

Chemical and Mineralogical Conversion of Andisols following Invasion by Bracken Fern

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ABSTRACT

Andisols support $\approx 200\,000$ ha of mid-elevation grand fir (*Abies grandis* [Dougl. ex D. Don] Lindl.) forests in the Pacific Northwest region that are characterized by little or no natural conifer regeneration following removal of the forest canopy. Previous work suggests that the properties of these Andisols have been altered as a result of the establishment of successional communities dominated by bracken fern (*Pteridium aquilinum* [L.] Kuhn) in deforested areas. In this study, we compared soil properties in a 30-yr-old bracken fern site (clear-cut in 1965), a natural bracken fern site that is estimated to be centuries old, and an adjacent undisturbed forest in the Clearwater National Forest of northern Idaho. Results indicate that changes in chemical properties have accompanied establishment of successional communities. Mean weighted pH within the ash cap of the 30-yr-old bracken fern site (4.6) is significantly lower than that of the undisturbed forest (5.2). Mean values for Al saturation range from 27% in the undisturbed forest to 52% in the 30-yr-old bracken fern site; organic C is also lower in the undisturbed forest (37 g/kg) than in the 30-yr-old bracken fern site (54 g/kg). The dominant secondary mineralogical component of soils of the undisturbed forest is inorganic, short-range-order Al-Fe minerals, while metal-humus complexes are dominant in the bracken-fern-influenced soils. Data indicate that bracken fern successional communities are responsible for a shift from allophanic to nonallophanic properties in these soils, probably due to increased levels of soil organic C associated with bracken fern and a subsequent increase in formation of Al-humus complexes. Furthermore, such a mineralogical shift may contribute to the observed problems with conifer regeneration.

SOME MID-ELEVATION ECOSYSTEMS in the inland Pacific Northwest consist of stands of grand fir forest in a patchwork or mosaic pattern with various shrub and forb communities. These ecosystems are collectively referred to as the Grand Fir Mosaic (Ferguson and Adams, 1994). Soils of the GFM are strongly influenced by volcanic ash from the eruption of Mount Mazama, which created Crater Lake, OR, approximately 6800 yr ago, and are accordingly classified as Andisols (Bacon, 1983; Soil Survey Staff, 1994). Another defining characteristic of the GFM in northern Idaho is that following removal of forest canopy as a result of timber harvest or natural disturbance, successional communities dominated by bracken fern are quickly established. Furthermore, these deforested areas appear to remain in an arrested state of secondary succession, as little or no natural conifer regeneration is observed where bracken-fern-dominated successional communities have become established (Ferguson and Boyd, 1988). This lack of natural conifer regeneration in cleared areas of the GFM became appar-

ent following initiation of timber harvesting in the 1960s, with subsequent studies showing that competition and allelopathy attributable to bracken fern are not the only factors contributing to seedling mortality (Ferguson and Adams, 1994). This work has prompted a more detailed examination of Andisols of the GFM and their potential role in the forest regeneration problem.

Although few researchers have considered the effects of bracken fern on soil formation, it has been suggested that bracken fern can influence the soil in which it is growing. Jarvis and Duncan (1976) reported a change in soil morphology, from a brown earth to a more heavily podzolized soil, across a zone in the British Isles where vegetation changed from bracken fern to heather (*Calluna vulgaris* [L.] Hull). Leamy et al. (1980) noted that Andisols on the North Island of New Zealand rarely display thick dark humus horizons except where native podocarp forest was converted to bracken fern. In the GFM of northern Idaho, A horizons of Andisols invaded by bracken fern are somewhat darker than in the native forest soil (Sommer, 1991). This alteration is reflected in the soil classification changing from Haplocryands under the native forest to Fulvicryands in the bracken-fern-dominated successional communities (Sommer, 1991; Soil Survey Staff, 1994). Sommer (1991) found significant differences in pH and extractable Mn between the undisturbed forest soils and soils supporting a bracken fern community. Additionally, quantities of KCl-extractable Al were as much as 100 times greater in bracken-fern-influenced soils than in adjacent undisturbed forest soils, but differences were not statistically significant due to high variability. These data nevertheless suggest that canopy removal and bracken fern establishment have resulted in chemical alteration of GFM soils.

Andisol mineralogy is dominated by the presence of various organic and inorganic short-range-order constituents, and Andisols can be classified as either allophanic or nonallophanic depending on the relative abundance of these components (Shoji et al., 1985). Allophanic Andisols are dominated by allophane, imogolite, and Al-humus complexes, with lesser amounts of crystalline clay minerals. These soils are moderately to strongly acid, and have low KCl-extractable Al and low Al saturation (Shoji et al., 1985; Nanzyo et al., 1993). Nonallophanic Andisols have Al-humus complexes and crystalline clay minerals as their dominant mineralogy, and contain a substantially smaller proportion of allophane and imogolite compared with allophanic Andisols. In addition, nonallophanic soils are strongly to very strongly acid, have high KCl-extractable Al, and commonly exhibit Al toxicity (Shoji et al., 1985; Nanzyo et al., 1993). In the Pacific Northwest, nonallophanic Andisols have been

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reported along the Oregon coast (Baham and Simonson, 1985). There are, however, no reports of nonallophanic Andisols occurring in the colder and drier forested areas of northern Idaho.

Field observations and the results of previous studies conducted within the GFM have led to the hypothesis that bracken fern communities are causing a conversion from allophanic to nonallophanic Andisols. This hypothesis is based on our assumption that bracken fern establishment has resulted in chemical and mineralogical alteration of soils that were initially similar. While we cannot completely rule out the possibility that bracken fern simply selects for and becomes established on nonallophanic soils, available evidence suggests this is not the case. Andisols with nonallophanic characteristics such as dark A horizons (melanic epipedons) are inevitably associated with vegetation types that produce large quantities of organic matter (Shoji et al., 1993), and bracken fern is known to produce large amounts of above- and belowground biomass annually (Ferguson and Adams, 1994). Also, volcanic-ash-influenced soils of northern Idaho that are forested typically develop allophanic characteristics (McDaniel et al., 1993), and Andisols with nonallophanic characteristics have not been observed within undisturbed, forested areas of the GFM. In combination, these observations suggest it is the establishment of bracken fern that is responsible for subsequent alteration of soil properties.

A shift from allophanic to nonallophanic properties is accompanied by formation of a highly reactive pool of organically complexed Al, which potentially could result in toxic levels of Al^{3+} in soil solution. If such a shift is occurring in soils of the GFM, it may play a key role in the observed regeneration problem. Although Andisols have been widely studied, a conversion of allophanic to

nonallophanic mineralogy has not been documented in the literature. Therefore, the objectives of this research were to: (i) determine changes in chemical properties of Andisols that have been invaded by bracken fern, especially those properties that may be detrimental to plant growth; and, (ii) examine and compare mineralogy of Andisols supporting bracken fern successional plant communities relative to adjacent undisturbed forest.

MATERIALS AND METHODS

Study Area

The GFM occurs in the 1300- to 1800-m elevational range of the Clearwater River drainage of northern Idaho, and in the Blue Mountains of northeastern Oregon and southeastern Washington (Fig. 1). The study area is located at an elevation of 1463 m, approximately 3 km south of Eagle Point in the Clearwater National Forest, Section 35, R7E, T40N. Parent materials in the study area include volcanic ash, which averages ~60 cm in thickness. The ash overlies soil derived from a fine-grained igneous rock that is chemically similar to granite. The study area was selected to allow sampling and comparison of soils under three different vegetation types or treatments. The treatments include: (i) relatively undisturbed forest; (ii) a 30-yr-old bracken fern site that was clear-cut and invaded by bracken fern in 1965; and (iii) a natural bracken fern site that existed prior to timber harvest (as indicated by 1956 aerial photography). The 1.5-ha "natural" bracken fern site is estimated to be hundreds of years old (Ferguson and Adams, 1994), perhaps forming as a result of a stand-replacing fire or disease. Because treatment locations are in close proximity to one another (<150 m apart) and occur on similar slopes (9–22%), aspects (43–134°), and parent materials, the age or type of plant community is the only observable factor that differs significantly. Available evidence indicates that all soils were similar prior to any disturbance and can therefore be

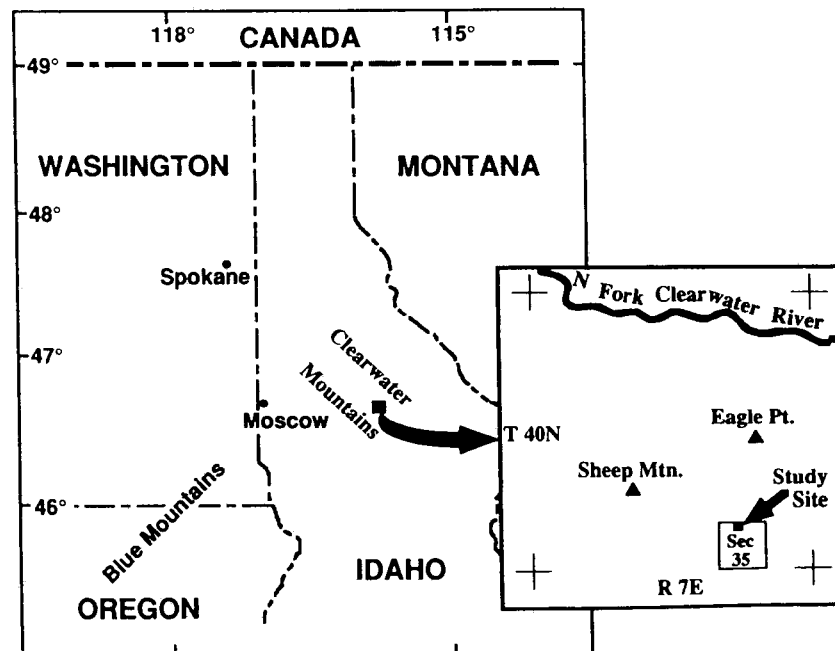


Fig. 1. Location of the study area in northern Idaho; inset shows location of the sampling site. The Grand Fir Mosaic occurs primarily within areas of the Clearwater and Blue Mountains.

used to assess the impacts of bracken fern establishment on soil properties.

Within each treatment, two pedons located 10 to 25 m apart on similar slopes, aspects, and microtopography were excavated by hand and described using standard horizon designations and descriptions (Soil Survey Division Staff, 1993). A minimum of three subsamples was collected across the lateral exposure of each genetic mineral horizon in each pedon and composited; composite samples were used for laboratory analyses.

Laboratory Methods

Samples were air dried, gently crushed, and sieved to obtain the 2-mm size fraction on which all analyses were conducted. The relative influence of volcanic ash was determined by NaF-pH (Fieldes and Perrott, 1966), P retention (Blakemore et al., 1981), and the percentage of glass shards within the very fine sand fraction as determined by petrographic microscopy. Chemical analyses of the soil included pH of a 1:1 (soil/water) mixture measured with a standard pH electrode, exchangeable cations by NH_4OAc (pH = 7) extraction (Soil Conservation Service, 1984), organic C by rapid dichromate oxidation (Nelson and Sommers, 1982), exchangeable H^+ and Al^{3+} by KCl extraction (Thomas, 1982), and Al saturation as a percentage of the ECEC (NH_4OAc -extractable bases + KCl-extractable acidity). Particle-size distribution and separation were performed by using sieving and centrifugation procedures: samples were treated with NaOCl to destroy organic aggregating agents (Anderson, 1963) and dispersed using sodium hexametaphosphate and sonification (Gee and Bauder, 1986).

To assess differences in mineralogy, Al and Fe were partitioned into various operationally defined forms using selective dissolution techniques. Extraction with sodium pyrophosphate was used to estimate Fe and Al contained in metal-humus complexes (McKeague, 1967). Aluminum contained in inorganic, short-range-order minerals such as allophane and imogolite was estimated by subtracting pyrophosphate-extractable Al from that extracted with acid ammonium oxalate (pH 3). Similarly, Fe contained in poorly crystalline Fe (hydr)oxides was estimated by subtracting pyrophosphate-extractable Fe from that extracted with acid ammonium oxalate (Soil Conser-

vation Service, 1984; Jackson et al., 1986). Extracts were analyzed for Fe and Al using inductively coupled plasma spectroscopy. X-ray diffraction analysis was used to study the crystalline mineralogical components; treatments included Mg saturation, Mg saturation and glycerol solvation, K saturation, and K saturation plus 550°C heat (Whittig and Allardice, 1986). Formamide was used to differentiate kaolinite from halloysite (Churchman et al., 1984; Theng et al., 1984). All analyses except for x-ray diffraction were run in duplicate and reported as means. Student's *t*-tests were performed using weighted averages for the volcanic ash cap to determine any statistically significant differences ($\alpha = 0.05$) among sites.

RESULTS AND DISCUSSION

Morphology and Volcanic Ash Influence

All soils of the study area are mantled with volcanic-ash-rich horizons that have redder hues and siltier textures than the underlying horizons (Table 1). Sodium fluoride-pH values within the ash cap are high and range from 10.1 in the A horizon of the 30-yr-old bracken fern site to 11.6 in the Bw2 horizon of the same pedon (Table 1). In this procedure, values above 9.4 indicate the presence of allophane and/or Al, Fe (hydr)oxides (Fieldes and Perrott, 1966). The data indicate that these soils have a relatively large amorphous phase, which is capable of exchanging hydroxyl (OH^-) groups in the presence of F^- . The relatively high NaF-pH values found in lower horizons of the bracken-fern-influenced soils are probably due to mixing of volcanic ash throughout the profile. This mixing may result from the increase in gopher activity that follows disturbance or by tree throw that occurred prior to canopy removal. Phosphorus-retention values in the ash caps are also high, ranging from 66% in the natural bracken fern site to 96% in the 30-yr-old bracken fern site. Glass shard percentages within the very fine sand fractions range from 16 to 38 (Table 1); lower glass percentages in the bracken fern

Table 1. Classification and selected properties of representative pedons supporting undisturbed forest and successional bracken fern communities.

Plant community	Classification	Pedon	Horizon	Depth	Moist color	Texture†	Glass in very fine sand	P retention	NaF-pH	Organic C
				cm			%			g/kg
Undisturbed forest	Typic Hapludand	U1	A	0-8	7.5YR 2.5/2	sil	38	92	11.0	69
			Bw1	8-35	7.5YR 3/3	sil	32	95	11.4	34
			Bw2	35-62	7.5YR 3/3	sil	32	87	11.2	27
			2Bw3	62-79	10YR 4/4	l	— ‡	96	9.4	4
			2Bw4	79-95	10YR 4/4	l	—	96	9.0	4
			2Cr	95+	10YR 4/4	l	—	53	9.0	4
30-yr-old bracken fern glade	Alic Fulvudand	A1	A	0-15	7.5YR 2.5/2	sil	28	87	10.1	95
			Bw1	15-29	7.5YR 2.5/2	sil	26	96	11.5	54
			Bw2	29-45	7.5YR 2.5/3	sil	27	96	11.6	42
			2Bw3	45-69	10YR 3/4	l	—	53	10.8	5
			2C	69+	10YR 4/4	l	—	30	9.4	3
Natural bracken fern site	Alic Hapludand	N1	A	0-12	7.5YR 2.5/3	sil	21	66	10.4	63
			Bw1	12-29	7.5YR 2.5/3	sil	18	77	11.0	39
			Bw2	29-48	7.5YR 2.5/3	sil	16	89	11.3	40
			Bw3	48-69	7.5YR 3/3	l	—	88	11.4	41
			2Bw4	69-82	10YR 4/6	l	—	74	11.3	36
			2Cr	82+	10YR 4/4	l	—	24	10.7	4

† sil = silt loam, l = loam.

‡ Samples were not analyzed.

soils may reflect a greater amount of mixing by gophers.

High NaF-pH, P retention, and glass shard content indicate that volcanic ash is a dominant parent material and has a significant effect on soil properties. Accordingly, soils within the undisturbed forest are classified as Typic Hapludands (Soil Survey Staff, 1994). The 30-yr-old bracken fern site soils are classified as Alic Fulvudands; the fulvic great group indicates a higher C content in the upper 40 cm of the soil compared with the Hapludands of the undisturbed forest (Soil Survey Staff, 1994). Soils of the natural bracken fern site are classified as Alic Hapludands, based on KCl-extractable Al >2 cmol_c/kg (Table 2) (Soil Survey Staff, 1994). The slightly darker colors at depth within the ash cap of bracken fern soils may reflect the large, annual input of bracken fern biomass into the soil each year as well as increased mixing of the ash cap through gopher activity.

Chemical Properties

Soil pH is significantly lower in the bracken-fern-influenced soils than in the undisturbed forest. Mean pH values within the volcanic ash cap range from 4.6 in the 30-yr-old bracken fern soil to 5.2 in the undisturbed forest soil (Table 2). The older, natural bracken fern soil is intermediate between the two sites, with a pH of 4.8, and does not differ significantly from the 30-yr-old bracken fern soil. Several factors such as precipitation, soil age, nutrient uptake by plants, and inputs of acid litter to the forest floor contribute to high acidity associated with forest soils (Gilliam, 1991). Since vegetation is presumed to be the main variable in this study, we conclude that bracken fern establishment appears to have an acidifying effect on the soil through the addition of acid litter and/or high rates of nutrient uptake. Although lowering of soil pH has been reported following the removal of forest vegetation (Dahlgren and Driscoll, 1994), bracken fern appears to contribute to and maintain acid conditions relative to the undisturbed forest vegetation. These pH data are consistent with the conversion of allophanic to nonallophanic Andisols. Nonallophanic Andisols commonly have a pH(H₂O) range of 4.8 to 5.3, compared with a range in allophanic Andisols of 5.0 to 6.0 (Nanzoy et al., 1993). Furthermore, Al toxicity has been reported in nonallophanic Andisols in Japan with pH <5 (Shoji et al., 1980).

Organic C ranges from 37 g/kg in the undisturbed

forest soil to 54 g/kg in the 30-yr-old bracken fern soil (Table 2). The natural bracken fern soil is intermediate, with 46 g/kg organic C (Table 2). Dahlgren et al. (1991) found that large quantities of soluble organic C become immobilized or decomposed within the A1 horizons of nonallophanic Andisols. The increase of organic C relative to the undisturbed forest, attributable to the large amount of biomass added to the soil each year by the bracken fern, increases the potential for the preferential formation of Al-humus complexes. This process is known as the antiallophanic effect, since Al is complexed by organic compounds and is therefore unavailable for formation of inorganic aluminosilicates such as allophane and imogolite (Dahlgren et al., 1993).

Aluminum extractable by KCl, which reflects Al available for exchange with soil solution, is also elevated in the bracken fern soils relative to the undisturbed forest. Mean values for the ash cap are significantly different between the undisturbed forest and the natural bracken fern glade, increasing from 1.5 to 3.5 cmol_c/kg (Table 2). Aluminum extractable by KCl is also the only chemical property showing a significant difference between the bracken fern treatments (Table 2). The increase in exchangeable Al, along with a decrease in pH from the undisturbed forest soil, creates a more hostile environment for plant growth. These changes are also consistent with our hypothesis that soils supporting bracken fern communities are being converted to nonallophanic Andisols.

Aluminum saturation percentage is significantly higher in the bracken-fern-influenced soils relative to that of the undisturbed forest soil. Aluminum saturation in the 30-yr-old bracken fern soil has almost doubled from 27 to 52% in the undisturbed forest soil (Table 2). These data suggest that Al may be more available for plant uptake within the bracken-fern-influenced soils where seedling mortality is high.

Mineralogy

Selective dissolution techniques indicate different trends in the distribution of organic and inorganic secondary Fe in the ash caps among the various treatments. Organically complexed Fe is relatively low in the soils of the undisturbed forest and does not form a distinct zone of accumulation (Fig. 2). In contrast, Fe present as Fe-humus complexes in the ash-influenced surface horizons of the 30-yr-old bracken fern site is twice that of the undisturbed site; the depth distribution also indicates accumulation in the A horizon. Organically complexed Fe is highest in the ash cap of the natural bracken fern soil and its depth distribution shows an accumulation deeper in the ash cap. The accumulation of Fe-humus complexes with depth may indicate that podzolization is occurring in this soil or could be a result of mixing by gophers. Although the total Fe found in humus complexes and short-range-order minerals is not significantly different among the ash caps of the various sites, the proportion of Fe contained in Fe-humus complexes is significantly higher in some horizons of the natural bracken fern glade. These data indicate that formation of

Table 2. Selected chemical properties of the soils. Values represent means of weighted averages for the ash-influenced horizons of the two pedons sampled at each site.

Site	pH	Organic	KCl-Al	Al saturation
		C		
		g/kg	cmol _c /kg	% of ECEC†
Undisturbed forest	5.2a‡	37a	1.5a	27.4a
30-yr-old bracken fern	4.6b	54b	2.6a	51.9b
Natural bracken fern	4.8b	46b	3.5b	47.9b

† ECEC = effective cation exchange capacity (exchangeable bases + KCl-acidity).

‡ Within a column, means followed by the same letter are not significantly different at $\alpha = 0.05$.

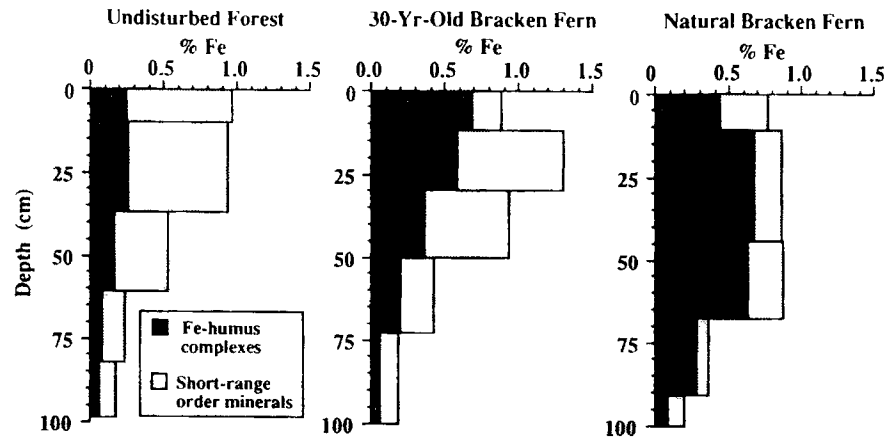


Fig. 2. Depth distribution of Fe in soil fractions as determined by selective dissolution techniques. Each graph represents the mean of two pedons sampled within the treatment.

metal-humus complexes is a more dominant soil-forming process in the natural bracken fern soil relative to the forest community.

Results of selective dissolution techniques for Al are similar to those observed with Fe. In the undisturbed forest, Al-humus complexes decrease slightly with depth (Fig. 3). Inorganic, short-range-order Al minerals such as allophane and imogolite are the dominant form of secondary Al in the ash-influenced horizons of the undisturbed forest soils. Although the amount of Al found in Al-humus complexes is similar in the A horizons of all sites, the bracken-fern-influenced soils show accumulations of Al-humus complexes in the Bw1 and Bw2 horizons. Aluminum-humus complexes have increased in the Bw1 horizon of the 30-yr-old bracken fern soils, relative to the undisturbed forest, with a greater proportion of the secondary Al occurring in this form. Aluminum-humus complexes are abundant throughout the ash cap of the natural bracken fern soil and account for approximately 80 to 91% of the secondary Al. The 30-yr-old and natural bracken fern glade soils also show a different distribution of Al-humus complexes with depth than the undisturbed forest. Accumulations of organically bound Al are evident within the Bw1 and Bw1-Bw2 horizons of the 30-yr-old and natural bracken fern

glade soils, while Al-humus complexes decrease with depth in the undisturbed forest. Although podzolization does not appear to be a dominant soil-forming process within the undisturbed forest soil, it is more prominent in the 30-yr-old bracken fern soil, and is best expressed in the natural bracken fern soil. Since all other factors (precipitation, landscape position) contributing to podzolization are the same at each site, it appears that bracken fern produces a larger quantity and/or different types of organic acids that are capable of chelating Fe and Al. This is responsible for the different distribution of Al-humus complexes with depth in the bracken-fern-influenced soils compared with the undisturbed forest soil. As with Fe, repartitioning of secondary Al appears to occur without the total amount of secondary Al changing. This indicates a shift from inorganic short-range-order minerals, primarily allophane, imogolite, and ferrihydrite, to Fe- and Al-humus complexes. Because Al-humus complexes are the dominant form of active Al in humus-rich horizons of Andisols (Dahlgren et al., 1993), and therefore control Al availability to soil solution and plants, the shift to an Al-humus-dominated mineralogy may be of considerable ecological significance.

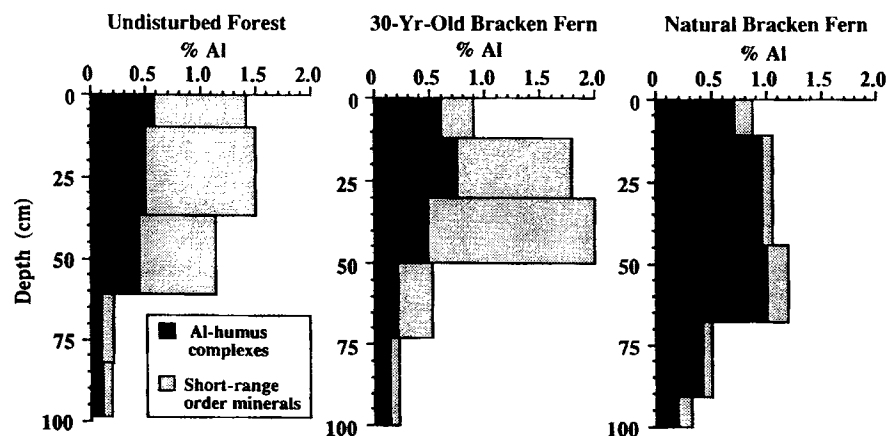


Fig. 3. Depth distribution of Al in soil fractions as determined by selective dissolution techniques. Each graph represents the mean of two pedons sampled within the treatment.

X-ray Diffraction

Although the clay-sized, crystalline layer silicate component of Andisols is relatively small, identification of these minerals can also provide some insight into soil-forming processes. X-ray diffraction patterns of Bw1 horizons from each of the sites show major peaks at 1.4 and 0.7 nm (Fig. 4). The 0.7-nm peaks correspond to a kaolin (1:1) mineral; following treatment with formamide, these peaks did not expand to 1.0 nm (data not shown), indicating that this mineral phase is kaolinite rather than halloysite in all three of the soils (Churchman et al., 1984; Theng et al., 1984).

The 1.4-nm peaks correspond to a nonexpanding 2:1 layer silicate mineral, similar to hydroxy-Al-interlayered vermiculite reported in Andisols and volcanic-ash-influenced Spodosols of northern Idaho (McDaniel et al., 1993). While this mineral phase is present in all three of the soils, a difference among sites is the degree to which the 1.4-nm peaks collapse to 1.0 nm with K saturation and heat treatments. The Bw1 horizons from the undisturbed forest and the 30-yr-old bracken fern soils show very little collapse of the 1.4-nm peak with K saturation; after heating to 550°C, a pronounced hump can be seen on the low-angle side of the 1.0-nm peak (Fig. 4). X-ray diffraction patterns of the natural bracken fern soil show the most complete collapse of the 1.4-nm peak with K saturation and heating. Unlike the patterns for the undisturbed and 30-yr-old bracken fern soils, there is no pronounced hump or shoulder on the low-angle side of the 1.0-nm peak, indicating comparatively less hydroxy-Al interlayering (Barnhisel and Bertsch, 1989).

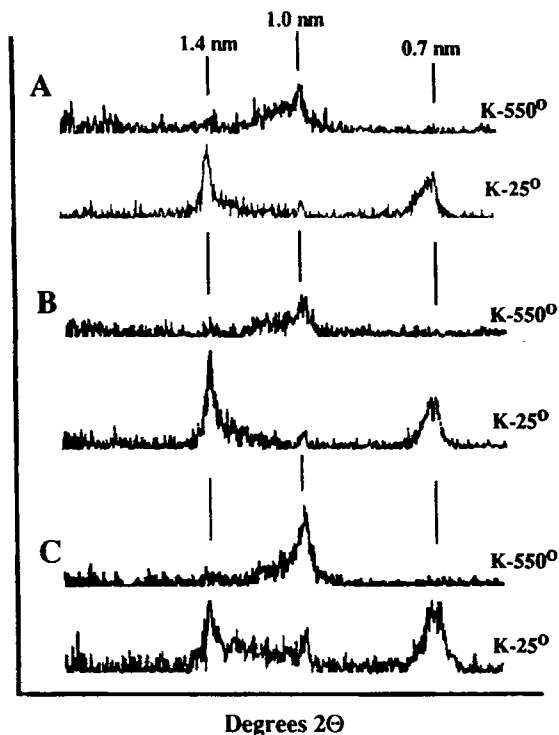


Fig. 4. X-ray diffraction patterns for clay fractions of Bw1 horizons from (A) undisturbed forest, (B) a 30-yr-old bracken fern site, and (C) a natural bracken fern site.

These results indicate that the crystalline, 2:1 minerals in the undisturbed forest and the 30-yr-old bracken fern soils contain more hydroxy-Al interlayering than do the older natural bracken fern soils. This observation, in combination with the selective dissolution data, suggests that a more active pool of organic complexing agents present in the natural bracken fern soil is acting as a sink for available Al, thereby preventing it from forming hydroxy-Al interlayers in the 2:1 layer silicates. Although this mineralogical change is not seen in the 30-yr-old bracken fern soil, it is evident in soils supporting bracken fern communities that are believed to be centuries old.

CONCLUSIONS

Data from this study indicate that chemical and mineralogical properties of Andisols in the GFM of northern Idaho are being altered following invasion by bracken fern successional plant communities. Furthermore, alteration of these chemical and mineralogical properties appears to be relatively rapid — significant alteration is evident in soils that have supported bracken fern communities for as little as 30 yr. The observed changes are consistent with a conversion of allophanic Andisols to Andisols with nonallophanic character. The development of nonallophanic characteristics following invasion by bracken fern has resulted in soils that have lower pH and higher exchangeable Al, both of which can have significant implications for plant growth. Soils supporting bracken fern also are characterized by higher organic C and a repartitioning of secondary Al and Fe from inorganic compounds into organic complexes. Rapid development of this larger pool of organically bound Al may inhibit forest regeneration through its influence on Al activity in soil solution.

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