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Effects of clearcutting and soil mixing on soil properties and understorey biomass in western red cedar and western hemlock forests on northern Vancouver Island, Canada

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Abstract

On northern Vancouver Island in British Columbia it has been hypothesised that the cultivation effect of repeated windthrow is the cause of the higher nutrient availability in windstorm-derived, natural second-growth stands of western hemlock and amabilis fir (the HA type), compared with adjacent old-growth stands of western red cedar with a smaller component of hemlock, and a dense understorey of the ericaceous shrub, salal (the CH type). In 1988 an experiment was established in a clearcut area containing examples of these two forest types. The experiment was designed to simulate the effects of a broadscale windthrow by mixing mineral and organic horizons using a large rake attached to an excavator. In this study, a range of soil physical and chemical properties, and the biomass of understorey plants, were measured 4.5 years after treatment in uncut, clearcut, and clearcut and mixed plots of the two types. In the HA type, clearcutting and soil mixing decreased surface organic matter and moisture content, and increased the rate of decomposition of cellulose. It had little effect on the rate of microbial activity measured using CO_2 evolved in laboratory incubation, or N and P measured after KCl extraction, anaerobic incubation, or using ion-exchange resin bags in situ. In the CH type, the treatment decreased mineralisable N and phosphate-P held on resin bags, and the rates of cellulose decomposition and CO_2 evolution. Mixing markedly decreased the cover of salal compared with both the clearcut only and the uncut treatment. The anticipated benefits of mixing and soil disturbance (increased soil nutrient availability brought about by the mixing of mineral and organic horizons) have not occurred. This was probably because the mixing treatment brought humus material from deeper in the soil profile to the surface. Decomposition of this material is limited more by its poorer quality for decomposers (lower N concentration, and possibly higher tannins) than by soil microclimate.

Keywords: Soil nutrient availability; Disturbance; Windthrow; Cultivation; Decomposition

1. Introduction

Pedoturbation, or soil disturbance and mixing, is an important pedogenic process that occurs naturally in forest soils through the activities of animals or plants, or through physical mechanisms, such as freezing and thawing, or swelling and shrinking of clays (Johnson et al., 1987). Disturbance by ploughing or some other

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form of cultivation is also a common site preparation practice before establishment of trees in plantations. This disturbance aims to increase early growth of planted seedlings by creating more favourable conditions of moisture, aeration and nutrient availability, and decreasing competition from non-crop vegetation (Burger and Pritchett, 1988).

Pedoturbation as a result of tree falls is a widespread phenomenon in forests (Lyford and MacLean, 1966; Dunn et al., 1983; Cremeans and Kalisz, 1988), which has a significant impact on many aspects of forest ecosystem functioning (Nakashizuka, 1989; Schaetzl et al., 1989; Peterson et al., 1990). Tree falls create a variety of soil microsites within a stand, depending on whether the trees snap off, the roots are uplifted and form a hinge, or the root ball rotates within the soil profile (Beatty and Stone, 1986). Uplifting or rotation of the roots of larger trees results in a major disturbance to the soil profile, with an effect similar to mechanical ploughing (Armson, 1977). Tree falls caused by wind (windthrow) have been suggested as an important mechanism for maintaining forest productivity in some areas. For example, in the coastal forests of south-east Alaska, windthrow is considered to be the only form of disturbance occurring often enough to keep soils in a juvenile, or semi-mature stage of development. Mature soils in this region are not as favourable for tree growth, because of the negative effects of podzolisation on nutrient immobilisation, and the development of impermeable horizons (Ugolini et al., 1990).

The forests on better-drained sites on northern Vancouver Island in British Columbia are dominated by two forest types: an old-growth type consisting mainly of western red cedar (*Thuja plicata*) with a smaller component of western hemlock (*Tsuga heterophylla*) (the CH type), and a more uniform, second-growth type consisting western hemlock and amabilis fir (*Abies amabilis*), which largely originated following a widespread windstorm in 1905 (the HA type). Both types have thick mor humus (of 10 cm-1 m depth) overtopping podzolic mineral horizons.

Following clearcutting of these two types, major differences have been observed in the productivity of planted and naturally regenerated seedlings (Weetman et al., 1989a,b). Seedlings planted on the CH type grow slowly and exhibit symptoms of nutrient deficiency, whereas those on the HA type grow relatively rapidly and show no sign of nutrient deficiency. This slower growth on the old-growth sites is partly due to lower forest-floor nutrient availability in the CH type (Prescott et al., 1993), and partly to competition for the limited nutrients from the ericaceous shrub salal (*Gaultheria shallon*) which resprouts rapidly from rhizomes on the CH sites following clearcutting and slash burning (Messier and Kimmins, 1991; Messier, 1993). Differences in the nutritional conditions in the two forest types have been attributed to the history of windthrow in the HA stands. It has been hypothesised that windthrow improved the physical condition of the soil and increased nutrient availability by periodically mixing organic horizons with mineral soil (Lewis, 1982; De Montigny, 1992), in a similar way to the changes observed in coastal Alaska.

In 1988 an experiment was established in a clearcut and slashburnt area containing sites previously occupied by both forest types. The objective was to simulate the effect of extensive windthrow by mixing the mineral and organic soils using a large rake attached to an excavator. This paper compares a range of soil properties and the biomass of understorey plants in clearcut, clearcut and mixed, and uncut sites of the two forest types, and evaluates the results in terms of our current understanding of differences in ecological functioning between the two forest types.

2. Methods

2.1. Study area

The study was conducted on a gently undulating coastal plain about 100 m in elevation on northern Vancouver Island, British Columbia, near the town of Port McNeill (latitude 50°60′N), in Block 4 of Tree Farm Licence 25 operated by Western Forest Products Ltd. This area is in the very wet maritime subzone of the Coastal Western Hemlock biogeoclimatic zone (Pojar et al., 1991), which occupies the lower and middle altitudes of Vancouver Island and the coastal mainland of British Columbia. The structure of the two types has been described previously by Keenan (1993). The old-growth CH type is structurally diverse, with trees ranging in age up to 1000 years, 260 cm in diameter, and 45 m in height. The understorey is dominated by salal, with a smaller percentage of *Vaccinium* spp., ferns (*Blechnum* spp.), and a thick ground cover of mosses (*Hylocomium splendens* and *Rhytidiadelphus loreus*). The HA type consists of western hemlock and amabilis fir at a stocking of about 650 stems ha^{-1}, with relatively normal diameter class distributions. The mean diameter is about 50 cm, maximum diameter about 80 cm, and dominant height about 45 m. The understorey in these stands is dominated by advanced regeneration of hemlock and fir, and by similar mosses and ferns to those in the CH type. A full plant nomenclature has been given by Hitchcock and Cronquist (1973).

The mean annual precipitation at Port Hardy airport, 15 km from the study area, is approximately 1700 mm, with 65% falling between October and February. Although less rain falls in summer, rainfall during the growing season is sufficient to prevent any soil moisture deficit. Hours of sunshine range from an average of 6.4 h day^{-1} in July to 1.5 h day^{-1} in December, reflecting the frequent occurrence of fog in the summer and frontal clouds in the winter. Mean annual temperature is 7.9°C and the daily average ranges from 2.4°C in January to 13.8°C in August. Mineral soils are predominantly well-drained to somewhat imperfectly drained, medium-textured, humoferric podzols (Agriculture Canada, 1987), derived from compact till of periglacial and fluvio-glacial origin.

2.2. Experimental design and treatments

The experiment was established in a 97 ha area containing a mosaic of the two forest types. The area was clearcut during 1986 and slashburned in the spring of 1987. The mixing treatment was part of a larger experiment aimed at investigating the growth of cedar and hemlock seedlings planted at three densities, with and without fertilization, and with and without soil mixing, on the two forest types. In total, 32 plots (16 in each forest type) had the soil mixed, and half of these were planted with cedar and half with hemlock at 2500 stems ha^{-1}. The mixing treatment was carried out in January 1988 with a three-tined rake attached to a Caterpillar 215 excavator. The forest floor and mineral soil were thoroughly mixed, salal rhizomes were removed by hand from the disturbed soil, and the slash was redistributed to facilitate planting.

Soil sampling and other field measurements in this study were carried out on 22 plots, 16 in the clearcut and burnt experimental area—four unmixed (the CC treatment) and four mixed (the CCM treatment) in each of the two forest types—and on the three surrounding sites containing uncut stands of the CH and HA forest types (the UC treatment).

2.3. Soil properties

Soil samples were collected in July 1992, 4.5 years after treatment. Ten samples were collected from each plot. Near each of five sample points, the vegetation cover and litter were removed and two samples of the 0–20 cm soil layer were extracted. These two samples were combined, giving five samples per plot for analyses. Samples were kept in coolers in the field and transported to the laboratory within 4 days. In the laboratory, larger roots and stones were removed and organic samples were passed through a 5 mm sieve; predominantly mineral samples were passed through a 2 mm sieve. After sieving, samples were stored at 4°C until they were analysed.

Extractable nitrate, ammonium and phosphate were determined colorimetrically using a Technicon Autoanalyzer (Tarrytown, NY, USA), after shaking 5 g of fresh mass of each sample in 100 ml of 2 M KCl for 1 h. Mineralisable nitrate and ammonium were determined by subtracting the initial extractable amounts from the amounts extracted after an anaerobic incubation of 5 g of fresh mass in 25 ml of distilled water for 7 days at 30°C. Soil moisture content was estimated after oven drying a subsample at 105°C for 24 h, and organic matter content by the loss on ignition after 4 h at 500°C. Soil pH was measured on one bulked and homogenised sample of the five samples from each plot using a glass electrode in a 1:4 soil–water mixture.

Nutrient availability was measured using ion-exchange resin bags (Binkley and Matson, 1983; Gibson, 1986; Binkley et al., 1986). In April 1992, bags containing cation and anion exchange resins (21 g Amberlite IRC-50 C.P. RCOO-H, and 29 g Amberlite IRC-45 C.P. RNH3-OH), were buried at 20 cm depth at nine points in each plot. These were removed in August 1992, air dried, mixed with 200 ml of 2 M KCl and shaken for 1 h. The extract was analysed for ammonium-N, nitrate-N and phosphate-P using the methods described above.

Cellulose is a readily available form of carbon and energy source for decomposers, and its decomposition rate has been well correlated with that of conifer litter in Alaskan taiga forests (Fox and VanCleve, 1983).

A disc of cellulose of 4.25 cm diameter (Whatman No. 1 filter paper) enclosed in a nylon mesh bag with a pore size of 1 mm was buried at 20 cm depth for the 4 month period at the same point as each resin bag. After collection, soil particles were washed off and the paper remaining was oven dried for 24 h at 70°C and weighed.

The rate of CO_2 evolution from soil is an indicator of microbial activity. The effect of treatments on CO_2 evolution is therefore an indication of the effect of treatment on conditions for microbial decomposers. CO_2 evolution was assessed in the laboratory. About 80 g (wet weight) of each soil sample was removed from refrigeration and placed in a 500 ml mason jar at laboratory room temperature (about 25°C). The jars were left open for 2 days at room temperature, then sealed. Twenty-four hours after sealing, a 0.2 ml sample of gas was withdrawn through a rubber seal in the lid of each jar using a syringe. The CO_2 concentration of this gas sample was measured using an IR gas analyser. Five mason jars were filled with marbles to about the same level as those with soil. The average value from these blank samples was subtracted from the measured concentration, and this adjusted value was converted to milligrams of CO_2 released per dry gram of soil over the 24 h period.

2.4. Understorey vegetation

Above-ground biomass of understorey plants was estimated by clipping all vegetation within five systematically located 1 m^2 quadrats in each plot. Each sample was separated into species, divided into stem, leaf and flowers, and weighed. Moisture content was determined by drying a sub-sample of the biomass of each species at 70°C for 24 h, and then used to convert each sample to oven-dry mass.

2.5. Statistical analysis

The results were analysed as a 2×3 factorial using a randomised design. The factors were forest types (CH and HA) and treatment (UC, CC, and CCM). There were three plot replicates for the uncut forest, and four for the clearcut and clearcut and mixed treatments, with five to nine samples for each plot. The sample mean was calculated for each plot, and these means were used as the replicates in an analysis of variance. Treatment means within each forest type were compared using orthogonal contrasts after the ANOVA. Bartlett's test (Sokal and Rohlf, 1981) was used to compare the homogeneity of variances of the means. If they varied significantly, log or square-root transformations were used in the ANOVA, but only the untransformed means and standard errors are shown in the results. All analyses were performed using SYSTAT (Wilkinson, 1990).

3. Results

3.1. Soil moisture, temperature, and organic matter content

Soil physical properties are shown in Table 1. Gravimetric moisture content was slightly higher

Table 1
Soil physical properties in uncut, clearcut, and clearcut and mixed old-growth western red cedar and western hemlock (CH) and second-growth western hemlock and amabilis fir (HA) stands on northern Vancouver Island, British Columbia; means, with standard errors of the mean given in parentheses

	CH			HA		
	UC	CC	CCM	UC	CC	CCM
Moisture content (%)	78 (1.3)[a]	71 (1.8)[a]	60 (5.0)[b]	70 (2.0)[x]	72 (1.5)[x]	59 (2.8)[y]
Organic matter content (%)	86 (2.1)[a]	77 (5.2)[a]	52 (10.3)[b]	82 (6.7)[x]	86 (6.1)[x]	53 (6.0)[y]

Within each forest type, means followed by different letters were significantly different ($\alpha \leqslant 0.05$), using orthogonal contrasts following the ANOVA.

in the UC–CH (78%) than the UC–HA (70%), which may be indicative of higher transpiration from the denser canopy of the second-growth HA stands. Moisture content was lower in the CC plots on the CH type, but not on the HA type. Soil moisture has generally been observed to increase after clearcutting, because of the greater transpiration and rainfall interception by the tree canopy (McColl, 1977; Adams et al., 1991), although reductions in moisture content have been observed in other studies (Edwards and Ross-Todd, 1983; Hendrickson et al., 1985). Moisture content on the CCM plots was significantly lower ($\alpha \leqslant 0.05$) in both forest types (about 60%). This decrease could be due to (1) the mixing of organic and mineral soil layers during cultivation, which increased the mineral content at the soil surface, leading to increased thermal conductivity and heat admittance, and increased temperature below the soil surface, and therefore increased evaporation, (2) the lower moisture-holding capacity of mineral soil compared with organic matter, and/or (3) higher rates of infiltration owing to the mixing treatment (Ross and Malcolm, 1982).

Organic matter content in both forest types was significantly lower ($\alpha \leqslant 0.05$) in the CCM (52–53%) than the other two treatments (82–86% and 77–86% for the UC and CC treatments, respectively). This reduction in organic matter content was primarily due to the mixing of the mineral and organic horizons in the CCM plots.

3.2. Soil nutrients and microbial activity

Estimates of pH, nutrient status (by KCl extraction, anaerobic mineralisation, and buried ion-exchange resin bags), and rate of microbial activity (evolved CO_2 and decomposition of cellulose) are shown in Table 2. The pH was similar in the UC and CC treatments in both the CH and HA types (3.8–4.1), and significantly higher ($\alpha \leqslant 0.05$) in the CCM plots on the two forest types (4.6). This increase was probably due to the mixing of the more acidic organic matter with the less acidic mineral soil during cultivation.

Extractable ammonium-N and P were significantly higher ($P=0.006$, $P=0.022$) in soil from the HA than the CH type. Mineralisable ammonium was also higher in the HA type across the three treatments, but this difference was not significant ($P=0.171$). The order of magnitude of these differences is similar to those previously reported by Prescott et al. (1993), although they reported larger differences in ammonium mineralised in an aerobic incubation.

In the HA type extractable P was a significantly higher ($\alpha \leqslant 0.05$) in the CC than the UC treatments, but, except for this, clearcutting alone generally had no significant effect on extractable or mineralisable nutrients in either forest type.

Mineralisable ammonium-N was significantly lower ($\alpha \leqslant 0.05$) on the CCM plots than the other two treatments in the CH type, but not in the HA type. Extractable P was significantly lower on the CCM–CH plots than on the CC treatment. In the

Table 2
Soil chemical properties and microbial activity in uncut, clearcut and clearcut and mixed treatments in the CH and HA forest types; means with standard errors given in parentheses

	CH						HA						P^1
	UC		CC		CCM		UC		CC		CCM		
Extractable ($\mu g\ g^{-1}$)													
nitrate	12	(0.6)[a]	12	(0.3)[a]	11	(0.5)[a]	13	(0.4)[x]	12	(0.3)[x]	12	(0.2)[x]	0.175
ammonium	34	(2.3)[a]	39	(4.7)[a]	30	(3.0)[a]	44	(6.4)[x]	41	(1.8)[x]	46	(0.9)[x]	0.006
phosphate	6	(1.0)[ab]	14	(5.3)[a]	4	(1.1)[b]	9	(2.0)[x]	19	(1.2)[y]	13	(2.1)[y]	0.022
Mineralisable ($\mu g\ g^{-1}$)													
ammonium	48	(9.1)[a]	48	(7.5)[a]	20	(5.6)[b]	54	(3.8)[x]	49	(8.2)[x]	37	(4.3)[x]	0.171
Resin ($\mu g\ g^{-1}$)													
nitrate	36	(1.6)[a]	36	(3.5)[a]	45	(8.8)[a]	53	(19.9)[x]	49	(5.5)[x]	48	(4.9)[x]	0.124
ammonium	270	(37.8)[a]	262	(3.1)[a]	435	(67.0)[a]	536	(117.7)[x]	1370	(68.5)[x]	1010	(22.1)[x]	0.003
phosphate	312	(19.7)[a]	114	(27.3)[ab]	39	(17.8)[b]	89	(48.1)[x]	117	(19.6)[x]	157	(62.0)[x]	0.596
Evolved C ($\mu g\ g^{-1}$ organic matter day^{-1})	270	(24.3)[a]	197	(29.9)[ab]	98	(20.7)[b]	249	(14.8)[x]	196	(57.7)[x]	187	(17.2)[x]	0.430
Cellulose decomposition (% wt. loss)	45	(5.2)[ab]	58	(5.9)[b]	26	(5.9)[a]	31	(7.2)[x]	33	(8.0)[x]	59	(5.5)[y]	[2]
pH	3.8	(0.12)[a]	4.1	(0.18)[ab]	4.6	(0.19)[b]	4.0	(0.23)[x]	3.9	(0.22)[x]	4.6	(0.18)[y]	0.795

[1] P values for differences between forest types using a two-way ANOVA.
[2] Indicates a significant interaction ($\alpha \leqslant 0.001$) between site and treatment.
Within forest type, values followed by different letters were significantly different ($\alpha \leqslant 0.05$) using orthogonal contrasts following the ANOVA. Log transformed values were compared for resin ammonium, but the untransformed mean and standard error are shown.

HA type, mean extractable P was significantly higher ($\alpha \leqslant 0.05$) in the CCM than the UC treatment. The mean of the sample values for mineralisable N was lower in the CCM–HA than the other two treatments, but this difference was not statistically significant.

The ions held on buried exchange resins provide an estimate of the labile pool of nutrients that have been mineralised in the soil but not yet taken up by plant roots (Binkley et al., 1986). Ammonium-N was significantly higher ($P=0.003$) across all treatments in the HA type compared with the CH, but the other ions were not significantly different. Clearcutting alone had no significant effect on this labile pool in the CH type. This suggests either that nutrient mineralisation was lower in the CC treatment, or that nutrient uptake by salal is of the same order of magnitude as the uptake by the old-growth CH stands. Above-ground salal biomass in the CC was similar to the UC treatment (Fig. 1), but because below-ground biomass reaches a maximum 5 years after clearcutting and burning (Messier and Kimmins, 1991), total biomass is likely to be higher in the CC plots. Thus, the nutrient demand by salal on the clearcuts may equal the total demand in the old-growth stands.

In the HA type, the mean of the samples for resin ammonium in the CC treatment was more than double that in the uncut forest, and the mean for the CCM plots was also considerably higher than the UC plots. However, these differences were not significant ($\alpha \leqslant 0.05$).

The rate of CO_2 evolved per gram of soil organic matter measured in the laboratory is an index of size and activity of soil microbial populations. Rates were similar in the UC–CH and UC–HA stands, and about 20–25% lower on the CC plots in both forest types, although these differences were not significant. There was no significant difference in CO_2 evolved on the CCM plots compared with the CC only treatment in the HA type. In the CH type, CO_2 evolution was significantly lower ($\alpha \leqslant 0.05$) in the CCM treatment compared with the UC forest.

Cellulose is a form of readily available carbon

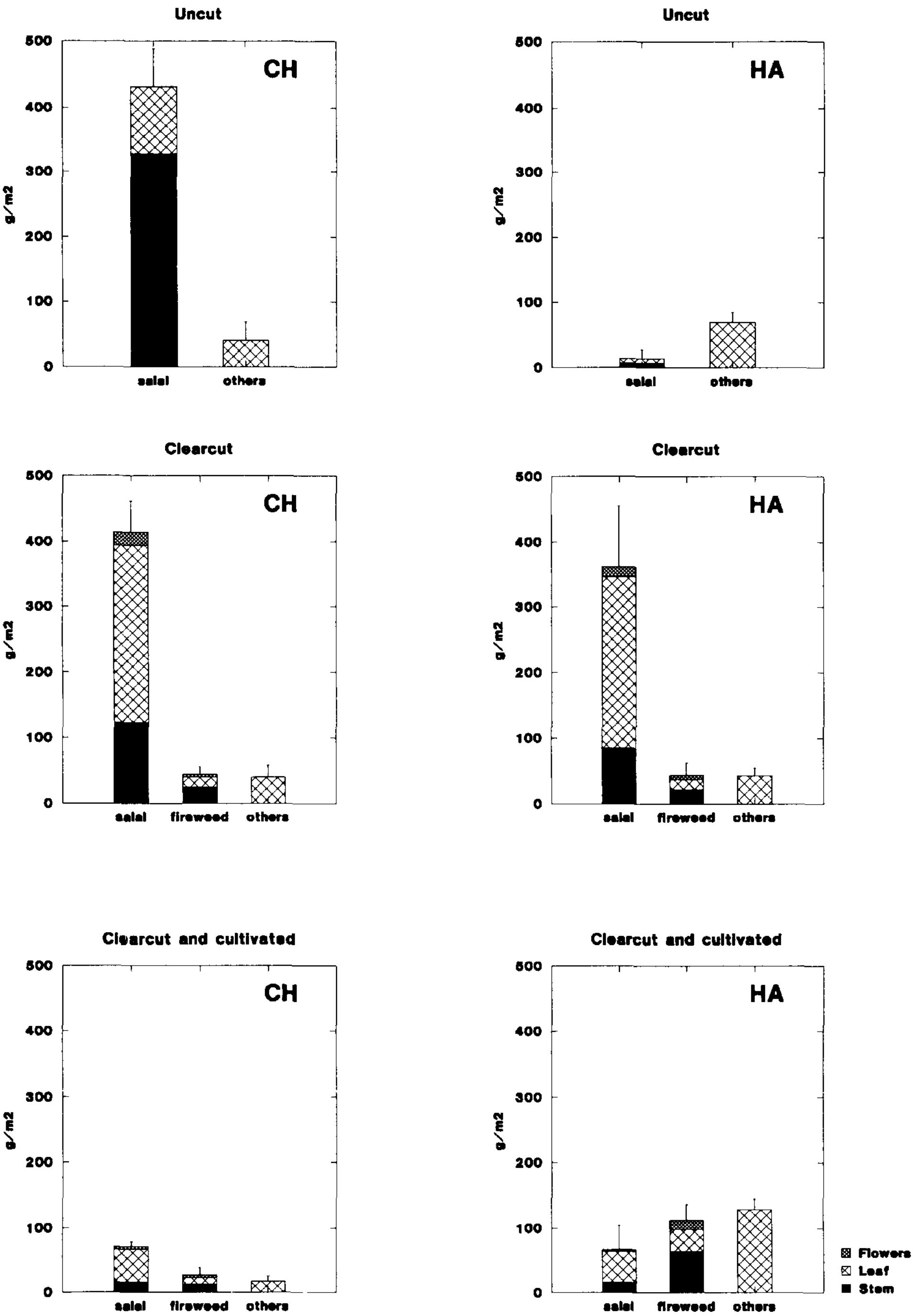

Fig. 1. Above-ground biomass of understorey species in the uncut forest, and after clearcutting, and clearcut and soil mixing in two adjacent forest types on northern Vancouver Island—an old-growth, cedar–hemlock (CH) type, and a second-growth hemlock–amabilis fir (HA) type. Values are the means from three plots in the uncut forest, and four plots in the treated areas; five 1 m^2 samples per plot. Bars indicate standard errors of each mean.

for decomposers, and its decomposition rate in soil is an indication of demand for available carbon. This depends on microbial population size, environmental conditions for decomposers (e.g. water, temperature), and the extent to which other nutrients are limiting microbial activity. The effect of the treatments on cellulose decomposition was different in each forest type. In the CH type decomposition was significantly slower ($\alpha \leqslant 0.05$) in CCM treatment (26% mass loss) than in the CC only treatment (58%). This lower rate of decomposition is in general agreement with the estimates of nutrient availability from extraction, mineralisation, and resin bags in the CH type. Therefore the availability of nutrients may be limiting decomposition in the CCM treatment in this type.

In the HA type, mass loss was significantly faster ($\alpha \leqslant 0.05$) in the CCM (59%) than in the other two treatments (31–33%). However, given that other indices of nutrient availability were generally no higher in this treatment, the reason for the increased rate of cellulose decomposition is unclear.

3.3. Understorey biomass

Above-ground understorey biomass in each site–treatment combination is shown in Fig. 1. Understorey biomass was much greater in the UC–CH than the UC–HA stands, owing the more open structure of the CH stands, and the high quantity of salal in the understorey. In the HA stands there was a minor component of salal and the 'others' component was largely coniferous advanced growth. Estimates from the CC plots on both the CH (414 g m^{-2}) and the HA (362 g m^{-2}) types indicated that, almost 5 years after cutting and burning, above-ground salal biomass had recovered to levels similar to that in the UC–CH stands (431 g m^{-2}), but was not yet at the maximum for CC sites in this area: 557 g m^{-2} reported 8 years after clearcutting and slash burning (Messier and Kimmins, 1991). The allocation to different plant parts in salal was different between the two treatments. In the CC area there was a much greater proportion in leaf than in stem components. Below-ground biomass is also likely to be much higher than in the UC–CH stands. Salal allocates a large proportion of biomass below ground following clearcutting (Messier and Kimmins, 1991), whereas allocation to fine roots in the UC stands is much lower (Messier, 1993). This large increase in leaf and fine root biomass following clearcutting and burning may explain the possible equivalence of nutrient uptake between the UC and CC treatments suggested above. On the HA sites, the biomass of salal increased substantially following clearcutting. This originates from small clumps surviving under the dense canopy of the HA stands; salal resprouts rapidly from rhizomes, and the burning treatment probably gives it an advantage over regenerating conifers. Unburnt HA stands are rapidly reoccupied by the dense stocking of conifer advanced growth following clearcutting.

The above-ground biomass of salal in both forest types was five times lower on the mixed plots than on the CC and UC treatments. Other species in the CH type were not greatly affected by mixing, but the biomass of fireweed and other species in the CCM plots in the HA type was more than twice that on the CC plots. These species may be benefiting from the increased availability of nutrient-rich sites brought about by the reduction in salal by the mixing treatment in the HA type.

4. Discussion

In general, the soil mixing treatment had no major effect on soil nutrients in the HA type and a detrimental impact in the CH type. These results, almost 5 years after the initial treatment, suggested that the anticipated benefits of mixing and soil disturbance (i.e. increased aeration and soil nutrient availability through the mixing of mineral and organic horizons, and the bringing to the surface of buried organic material where it can decompose more rapidly) have not occurred. Other studies indicated that the podzols in this area have a B horizon with low nutrient and organic matter content (Keenan, 1993). This contrasts with the higher organic matter content of this horizon in coastal Alaskan forest soils, where the benefits of soil mixing and windthrow have been documented (Ugolini et al., 1990). Organic material from deeper in the forest floor in the CH type have lower extractable and mineralisable N and P concentrations, compared with similar material in the HA type (Prescott et al., 1993). The chemical structure of this deeper humus material also differs, possibly owing to tannins leaching from salal (De Montigny et al., 1993). Therefore, nutrients in these layers may be held in complexes that a relatively resistant to decomposition and mineralisation. Mixing these layers with the L and F layers, which have higher available nutrients, has resulted in decreased nutrient availability in the CH type.

Given that the experimental treatment that was applied adequately simulated the effects of windthrow, the results of this study suggest that short-term effects of disturbance and mixing of the organic and mineral horizons were not the main cause of differences in nutrient availability and forest productivity between the two forest types. However, the treatment may differ from extensive windthrow in a number of ways. First, overturning of tree boles and lifting of roots may expose a greater area of mineral soil than was the case with this treatment. Second, some of this mineral soil is raised and gradually deposited in the pit created by the overturned roots, probably creating a more aerated soil with lower bulk density. Finally, a large amount of green foliage is deposited on the forest floor following a windthrow, and this may lead to short-term increases in nutrient availability. The mixing treatment in this study did not result in green foliage being deposited.

In general, N availability is a function of rate of decay of organic matter, and the balance between immobilisation and mineralisation during the process of decay. In temperate coniferous forests, when climatic factors are constant, these processes are associated with the chemical composition and physical structure of the litter inputs, particularly the concentration of N, and the concentration of recalcitrant, lignolytic carbon compounds (Swift et al., 1979). These two forest types have had long periods of dominance by different species. Under the N-limited conditions in this study area, cedar foliage has lower N concentration and higher contents of secondary compounds, and decays more slowly than hemlock foliage (Keenan, in preparation). Cedar wood also decays at a slower rate than hemlock (Sollins, 1981), because it contains secondary carbon compounds of high biotoxicity (Minore, 1983). In this locality, the topography is subdued, and disturbance owing to soil movement is rare. There has also been little intense wildfire, and the major disturbance to the forest cover is treefalls during windstorms, which result in large amounts of organic matter being deposited on the forest floor. These conditions allow the chemical characteristics of the species to express themselves fully within the vegetation soil system.

The lower N availability in forest floor of the CH type is therefore more likely to be a caused by the slower organic matter turnover and nutrient supply from more recalcitrant cedar foliar and woody litter, and differences in chemical structure of carbon–nitrogen compounds deeper in the organic profile. However, over the longer term, changes brought about by exposing deeper organic layers and the mineral soil may have a positive influence on nutrient availability and on productivity. Continued remeasurement of nutrient availability indices in this experiment would allow these potential developments to be monitored.

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