ECTOMYCORRHIZAL FORMATION IN HERBICIDE-TREATED SOILS OF DIFFERING CLAY AND ORGANIC MATTER CONTENT*

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Abstract. Herbicides are commonly used on private timberlands in the western United States for site preparation and control of competing vegetation. How non-target soil biota respond to herbicide applications, however, is not thoroughly understood. We tested the effects of triclorpyr, imazapyr, and sulfometuron methyl on ectomycorrhizal formation in a greenhouse study. Ponderosa pine, Douglas-fir, and white fir seedlings were grown in four forest soils ranging in clay content from 9 to 33% and organic matter content from 3 to 17%, and treated with commercial formulations of each herbicide at 0, 1.0, and 2.0 times the recommended field rate. Many of the possible herbicide-soil combinations resulted in reduced seedling growth. Root development was particularly sensitive to the three herbicides, with an average of 51% fewer root tips compared to the control treatment. The ability of mycorrhizal fungi to infect the remaining root tips, however, was uninhibited. Mycorrhizal formation was high, averaging 91% of all root tips, regardless of herbicide, application rate, soil type, or conifer species. In agreement, soil microbial biomass and respiratory activity were unaffected by the herbicide treatments. The results show that these herbicides do not alter the capability of mycorrhizal fungi to infect roots, even at concentrations detrimental to seedling growth.

Keywords: imazapyr, mycorrhizae, root growth, sulfometuron methyl, triclopyr

1. Introduction

Ectomycorrhizae are well recognized for their role in conifer nutrition (Perry, 1994). Ubiquitous in most forests, their complex network of fungal hyphae increase the effective rooting area of host plants, often leading to improved nutrient uptake, seedling survival, and tree growth. Although uptake of phosphorus in infertile soils is considered their primary function, assimilation and transport of most plant nutrients has also been credited to the fungus-plant symbiosis (Allen, 1991). How ectomycorrhizae respond to anthropogenic disturbance, therefore, is important when assessing ecosystem health and integrity in managed forests.

With regard to herbicides, no clear pattern of mycorrhizal suppression has been demonstrated in literature. Pure culture studies have shown few herbicidal effects on fungal growth at predicted field concentrations, yet suppression of growth at higher concentrations (Kelley and South, 1980; Chakravarty and Sidhu, 1987; Chakrav-

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arty and Chatarpaul, 1990a). Only a few fungal species and herbicides have been examined, however, and the applicability of these *in vitro* studies to field conditions is uncertain given the complexity of fungal communities, soil types, and environmental factors that influence forest ecosystems. Still, they do not indicate any drastic negative effects. Results from field, nursery, and greenhouse studies have varied somewhat with herbicide and soil type. Most studies indicate no adverse effects of selected herbicides on ectomycorrhizal development (Trappe, 1983; Harvey *et al*., 1985; Chakravarty and Chatarpaul, 1990b; Sidhu and Chakravarty, 1990). However, Chakravarty and Sidhu (1987) found a decline in ectomycorrhizae on *Pinus contorta* and *Picea glauca* seedlings following application of hexazinone, while Marks and Becker (1990) noted that ectomycorrhizal formation and physiology was altered by propazine. Stimulation of ectomycorrhizae following application of simazine was also found in a sandy soil, presumably due to indirect, positive effects of weed control on tree growth (Smith and Ferry, 1979).

Little research has been conducted on ectomycorrhizal-herbicide interactions in the past decade, leaving a knowledge gap with respect to currently-preferred herbicides. At present, triclopyr, imazapyr, and sulfometuron methyl are among the most popular herbicides used in California forests (Calif. Dept. Pesticide Regulation, 2000). Whether these compounds affect ectomycorrhizae is unknown. Indications from pure culture studies suggest a potential suppression of ectomycorrhizal fungi by triclorpyr (Sidhu and Chakravarty, 1990). Likewise, sulfometuron methyl has been shown to reduce soil microbial biomass in Christmas tree plantations (Arthur and Wang, 1999), although its affect, and that of imazapyr, on ectomycorrhizae is untested. Our objective was to determine whether these compounds suppress ectomycorrhizal formation on tree species common to mixed-conifer forests in the western United States. Seedlings were grown in forest soils of differing clay and organic matter content to determine the influence of soil properties on herbicide toxicity.

2. Materials and Methods

Our greenhouse experiment was a factorial combination of seven herbicide treatments, three conifer species, and four forest soils. Five replications of each of the 84 herbicide-conifer-soil combinations were included in a completely randomized experimental design. Herbicide treatments included commercial formulations of sulformeturon methyl (Oust® (Dupont, Wilmington, DE, U.S.A.) applied at 0.14, 0.28 kg active ingredient ha^{-1}), triclopyr (Garlon 4® (Dow AgroSciences LLC, Indianapolis, IN, U.S.A.) applied at 4.5 and 9.0 kg active ingredient ha^{-1}), and imazapyr (Arsenal® (BASF Corporation, Research Triangle Park, NC, U.S.A.) applied at 1.1 and 2.1 kg active ingredient ha^{-1}), plus a non-herbicide control. These concentrations are 1.0- and 2.0-times the recommended field rate for conifer site preparation in the western United States. Stratified seeds of ponderosa pine (*Pinus*

TABLE I

Selected characteristics of the four soils used to test mycorrhizal response to triclopyr, imazapyr, and sulfometuron methyl

	Sandy loam (low OM)	Sandy loam (high OM)	Loam	Clay loam
Soil origin	Weathered granite	Granodiorite	Volcanic mudflow	Basalt
Great group	Xerochrept	Dystroxerept	Haploxeralf	Palexerult
Clay content (%)	9	9	20	33
OM content (g kg^{-1})	39	99	162	172
pH	6.4	6.2	5.8	5.8
Cation exchange capacity ($cmol_c$ kg^{-1})	Not determined	16.9	43.8	21.3

ponderosa), Douglas-fir (*Pseudosuga menziesii*), and white fir (*Abies concolor*), collected from Northern California forests, were planted in 250 mL pots (5 cm diam., 18 cm tall) containing ca. 150 g soil. The four soils were collected from mixed-conifer forests in Northern California, and chosen to provide a wide range of clay and organic matter contents (Table I). Each soil was sieved (8 mm) and mixed thoroughly prior to planting. No mycorrhizal inoculum was added. Twenty additional seedlings of each conifer species were grown concurrently to determine the timing of lateral root development and ectomycorrhizal formation. The extra seedlings were sampled on a weekly basis throughout the experiment.

Soils were watered daily with tap water during the first week after sowing, then twice weekly until harvest. We chose non-sterile water since (i) axenic conditions were not crucial to the experimental objective, (ii) qualitative estimates of the general fungal population in our tap water using fluorescent microscopy were extremely low, and (iii) it was readily accessible and more reflective of non-sterile rainwater. Any ectomycorrhizal propagules added in the water were thus considered a component of soil fungal community. Each pot was weighed periodically during the first two months and adjusted to field capacity as necessary, thus ensuring no herbicide loss by leaching of gravitational water. Treatments were thinned to one seedling pot^{-1} within 3 weeks of planting. Pine seedling were grown for 4 months, from February through May 2002, and Douglas-fir and white fir seedlings were grown an extra month, from February through June 2002, to account for their slower development. There was no supplemental lighting, and greenhouse temperatures ranged from 20 to 29 °C.

Herbicide solutions were applied to the soil surface at the onset of lateral root development, 45 d after planting ponderosa pine, and 55 d after planting Douglas-fir and white fir. Our decision to postpone herbicide application until lateral roots had formed was based on a preliminary study which indicated excessive seedling mortality if applied beforehand. No visual signs of mycorrhizal development were evident at the time of application.

At harvest, roots were gently washed free of adhering soil with tap water, and stored for a maximum of 14 d at 4 °C prior to microscopic determination of total and ectomycorrhizal root tips (Agerer, 1994). Following completion of mycorrhizal counts, the seedlings were dried at 60 °C until no further weight loss and weighed for total, root, and lateral root biomass. Soil samples from pots used to grow ponderosa pine seedlings were analyzed for microbial biomass and respiration immediately following harvest. Microbial biomass was measured by substrate-induced respiration (Anderson and Domsch, 1978), using 25 g (dry weight equivalent) soil and 5 g kg^{-1} glucose. Respiration was measured on 25 g samples during the initial 4 hr after harvesting (Zibilske, 1994). Carbon dioxide produced during microbial biomass and respiration incubations was measured with an infra-red gas analyzer (LI-6200, LI-COR®, Lincoln, NE, U.S.A.).

Herbicide effects on microbial biomass, respiration, seedling growth, root-tip number, and percent mycorrhizae were tested by analysis of variance, and Dunnett's mean separation was used to test differences between the herbicide treatments and the control for each conifer-soil type combination.

3. Results

3.1. Ponderosa pine

There was considerable herbicide damage to the pine seedlings. Triclopyr and imazapyr were lethal to seedlings in the coarse-textured soils, while plant dry weight was significantly lower in 13 out of 21 soil-herbicide combinations when compared to the control (Table II). The decline in plant growth varied with soil texture: the two sandy loam soils were most sensitive to the herbicides (42% less growth than the control), followed by the clay (23% less growth than the control) and loam (17% less growth than the control) soils. Root growth was strongly inhibited by the herbicides. Significantly fewer root tips were found for 15 out of 21 soil-herbicide combinations when compared to the control. Total- and lateral-root biomass showed comparable declines (data not shown). Imazapyr produced the largest decline in root tips, with an average of 47 root tips $plant^{-1}$ compared to 366 root tips $plant^{-1}$ for the control.

Nearly all root tips (94%) were mycorrhizal regardless of soil or herbicide treatment (Table II). Mycorrhizal formation was unrelated to the level of herbicide damage to roots. For example, imazapyr severely restricted root-tip formation, yet those that formed were virtually 100% mycorrhizal. Other treatments, such as sulfometuron methyl and triclopyr in the clay soil, had no affect on root-tip number or mycorrhizal formation. Field-rate applications of sulfometuron methyl

TABLE II

Ponderosa pine seedling response to herbicide applications at the recommended field rate (1×) and twice the recommended rate (2×). An asterisk (*) within a column and soil type signifies a significantly lower value than the control at $P = 0.05$

Soil	Treatment	Survival (%)	Plant dry wt (g plant^{-1})	Root tips (# plant^{-1})	Mycorrhizae (%)
Sandy loam (low OM)	Control	100	0.33	301	91
	Sulfometuron (1×)	100	0.23*	107*	94
	Sulfometuron (2×)	100	0.25*	77*	90
	Triclopyr (1×)	40	0.13*	140*	92
	Triclopyr (2×)	0	–	–	–
	Imazapyr (1×)	80	0.20*	1*	100
	Imazapyr (2×)	0	–	–	–
Sandy loam (high OM)	Control	100	0.44	460	96
	Sulfometuron (1×)	100	0.32*	156*	90*
	Sulfometuron (2×)	100	0.33*	159*	94
	Triclopyr (1×)	40	0.18*	280*	87*
	Triclopyr (2×)	0	–	–	–
	Imazapyr (1×)	100	0.18*	23*	100
	Imazapyr (2×)	80	0.19*	22*	100
Loam	Control	100	0.34	468	92
	Sulfometuron (1×)	100	0.36	384	91
	Sulfometuron (2×)	100	0.33	223*	88
	Triclopyr (1×)	100	0.30	345*	96
	Triclopyr (2×)	40	0.20*	524	96
	Imazapyr (1×)	100	0.27	105*	99
	Imazapyr (2×)	100	0.24	59*	99
Clay loam	Control	100	0.32	234	84
	Sulfometuron (1×)	100	0.33	293	90
	Sulfometuron (2×)	100	0.29	162	78
	Triclopyr (1×)	100	0.25	205	97
	Triclopyr (2×)	20	0.16*	176	100
	Imazapyr (1×)	100	0.23*	57*	99
	Imazapyr (2×)	100	0.22*	58*	99

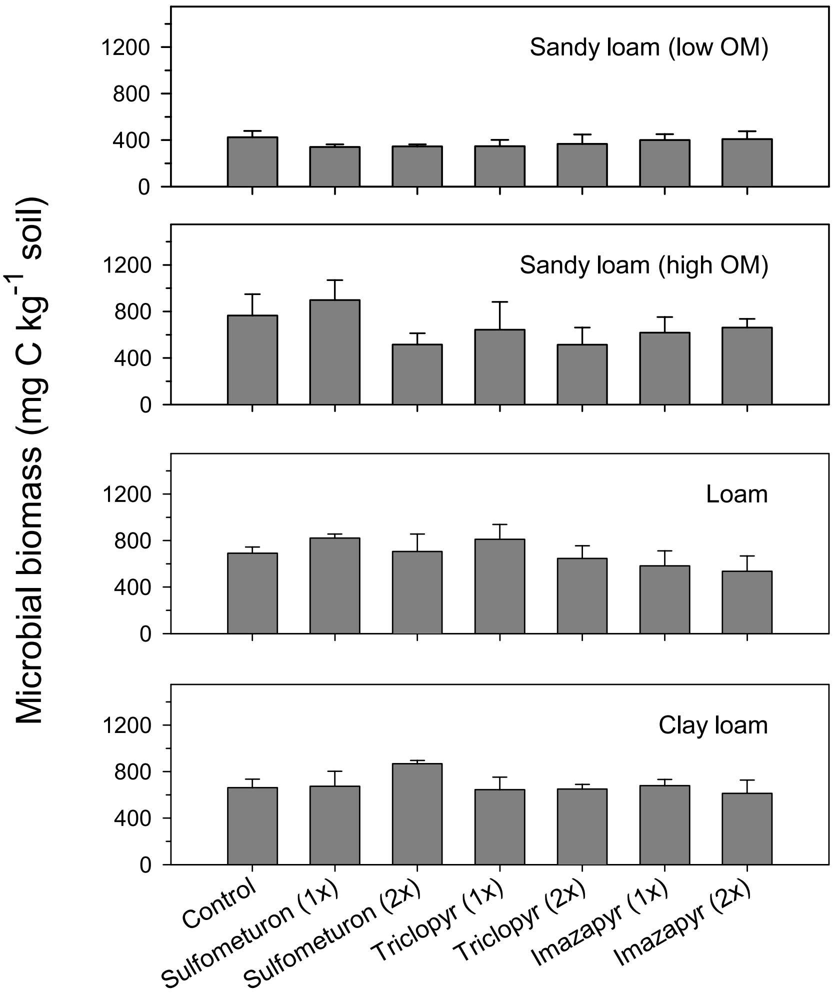

Figure 1. Microbial biomass in herbicide-treated soils of varying texture and organic matter content. Herbicides were applied at normal (1×) and twice (2×) the recommended field rate, and microbial biomass was determined 2–3 months after application.

and triclopyr to the sandy loam (high OM) soil resulted in the only statistically significant, albeit minor, declines in mycorrhizae. Variation in percent mycorrhizae was low among replicate samples. The coefficient of variation for the four soils ranged from 2.9 to 8.7%.

Soil microbial biomass and respiration were measured within 4 hr of seedling harvest to test herbicide effects on general microbial properties. Microbial biomass varied with soil type, but was unaffected by herbicide treatment (Figure 1). The only exception was a slight, statistically non-significant (at $P = 0.10$) decline in microbial biomass for the sandy loam (high OM) soil treated with the highest rate of sulfometuron methyl or tricloyr. Similarly, no significant changes in microbial respiration were found due to herbicide treatment.

3.2. Douglas-fir

Douglas-fir seedlings were generally more tolerant than ponderosa pine to the selected herbicides. No mortality was found, and plant dry weight was significantly lower in only 5 out of 24 soil-herbicide combinations when compared to the control (Table III). Only the sandy loam (low OM) soil showed a general decline in growth due to herbicide treatments. Root-tip formation, in contrast, was strongly affected by all herbicides. Nineteen out of 24 soil-herbicide combinations had significantly fewer root tips than the control.

Like ponderosa pine, the majority of root tips (90%) were ectomycorrhizal regardless of herbicide treatment or soil type. The field rate application of imazapyr on the sandy loam (high OM) soil produced the largest decline in ectomycorrhizae, although the decline was not matched by doubling the concentration of imazapyr.

3.3. White fir

Seedling growth was moderately affected by the herbicide treatments. Survival was near 100% and plant dry weight was reduced in only one out of 24 soil-herbicide combinations compared to the control (Table IV). Root-tip formation was less sensitive to the herbicides compared to the other two conifers, with imazapyr causing the only consistent decline in the sandy loam and loam soils.

Again, ectomycorrhizal formation was high (93%) when averaged for all soils and herbicides. Imazapyr produced the only statistically significant decline (P = 0.10) in ectomycorrhizae. Field-rate applications of imazapyr resulted in 21 and 9% less ectomycorrhizae than the control in the loam and clay soils, respectively.

4. Discussion

With few exceptions, ectomycorrhizal formation was uninhibited by triclopyr, imazapyr, and sulfometuron methyl at concentrations as high as twice the recommended field rate. Ectomycorrhizae were found on 91% of all root tips when averaged across herbicide treatments. Only seven out of 69 possible herbicide-conifer-soil combinations resulted in a statistically significant reduction in ectomycorrhizae. Of these seven, the decline was random by soil type, conifer species, and herbicide concentration. Further, the decline was not pronounced: mycorrhizal root tips accounted for more than two-thirds of all root tips regardless of treatment. Common indices of microbial community size and activity (biomass, respiration) also were unaffected by herbicide treatment.

In contrast, root growth showed moderate damage from all three herbicides. Root tips were reduced significantly in nearly two-thirds of the possible herbicide-

TABLE III

Douglas-fir seedling response to herbicide applications at the recommended field rate (1×) and twice the recommended rate (2×). An asterisk (*) within a column and soil type signifies a significantly lower value than the control at $P = 0.05$

Soil	Treatment	Survival (%)	Plant dry wt (g plant^{-1})	Root tips (# plant^{-1})	Mycorrhizae (%)
Sandy loam (low OM)	Control	100	0.20	168	94
	Sulfometuron (1×)	100	0.18	57*	74*
	Sulfometuron (2×)	100	0.18	82*	85
	Triclopyr (1×)	100	0.13*	122	95
	Triclopyr (2×)	100	0.11*	140	100
	Imazapyr (1×)	100	0.15	23*	97
	Imazapyr (2×)	100	0.13*	34*	94
Sandy loam (high OM)	Control	100	0.24	307	91
	Sulfometuron (1×)	100	0.25	126*	80
	Sulfometuron (2×)	100	0.21	97*	74
	Triclopyr (1×)	100	0.16	143	93
	Triclopyr (2×)	100	0.15*	277	98
	Imazapyr (1×)	100	0.23	71*	68*
	Imazapyr (2×)	100	0.21	63*	87
Loam	Control	100	0.25	311	93
	Sulfometuron (1×)	100	0.25	279	95
	Sulfometuron (2×)	100	0.23	168*	92
	Triclopyr (1×)	100	0.22	151*	95
	Triclopyr (2×)	100	0.24	84*	96
	Imazapyr (1×)	100	0.23	169*	85
	Imazapyr (2×)	100	0.22	128*	84
Clay loam	Control	100	0.21	259	96
	Sulfometuron (1×)	100	0.23	152*	89
	Sulfometuron (2×)	100	0.23	114*	84
	Triclopyr (1×)	100	0.16	83*	97
	Triclopyr (2×)	100	0.15*	84*	99
	Imazapyr (1×)	100	0.23	99*	88
	Imazapyr (2×)	100	0.21	52*	99

TABLE IV

White fir seedling response to herbicide applications at the recommended field rate (1×) and twice the recommended rate (2×). An asterisk (*) within a column and soil type signifies a significantly lower value than the control at $P = 0.05$

Soil	Treatment	Survival (%)	Plant dry wt (g plant^{-1})	Root tips (# plant^{-1})	Mycorrhizae (%)
Sandy loam (low OM)	Control	100	0.20	231	97
	Sulfometuron (1×)	100	0.23	135	91
	Sulfometuron (2×)	100	0.20	85*	93
	Triclopyr (1×)	100	0.27	222	94
	Triclopyr (2×)	80	0.21	105	99
	Imazapyr (1×)	100	0.16	80*	92
	Imazapyr (2×)	100	0.16	65*	98
Sandy loam (high OM)	Control	100	0.31	183	94
	Sulfometuron (1×)	100	0.26	76*	95
	Sulfometuron (2×)	100	0.25	96*	93
	Triclopyr (1×)	80	0.23	121	99
	Triclopyr (2×)	20	0.15*	150	93
	Imazapyr (1×)	100	0.20	59*	88
	Imazapyr (2×)	100	0.18	79*	100
Loam	Control	100	0.32	295	95
	Sulfometuron (1×)	100	0.26	224	93
	Sulfometuron (2×)	100	0.29	211	97
	Triclopyr (1×)	100	0.37	185	87
	Triclopyr (2×)	80	0.32	131*	98
	Imazapyr (1×)	100	0.32	140*	75
	Imazapyr (2×)	100	0.26	119*	83
Clay loam	Control	100	0.28	127	98
	Sulfometuron (1×)	100	0.26	97	94
	Sulfometuron (2×)	100	0.31	117	94
	Triclopyr (1×)	100	0.27	110	94
	Triclopyr (2×)	100	0.27	110	98
	Imazapyr (1×)	100	0.24	118	89*
	Imazapyr (2×)	100	0.23	78	84*

conifer-soil combinations. This finding supports the observation of Trappe *et al.* (1984) that mycorrhizae can be unaffected even when moderate damage occurs to the host. Differential responses by seedlings and soil organisms partially reflects the plant-specific mode of action of the herbicides, which varies from inhibition of protein synthesis (imazapyr) and cell division (sulfometuron methyl), to uncontrolled cell division and elongation (triclopyr). Also, it reflects the acknowledged ability of mycorrhizal fungi to infect host plants and thrive in stressed environments (Allen, 1991).

Mycorrhizal indifference to herbicide treatment was independent of soil type. Although far from a complete survey of forest soils, the soils used in our experiment represented a wide range of clay and organic matter content. This consistency in ectomycorrhizal response between soils can be attributed, in part, to herbicide chemistry. Triclopyr, imazapry, and sulfometuron methyl are weak acids, negatively charged in the pH range of the four soils (5.8–6.4). Consequently, they are repelled by the net negative charge of soils, and remain active in solution until degraded or leached through the profile. Sorption only occurs in soils with anionic-exchange sites, such as those containing appreciable levels of iron and aluminum oxides, or in soils below pH 5, where the protonated herbicides can bind to organic matter (Wehtje *et al.*, 1987; Johnson *et al.*, 1995; Pusino *et al.*, 1997). Clearly the herbicides were not strongly adsorbed in our study as noted by the reduction in root-tip formation in many of the soil-herbicide combinations. The uniform response by ectomycorrhizae in these diverse soils, therefore, indicates that soil physio-chemical properties have little influence in predicting ectomycorrhizal response to triclopyr, imazapyr, and sulfometuron methyl.

Our results agree well with previous findings of herbicides and how they affect ectomycorrhizae. Nearly all studies conducted in forest or nursery soils have found no detrimental effects of assorted herbicides on mycorrhizal formation (Smith and Ferry, 1979; Trappe, 1983; Harvey *et al.*, 1985, Marks and Becker, 1990; Sidhu and Chakravarty, 1990). Only Marks and Becker (1990) report a suppression of mycorrhizal formation in the first 6 months following addition of propazine to soil. In addition to our findings for triclopyr, imazapyr, and sulfometuron methyl, the list of compounds showing no damage to ectomycorrhizal formation in soil include glyphosate, hexazinone, simazine, chlorthal dimethyl, bifenox, DCPA, and napropamide. In comparison, herbicide effects have been limited to pure cultures studies with high herbicide concentrations (Kelley and South, 1980; Chakravarty and Sidhu, 1987; Chakravarty and Chatarpaul, 1990) or pot studies in which inoculated seedlings are grown in artificial media (Chakravarty and Sidhu, 1987; Sidhu and Chakravarty, 1990). Tolerance of ectomycorrhizae to selected herbicides in native soil supports the theory of Domsch *et al.* (1983) that herbicide side-effects are overshadowed by the large, natural variation of complex soil environments.

We conclude that triclopyr, imazapyr, and sulfometuron methyl are not suppressive to ectomycorrhizae in forest soils. Herbicide damage to ponderosa pine, Douglas-fir, and white fir seedlings did not alter the ability of ectomycorrhizal fungi to infect the host. Our findings provide a coarse-level understanding of herbicides and their affect on soil biota. A remaining question is whether or not ectomycorrhizal diversity and function are compromised by herbicides.

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