingly valuable to understand key drivers and responses in these systems.

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Statement of authorship A.E. conceived and designed the experiment, conducted the final analyses, and wrote the manuscript; B.L. and S.M. helped design and conduct the experiment, helped collect and analyze the data, and edited the manuscript.

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