Robert P. Griffiths[1] and **Trina Filan** Department of Forest Science, Oregon State University, Richardson Hall, Corvallis, Oregon 97331

Effects of Bracken Fern Invasions on Harvested Site Soils in Pacific Northwest (USA) Coniferous Forests

Abstract

Bracken ferns are known to dominate early successional vegetative assemblages in disturbed coniferous forests of the Pacific Northwest often resulting in a suppression of conifer seedling establishment. This study was designed to explore mechanisms by which this suppression might occur. Bracken fern induced changes in forest soils were studied at 10 separate sites in the Oregon Cascade Mountains in or near the H. J. Andrews Experimental Forest. All sites contained uncut mature forests and adjacent harvested stands that had been clear-cut 15–20 years prior to this study. Each harvested unit contained areas dominated by bracken fern. Of the 10 harvested units studied, six also had areas dominated by woody shrubs. Samples were collected both in spring/early summer when soils were relatively cool and moist and in summer/early fall when soils were warmer and drier. In spring/early summer, fern plots were significantly cooler than mature forest or nearby shrub areas. Fern soils were also significantly lower in K and NO3-N, and had lower denitrification enzyme activity (DEA) rates. In summer/early fall, NH4-N, NO3-N, DEA, and phosphatase activity were all significantly lower in fern plots. Of all variables, mineral N pools showed the strongest consistent trends differentiating fern from conifer soils. Our data suggest that bracken fern may have a competitive advantage by sequestering N to the point that reduced soil mineral N pools limit growth of competing vegetation.

Introduction

Over the past 30+ years, there has been a great deal of interest in the ecology of bracken fern (*Pteridium aquilinum* (L.) Kuhn.) because they are known to: (1) produce toxins implicated in causing cancers and other illness in livestock (Smith and Taylor 1986, Smith and Taylor 1995, Smith et al. 2004), and (2) exclude the establishment of conifer seedlings in disturbed forest settings (Ferguson and Boyd 1988, Sommer et al. 1991, Ferguson and Adams 1994). Forest ecologists and managers have noted the exclusionary characteristics of these ferns in both natural fern glens and in early succession stages after major disturbances associated with fires and stand harvest (Ferguson and Boyd 1988, Sommer et al. 1991, Ferguson and Adams 1994). In some cases, bracken fern patches have excluded conifer seedlings despite several post-harvest planting efforts (Ferguson and Adams 1994). Even when seedlings do survive, bracken fern can retard seedling growth (Dimock 1964).

In undisturbed ecosystems, bracken fern is commonly found in both mature forest and semi-open woodlands (Page 1976, Watt 1976). After a major forest disturbance, an extensive underground rhizome system allows it to rapidly colonize a disturbed site storing large amounts of nutrients during rapid frond development (Watt 1940, Page 1986, Lederle and Mroz 1991) and shading out other vegetation (Ouden et al. 2000) making them highly competitive with other vegetation for light, nutrients, and water (Pitman and Pitman 1986). Fronds falling from these ferns are also heavy and can bury and crush fragile seedlings (Koroleff 1954). In addition, they produce highly allelopathic compounds (Del Moral and Cates 1971, Smith and Taylor 1986, Lee and Cooke 1989) timing their greatest allelopathic potential to correspond with primary growth periods of other species (Gliessman 1976).

A number of management techniques have been suggested to ameliorate the adverse effects of bracken fern on seedling reestablishment after forest disturbance, but these are hampered by an incomplete knowledge of the mechanisms by which these plants suppress competing vegetation (Ferguson and Boyd 1988). Although this fern's natural history and ecology have been extensively studied (Watt 1940, Cody and Crompton 1975, Page 1976, Watt 1976, Page 1986, Ouden et al. 2000), little is known of its influence on forest soils (Johnson-Maynard et al.1997, Johnson-Maynard et al. 1998).

The main objective of this research was to add to the understanding of how these plants affect forest soils and by inference, to elucidate competitive

[1]Author to whom correspondence should be addressed: E-mail: griffithsr@fsl.orst.edu.

mechanisms. More specifically, based on reports of Watt (1940), Page (1986), Lederle and Mroz (1991), we wanted to test the hypothesis that the competitive advantage of bracken fern is due in large part to nutrient sequestration. To this end we measured chemical and biochemical properties of soils associated with bracken fern plots in young harvested stands and compared these with those in adjacent undisturbed conifer-dominated plots. In addition, we included shrub-dominated plots in close proximity to bracken fern plots thus providing information on a different vegetation type within the same harvested unit. The first sampling was done in the spring/early summer when the soils were moist and cool. In contrast, a second set of samples were taken in the late summer/early fall when the soils were at the driest and warmest for the year. If similar trends were observed during these contrasting seasons, our observations should reflect soil conditions for much of the year.

Materials and Methods

Site Descriptions

The ten study sites (Table 1) were in or near the H.J. Andrews Experimental Forest (HJA) located in the Oregon Central Cascade Mountains (Figure 1). Descriptions of vegetation, climate and topography are well documented (Franklin and Dyrness 1988, Greenland 1994). Study sites were typical of mountain hemlock (*Tsuga mertensiana*

TABLE 1. Site descriptions including sample sets, site aspect, slope and elevation. All sites adjacent to one another were considered as one treatment set. Each set contained a recently harvested section dominated by bracken fern and a site dominated by mature or old growth conifers. Six sets also contained sample plots in the harvested area dominate by shrubs.

	Treatment sets			Aspect	Slope	Elevation
Set#	Conifer	Fern	Shrub	(deg)	(deg)	in m
1	X	X		230	16	1014
2	X	X		230	12	1020
3	X	X	X	200	28	1472
4	X	X	X	75	29	1480
5	X	X	X	90	18	1180
6	X	X	X	70	10	1354
7	X	X	X	175	24	1406
8	X	X		250	25	1408
9	X	X		190	13	1428
10	X	X	X	300	7	1347

Figure 1. Location of the H. J. Andrews Experimental Forest relative to the state of Oregon

(Bong.) Carr.) zones (Franklin and Dryness 1988). Site elevations ranged from approximately 1000 to 1500 meters (Table 1). At each site, mineral soils were collected in paired treatment sets (mature and harvested units). At six sites, the sets also included a harvested area dominated by wood shrubs. The harvested sites were clear-cut and replanted within the last 15-20 years. These sites were paired so that both mature stands and adjacent harvested units had approximately the same soil type, slope, elevation and aspect. In each of the harvested stands, soils were collected in areas dominated by bracken fern which were essentially devoid of conifer seedlings.

Soil Sampling and Processing

Samples were collected in late spring/early summer and summer/early fall and early fall, 1997. Six mineral soil samples were taken along a randomly chosen transect through each vegetation type at a sampling interval of 5 m. Samples consisted of soil taken with a 4.7 cm corer to a depth of 10 cm beneath the litter layer. All samples from each site were mixed in a large plastic bag and returned to the laboratory in an ice chest and stored at 15°C until they were analyzed < 24 h after collection. Soil respiration rates were measured with a nondispersive, infrared CO_2 analyzer (Li-Cor®, LI-6200) for a period of one min after the gas chamber gas had reached ambient CO_2 concentration. When ever respiration measurements were taken, soil

temperatures were measured with a calibrated dial thermometer as reported by Griffiths and Swanson (2001).

Laboratory Analyses

Just prior to analysis, soils were sieved through a 2-mm sieve. Soil moisture, bulk densities, pH, and denitrification enzyme activity (DEA) were measured using methods outlined by Griffiths and Swanson (2001). Laboratory respiration was measured on sieved soils brought to 75% moisture by adding sterile deionized water. Twenty five ml Erlenmeyer flasks containing soils were sealed with serum-bottle stoppers and incubated at 24°C for 1 h before the first headspace CO_2 measurement was made. Flasks were incubated for another 2 h and headspace CO_2 concentration was again measured using a Hewlett Packard model 5890 GC. The detector signal was integrated using a Hewlett Packard model 3396 integrator (Hewlett Packard, Palo Alto, CA) that was calibrated by the external calibration method with known gas standards. The GC was equipped with a flame ionization detector with a methanizer in series, and a 2 m stainless steel column was packed with Poropak-R (50/80 or 80-100 mesh). Substrate-induced respiration (SIR) was measured in soils prepared as in respiration experiments except 0.1 ml of 1 M glucose solution (0.1 ml H_2O in the controls) was added to the reaction vessel. As was the case in the other respiration measurements, the reaction vessels were allowed a preincubation period of 1 h between sealing the vessels and the time zero measurement.

ß-glucosidase activity was determined by spectrophotometric assay (Caldwell et al. 1999). One mL of 10 mM *p*-nitrophenyl β-D glucopyranoside substrate was added to duplicate 1-mL subsamples containing a soil slurry (1 gdw in 1 mL deionized H_2O). The tubes were shaken and then placed with duplicate controls without substrate in a 30°C water bath for 2 h. After incubating, 1 mL of 10 mM *p*-nitrophenyl β-D glucopyranoside was added to the controls, and all reactions were immediately stopped by the addition of 2 mL of 0.1 M tris[hydroxymethyl]aminomethane at pH 12.0. The mixtures were centrifuged for 5 min at 500 × g. From the supernatant, 0.2 mL was diluted with 2.0 mL deionized water. The optical density was measured at 410 nm, and a standard curve was prepared from 0.02 to 1.0 µmol/mL *p*-nitrophenol (pNP). Phosphatase measurements were made using the same general procedure as for ß-glucosidase, except the substrate used was 1 mL of 50 mM *p*-nitrophenyl phosphate, the incubation period was 1 hour, and 2 mL of 0.5 M NaOH instead of 0.1 M tris[hydroxymethyl]aminomethane, was added to terminate the reaction (Tabatabai and Bremmer 1969). Total fungal and bacterial biomasses were determined by epifluorescent microscopy following the procedures of Ingham et al. (1991).

Total C and N were assayed on a Carlo-Erba model NA1500 C and N analyzer. NH4-N, Al and NO3-N concentrations were determined on KCl extracts using an Alpkem Rapid Flow autoanalyzer model 3000 using ICP. Potassium, Ca, and Mg concentrations were measured on BaCl soil extracts (Wright and Stuczynski, 1994).

Total and unreactive phenolics (most likely tannin) concentrations were measured using a standard colorimetric technique (Ryan et al.1990). Five g of soil was added to a 250 ml Erlenmeyer flask containing 50 ml of DI water and steamed for 1 hr. The supernatant was decanted into centrifuge tubes and centrifuged for 5 minutes at 1,000 × g then filtered through a 0.45 µm membrane filter and rinsed with distilled water. Three ml of the filtrate was added to 150 mg of casein and shaken for 3 h. This was centrifuged for 20 min at 1,000 × g. The supernatant was reacted with Folin-Cicalteau reagent in the presence of Na_2CO_3 to determine the concentration of unreactive phenolics in the sample. The assay was calibrated using known quantities of catechol. Total phenolics were measured in supernatant not reacted with casein.

Statistical Analysis

All statistical analyses were conducted with Statgraphics® Plus for Windows® (Statistical Graphics Corporation, Rockville, MD). The following variables were not normally distributed and were therefore log transformed for the ANOVA analysis; K, NH4-N, NO3-N, total and unreactive phenolics, laboratory respiration, phosphatase, bacterial and fungal biomass, and DEA. A separate AVOA analyses was made for each season. A multivariate analysis was conducted on the mean values for subsample replications for each variable by vegetation type. In all cases, a "*P*" value ≤ 0.05 was used to determine statistical significance. A multiple discriminant analysis was made by combining the data from both seasons using the

variables NO3-N, NH4-N-N, DEA and phosphatase activities (Hair et al. 1992).

Results

In spring/early summer, soil temperature was significantly lower in fern than in conifer plots (Table 2). This trend was also seen in summer/early fall but was not statistically significant (Table 3). The only other variables from the spring/early summer sampling showing significant differences were K ions, NH4-N, NO3-N, and denitrification potentials (DEA) (Table 2). The last three variables also showed significant differences in summer/early

TABLE 2. Soil characteristics in plots with different vegetation sampled in the spring/early summer. The numbers in ( ) indicate the number of plots for that type of vegetation. For individual variables, means followed by different letters were significantly different at $P \leq 0.05$.

Variable	Units	Conifer (10)	Fern (10)	Shrub (6)
Soil temperature	degrees C	11.6b	8.8a	11.9b
Soil moisture	percent	65.9	64.9	63.4
pH	pH	5.69	5.54	5.56
Bulk density	g cm^3	0.32	0.32	0.30
Total C	percent	10.9	9.6	11.2
Total N	percent	0.65	0.48	0.55
Al	µg gdm^{-1}	28.6	33.8	44.4
K	µg gdm^{-1}	39.1b	18.8a	30.5ab
Ca	mg/gdm	3.40	2.73	2.81
Mg	µg gdm^{-1}	392	209	271
NH4-N	µg gdm^{-1}	2.0a	2.1a	7.2b
NO3-N	µg gdm^{-1}	3.6b	0.2a	4.2b
Denitr. Potential	nmol N/gdm^{-1}-h	8.35b	1.43a	9.18b
Total phenolic	µg gdm^{-1}	46.3	47.1	53.3
Unreactive phenol.	µg gdm^{-1}	28.4	26.7	27.4
Field resp.	mgCm^2-min^{-1}	13.1	13.3	12.2
Laboratory resp.	µg C gdm^{-1} h^{-1}	0.74	0.95	0.75
Sub. Ind. Resp.	µg C gdm^{-1} h^{-1}	0.21	0.18	0.16
Bacterial biomass	µg biomass g^{-1}	73.5	62.6	108
Fungal biomass	µg biomass g^{-1}	446	593	547
Bact/fung biomass.		0.16	0.11	0.20
Phosphatase	µmol g^{-1} h^{-1}	0.07	0.08	0.03

TABLE 3. Soil characteristics in plots with different vegetation sampled in the summer/early fall.

Variable	Units	Conifer (10)	Fern (10)	Shrub (6)
Soil temperature	degrees C	17.5	14.9	18.5
Soil moisture	percent	45.0	52.4	72.4
pH	pH	5.43	5.19	5.19
Al.	µg gdm^{-1}	71a	133b	148b
NH4-N	µg gdm^{-1}	4.7b	2.3a	2.4ab
NO3-N	µg gdm^{-1}	4.3b	0.7a	2.2ab
Denitr. Potential	nmol N/gdm^{-1}-h	5.9b	1.6a	6.0b
Total phenolic	µg gdm^{-1}	63.6	74.7	66.9
Unreactive phenol.	µg gdm^{-1}	29.8	37.1	33.4
Field resp.	mgCm^2-min^{-1}	13.8	15.6	16.0
Laboratory resp.	µgC gdm^{-1} h^{-1}	0.40	0.45	0.48
Subs. Ind. Resp.	µgC gdm^{-1} h^{-1}	0.10	0.07	0.13
Bacterial biomass	µg biomass g^{-1}	73.3	93.1	127.3
Fungal biomass	µg biomass g^{-1}	109	191	98
Bact/fung biom		0.67	0.44	1.30
Phosphatase	µmol g^{-1} h^{-1}	0.10a	0.24b	0.04a
ß-glucosidase	µmol g^{-1} h^{-1}	0.08	0.07	0.09

fall (Table 3). In both seasons, NO3-N, and DEA were lowest in fern soils. In spring/early summer, shrub soils showed the greatest NH4-N values when compared with either conifer or fern soils. In summer/early fall fern soil NH4-N values were significantly lower that either conifer or shrub soils. The only other variables showing significant summer/early fall vegetation differences were Al ions and phosphatase, which were both higher in fern soils.

A discriminant analysis of different vegetation types using the data from both seasons and the variables denitrification potential, NO3-N, NH4-N and phosphatase activity showed three distinct groupings (first function differences at P = 0.0005). Both conifer and fern soils were separated with shrub functions generally falling between the other two vegetation types.

Discussion

The main objective of this research was to determine which soil factors might contribute to the apparent suppression of conifer seedling reestablishment by bracken fern after stand harvest. A number of explanatory mechanisms have been suggested in the literature over the last 30+ years. One suggestion was that bracken fern underground rhizome complexes compete with other vegetation by removing water and nutrients from forest soils (Lederle and Mroz 1991). For both seasons, no significant decreases in fern soil moisture were observed relative to other vegetation types therefore reduced moisture did not appear to be a factor.

In spring/early summer, Al concentrations were slightly higher in fern than conifer soils but this difference was not statistically significant (Table 2); however, summer/early fall Al concentrations showed differences that were both greater and statistically significant (Table 3). It is not known if these elevated Al concentrations could partially explain the exclusionary characteristics of bracken ferns. In another study comparing bracken fern soils with forest soils, elevated Al concentrations were found in bracken soils (Sommer et al. 1991). Studies of Al concentrations in fern soil lysimeter solutions have also shown elevated levels but these were not judged to be of sufficient toxicity to influence interplant competition (Johnson-Maynard et al. 1998).

Another mechanism suggested for vegetation exclusion by bracken fern is the production of phenolics originating from either the leaching of phenolic acids and tannins from fern fronds (Glass and Bohm 1969, Gliessman and Muller 1978) or from their decomposition (Rose et al. 1983). Soil total and unreactive phenolics were measured but no significant differences by vegetation type were observed suggesting that this was not an exclusionary factor.

Bacterial: fungal biomass ratios have been shown to be much higher in degraded forest sites where seedling reestablishment after clear cutting has not been successful (Elaine Ingham, Oregon State University, personal communication). Ingham has speculated that when bacteria dominate, there is poor conifer seedling survival, which could result in altered post disturbance vegetative succession (Perry et al. 1989). We speculated that bracken ferns might effectively shift bacterial: fungal biomass ratios in favor of bacteria and thus act to exclude conifer seedling establishment (Amaranthus and Perry 1987, Perry et al. 1987, Elaine Ingham, Oregon State University, personnel communication). Bacterial: fungal biomass ratios did not differ significantly by vegetation type and therefore did not appear to be a factor in seedling suppression.

Of the variables studied, mineralized N availability appears to be the most likely factor for conifer seedling exclusion by bracken fern. This is in agreement with the suggestion made by Lederle and Mroz (1991) who thought underground rhizome complexes might compete with other vegetation for nutrients. We did find significantly lower NO3-N levels ($P \leq 0.05$) in fern compared with conifer soils. The same was true for NH4-N^+ ion concentrations in the summer/early fall but not the spring/early summer. The reduction in mineral N availability in fern soils was further substantiated by denitrification enzyme activity (DEA) data. DEA was significantly lower in fern soils than either conifer or shrub soils suggesting low NO3-N and NH4-N availability to denitrifiers (Griffiths and Swanson, 2001). Although mineralized N, soil organic matter and moisture are all know to influence DEA levels (Tiedje 1982, Davidson and Swank 1986, Drury et al. 1991), the most likely limiting factor in the current study is mineralized N availability since there were no significant vegetation differences in soil moisture or total C and N.

It might be argued that the observed differences in mineralizable N and DEA between the

harvested and undisturbed forest sites might be due to the differences in site disturbance rather than vegetation type. This seems unlikely. Increased soil mineralized N concentrations have repeatedly been reported in recently harvested forest stands (Vitousek et al. 1979, Vitousek and Matson 1985, Bowden and Bormann 1986). This may be due to both a decrease in N uptake by vegetation and an increase in fine organic matter decomposition rates. The decrease in plant uptake is obviously driven by tree harvesting and the increase in decomposition rates is thought to be driven by microclimatic changes (Vitousek and Matson 1985, Pankow et al. 1991, Bradley et al. 1998).

In a recent HJA study of DEA in forest soils using nine sample sets, Griffiths and Swanson (2001) found DEA activities in harvested stands to be ~ six times higher than in adjacent undisturbed forest soils. The harvested stands in that study were in approximately the same locations and age as those used in the current study. In another study of mature and disturbed forest soils in the same general area also showed DEA levels that were ~ five times greater in harvested stands than in adjacent undisturbed forests (Griffiths et al., 2005). In the current study, we found DEA activities to be ~ four to six times less in the fern sites within harvested stands when compared with adjacent undisturbed forests. This makes our observations in fern soils even more compelling since, based on past studies, we would expect to find an increase in harvest site DEA levels. What we observed in the fern plots was a significant reduction in DEA levels.

It is possible that the ferns alter microbial activity in a way that either stimulates microbial growth, thus acting as a nutrient sink as N becomes incorporated into new microbial biomass, or suppressing decomposition thereby decreasing N mineralization. Neither of these appears to be the case. There were no significant differences by vegetation type for field respiration, SIR, laboratory respiration, or ß-glucosidiase. If the ferns were altering microbial activities, we would expect that some, if not all, of these variables would be altered. The only related variable showing a significant vegetation effect was phosphatase activity. Phosphatase activities were significantly higher in summer/early fall fern soils but this was not observed in the spring/early summer. These data along with the bacterial and fungal biomass data strongly suggest that ferns are not altering the microbial community in a way that would account for the differences seen in N chemistry. From this we conclude that the ferns themselves are reducing NO3-N and NH4-N concentrations which are reflected in low DEA levels. This sequestration may be sufficient to limit N availability to a degree that seedling establishment is suppressed. In spring/early summer, the plant nutrient K was also significantly lower in fern soils. Taken together these data suggest, that as Lederle and Mroz (1991) speculated, the competitive advantage bracken ferns show in disturbed forest soils maybe traced back to their ability to take up and sequester plant nutrients. These results open up a potentially useful area of future research into the field of bracken fern ecology.

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