

Effects of fungal seed pathogens under conspecific and heterospecific trees in a temperate forest

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Abstract: This study investigated the impacts of soil fungi on seeds of two eastern North American temperate-zone trees: *Acer saccharum* Marsh. (sugar maple) and *Tsuga canadensis* (L.) Carr (eastern hemlock). Seeds of each species were buried at locations dominated by either conspecifics or heterospecifics. Half were protected with fungicide, and the net consequences for survival and germination were assessed. Net effects of fungicide usually were positive, indicating that pathogens affected seeds more strongly than any potential mutualists. Losses of *A. saccharum* to fungi were modest, and almost identical in areas dominated by itself versus areas dominated by *T. canadensis*. In contrast, fungal impacts on *T. canadensis* were strongly habitat-dependent: losses to fungi were high in *T. canadensis*-dominated sites, but not in *A. saccharum*-dominated sites. This result is consistent with an accumulation of host-specific pathogens, either by a direct feedback between *T. canadensis* and its fungal enemies, or indirectly through modification of the soil environment. Even though these two trees share similar habitats, responses to fungicide indicate that their seeds are affected very differently by the soil environment.

Key words: *Acer saccharum*, fungi, pathogens, seed bank, *Tsuga canadensis*, seeds.

Résumé : L'auteur examine les impacts des champignons du sol sur les semences d'arbres de la zone tempérée de l'Amérique du Nord : *Acer saccharum* Marsh (érable à sucre) et *Tsuga canadensis* L. Carr (pruche de l'Est). Il a enterré des graines de chacune de ces espèces à des endroits dominés par des espèces conspécifiques ou hétérospécifiques, en en protégeant la moitié avec un fongicide, avant d'évaluer les conséquences sur leur survie et leur germination. Le fongicide exerce généralement des effets positifs, ce qui indique que les champignons pathogènes affectent plus fortement les graines que n'importe lequel organisme mutualiste. Les pertes chez l'*A. saccharum* par les champignons demeurent modestes, et presque identiques dans les endroits où il domine, vs ceux dominés par le *T. canadensis*. Au contraire, les impacts des champignons sur les graines du *T. canadensis* dépendent fortement de l'habitat, avec des pertes élevées dues aux champignons dans les sites dominés par le *T. canadensis*, mais non dans les sites dominés par l'*Acer saccharum*. Ce résultat concorde avec l'accumulation de pathogènes spécifiques à l'hôte, soit directement par une rétroaction directe entre le *T. canadensis* et ses ennemis fongiques, ou indirectement par des modifications de l'environnement édaphique. Bien que ces deux arbres partagent des habitats similaires, les réactions aux fongicides indiquent que leurs graines sont affectées très différemment par l'environnement édaphique.

Mots-clés : *Acer saccharum*, champignons, pathogènes, banque de semences, *Tsuga canadensis*, semences.

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Introduction

Pathogens can have important impacts on plant populations and communities (Dobson and Crawley 1994; Gilbert 2002; Van der Putten 2003). For example, soil fungi have been demonstrated to reduce tree seed and seedling survival and growth in a variety of temperate (e.g., Stanosz 1993; Zhong and van der Kamp 1999; Masaki and Nakashizuka 2002; Tomita et al. 2002; Packer and Clay 2000, 2003) and tropical (e.g., Augspurger 1983; Kitajima and Augspurger 1989; Forget 1997; Dalling et al. 1998) forest systems. These impacts often are spatially variable: mortality may be

higher in sites with large fungal populations, and lower in sites favoring trees' growth and defense (Augspurger 1984; Augspurger and Kelly 1984; Forget 1997; Zhong and van der Kamp 1999; DeWalt et al. 2004; O'Hanlon-Manners and Kotanen 2004a). As an example, white birch (*Betula papyrifera* Marsh.) experiences lower losses of seeds to fungi in fields rather than in forests, suggesting pathogens may contribute to the dependence of this species on open sites for recruitment (O'Hanlon-Manners and Kotanen 2004b).

Spatial variation in populations of pathogens can often be linked to variation in the physical or biotic environment. For example, wetter soils may sustain larger populations of harmful fungi (Blaney and Kotanen 2001; Schafer and Kotanen 2003). Consequently, treefall gaps or other relatively dry openings may provide a refuge from pathogens prevalent in the moist, shady understory (Augspurger 1984; Augspurger and Kelly 1984; Forget 1997; Wenny and Levey 1998; O'Hanlon-Manners and Kotanen 2004b). As another

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example, fungi may be more abundant in soils with greater organic content or a higher C:N ratio (Wardle 2002); this also might increase the risk of attack (Zhong and van der Kamp 1999). Plants themselves may affect pathogen populations by a variety of direct and indirect mechanisms. Indirect mechanisms may involve plants modifying soil C:N ratio or chemistry via the input of organic material, or modifying soil moisture by changing evapotranspiration rates (Wardle 2002; Van der Putten 2003). These soil changes can affect pathogen populations as described above. The best-studied direct mechanism is soil microbial feedback: the buildup of pathogen populations in response to the presence of host species (Van der Putten et al. 1993; Bever 1994; Bever et al. 1997; Mills and Bever 1998; Van der Putten 2003). This may render recruitment more difficult in areas dominated by conspecific adults, as originally suggested by Janzen (1970) and Connell (1971) (the "Janzen–Connell Hypothesis"). Studies providing evidence of density- or distance-dependent recruitment suggest that this model may be widely applicable in tropical forests (Clark and Clark 1984; Wills et al. 1997; Harms et al. 2000; Wright 2002; but see Hyatt et al. 2003 for a strong contrary view). Evidence from temperate regions is more limited, but suggests density-dependent predators and pathogens may similarly affect recruitment in forests (Packer and Clay 2000; Hille Ris Lambers et al. 2002). Soil feedback is not always negative: some species may cultivate mycorrhizae or other soil microflora that improve their own performance or reduce that of their competitors (Klironomos 2003; Callaway et al. 2004a, 2004b; Hood et al. 2004; Weber et al. 2005).

I designed this study to experimentally investigate the impacts of fungal pathogens (including true pathogens, seed decay fungi, and other antagonists) on seeds of two co-occurring temperate forest trees: *Acer saccharum* Marsh. (sugar maple) and *Tsuga canadensis* (L.) Carr (eastern hemlock). These species alter soil conditions in distinctly different ways (Pastor et al. 1984; Mladenoff 1987; Frelich et al. 1993; Finzi et al. 1998a, 1998b), with consequences for their recruitment. There is evidence that surface soil characteristics such as low pH, high soil carbon, and low nitrogen availability reduce recruitment by *A. saccharum* in *T. canadensis*-dominated areas, while a thick, dry layer of leaf litter inhibits recruitment of *T. canadensis* in *A. saccharum*-dominated sites (Frelich et al. 1993; Catovsky and Bazzaz 2000). These mutually negative interactions may explain why these two species tend to be negatively associated on a local (stand) scale (Frelich et al. 1993). However, it is possible that interactions with the soil microbial community might significantly modify these effects. In principle, microbes might respond to soil changes such that each tree species cultivates a pathogen community hostile to the other, further reducing heterospecific recruitment. Alternatively, soil changes and (or) the accumulation of species-specific pathogens predicted by the Janzen–Connell Hypothesis might favour microbial communities that cause each species to inhibit its own recruitment, though evidently not enough to eliminate the observed pattern of stand dominance. Thus, soil microbes might tend either to reinforce or to reduce stand stability.

My experiment tested the hypothesis that the net effect of soil fungi on seeds of each of my study species is more neg-

ative at sites where that tree is common versus sites where it is scarce. To accomplish this, I used fungicide to treat seeds in habitats dominated by both conspecifics and heterospecifics, with untreated controls. Comparison of fungicide-treated seeds versus untreated seeds allowed me to estimate the net effect of the soil fungal community: improved survival of fungicide-treated seeds indicates that the effects of pathogens outweighed the effects of any beneficial species. My results demonstrate that seeds of these two co-occurring tree species responded very differently to fungicide applications, suggesting that seed pathogens may play a different role in each case.

Materials and methods

Study site

This experiment was conducted at the University of Toronto's Koffler Scientific Reserve at Jokers Hill, Regional Municipality of York, in southern Ontario, Canada (44°02'N, 79°31'W, 300 m elevation a.s.l.). This 350 ha site lies within the Oak Ridges Moraine, and is characterized by prominent hills with a thin organic layer over deep glacial sands. Experimental plots were established throughout a single large (>1 km²) tract of mature forest near the centre of this property. The most abundant tree in this tract is *A. saccharum*, but *T. canadensis* occurs patchily throughout, generally in stands < 1 ha in area. Other species typical of the temperate Great Lakes Forest region also are present, notably including American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britton), and eastern white pine (*Pinus strobus* L.). Further information on this site may be found at www.zoo.utoronto.ca/jokershill/jh.html.

Experimental species

Acer saccharum is the dominant mature forest tree throughout much of southeastern Canada and the northeastern USA (Godman et al. 1990; Farrar 1995). This deciduous species is very shade-tolerant, and can persist for decades as small saplings in deep shade in the forest understory until a canopy gap opens (Godman et al. 1990; Farrar 1995). The winged seeds are dispersed from October to December (Schopmeyer 1974). These seeds do not persist long in the soil (Marquis 1975; Houle 1994), but germinate very early in spring, often while snow is still present (Godman et al. 1990, Farrar 1995). *Acer saccharum* seeds seem relatively resistant to fungal attack: O'Hanlon-Manners and Kotananen (2006) did not detect a significant improvement in seed survival in response to protection with fungicide.

Tsuga canadensis is a highly shade-tolerant, late-successional conifer, and co-occurs with *A. saccharum* throughout much of eastern North America (Anderson and Gordon 1994). The winged seeds are wind-dispersed during fall and winter (Fowells 1965; Godman and Lancaster 1990), and germinate in June or July in northern areas (Fowells 1965). *Tsuga canadensis* does not form a persistent seed bank (Marquis 1975; Hille Ris Lambers et al. 2002). Saplings frequently recruit on decaying logs and stumps (Godman and Lancaster 1990; Anderson and Gordon 1994), in part because seedlings are prone to smothering by leaf litter on the forest floor (Anderson and Gordon

1994), but also because these microhabitats provide a refuge from pathogenic fungi that reduce viability of seeds buried in soil (O'Hanlon-Manners and Kotanen 2004a).

Experimental methods

Sixteen experimental plots were established in June 2002, scattered throughout mature maple–beech–hemlock forest; 8 were located in eight different *T. canadensis*-dominated sites, and the remaining plots in eight *A. saccharum*-dominated sites. Sites were 10's to 100's of meters apart, and contained numerous large trees of the focal species. At each site, approximately 20 mL of fresh local soil was used to fill four seed bags, each made from a knee-high nylon stocking; this soil was collected from just below the surface organic layer, and was nearly pure sand. Fifteen seeds, provided from Ontario sources by the National Tree Seed Centre (Natural Resources Canada, Canadian Forest Service, Fredericton, New Brunswick), were added to each bag: seeds of *T. canadensis* to two bags per site, and seeds of *A. saccharum* to the other two. Although this is a modest sample size, it is not unreasonably small: a total of 960 seeds was used in this experiment (480 per species), and the demonstration of statistically significant results (see below) shows that this provided sufficient power for the detection of important treatment effects.

This experiment was designed to compare the net effects of the entire fungal community on buried seeds subjected to different treatments, rather than to estimate absolute levels of mortality or to isolate the effects of specific pathogens. One bag of each species was saturated with a broad-spectrum fungicide (1:100 solution of Maestro 75DF in water: Zeneca Corp., Ont.); the other was saturated with water as a control. The active ingredient in this fungicide (75% by weight) is captan (3a,4,7,7a-tetrahydro-2-[(trichloromethyl)thio]-1*H*-isoindole-1,3(2*H*)-dione), a nonsystemic heterocyclic nitrogen fungicide effective against a broad range of Oomycota, Ascomycota, and Basidiomycota (Sharvelle 1961; Torgeson 1969; Neergaard 1977); my lab has successfully used captan in a series of similar experiments (Blaney and Kotanen 2001, 2002; Schafer and Kotanen 2003; O'Hanlon-Manners and Kotanen 2004a, 2004b). It is expected that short-lived seeds should be concentrated near the soil surface (Baskin and Baskin 1998); thus, seed bags were buried as shallowly as practically possible (5–10 cm) in the surface soil layer, separated from one another by approximately 1 m. Fungicide and water treatments were re-applied at approximately monthly intervals by saturating the immediate site of burial of each bag; bags were far enough apart that significant cross-contamination seems unlikely. Use of seed bags may underestimate survival in natural soils (Van Mourik et al. 2005); however, this should not bias comparisons between experimental treatments.

These bags were retrieved in November 2002 and returned to the laboratory where seeds were recovered by sieving. Bags that were not recovered intact were excluded from analyses, as were any missing seeds. Field-germinated seeds were counted and removed, and the remaining seeds were transferred to germination treatments based on information provided by the National Tree Seed Centre, and shown to maximize germination in previous experiments (O'Hanlon-Manners and Kotanen 2006). *Tsuga canadensis* seeds were

placed in pots filled with potting soil, and initially placed in a germination chamber (12 h light/12 h dark, 25–5 °C, 90% humidity); in December, these pots were moved to a greenhouse. *Acer saccharum* seeds, which germinate best at low temperatures (Godman et al. 1990; Farrar 1995), were placed in plastic ziplock bags in a dark refrigerator (approximately 5 °C). These seeds were kept wet at all times. Seeds of both species were examined at monthly intervals until March (4 months), and classified as “germinated”, “intact” (firm and apparently undiseased), or “dead” (soft or rotten); the distinction between these categories generally was very obvious. Germinated and dead seeds were then removed. Seeds were classed as “surviving” if they germinated in either the field or the lab, or if they still remained intact by the end of the experiment.

Statistical analyses

Statistical analyses were performed using the EMS “Fit Model” routine of JMP 5 (2002, SAS Institute Inc., Cary, NC). Results for *A. saccharum* and *T. canadensis* were analyzed separately, since these species exhibited different responses; because these two analyses were based on seeds sharing the same plots, they are not fully independent. The proportion of recovered seeds that survived was analyzed with split-plot factorial ANOVAs (with site treated as a random block), following an arcsin–squareroot transformation (Kirk 1995). This is a more appropriate analysis than methods treating the fate of each seed as a binomial variable (e.g., logistic analyses) because it does not assume that the seeds within each bag are independent. The focus of this experiment was on responses to treatments rather than estimation of absolute levels of mortality. For instance, comparison of fungicide additions versus controls allows estimation of the net effect of the soil fungal community, including both harmful and beneficial species. Increased survival in response to fungicide addition therefore indicates that the influence of pathogens on survival exceeded that of mutualists, such as mycorrhizal fungi; the larger this increase, the more negative the net effect of the fungal community. Since some seeds germinated in the field, pathogens may include both seed pathogens and early seedling pathogens. It was expected that the positive influence of mycorrhizal species would be relatively small, since these primarily affect growth following root development, and thus are unlikely to strongly affect seed survival and germination. Means are reported \pm one standard error.

Results

Of the 64 experimental bags, 58 were recovered intact. These bags should have contained 870 seeds. The fate of 843 of these seeds (417 *A. saccharum* and 426 *T. canadensis*) could be determined; the remaining 3 *A. saccharum* and 24 *T. canadensis* seeds were not located or were lost during processing, and were excluded from analyses. Of these 843 seeds, 123 germinated in the field (all *T. canadensis*), while 244 *A. saccharum* seeds germinated in the lab versus 77 seeds of *T. canadensis*. Only 10 *A. saccharum* seeds and 0 (zero) *T. canadensis* seeds remained ungerminated but apparently intact at the end of the experiment; thus, misclassification of intact but dead seeds

Table 1. Results of ANOVAs (blocked by site) of the estimated proportion of *Acer saccharum* and *Tsuga canadensis* seeds that survived the experiment; see Fig. 1 for treatment means.

Factor	<i>Acer saccharum</i>				<i>Tsuga canadensis</i>			
	MS	df ^c	F ^d	p	MS	df ^c	F ^d	p
Habitat ^a	0.036	1	0.323	0.579	0.007	1	0.024	0.880
Site (habitat)	0.110	13	0.857	0.609	0.313	14	1.705	0.180
Treatment ^b	0.532	1	4.124	0.067	0.190	1	1.033	0.330
Habitat × treatment	0.000	1	0.002	0.968	1.077	1	5.867	0.032
Residual	0.129	11			0.184	12		

^aType of site where seeds were buried (*A. saccharum* vs. *T. canadensis* stands).

^bSeeds protected with fungicide vs. controls.

^cDegrees of freedom vary slightly as a consequence of missing data.

^dTests of "Habitat" are based on a synthesized denominator MS with Satterthwaite's degrees of freedom: *A. saccharum*: MS = 0.111; df = 13.9. *T. canadensis*: MS = 0.305; df = 15.0.

as living is unlikely to have strongly biased estimates of survival. Overall, 61% of *A. saccharum* seeds and 47% of *T. canadensis* seeds were judged to have survived the experiment (as germinated or intact); most of the remainder were obviously decayed, often with visible colonies of fungi or bacteria.

Analyses of overall survival (i.e., germinated seeds plus intact seeds) indicated that *A. saccharum* and *T. canadensis* responded to fungal pathogens in strongly contrasting ways (Table 1; Fig. 1). *A. saccharum* showed a marginally significant ($p = 0.07$) improvement in survival in response to fungicide (Table 1); however, this response was very similar (a 13%–14% increase) in both *A. saccharum*-dominated sites (control: 57% ± 6%; fungicide: 70% ± 6%) and *T. canadensis*-dominated sites (control: 51% ± 8%; fungicide: 65% ± 4%) (Fig. 1a), leading to a nonsignificant habitat effect and habitat × treatment interaction. In contrast, *T. canadensis* responded differently to fungicide in each habitat (Fig. 1b), leading to a significant habitat × treatment interaction (Table 1). In *T. canadensis*-dominated sites, fungicide improved seed survival from 38% ± 5% to 63% ± 7%: a 25% increase; in *A. saccharum*-dominated sites, survival was nearly unaffected, changing from 47% ± 10% to 44% ± 6%: a 3% decrease. Excluding seeds that failed to germinate did not alter patterns of significance for either species.

Discussion

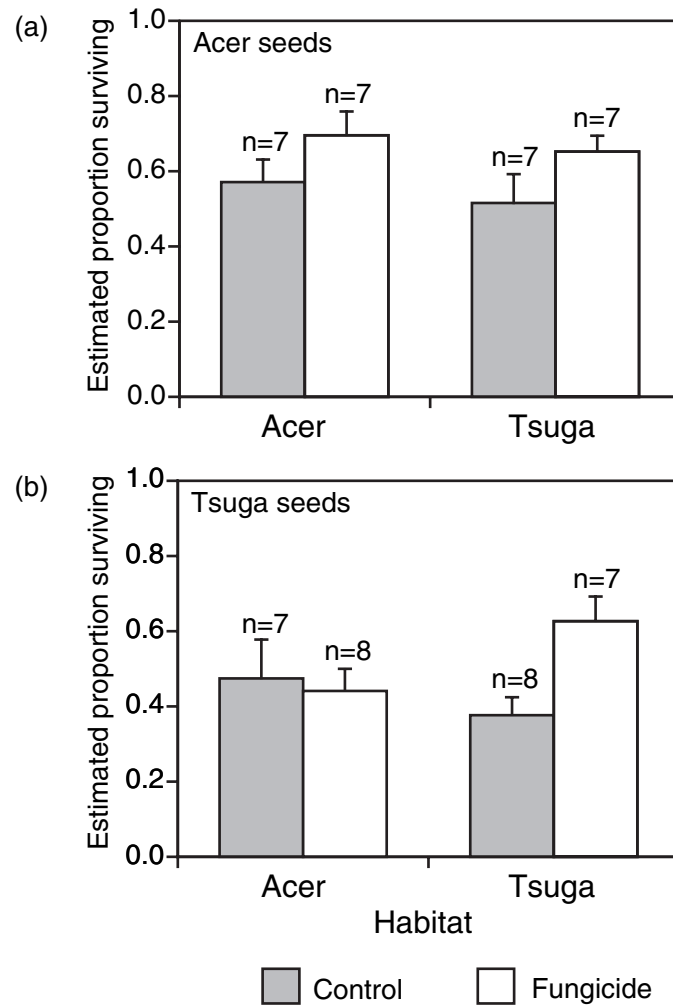
Previous research at this location has documented significant impacts of soil fungi on seeds in a variety of forest (O'Hanlon-Manners and Kotanen 2004a, 2004b, 2006) and nonforest (Blaney and Kotanen 2001, 2002; Schafer and Kotanen 2003) systems. The present study again demonstrates that soil fungal pathogens have the potential to affect the early stages of recruitment, likely including both seeds and germinating seedlings (e.g., Packer and Clay 2000). Although in principle the fungicide used might affect mutualists such as mycorrhizae, its net effects usually were positive, indicating that (as expected) pathogens affected seeds of both *A. saccharum* and *T. canadensis* more strongly than any potential mutualists. The improvement for *A. saccharum* was relatively modest, and was significant only at the $p = 0.07$ level (likely because of limited statistical power). The improvement for *T. canadensis* was much more substantial,

at least in conspecific-dominated sites: a 1.6-fold increase, suggesting greater susceptibility to fungal attack. Since this study was performed from summer to fall, while non-dormant seeds primarily occur in soil from winter to spring, there is a risk that the microbial communities experienced by seeds in this experiment differed from those naturally encountered (e.g., Lipson et al. 2002). However, over-winter studies previously conducted with the same species at the same site (O'Hanlon-Manners and Kotanen 2004a, 2006) also have found significant losses to seed fungi in *T. canadensis*, but not *A. saccharum*, suggesting patterns of mortality are similar. This study adds to accumulating evidence that pathogens present in the soil may play a significant (but underappreciated) role in reducing establishment success in both temperate and tropical forests.

The principal goal of the field experiment reported in this paper was to compare the impacts of seed-attacking fungi between sites where each tree species is common versus sites where it is scarce. These impacts differed markedly between the two study species. Losses of seeds of *T. canadensis* were strongly habitat-dependent: losses were high in *T. canadensis*-dominated sites, but not in *A. saccharum*-dominated sites. One possible explanation for this pattern may be that feedback between *T. canadensis* and the soil biota directly enhances populations of host-specific pathogens, as has for instance been shown for black cherry (*Prunus serotina* Ehrh.) (Packer and Clay 2000, 2003; Reinhart et al. 2003, 2005). A second possibility may be that *T. canadensis* modifies the physical environment around itself in such a way as to indirectly increase pathogen populations. For example, soil beneath *T. canadensis* tends to become enriched in carbon, while the rapid decomposition of *A. saccharum* leaf litter leads to lower soil organic content (Pastor et al. 1984; Frelich et al. 1993; Finzi et al. 1998b): more soil carbon may favor larger fungal populations (Wardle 2002). Knowing the identity of the pathogens involved might distinguish between these two possibilities: are they obligately host-specific, or facultatively pathogenic saprobes? Interestingly, when treated with fungicide, seeds of *T. canadensis* tended to perform better under conspecifics than heterospecifics, perhaps suggesting a positive effect of local soil composition or associated nonfungal biota.

Acer saccharum exhibited very different patterns of seed survival. Although fungi tended to reduce seed viability, es-

Fig. 1. Estimated proportion of seeds which survived the experiment. “Proportion surviving” includes both germinated seeds and ungerminated but apparently viable seeds. Seeds of (a) *Acer saccharum* and (b) *Tsuga canadensis* buried in two habitat types (*A. saccharum* vs. *T. canadensis* stands) were subjected to two experimental treatments (fungicide or control). Shown are means + standard errors; “n” indicates sample size. Sample sizes vary slightly because seed bags that were not recovered intact were excluded from the analyses. See Table 1 for results of significance tests.



timates of losses to fungi were almost identical in areas dominated by *A. saccharum* versus areas dominated by *T. canadensis*, suggesting changes in fungal populations were not more strongly reducing survival in *A. saccharum*-dominated sites. This absence of a habitat \times fungicide treatment interaction also suggests that while soil changes beneath *T. canadensis* may inhibit recruitment of *A. saccharum* (Frelich et al. 1993; Catovsky and Bazzaz 2000), the mechanism does not involve seed-attacking fungal pathogens, although it is always possible that pathogens may have stronger effects on later life history stages. One possible explanation for the consistency of fungal attack in *A. saccharum* may be that seed mortality was caused by generalists or unspecialized seed-decay fungi rather than host-specific pathogens. Alternatively, seeds may have been lost to specialist pathogens that are ubiquitous within maple-dominated landscapes, including embedded stands of *T. canadensis*. Reinhart and Callaway (2004) similarly reported that the effects of soil biota on seedlings of *Acer negundo* L. and *Acer platanoides* L. in their respective native

regions were equally negative under both conspecifics and heterospecifics, despite evidence of both specialist and generalist pathogens.

Results of this study suggest that interactions involving seed pathogens do not reduce the stability of *A. saccharum* stands. In contrast, they do seem to indicate that *T. canadensis* might have trouble recruiting in areas dominated by conspecifics. Despite this, studies elsewhere have found evidence that mature *T. canadensis* has positive or neutral effects on populations of its own saplings (Frelich et al. 1993; Catovsky and Bazzaz 2000, 2002), and established stands can persist for thousands of years (Foster and Zebryk 1993; Davis et al. 1998). Assuming these studies are representative, a potential explanation for this discrepancy may be that other factors outweigh any disadvantage resulting from seed pathogens accumulating near conspecifics. For example, dispersal limitation may be more important than other constraints on establishment (e.g., Hubbell et al. 1999); the heavy seed rain in established hemlock stands (Catovsky and Bazzaz 2000) may be great enough to out-

weigh any negative features of such sites. Hemlock stands may provide a refuge from the deep leaf layer annually deposited by deciduous trees, and thus improve seedling establishment (Frelich et al. 1993). *Tsuga canadensis* saplings may benefit because the deep shade beneath adults excludes most competitors from hemlock stands (Catovsky and Bazzaz 2000, 2002). Finally, the benefits provided by host-specific mutualists, such as mycorrhizae, may counteract the risks of host-specific disease. Maples are AM-mycorrhizal, while hemlocks instead rely on ectomycorrhizae; thus, positive feedbacks in sites dominated by the appropriate mycorrhizae might eventually outweigh negative interactions during seed dormancy and germination (e.g., Weber et al. 2005). Increased risk of seed mortality in *T. canadensis* stands may reduce the extent of such benefits, and thus the stability of established stands, but evidently not sufficiently to disrupt them.

One other possibility is that the ability of *T. canadensis* to establish on logs may help to buffer it against the impacts of soil fungi: logs may increase survival of seedlings by initially providing low-pathogen microsites (O'Hanlon-Manners and Kotanen 2004a). *Acer saccharum*, which generally recruits on the forest floor, may reduce pathogen attack with a different strategy. *Acer saccharum* may evade pathogens by germinating very early in the year, so that seedlings will be larger, tougher, thicker-barked, and therefore less vulnerable by the time warmer temperatures encourage the growth of many pathogens (see Seiwa 1998 for evidence from *Acer mono* Maxim.). Following germination, *A. saccharum* seedlings persist in a juvenile state for years or decades (Godman et al. 1990; Marks and Gardescu 1998); it may be that this metabolically active "seedling bank" is safer from pathogens than seeds exposed for long periods in a seed bank.

In summary, buried seeds of *T. canadensis* and *A. saccharum* responded differently to protection with fungicide: benefit for *T. canadensis* was markedly greater near conspecifics, while benefit for *A. saccharum* was smaller and spatially more homogeneous. These differing responses likely are related to interactions between these trees and both physical and biotic characteristics of the soil. Thus, even though these two shade-tolerant, mature forest trees occur in the same habitats, their seeds respond very differently to this shared environment.

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