

Early vegetation recovery and element cycles on a clear-cut watershed in western Oregon¹

HENRY L. GHOLZ,² GLENN M. HAWK, ALSIE CAMPBELL, AND KERMIT CROMACK, JR.

Department of Forest Science, College of Forestry, Oregon State University, Corvallis, OR, U.S.A. 97331

AND

ALFRED T. BROWN

The Watts Doctor, 5691-H. S.E. Internal Way, Milwaukie, OR, U.S.A. 97222

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Aboveground biomass and leaf area, net primary production, and nutrient cycling through vegetation were studied for 3 years after clear-cutting (stems only) of a 10.24-ha watershed in the Oregon Cascade Mountains. The riparian zone and four main habitats were analyzed separately. In 3 years, aboveground net primary production increased from 5 to 112 g·m⁻²·year⁻¹ in the ridgetop habitat; midsummer aboveground biomass increased from 8 to 196 g/m² in the riparian zone and from 198 to 327 g/m² on the ridgetop. Other values were intermediate to these. Litter fall of species with perennial aboveground parts averaged 20–27% of standing biomass. Native annuals, especially *Aralia californica* Wats., dominated the riparian zone. *Senecio sylvaticus* L., an introduced species, dominated most of the rest of the watershed, except for the ridgetop habitat, which was dominated by residual woody shrubs. Uptake of N exceeded losses in streamflow the 1st year and was six times greater in the 2nd; uptake of P and K in that year was 2.5 and 3 times greater than losses. In the 3rd year, total uptake of K (2.5 g·m⁻²·year⁻¹) equaled the preclear-cutting level, and uptake of N (1.3 g·m⁻²·year⁻¹) and P (0.3 g·m⁻²·year⁻¹) was about half that level. No correlation was found between plant uptake and nutrient loss in streamflow. Uptake of all elements exceeded return through leaching and litter fall by 16%, except that of Mg, which exceeded return by 44%. Because of early dominance by species with annuals, the proportion of elements redistributed internally by vegetation was generally low. The amount of nutrients in flux through vegetation, atmosphere, and stream was small in comparison to the amount lost in the removal of tree stems.

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Les auteurs ont étudié, pendant trois ans après coupe rase, la production de biomasse aérienne et la surface foliaire de la végétation, de même que la production primaire et le cycle des éléments dans un bassin de 10,24 ha des Cascade Mountains de l'Oregon. La zone riparienne et les quatre habitats dominants furent analysés séparément. En 3 ans la production primaire nette aérienne a augmenté de 5 à 112 g·m⁻²·an⁻¹ dans l'habitat de crête; la biomasse aérienne à la mi-été est passée de 8 à 196 g/m² dans la zone riparienne et de 198 à 327 g/m² dans la zone de crête. Les valeurs de production des autres habitats se situaient entre ces dernières. La production de litière des espèces à tissus aériens pérennes s'élevait à 20–27% de la biomasse sur pied. Des plantes annuelles indigènes, en particulier *Aralia californica* Wats. dominaient la zone riparienne. *Senecio sylvaticus* L., une espèce introduite, dominait la plus grande partie du reste du bassin, sauf l'habitat de crête qui était dominé par des arbustes ligneux résiduels. Le prélèvement de N fut plus élevé que les pertes par drainage la 1^{re} année et six fois plus élevé la 2^e année; les prélèvements de P et K la 2^e année étaient, respectivement, 2,5 et 3 fois plus élevés que les pertes par lessivage profond. Durant la 3^e année, le prélèvement total de K (2,5 g·m⁻²·an⁻¹) s'élevait au même niveau que celui d'avant coupe, alors que les prélèvements de N (1,3 g·m⁻²·an⁻¹) et de P (0,3 g·m⁻²·an⁻¹) étaient environ la moitié de ceux d'avant coupe. On n'a pas observé de corrélation entre le prélèvement d'éléments par la végétation et les pertes par lessivage profond. Pour tous les éléments, le prélèvement était 16% plus élevé que la restitution par le pluvio-lessivage et la chute de litière, à l'exception de Mg dont la prélèvement était de 44% supérieur à la restitution. En raison de la dominance des plantes annuelles au début de la colonisation des stations, la proportion des éléments recyclés par translocation interne était en général faible. Par comparaison aux quantités d'éléments exportés par la récolte des troncs d'arbres, les quantités d'éléments en circulation dans la végétation, l'atmosphère et les ruisseaux étaient faibles.

[Traduit par le journal]

Introduction

Revegetation is undoubtedly the most important factor in ameliorating the effects of severe ecological disturbance such as the clear-cutting of a forest. It may alter many processes and

lead to decreased losses of essential elements in erosion and streamflow (Vitousek and Reiners 1975; Vitousek 1977 1981).

First, as leaf area and evapotranspiration increase, the smaller volume of water percolating through the soil decreases dissolved-nutrient losses and erosion. Clear-cutting has been shown to increase streamflow from a mixed hardwood watershed in West Virginia (Kochenderfer and Wendel 1983), but the difference decreased annually over 10 years and was closely related to increases in dry-matter production ($r^2 = 0.915$). Streamflow from pine plantations in northern Florida returned to preharvest levels within 2–3 years (Swindel *et al.* 1982). Leaf area on these sites reached half its maximum only 2 years

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²Present address: School of Forest Resources and Conservation, University of Florida, Gainesville, FL, U.S.A. 32611.

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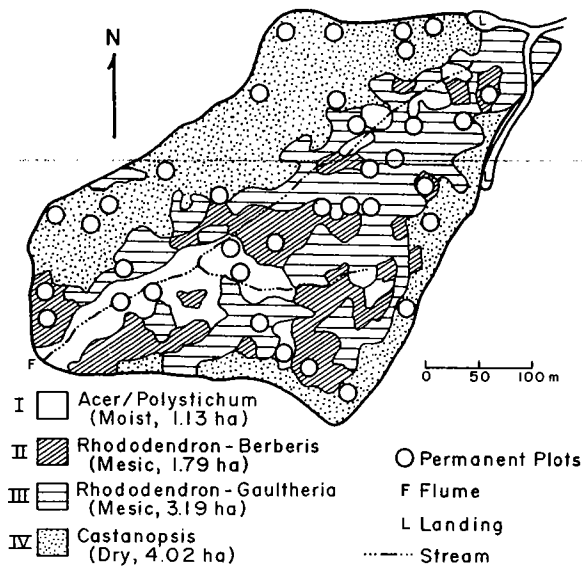


FIG. 1. Map of habitat types and locations of plots on WS-10. The 0.11-ha riparian zone is too narrow to be identified separately.

after harvest and its maximum in 10 years (Gholz and Fisher 1982). In a review of 94 studies through 1980, Bosch and Hewlett (1982) attempted to generalize the relationship between increased streamflow (or decreased evapotranspiration) and forest vegetation removal. The correlation was weak (hardwood forest, $r^2 = 0.506$; conifer forest, $r^2 = 0.650$), perhaps because the rate of canopy reestablishment varied.

Second, nutrient uptake may increase soon after clear-cutting if fast-growing perennial species such as pin cherry (*Prunus pensylvanica*), black locust (*Robinia pseudoacacia*), or red alder (*Alnus rubra*) (Marks 1974; Cole *et al.* 1977; Boring *et al.* 1981) become established. In these cases, uptake rates may reach preclear-cutting levels in 10 to 20 years (in Marks' study, they reached preclear-cutting levels in only 4 years).

Third, as fine roots bind the soil (O'Loughlin and Ziemer 1982) and vegetation reduces the impact of rain drops, erosion may be further reduced. Increasing shade may cool the soil, inhibiting the production of more mobile nutrient forms through mineralization and nitrification (Dominski 1971).

Although vegetation recovery is important, few quantitative studies of net primary production (NPP), nutrient uptake and return, leaf-area increase, and other vegetation processes of a watershed have been made during the first critical years after clear-cutting when streamflow increases and nutrient losses are greatest (Marks 1974; Likens *et al.* 1978; Snedaker 1980; Boring *et al.* 1981).

In this study, we examine the recovery of vegetation on a watershed in western Oregon for the first 3 years after clear-cutting, and quantify fluxes of nutrients in the internal cycle to determine how patterns change when a watershed is clear-cut. We compare the magnitude of internal fluxes with fluxes across the ecosystem boundary. We have subdivided the watershed to determine whether particular areas, such as the riparian zone, dominate the recovery process and are disproportionately important as a filter of dissolved ions. No other studies have addressed the relative importance of different zones across a watershed.

Study area

The study site, a 10.24-ha watershed (WS-10) in the H. J. Andrews

TABLE 1. Measurements of plant species on WS-10 permanent plots, taken in 1976, 1977, and 1978, and used in regression equations (Gholz *et al.* 1979)

Species	Measurement (cm)
<i>Acer circinatum</i>	Basal diameter
<i>Acer macrophyllum</i>	Basal diameter, dbh
<i>Adiantum pedatum</i>	Total length
<i>Amelanchier alnifolia</i>	Basal diameter
<i>Aralia californica</i>	Basal diameter
<i>Athyrium filix-femina</i>	Number of fronds; average frond length
<i>Berberis nervosa</i>	Percentage of cover
<i>Blechnum spicant</i>	Number of fronds; average frond length
<i>Castanopsis chrysophylla</i>	Basal diameter, dbh
<i>Corylus californica</i>	Basal diameter, dbh
<i>Cornus nuttallii</i>	Basal diameter, dbh
<i>Dryopteris austriaca</i>	Number of fronds; average frond length
<i>Epilobium angustifolium</i>	Total stem length
<i>Epilobium paniculatum</i>	Basal diameter, plant height
<i>Epilobium watsonii</i>	Plant height
<i>Gaultheria shallon</i>	Percentage of cover
<i>Holodiscus discolor</i>	Basal diameter
<i>Oxalis oregana</i>	Percentage of cover
<i>Petasites frigidus</i>	Leaf blade length
<i>Polystichum munitum</i>	Number of fronds; average frond length
<i>Pseudotsuga menziesii</i>	Basal diameter, dbh
<i>Rhododendron macrophyllum</i>	Basal diameter, dbh
<i>Rhamnus purshiana</i>	Basal diameter, dbh
<i>Ribes</i> spp.	Basal area, dbh
<i>Rubus</i> spp.	Basal diameter, dbh
<i>Salix</i> spp.	Basal diameter, dbh
<i>Senecio sylvaticus</i>	Total stem length
<i>Stachys cooleyae</i>	Total length
<i>Symphoricarpos mollis</i>	Basal diameter
<i>Taxus brevifolia</i>	Basal diameter, dbh
<i>Thuja plicata</i>	Basal diameter, dbh
<i>Tsuga heterophylla</i>	Basal diameter, dbh
<i>Vaccinium</i> spp.	Basal diameter, dbh
<i>Xerophyllum tenax</i>	Clump basal diameter; compressed clump length

NOTE: Percentage of cover, estimated for all species, is given only if it was an equation variable. Diameter at breast height (dbh) of all trees ≥ 5 cm was measured on each plot.

Experimental Forest (44°N, 122°30'W) 60 km east of Eugene, Oregon, was gauged by the United States Forest Service and was monitored for input and loss of elements as part of the International Biological Program from 1973 to 1975. It has since been monitored as part of other continuing projects. Five plant communities, a riparian zone and four habitats (one moist, two mesic, and one dry, described by Hawk 1979) form a progression up a steep slope (Fig. 1). Soils are generally deep, well-drained, typic dystochrepts, underlain by andesitic tuffs and breccias at a variable depth (Anonymous 1960; Harr 1977; James 1977). Mean annual precipitation is 2300 mm, with 80% falling from October through April, and mean annual temperature is 8.5°C (1972–1976 averages from Waring *et al.* 1978). Snow is frequent in the winter, although deep and long-lasting snowpacks are rare.

Before clear-cutting, the stands were old-growth Douglas-fir (*Pseudotsuga menziesii* Mirb. (Franco) var. *menziesii*) with a well-developed understory of western hemlock (*Tsuga heterophylla* Raf. (Sarg.)). Aboveground NPP averaged $800 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$, belowground NPP was presumed to be 20% of aboveground NPP, and aboveground biomass increments were negative (Grier and Logan 1977). Understory vegetation ranged from sparse herbs, ferns, and

TABLE 2. Ground cover (± 1 SE, excluding stems and stumps) on the four main terrestrial habitats in WS-10 for 1973 and the first 3 years after clear-cutting

Habitat	Litter (%)				Mineral soil (%)				Rock (%)			Moss (%)				Down logs (%) 1976-1978
	1973	1976	1977	1978	1973 ^a	1976	1977	1978	1976	1977	1978	1973	1976	1977	1978	
1 (moist)	50	56 (12)	63 (11)	63 (5)	3	32 (5)	26 (7)	29 (7)	1.4 (1.2)	0.4 (0.4)	0.5 (0.4)	49	7 (4)	3 (1)	3 (3)	10 (6)
2 (mesic)	73	74 (5)	82 (4)	76 (5)	6	17 (4)	10 (3)	16 (3)	0.2 (0.2)	0.4 (0.3)	0.3 (0.2)	24	7 (2)	3 (1)	1 (1)	5 (2)
3 (mesic)	73	62 (7)	82 (4)	71 (4)	3	25 (7)	15 (4)	23 (4)	1.4 (0.9)	0.4 (0.2)	0.3 (0.2)	14	7 (3)	3 (1)	1 (1)	3 (1)
4 (dry)	87	79 (4)	87 (2)	75 (2)	4	15 (3)	7 (2)	17 (3)	0.0 (0.1)	0.0 (0.1)	0.1 (0.1)	10	2 (1)	1 (0)	1 (1)	4 (1)
Mean	76	70	82	73	4	21	12	20	0.7	0.3	0.2	18	5	2	1	4

NOTE: Totals for 1976, 1977, and 1978 can be >100% because down logs were often suspended over other ground-cover types. Mean percentages are weighted by the proportion of habitat area to total watershed area.

^aMineral soil for 1973 includes rock cover.

deciduous shrubs in the moist habitat to dense, evergreen, woody shrubs in the dry habitat. Preclear-cutting nutrient cycles for WS-10 have been described by Sollins *et al.* (1980).

Hawk (1979) established a series of thirty-six 10 × 15 m permanent plots in 1973, distributed in proportion to the area of the four main habitat types (Fig. 1). Each contained sixteen 1 × 1 m subplots that were the basic units of study for this project. We subjectively delineated the riparian zone (0.11 ha) in fall 1975 after the clear-cutting as an area 1 to 15 m wide, depending on the slope, along the perennial portions of both branches of the first-order stream draining the watershed (Fig. 1).

In summer 1975, WS-10 was clear-cut. Boles of cut trees and unmerchantable woody material >20 cm in diameter or >2.4 m in length, including many logs lying on the ground, were removed, so that large woody slash was disposed of without burning. In 1976, the watershed was planted with 2-year-old bare-root seedlings of Douglas-fir on a 2.4 × 2.4 m spacing.

Methods

Estimating organic mass, distribution, and production

Each 1 × 1 m subplot was surveyed in early August 1976, 1977, and 1978 for vegetation dimensions and the percentage of cover by logs, bare soil, rock, and litter. Data for 1973, when the plots were established and surveyed, were used for comparisons.

To obtain accurate estimates of aboveground plant biomass for each year after clear-cutting, we measured various dimensions of all plants on the 36 plots in the four main habitats. (The riparian zone was sampled separately; see following section.) These measurements were coupled with those from destructive sampling, mainly off WS-10, to derive regression equations for computing annual biomass of foliage and wood ("dimension analysis," Whittaker and Marks 1975).

Because harvest was in progress in August 1975 and vegetation surveys were impossible to make, we assumed that biomass of perennial vegetation in 1975 was equal to that in 1976. In 1975-1976, the 36 plots were relocated and riparian transects and sampling procedures were initiated. The residual plants in 1976 more closely resembled understory, shade-growing plants than sun-growing plants; therefore, we used biomass equations based on data from understories of other old stands in the area (Gholz *et al.* 1979) for computing the 1976 biomass. For 1977 and 1978, we used equations generated from destructive sampling in nearby clearcuts and from sampling on WS-10 itself. The implications of these decisions are addressed in the discussion. All equations have been fully documented by Gholz *et al.* (1979).

Variables measured on each 1 × 1 m subplot are listed in Table 1. Although foliage losses from logging injury were not directly assessed, many measurements used in the equations, such as percentage of cover or number of fronds, account for such damage. All-sided leaf area was calculated for each species from foliage bio-

mass and specific leaf area (square centimetres of leaf blade area per gram dry mass) of samples collected during plot surveys. Diameter of most woody shrubs was measured at the litter surface (Table 1). Stem lengths were measured mainly on summer spike-producing species, such as *Senecio sylvaticus* L. and *Epilobium* spp. Ferns were measured for number of fronds and average frond lengths. Biomass of herbs and minor species for which equations were unavailable was computed by equations for species of similar morphology, or as a linear function of percentage of cover and the average specific leaf area (200 cm²/g). Data were expressed in grams per plant, grams per clump (when individual whole plants such as *Polystichum munitum* (Kaulf.) Presl and *Xerophyllum tenax* (Pursh) Nutt. were not discernable), or grams per square metre (where percentage of cover was an equation variable). Data for each species, plot, and habitat type included foliage biomass (new and old for evergreen species), branch biomass (if separated), stem biomass, and leaf surface area.

Riparian zone vegetation was surveyed on thirty 1-m wide transects located at regular intervals perpendicular to the stream channel. Because logging had left only a sparse community in 1976, every leaf was counted and all woody plant parts were measured. A subsample was randomly selected from each species for determining dry mass. Vegetation in the transects in 1977 and 1978 was measured in the same way as that elsewhere on the watershed (Table 1).

Aboveground litter production on WS-10 was sorted into three classes, "foliage," "wood and bark," and "other" (e.g., flower parts), then dried at 70°C for 24 h and weighed to 1 mg. Six collection techniques were used.

(1) Fruit ("other" classification) and woody debris were collected from October 1977 through September 1978 in 1 × 1 m litter traps randomly placed in numbers proportional to habitat area. Woody litter fall for each habitat in 1975-1976 and 1976-1977 was computed as (woody biomass ÷ total biomass in August 1976-1977) × woody litter fall in 1977-1978.

(2) Foliage litter of *Rhododendron macrophyllum* G. Don, a common woody shrub on WS-10, was estimated by counting leaves by age-class, marking them, and collecting fallen leaves monthly from October 1977 through September 1978 from plants of various sizes, 10 in a moist and 10 in a dry area. Litter fall for the entire watershed was estimated from the linear relationship between peak August biomass and annual litter production for both areas (Fig. 2).

(3) Foliage litter of *Gaultheria shallon* Pursh and *Berberis nervosa* Pursh (the two most common low evergreen shrubs) was measured on 10 1 × 1 m plots with 2 to 100% cover in the *Rhododendron* areas. Dead leaves were removed initially, then newly fallen dead leaves were collected monthly from August 1977 through July 1978. Litter fall was calculated as in technique 2 from a linear relationship between annual litter production and August foliage mass (Fig. 2).

(4) Ten clumps each of *Polystichum* and *Xerophyllum* of different sizes were surrounded by colored tape, measured, and cleared of dead

TABLE 3. Mid-August aboveground biomass and leaf area of all vegetation (± 1 SE) and the percentage of biomass and leaf area contributed by invading annual species (± 1 SE), by habitat type

Habitat	Foliage biomass (g/m ²)			Stem and branch biomass (g/m ²)			Leaf area (m ² /m ²)		
	1976	1977	1978	1976	1977	1978	1976	1977	1978
(a) All vegetation									
Riparian zone	6.0	80.4(26.4)	98.1(29.8)	2.0	95.0(45.3)	97.9(44.4)	0.13	1.96	2.43
1 (moist)	11.3(4.0)	10.8(3.8)	44.4(11.9)	15.6(8.7)	34.1(14.7)	112.1(58.7)	0.2(0.1)	0.2(0.1)	0.8(0.2)
2 (mesic)	21.5(7.3)	33.8(11.3)	80.5(15.8)	49.5(19.2)	76.8(22.6)	144.6(39.8)	0.4(0.2)	0.6(0.2)	1.4(0.2)
3 (mesic)	15.7(4.1)	25.1(4.3)	73.9(24.2)	74.0(55.2)	106.2(55.5)	161.7(86.1)	0.4(0.2)	0.6(0.2)	1.3(0.4)
4 (dry)	66.1(15.1)	92.1(15.2)	132.6(13.4)	131.5(50.2)	153.2(53.1)	194.4(62.5)	1.2(0.3)	1.4(0.3)	2.1(0.3)
Mean	36.0	51.9	95.1	85.1	111.4	164.5	0.7	0.9	1.6
Habitat	Foliage biomass (%)			Stem and branch biomass (%)			Leaf area (%)		
	1976	1977	1978	1976	1977	1978	1976	1977	1978
(b) Proportion contributed by invading annual species									
Riparian zone	<0.1	9.5	5.3	<0.1	23.0	7.8	<0.1	14.9	6.9
1 (moist)	0.1(0.2)	49.4(17.9)	45.6(14.6)	0.2(0.1)	61.5(14.9)	69.4(13.4)	0.2(0.3)	56.2(15.6)	49.3(14.7)
2 (mesic)	0.1(0.0)	26.5(5.0)	34.0(12.4)	0.1(0.0)	50.4(7.6)	48.0(12.9)	0.3(0.3)	27.6(5.3)	32.6(11.8)
3 (mesic)	0.2(0.1)	31.9(5.8)	32.5(9.6)	0.1(0.0)	62.9(9.6)	57.7(9.3)	0.2(0.2)	34.0(6.3)	34.2(9.2)
4 (dry)	0.0(0.0)	6.5(2.8)	2.1(2.8)	0.0(0.0)	19.0(6.5)	13.6(3.4)	0.2(0.2)	7.7(3.1)	3.9(1.0)
Mean	0.1	22.7	22.4	0.1	42.9	39.5	0.2	24.8	23.4

NOTE: Means are weighted by the proportion of habitat area to total watershed area.

plant material. New dead material was removed from the taped areas monthly in 1977–1978. Litter production was calculated as in technique 2 from linear relationships (Fig. 2). Litter fall relationships derived in 1977–1978 by techniques 2–4 were used with plant measurements from 1975–1976 and 1976–1977 for estimating foliar litter fall.

(5) Peak foliage litter fall of deciduous species was calculated as August foliage biomass corrected downward to account for loss in mass before abscission. The correction factor was determined by sampling at least five leaves from at least three plants of each of the 10 most common deciduous species in each habitat, once in early August and again as they senesced in 1976, 1977, and 1978, and by comparing specific leaf areas.

(6) Litter fall of species with annual aboveground parts was assumed to be 100% of August biomass.

(7) Litter fall for herbs not otherwise tallied was assumed to be 50% of their total standing crop (about half of these species had annual aboveground parts).

No estimate of belowground NPP was made. Aboveground NPP was calculated as the sum of annual increment in perennial biomass plus litter fall (which included turnover of annuals).

Element sampling and analysis

For element determinations, litter fall was composited in three replicates per year of "foliage," "wood and bark," and "other" samples. Samples for estimating element concentrations in standing plant biomass were collected in early August of each year. Replicated foliage samples, including the petioles or rachis, were collected from random points in each habitat and the riparian zone for 15 major species in 1976, 20 species in 1977. Twenty-two species from the riparian zone were collected in 1978. Ten random samples (1 × 1 m ground area) per habitat type were made for "miscellaneous herbs." In 1976, because of the small leaf biomass in the riparian zone, a single composite sample was made for all species. In August 1977, from 3 to 20 5-cm-long stem sections were removed from seven species on WS-10 or nearby clear-cut watersheds. Data for three other species were available from Russel (1973).

All samples were dried to 70°C, ground to pass a 0.16-mm screen in a Wiley Mill, and analyzed for N, P, K, Na, Mg, and Ca. N concentrations were determined by the micro-Kjeldahl method (Jackson 1958), and P by the molybdate-blue method, with ascorbic

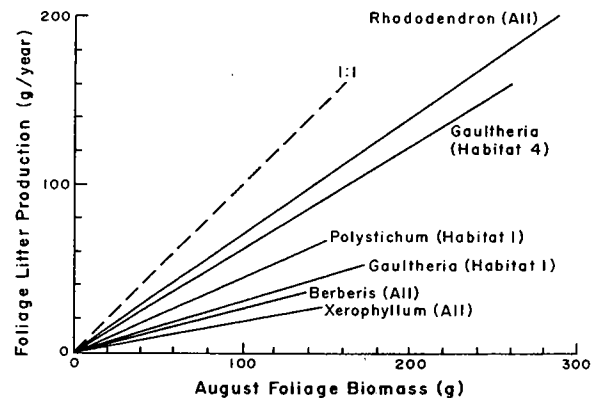


FIG. 2. Annual foliar litter production of selected evergreen species as a function of August 1978 foliage biomass on WS-10. Values per stem for *Rhododendron*, per clump for *Polystichum* and *Xerophyllum*, and per square metre for *Gaultheria* and *Berberis* correspond to August biomass estimates obtained from the various regression equations.

acid as the reducing agent (Rand 1976). Samples for cation analysis were first digested with perchloric–nitric acid, and cations were determined by standard methods of atomic absorption spectroscopy.

Internal redistribution, the proportion of elements annually relocated from foliage of perennials before senescence, was calculated as the difference between the amount of the elements in August foliage and the amount in litter fall of the eight major perennial species: *Xerophyllum*, *Gaultheria*, *Castanopsis chrysophylla* (Dougl.) A. DC., *Acer macrophyllum* Pursh and *A. circinatum* Pursh, *Rhododendron*, *Berberis*, and *Polystichum*. In each habitat where they were encountered, five individuals of each species were monitored. Specific leaf areas (square centimetres per gram) and nutrient concentrations of each species were determined from the oldest age class of foliage in August 1977 and from new litter collected throughout September (when no precipitation was recorded). By combining the changes in weight and nutrient concentrations, we calculated the amounts of internal redistribution. Leaching was not measured di-

TABLE 4. Estimates of mean annual litter fall, aboveground biomass increment, and aboveground net primary production (NPP) for the first 3 years after clear-cutting WS-10

Period	Habitat	Litter fall (L)				Total	Biomass increment (ΔB) ^c	NPP (L + ΔB)
		Foliage ^a	Wood and bark	Annual plant species	Other ^b			
Nov. 1975– Oct. 1976	Riparian zone	4.5	<0.1	<0.1	—	4.5	0	4.5
	1	5.1	0.8	<0.1	1.2	7.1	0	7.1
	2	9.2	1.0	<0.1	1.6	11.8	0	11.8
	3	8.1	3.8	<0.1	1.5	13.5	0	13.5
	4	31.5	4.7	<0.1	3.5	39.7	0	39.7
	Mean	17.3	3.3	<0.1	2.3	22.9	0	22.9
Nov. 1976– Oct. 1977	Riparian zone	18.1	4.5	62.4	—	85.0	97.0	182.0
	1	7.2	1.8	19.1	1.4	29.5	-5.6	23.9
	2	19.3	1.5	29.3	2.2	52.3	-0.2	52.1
	3	17.6	5.4	30.7	2.0	55.7	3.9	59.6
	4	51.7	5.5	12.3	7.2	76.7	38.0	114.7
	Mean	30.3	4.4	22.3	4.0	60.5	15.7	76.1
Nov. 1977– Oct. 1978	Riparian zone	15.4	4.5	90.5	—	110.4	1.7	112.1
	1	33.8	6.0	90.6	3.9	134.3	19.0	153.3
	2	47.1	2.8	74.6	5.4	129.9	55.1	185.0
	3	56.3	8.2	118.0	8.6	191.1	-10.6	180.5
	4	71.8	6.9	13.6	15.2	107.5	79.7	187.2
	Mean	57.9	6.5	66.1	10.1	140.7	40.1	180.7

NOTE: Means are weighted by the ratio of habitat area to total watershed area. All values are in grams per square metre per year.

^aFoliage values do not include turnover of annual plant species.

^bNo estimate was obtained for the riparian zone.

^c ΔB for 1975–1976 is assumed to be 0. Values do not include annual plant turnover.

rectly but was computed by mass balance for each species and year as the amount of a nutrient in foliage that could not be accounted for by litter fall, internal redistribution, and new (≤ 1 -year-old) foliage. Annual uptake was calculated as the sum of elements in biomass increment, litter fall, and leaching. Values for the entire watershed were computed from means for habitat types weighted in proportion to the area of each habitat.

Results

Forest floor cover

The percentage of the ground covered by litter (O_1 and O_2 layers) did not change significantly as a result of the clear-cutting and only ranged from 70 to 80% over the watershed in 1973 and 1976 through 1978. In all years, before or after the clear-cutting, the moist habitat had the lowest litter cover (significantly different from other habitats at $p = 0.05$). In the original stands, lower litter cover in the moister habitats was balanced by increased bryophyte cover. Bryophytes were essentially eliminated by the logging and replaced by bare soil, and had shown no recovery by 1978. Decreases in moss cover and increases in bare soil were highly significant ($p \leq 0.05$). The percentage covered by rocks and logs was constant through the 3rd year.

The average cover of fallen logs in the preharvest stands was about 20% (Sollins *et al.* 1980). As mean log cover in 1976, 1977, and 1978 was only 4%, as much as 80% of the 190 Mg/ha of the original fallen log biomass (Grier and Logan 1977) was removed during the clear-cutting.

Biomass and leaf area

The vegetation on WS-10 in 1976, 1 year after logging, represented essentially all residual biomass. Few species had

invaded and little or no sprouting had occurred. The range in individual plot values was substantial, owing to uneven distribution of logging damage and variation in preclear-cutting understorey biomass.

Peak biomass and leaf area generally more than doubled in 3 years (Table 3). All increases from 1976 to 1978 were statistically significant ($p \leq 0.05$), although some year-to-year changes were not. Annual increase was greatest in the riparian zone in 1976–1977 because of sprouts of residual shrub species (especially *Cornus nuttallii* Aud. ex T. & G. and *Acer* spp.), and because of reinvasion of indigenous annuals, mainly *Aralia californica* Wats.

We classified 14 species, all herbaceous, as "invaders," that is, species not present in 1973. *Senecio sylvaticus* (an introduced annual) and *Epilobium angustifolium* L. (a native annual) represented 95% of the invading biomass and leaf area, *Senecio* alone about 90%. Less than 15% of riparian leaf area over the 3 years was from invading species (Table 3b). In marked contrast, more than 50% of the biomass of habitats 1, 2, and 3 and leaf area habitat 1 was made up of invading species by 1977, an increase from essentially 0 in 1976 (Table 3b). Few such species invaded the dry habitat (Table 3b), which may attest to the poor competitive ability of *Senecio* under dry conditions (West and Chilcote 1968).

Although leaf area more than doubled from 1976 to 1978, the watershed mean in 1978 was still only 6% that of the original stand (Table 3a). The relative increase was least in dry habitat 4, 8.4% of the original value by 1978. Values for the riparian zone, which 3 years after logging had by far the greatest leaf area, 2.4 m²/m² (Table 3a), could not be compared because no preharvest values were available.

TABLE 5. Element contents (grams per square metre) in standing crops, August 1976, 1977, and 1978

Year	Habitat	N	P	K	Na	Mg	Ca
1976 ^a	Riparian zone	0.16	0.03	0.24	0.002	0.02	0.16
	1	0.20	0.03	0.22	0.002	0.03	0.15
	2	0.33	0.05	0.33	0.003	0.08	0.40
	3	0.38	0.07	0.35	0.003	0.06	0.54
	4	0.88	0.14	0.62	0.007	0.15	0.94
	Mean	0.55	0.09	0.44	0.005	0.10	0.63
1977	Riparian zone	1.56(16)	0.35(12)	2.29(29)	0.033(40)	0.67(15)	1.78(16)
	1	0.30(62)	0.06(82)	0.66(84)	0.008(75)	0.14(47)	0.31(61)
	2	0.67(42)	0.15(49)	1.20(70)	0.017(76)	0.36(28)	0.78(36)
	3	0.60(41)	0.14(49)	1.23(71)	0.009(67)	0.24(11)	0.87(32)
	4	1.24(7)	0.19(13)	1.53(21)	0.013(77)	0.69(2)	1.41(7)
	Mean	0.84(30)	0.15(38)	1.28(52)	0.012(74)	0.43(15)	1.01(26)
1978	Riparian zone	2.02(5)	0.48(8)	3.01(9)	0.015(7)	0.85(4)	1.62(6)
	1	1.41(68)	0.34(73)	3.07(86)	0.045(73)	0.51(77)	1.15(81)
	2	1.61(49)	0.32(63)	2.91(75)	0.046(78)	0.84(38)	1.76(44)
	3	1.54(69)	0.38(73)	4.14(84)	0.029(86)	0.52(27)	1.65(72)
	4	1.95(9)	0.30(12)	1.97(13)	0.017(12)	1.20(1)	2.14(4)
	Mean	1.70(42)	0.33(47)	2.94(55)	0.029(54)	0.85(24)	1.81(41)

NOTE: The percentage contribution of invading annual species is in parentheses. Means are weighted by the proportion of habitat area to total watershed area.

^aThe invading annual species represented <0.1% in 1976.

Litter fall

Because of the variety of methods used to determine litter fall, means for habitat and year were not compared statistically. In 1977 and 1978, most litter fell in August, September, and October in all habitats. Large September peaks for litter classified "other" in dry habitat 4 reflected large and sudden input of *Castanopsis* fruits.

We estimate that the average total litter produced annually on WS-10 increased by a factor of 6 from 1976 to 1978 (Table 4). Turnover of species with annual tops, primarily *Senecio*, increased from <0.1 g/m² in 1975–1976 to an average 66.1 g/m² in 1977–1978. In that year, foliage from perennial species contributed 57.9 g/m²; wood and bark and other litter added <18 g/m².

Litter fall in 1975–1976 was almost an order of magnitude less in the riparian zone than in the dry habitat. In the riparian zone, it increased 19 times by 1976–1977, and was greatest in that habitat. By 1977–1978, the dry habitat and riparian zone were producing the least litter over the watershed as *Senecio* turnover increased to a maximum in the intermediate habitats.

Net primary production (NPP)

Litter fall was a far greater component of NPP than was biomass increment in the first three postclear-cutting years (Table 4). In 1975–1976, virtually all NPP was foliar litter fall from residual vegetation. However, in 1976–1977, about one-third of NPP was production by annuals (mainly invaders) in proportions ranging from 10% in dry habitat 4 to 80% in moist habitat 1. By 1977–1978, the contribution of annuals to NPP had risen to a mean 37%, ranging from 7% in the dry habitat to 81% in the riparian zone. *Aralia* was the most important species in the riparian zone and *Senecio* was most important elsewhere.

The great increase in NPP in the riparian zone from 1975–1976 to 1976–1977 was a consequence of both biomass increment and litter fall. Much of the increment occurred in

clumps of *Cornus* and *Acer circinatum*. Few sprouts died in 1977–1978, but there was little additional sprouting. NPP by annuals and litter production by perennials increased 30% in 1977–1978; perennial biomass increment was minor.

Biomass increment varied markedly over the watershed throughout the study. Habitats 1 and 2 had negative values in 1977; habitat 3 was near zero in 1977, negative in 1978 (negative values result when mortality is greater than the biomass increase of the remaining live vegetation). By 1978, above-ground NPP was 20% (moist habitat 1) to 29% (mesic habitat 3) that of preharvest old-growth forests and was rather uniform over the upper portions of the watershed (Table 3).

Element distribution

Analyses of N, P, K, Ca, Mg, and Na in the foliage and wood of the major species from WS-10⁴ showed that foliage of a given species from the riparian zone or moist habitats had higher concentrations of all nutrients than foliage from dryer habitats. Annual species also had higher concentrations in both foliage and stems than perennial species; in particular, *Senecio* and *Aralia* had more N and K than the other six invading species. Concentrations did not consistently change from 1976 through 1978 for a given species at a given location. Litter fall analyses indicated that nutrient concentrations were always lowest in woody litter. The "other" category had consistently higher N and K concentrations and lower Mg and Ca concentrations than did foliage, but showed no trend for P or Na.

Contents of the six elements in August 1976, 1977, and 1978 standing crops are given in Table 5 as the product of biomass and element concentration computed for each species and summed over species by habitat. In 1977, *Senecio* and *Epi-lobium* contained more than 80% of aboveground P and K. In 1978, they contained more than 80% of K in moist habitat 1 and mesic habitat 3, and a similar percentage of Na in habitat 3 and

⁴Data and statistical analyses are available from H. L. Gholz.

TABLE 6. Summary of element dynamics associated with vegetational recovery of WS-10 for the 3 years after tree harvest

Component	Year	N	P	K	Na	Mg	Ca
Atmospheric input ^a (g·m ⁻² ·year ⁻¹)		0.20	0.03	0.12	0.55	0.12	0.31
Aboveground return (g·m ⁻² ·year ⁻¹)							
Litter fall	1975-1976	0.153	0.023	0.051	0.001	0.031	0.187
	1976-1977	0.364	0.072	0.464	0.004	0.102	0.408
	1977-1978	0.891	0.165	1.595	0.011	0.214	1.272
Leaching	1975-1976	0.052	0.006	0.073	0.000	0.008	0.004
	1976-1977	0.079	0.014	0.256	0.022	0.018	0.009
	1977-1978	0.146	0.057	0.562	0.038	0.150	0.073
Total leaching + litter fall	1975-1976	0.206	0.029	0.124	0.001	0.039	0.191
	1976-1977	0.443	0.086	0.720	0.026	0.120	0.417
	1977-1978	1.037	0.222	2.157	0.49	0.364	1.345
Peak standing crop (g/m ²)	1975-1976	0.55	0.09	0.44	0.010	0.10	0.63
	1976-1977	0.83	0.15	1.28	0.012	0.43	1.01
	1977-1978	1.70	0.33	2.94	0.029	0.85	1.81
Intracommunity (g·m ⁻² ·year ⁻¹)							
Increment	1975-1976	0	0	0	0	0	0
	1976-1977	0.051	0.012	0.155	0.001	0.113	0.093
	1977-1978	0.194	0.036	0.274	0.002	0.161	0.205
Internal redistribution	1975-1976	0.057	0.004	0.061	0.0001	0.009	-0.026
	1976-1977	0.014	0.003	0.149	0.0004	0.027	-0.067
	1977-1978	0.049	0.032	0.225	0.0003	0.091	-0.446
Total aboveground uptake (aboveground return + increment, g·m ⁻² ·year ⁻¹)	1975-1976	0.206	0.029	0.124	0.001	0.039	0.191
	1976-1977	0.505	0.098	0.875	0.027	0.233	0.510
	1977-1978	1.303	0.258	2.431	0.051	0.525	1.550
Total uptake : total return	1975-1976	1.00	1.00	1.00	1.00	1.00	1.00
	1976-1977	1.11	1.14	1.22	1.04	1.94	1.22
	1977-1978	1.18	1.16	1.13	1.04	1.44	1.15
Total uptake : input	1975-1976	1.03	0.97	1.03	0.00	0.33	0.62
	1975-1977	2.53	3.27	7.29	0.05	1.94	1.65
	1977-1978	6.52	8.60	20.26	0.09	4.38	5.00
Total uptake : preharvest uptake	1975-1976	0.10	0.05	0.06	0.01	NA	0.05
	1976-1977	0.25	0.17	0.42	0.18	NA	0.12
	1977-1978	0.64	0.45	1.16	0.34	NA	0.37
Total dissolved element loss in streamflow ^b	1975-1976	0.13	0.12	0.6	4.1	1.6	7.2
	1976-1977	0.08	0.04	0.3	1.8	0.7	3.5
	1977-1978	0.21	0.11	0.6	0.4	1.5	5.3
Total uptake : total dissolved element loss in streamflow	1975-1976	1.59	0.24	0.21	0.00	0.02	0.03
	1976-1977	6.31	2.45	2.92	0.02	0.33	0.15
	1977-1978	6.21	2.35	4.05	0.01	0.35	0.26

NOTE: Values are watershed means weighted by the proportion of habitat area to total watershed area. NA, not applicable.

^aWeighted mean values for 1972-1974 from Fredriksen (1975).

^bStreamflow for the 3 water years (Oct. 1 - Sept. 30) were 196, 76, and 186 cm (R. L. Frederiksen, U.S. Forest Service Forestry Sciences Laboratory, Corvallis, Oregon, personal communication).

of Ca in habitat 1. Total standing crop increased from 1976 to 1978 by factors of 2.9 for Ca, 3.1 for N, 3.7 for P, 5.8 for Na, 6.7 for K, and 8.5 for Mg.

Across WS-10 from 1975 to 1978, standing crops, leaching and litter fall, perennial biomass increment, and uptake steadily increased. Leaching plus litter fall was similar to uptake, so that biomass increments were small but uptake rates relatively large (Table 6). By the end of the first year, uptake rates for N, P, and K equaled atmospheric input, and by 1978, uptake for all elements except Na substantially exceeded atmospheric input (Table 6). Uptake of K equaled that of preharvest stands by 1978. Uptake of the other elements, including Na, ranged from 37 to 64% of preharvest values. In the 1st year, uptake of N was 1 to 6 times losses at the stream gauge; in the 2nd year, uptake of N, P, and K was 2.5 to 6 times losses. However, over all 3 years, Na, Mg, and Ca losses were still much larger than uptake.

Internal redistribution of nutrients in the foliage, expressed as a maximum percentage of total uptake for 1975 to 1978, ranged from 4% for N to 17% for K and Mg. Ca ranged from -13 to -29%, indicating accumulation in older leaf material (Table 6).

Discussion

Vegetation dynamics after clear-cutting

WS-10 was harvested in a manner atypical for the western Cascade Mountains. However, the method of disposal of slash by removal to the landings instead of by burning in place will undoubtedly be used more frequently because it prevents air pollution, provides a relatively clear site for planting conifer seedlings, and reduces chances for wildfires later. On WS-10, this approach yielded a mix of residual shrubbery and invading herbaceous species, depending upon the degree of disturbance at a given location, that was similar to the pattern typical for

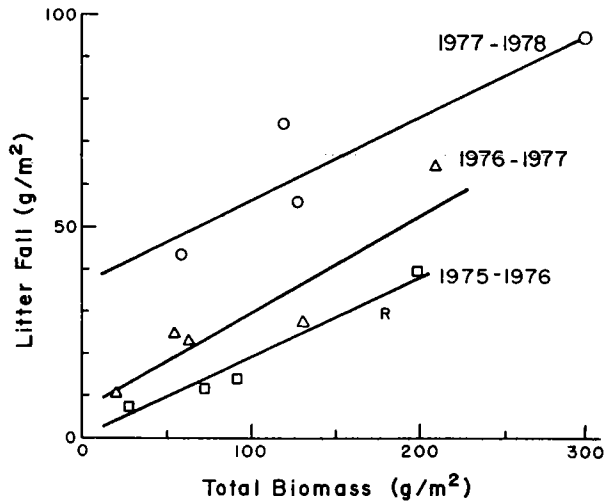


FIG. 3. Annual litter fall of perennial species and August standing biomass for the 3 years after clear-cutting on WS-10. The 1977-1978 riparian point is indicated as "R", and was not included in the regression for that year. Slopes for the 3 years were 0.19 ($n = 5$, $r^2 = 0.96$), 0.23 ($n = 5$, $r^2 = 0.75$), and 0.20 ($n = 4$, $r^2 = 0.83$), respectively.

burned clear-cuts in the area (Dyrness 1973). Dominance by *Senecio* was not expected without a burn (West and Chilcote 1968; Dyrness 1973) but occurred nonetheless. Other introduced species (particularly *Senecio jacobea*) are apparently increasing in importance after clear-cutting of other watersheds in the area (W. A. McKee, personal communication). However, it is premature to suggest a shift from dominance by *Senecio sylvaticus*.

During 1976, 1977, and 1978, the dry ridgetop habitat consistently had less *Senecio* than the other habitats and riparian zone. The ridgetop originally had a dense woody shrub understory (Grier and Logan 1977; Hawk 1979) that remained largely undamaged by the harvest, except at landings. Competition, lack of water, or the relatively low concentrations of N in the soil solution after harvest (Sollins and McCorison 1981) could have affected *Senecio* establishment in this area. Although the permanent plots were not surveyed in 1979 or 1980, they were observed in mid-July 1979 and in mid-August 1980. In 1979 *Senecio* was present only in low amounts, and by 1980 it appeared to be absent.

The nitrogen-fixing *Ceanothus velutinus* did not invade, as it commonly does elsewhere in the area, because its seeds require fire for germination (Youngberg and Wollum 1976). *Alnus rubra* does occur in the area, and we observed a few individuals in the riparian zone after the clear-cutting. However, with the summer drought of the western Cascade Mountains, it is largely limited to moister, north-facing slopes and riparian zones. Whether it will become dominant in the WS-10 riparian zone will be apparent only in the next 5 to 10 years.

Biomass, leaf area, and NPP

We decided to use preclear-cutting (shade) equations for estimating biomass of residual species in 1976 because of our inability to follow the vegetation changes between August 1975 and August 1976. The effects of the change from shade (preclear-cutting) to sun (postclear-cutting) vary among species, as shown by slopes of the regression lines relating foliage and wood biomass to plant dimensions (such as diameter) of

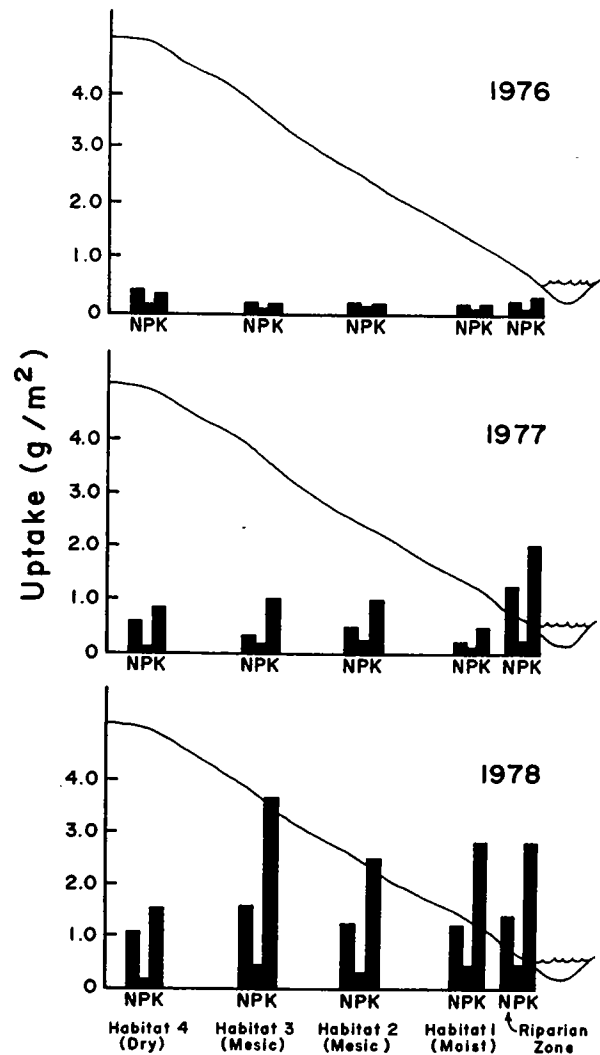


FIG. 4. Profiles of N, P, and K uptake across WS-10 for the 3 years after clear-cutting (1975-1976, 1976-1977, 1977-1978).

shade-growing and sun-growing plants of the same species (Gholz *et al.* 1979). Apparently some woody shrubs (e.g., *Rhododendron*, *Acer*) greatly decrease leaf biomass after clear-cutting; others (e.g., *Gaultheria*) increase biomass. Often leaf biomass per plant is little affected, but because specific leaf areas are greatly reduced (Gholz *et al.* 1976; Gholz 1978), plant leaf areas are as well. For example, *Rhododendron* in the sun retains only one-third to one-half of its leaf area in the shade, mainly because of decreased specific leaf area (Gholz 1978). Some species (e.g., *Berberis*) showed no adjustment. Observations in 1977-1978 lead us to believe that adjustment by species that adapt takes at least 1 year. For example, in 1977-1978, *Rhododendron* was replacing about 80% of its foliage annually; most other major evergreen species were replacing much less per year (see slopes in Fig. 2).

Biomass of the planted Douglas-fir was less than 5% of total aboveground biomass through 1978. We expect that it will dominate foliage mass after 10-15 years, although Turner and Long (1975) indicate that maximum leaf biomass may not be reached for 30 years or more.

During our 3-year study, NPP per unit area increased most rapidly in the riparian zone. Production in years 2 and 3, after invading species became established and residual vegetation had adjusted, increased substantially across the rest of the

watershed. We believe that the annual percentage increases in NPP will decrease from year to year, so that production will increase asymptotically to some maximum value, probably near the preclear-cutting values of $600\text{--}900\text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ (Grier and Logan 1977).

Plotting litter production against August standing biomass of perennial species of the separate habitats (Fig. 3) yields linear relationships over the 3 years; slopes of the lines are not statistically different. They indicate that an average 21% of the standing biomass of perennials turned over each year (average turnover = 4.8 years). The only anomaly occurred in the riparian zone in 1977–1978 because production was overwhelmingly dominated by annuals even after a year of abundant sprouting by woody plants. As the canopy closes and steady-state leaf litterfall is approached, the slope of the lines should approach zero, indicating that a greater proportion of NPP is being allocated to biomass increment than to detrital production. Constant slopes from 1976 through 1978 indicate that the pattern of energy allocation by perennials on WS-10 was similar (with the one exception).

Element cycling

Because the habitats from wettest to driest form a topographical sequence from streamside to ridgetop, values for nutrient uptake in the habitats constitute a series of profiles over the watershed (see N, P, and K in Fig. 4). The 1st-year increase of *Aralia* in the riparian zone, the 2nd-year increase of *Senecio* in the middle three habitats, and the slow rate of increase of residual vegetation on the ridges can be clearly seen. By 1977–1978, 3 years after harvest, the uptake rates of N, P, and K were similar across habitats, although less K was taken up in the dry habitat (reflecting the absence of *Senecio*).

Without more detailed profiles of the quantities of nutrients in solution, and without estimates of immobilization in decaying root systems and litter, we cannot directly link changes in the streamflow chemistry to plant uptake after clear-cutting. Likewise, it would be frivolous to predict losses had uptake been suppressed, as it may have been in 1976–1977, a very dry year (Table 6). However, we can gauge the relative significance of vegetation uptake by comparing it with element fluxes into and out of the watershed over the same time, with uptake of the preharvest old-growth forest, and with results of other studies of nutrient cycling.

Comparisons of vegetation uptake to atmospheric input can be misleading. Sollins *et al.* (1980), using a mass balance approach to analyze preharvest stands on WS-10, determined that most Na, K, Ca, and Mg input was a result of mineral weathering, the weathering input similar in magnitude both to losses from the root zone and to amounts taken up by and cycled through the vegetation. We have no estimates of nitrogen fixation, although we assume that this input on WS-10 was small because of the absence of N-fixing species. In the preharvest stands, fixation amounted to $0.3\text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$, mainly by the lichen *Lobaria oregana* (Tuck.) Müll. Arg. in the old-growth canopy (Sollins *et al.* 1980). The lichen was decimated during clear-cutting. Where a Douglas-fir forest was clear-cut and slash burned, N_2 fixation was estimated to be $10\text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ in a succeeding 17-year-old stand of *C. velutinus* (McNabb and Cromack 1983).

We found no direct correspondence between reduced vegetation uptake after clear-cutting and increased streamflow losses (except the unexplained correspondence of Na). Sollins *et al.* (1980), in the preclear-cut stands, found that fluxes of the

elements we studied decreased markedly from root zone to subsoil solution to stream, changes not completely explained but which could also account for the lack of correspondence in our study. However, we have no data comparable to those of Sollins *et al.* (1980) for quantitative losses of nutrients out of the root zone after clear-cutting. Several other studies have indicated that processes other than plant uptake may control losses soon after clear-cutting (e.g., Likens *et al.* 1978; review by Vitousek and Melillo 1979), although vegetation recovery may indirectly affect these processes. Sollins and McCorison (1981) indicated that although N concentrations were greater in the soil solution after the clear-cutting of WS-10 than before, total quantities of N lost from the root zone were small in either case. Ratios of WS-10 uptake for 1975 through 1978 to losses from the root zone on old-growth stands before clear-cutting (Sollins *et al.* 1980) were similar to ratios of uptake to losses in streamflow after clear-cutting (Table 6). This again indicates that the postclear-cutting N cycle through the vegetation was well developed after only 3 years, but that it may have had little effect on other portions of the ecosystem N cycle.

An important mechanism for obtaining the nutrients that support primary production, in addition to uptake from the soil solution, is reabsorption from senescing foliage. During the 3 years after clear-cutting, the proportions of such internal redistribution of mobile elements were generally small relative to those of the original stands (Table 6) and of other intact, mature forest vegetation (Cole *et al.* 1977; Sollins *et al.* 1980; Ryan and Bormann 1982), mainly because annual species were dominant. Internal redistribution for individual perennial species varied and was sometimes substantial (H. L. Gholz, unpublished data), but in spite of some exceptional species, it is clear that most nutrient demands on the watershed over the 3 years were met by uptake from the soil solution.

In comparison to rates on WS-10 during the first 2 years, rates of nutrient accumulation were very high on a clear-cut North Carolina watershed dominated by the nitrogen-fixer *Robinia pseudo-acacia* (Boring *et al.* 1981). Clear-cuts in Oregon dominated by *Ceanothus* have also shown high accumulation of N and biomass (Youngberg and Wollum 1976; Cole *et al.* 1977). At Hubbard Brook, stands of *Prunus pensylvanica*, not a nitrogen fixer, were also more productive in the first 1 to 2 years (Marks and Bormann 1972). (Both aboveground and belowground components were included in the latter study.) The rates of recovery on WS-10 are similar to those without *Prunus* invasion on WS-2 at Hubbard Brook (Bormann and Likens 1979). We conclude from these comparisons that revegetation over WS-10 as a whole occurred more slowly than after similar disturbances elsewhere. However, rates of recovery in the mesic downslope habitats on WS-10 were similar to the higher rates elsewhere.

Finally, the magnitude of vegetation uptake and watershed solution losses must be compared with the removal of elements in tree boles by clear-cutting. For example, N removed in boles was $57\text{ g}/\text{m}^2$ (Cromack *et al.* 1979); uptake for 1976–1978 was 0.2, 0.5, and $1.3\text{ g}/\text{m}^2$; and streamflow losses for the same years were 0.13, 0.08, and $0.21\text{ g}/\text{m}^2$. Clearly, in the Pacific Northwest, the impact of harvesting and revegetation uptake on solution losses is of small consequence compared with the one-time removal of elements during clear-cutting.

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TABLE 5. Element contents (grams per square metre) in standing crops, August 1976, 1977, and 1978

Year	Habitat	N	P	K	Na	Mg	Ca
1976 ^a	Riparian zone	0.16	0.03	0.24	0.002	0.02	0.16
	1	0.20	0.03	0.22	0.002	0.03	0.15
	2	0.33	0.05	0.33	0.003	0.08	0.40
	3	0.38	0.07	0.35	0.003	0.06	0.54
	4	0.88	0.14	0.62	0.007	0.15	0.94
	Mean	0.55	0.09	0.44	0.005	0.10	0.63
1977	Riparian zone	1.56(16)	0.35(12)	2.29(29)	0.033(40)	0.67(15)	1.78(16)
	1	0.30(62)	0.06(82)	0.66(84)	0.008(75)	0.14(47)	0.31(61)
	2	0.67(42)	0.15(49)	1.20(70)	0.017(76)	0.36(28)	0.78(36)
	3	0.60(41)	0.14(49)	1.23(71)	0.009(67)	0.24(11)	0.87(32)
	4	1.24(7)	0.19(13)	1.53(21)	0.013(77)	0.69(2)	1.41(7)
	Mean	0.84(30)	0.15(38)	1.28(52)	0.012(74)	0.43(15)	1.01(26)
1978	Riparian zone	2.02(5)	0.48(8)	3.01(9)	0.015(7)	0.85(4)	1.62(6)
	1	1.41(68)	0.34(73)	3.07(86)	0.045(73)	0.51(77)	1.15(81)
	2	1.61(49)	0.32(63)	2.91(75)	0.046(78)	0.84(38)	1.76(44)
	3	1.54(69)	0.38(73)	4.14(84)	0.029(86)	0.52(27)	1.65(72)
	4	1.95(9)	0.30(12)	1.97(13)	0.017(12)	1.20(1)	2.14(4)
	Mean	1.70(42)	0.33(47)	2.94(55)	0.029(54)	0.85(24)	1.81(41)

NOTE: The percentage contribution of invading annual species is in parentheses. Means are weighted by the proportion of habitat area to total watershed area.

^aThe invading annual species represented <0.1% in 1976.

Litter fall

Because of the variety of methods used to determine litter fall, means for habitat and year were not compared statistically. In 1977 and 1978, most litter fell in August, September, and October in all habitats. Large September peaks for litter classified "other" in dry habitat 4 reflected large and sudden input of *Castanopsis* fruits.

We estimate that the average total litter produced annually on WS-10 increased by a factor of 6 from 1976 to 1978 (Table 4). Turnover of species with annual tops, primarily *Senecio*, increased from <0.1 g/m² in 1975–1976 to an average 66.1 g/m² in 1977–1978. In that year, foliage from perennial species contributed 57.9 g/m²; wood and bark and other litter added <18 g/m².

Litter fall in 1975–1976 was almost an order of magnitude less in the riparian zone than in the dry habitat. In the riparian zone, it increased 19 times by 1976–1977, and was greatest in that habitat. By 1977–1978, the dry habitat and riparian zone were producing the least litter over the watershed as *Senecio* turnover increased to a maximum in the intermediate habitats.

Net primary production (NPP)

Litter fall was a far greater component of NPP than was biomass increment in the first three postclear-cutting years (Table 4). In 1975–1976, virtually all NPP was foliar litter fall from residual vegetation. However, in 1976–1977, about one-third of NPP was production by annuals (mainly invaders) in proportions ranging from 10% in dry habitat 4 to 80% in moist habitat 1. By 1977–1978, the contribution of annuals to NPP had risen to a mean 37%, ranging from 7% in the dry habitat to 81% in the riparian zone. *Aralia* was the most important species in the riparian zone and *Senecio* was most important elsewhere.

The great increase in NPP in the riparian zone from 1975–1976 to 1976–1977 was a consequence of both biomass increment and litter fall. Much of the increment occurred in

clumps of *Cornus* and *Acer circinatum*. Few sprouts died in 1977–1978, but there was little additional sprouting. NPP by annuals and litter production by perennials increased 30% in 1977–1978; perennial biomass increment was minor.

Biomass increment varied markedly over the watershed throughout the study. Habitats 1 and 2 had negative values in 1977; habitat 3 was near zero in 1977, negative in 1978 (negative values result when mortality is greater than the biomass increase of the remaining live vegetation). By 1978, above-ground NPP was 20% (moist habitat 1) to 29% (mesic habitat 3) that of preharvest old-growth forests and was rather uniform over the upper portions of the watershed (Table 3).

Element distribution

Analyses of N, P, K, Ca, Mg, and Na in the foliage and wood of the major species from WS-10⁴ showed that foliage of a given species from the riparian zone or moist habitats had higher concentrations of all nutrients than foliage from dryer habitats. Annual species also had higher concentrations in both foliage and stems than perennial species; in particular, *Senecio* and *Aralia* had more N and K than the other six invading species. Concentrations did not consistently change from 1976 through 1978 for a given species at a given location. Litter fall analyses indicated that nutrient concentrations were always lowest in woody litter. The "other" category had consistently higher N and K concentrations and lower Mg and Ca concentrations than did foliage, but showed no trend for P or Na.

Contents of the six elements in August 1976, 1977, and 1978 standing crops are given in Table 5 as the product of biomass and element concentration computed for each species and summed over species by habitat. In 1977, *Senecio* and *Epilobium* contained more than 80% of aboveground P and K. In 1978, they contained more than 80% of K in moist habitat 1 and mesic habitat 3, and a similar percentage of Na in habitat 3 and

⁴Data and statistical analyses are available from H. L. Gholz.

TABLE 6. Summary of element dynamics associated with vegetational recovery of WS-10 for the 3 years after tree harvest

Component	Year	N	P	K	Na	Mg	Ca
Atmospheric input ^a (g·m ⁻² ·year ⁻¹)		0.20	0.03	0.12	0.55	0.12	0.31
Aboveground return (g·m ⁻² ·year ⁻¹)							
Litter fall	1975-1976	0.153	0.023	0.051	0.001	0.031	0.187
	1976-1977	0.364	0.072	0.464	0.004	0.102	0.408
	1977-1978	0.891	0.165	1.595	0.011	0.214	1.272
Leaching	1975-1976	0.052	0.006	0.073	0.000	0.008	0.004
	1976-1977	0.079	0.014	0.256	0.022	0.018	0.009
	1977-1978	0.146	0.057	0.562	0.038	0.150	0.073
Total leaching + litter fall	1975-1976	0.206	0.029	0.124	0.001	0.039	0.191
	1976-1977	0.443	0.086	0.720	0.026	0.120	0.417
	1977-1978	1.037	0.222	2.157	0.49	0.364	1.345
Peak standing crop (g/m ²)	1975-1976	0.55	0.09	0.44	0.010	0.10	0.63
	1976-1977	0.83	0.15	1.28	0.012	0.43	1.01
	1977-1978	1.70	0.33	2.94	0.029	0.85	1.81
Intracommunity (g·m ⁻² ·year ⁻¹)							
Increment	1975-1976	0	0	0	0	0	0
	1976-1977	0.051	0.012	0.155	0.001	0.113	0.093
	1977-1978	0.194	0.036	0.274	0.002	0.161	0.205
Internal redistribution	1975-1976	0.057	0.004	0.061	0.0001	0.009	-0.026
	1976-1977	0.014	0.003	0.149	0.0004	0.027	-0.067
	1977-1978	0.049	0.032	0.225	0.0003	0.091	-0.446
Total aboveground uptake (aboveground return + increment, g·m ⁻² ·year ⁻¹)	1975-1976	0.206	0.029	0.124	0.001	0.039	0.191
	1976-1977	0.505	0.098	0.875	0.027	0.233	0.510
	1977-1978	1.303	0.258	2.431	0.051	0.525	1.550
Total uptake : total return	1975-1976	1.00	1.00	1.00	1.00	1.00	1.00
	1976-1977	1.11	1.14	1.22	1.04	1.94	1.22
	1977-1978	1.18	1.16	1.13	1.04	1.44	1.15
Total uptake : input	1975-1976	1.03	0.97	1.03	0.00	0.33	0.62
	1975-1977	2.53	3.27	7.29	0.05	1.94	1.65
	1977-1978	6.52	8.60	20.26	0.09	4.38	5.00
Total uptake : preharvest uptake	1975-1976	0.10	0.05	0.06	0.01	NA	0.05
	1976-1977	0.25	0.17	0.42	0.18	NA	0.12
	1977-1978	0.64	0.45	1.16	0.34	NA	0.37
Total dissolved element loss in streamflow ^b	1975-1976	0.13	0.12	0.6	4.1	1.6	7.2
	1976-1977	0.08	0.04	0.3	1.8	0.7	3.5
	1977-1978	0.21	0.11	0.6	0.4	1.5	5.3
Total uptake : total dissolved element loss in streamflow	1975-1976	1.59	0.24	0.21	0.00	0.02	0.03
	1976-1977	6.31	2.45	2.92	0.02	0.33	0.15
	1977-1978	6.21	2.35	4.05	0.01	0.35	0.26

NOTE: Values are watershed means weighted by the proportion of habitat area to total watershed area. NA, not applicable.

^aWeighted mean values for 1972-1974 from Fredriksen (1975).

^bStreamflow for the 3 water years (Oct. 1 - Sept. 30) were 196, 76, and 186 cm (R. L. Frederiksen, U.S. Forest Service Forestry Sciences Laboratory, Corvallis, Oregon, personal communication).

of Ca in habitat 1. Total standing crop increased from 1976 to 1978 by factors of 2.9 for Ca, 3.1 for N, 3.7 for P, 5.8 for Na, 6.7 for K, and 8.5 for Mg.

Across WS-10 from 1975 to 1978, standing crops, leaching and litter fall, perennial biomass increment, and uptake steadily increased. Leaching plus litter fall was similar to uptake, so that biomass increments were small but uptake rates relatively large (Table 6). By the end of the first year, uptake rates for N, P, and K equaled atmospheric input, and by 1978, uptake for all elements except Na substantially exceeded atmospheric input (Table 6). Uptake of K equaled that of preharvest stands by 1978. Uptake of the other elements, including Na, ranged from 37 to 64% of preharvest values. In the 1st year, uptake of N was 1 to 6 times losses at the stream gauge; in the 2nd year, uptake of N, P, and K was 2.5 to 6 times losses. However, over all 3 years, Na, Mg, and Ca losses were still much larger than uptake.

Internal redistribution of nutrients in the foliage, expressed as a maximum percentage of total uptake for 1975 to 1978, ranged from 4% for N to 17% for K and Mg. Ca ranged from -13 to -29%, indicating accumulation in older leaf material (Table 6).

Discussion

Vegetation dynamics after clear-cutting

WS-10 was harvested in a manner atypical for the western Cascade Mountains. However, the method of disposal of slash by removal to the landings instead of by burning in place will undoubtedly be used more frequently because it prevents air pollution, provides a relatively clear site for planting conifer seedlings, and reduces chances for wildfires later. On WS-10, this approach yielded a mix of residual shrubbery and invading herbaceous species, depending upon the degree of disturbance at a given location, that was similar to the pattern typical for

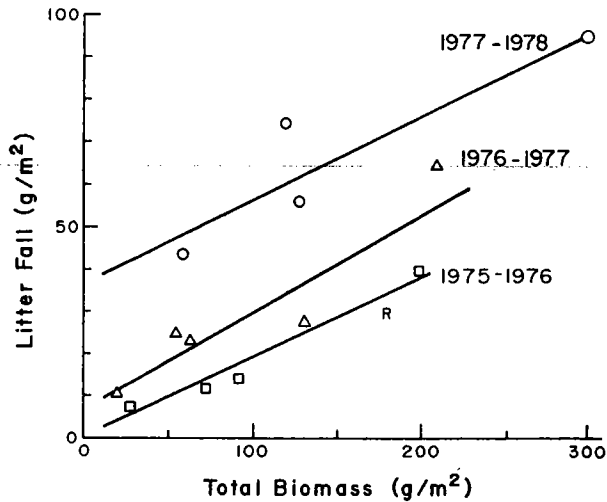


FIG. 3. Annual litter fall of perennial species and August standing biomass for the 3 years after clear-cutting on WS-10. The 1977–1978 riparian point is indicated as “R”, and was not included in the regression for that year. Slopes for the 3 years were 0.19 ($n = 5$, $r^2 = 0.96$), 0.23 ($n = 5$, $r^2 = 0.75$), and 0.20 ($n = 4$, $r^2 = 0.83$), respectively.

burned clear-cuts in the area (Dyrness 1973). Dominance by *Senecio* was not expected without a burn (West and Chilcote 1968; Dyrness 1973) but occurred nonetheless. Other introduced species (particularly *Senecio jacobea*) are apparently increasing in importance after clear-cutting of other watersheds in the area (W. A. McKee, personal communication). However, it is premature to suggest a shift from dominance by *Senecio sylvaticus*.

During 1976, 1977, and 1978, the dry ridgetop habitat consistently had less *Senecio* than the other habitats and riparian zone. The ridgetop originally had a dense woody shrub understory (Grier and Logan 1977; Hawk 1979) that remained largely undamaged by the harvest, except at landings. Competition, lack of water, or the relatively low concentrations of N in the soil solution after harvest (Sollins and McCorison 1981) could have affected *Senecio* establishment in this area. Although the permanent plots were not surveyed in 1979 or 1980, they were observed in mid-July 1979 and in mid-August 1980. In 1979 *Senecio* was present only in low amounts, and by 1980 it appeared to be absent.

The nitrogen-fixing *Ceanothus velutinus* did not invade, as it commonly does elsewhere in the area, because its seeds require fire for germination (Youngberg and Wollum 1976). *Alnus rubra* does occur in the area, and we observed a few individuals in the riparian zone after the clear-cutting. However, with the summer drought of the western Cascade Mountains, it is largely limited to moister, north-facing slopes and riparian zones. Whether it will become dominant in the WS-10 riparian zone will be apparent only in the next 5 to 10 years.

Biomass, leaf area, and NPP

We decided to use pre-clear-cutting (shade) equations for estimating biomass of residual species in 1976 because of our inability to follow the vegetation changes between August 1975 and August 1976. The effects of the change from shade (preclear-cutting) to sun (postclear-cutting) vary among species, as shown by slopes of the regression lines relating foliage and wood biomass to plant dimensions (such as diameter) of

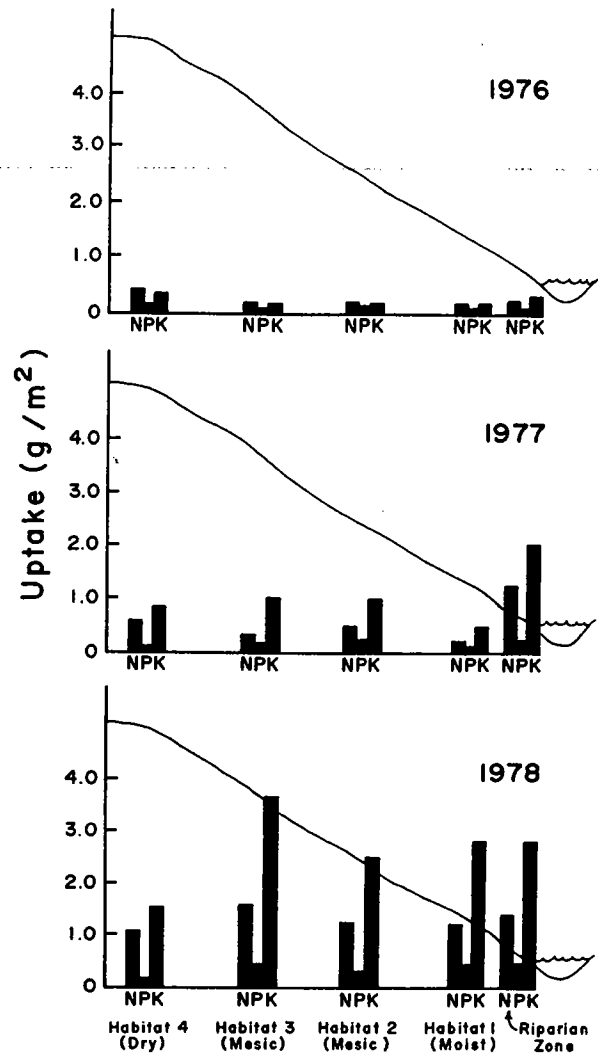


FIG. 4. Profiles of N, P, and K uptake across WS-10 for the 3 years after clear-cutting (1975–1976, 1976–1977, 1977–1978).

shade-growing and sun-growing plants of the same species (Gholz *et al.* 1979). Apparently some woody shrubs (e.g., *Rhododendron*, *Acer*) greatly decrease leaf biomass after clear-cutting; others (e.g., *Gaultheria*) increase biomass. Often leaf biomass per plant is little affected, but because specific leaf areas are greatly reduced (Gholz *et al.* 1976; Gholz 1978), plant leaf areas are as well. For example, *Rhododendron* in the sun retains only one-third to one-half of its leaf area in the shade, mainly because of decreased specific leaf area (Gholz 1978). Some species (e.g., *Berberis*) showed no adjustment. Observations in 1977–1978 lead us to believe that adjustment by species that adapt takes at least 1 year. For example, in 1977–1978, *Rhododendron* was replacing about 80% of its foliage annually; most other major evergreen species were replacing much less per year (see slopes in Fig. 2).

Biomass of the planted Douglas-fir was less than 5% of total aboveground biomass through 1978. We expect that it will dominate foliage mass after 10–15 years, although Turner and Long (1975) indicate that maximum leaf biomass may not be reached for 30 years or more.

During our 3-year study, NPP per unit area increased most rapidly in the riparian zone. Production in years 2 and 3, after invading species became established and residual vegetation had adjusted, increased substantially across the rest of the

watershed. We believe that the annual percentage increases in NPP will decrease from year to year, so that production will increase asymptotically to some maximum value, probably near the preclear-cutting values of $600\text{--}900\text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ (Grier and Logan 1977).

Plotting litter production against August standing biomass of perennial species of the separate habitats (Fig. 3) yields linear relationships over the 3 years; slopes of the lines are not statistically different. They indicate that an average 21% of the standing biomass of perennials turned over each year (average turnover = 4.8 years). The only anomaly occurred in the riparian zone in 1977–1978 because production was overwhelmingly dominated by annuals even after a year of abundant sprouting by woody plants. As the canopy closes and steady-state leaf litterfall is approached, the slope of the lines should approach zero, indicating that a greater proportion of NPP is being allocated to biomass increment than to detrital production. Constant slopes from 1976 through 1978 indicate that the pattern of energy allocation by perennials on WS-10 was similar (with the one exception).

Element cycling

Because the habitats from wettest to driest form a topographical sequence from streamside to ridgetop, values for nutrient uptake in the habitats constitute a series of profiles over the watershed (see N, P, and K in Fig. 4). The 1st-year increase of *Aralia* in the riparian zone, the 2nd-year increase of *Senecio* in the middle three habitats, and the slow rate of increase of residual vegetation on the ridges can be clearly seen. By 1977–1978, 3 years after harvest, the uptake rates of N, P, and K were similar across habitats, although less K was taken up in the dry habitat (reflecting the absence of *Senecio*).

Without more detailed profiles of the quantities of nutrients in solution, and without estimates of immobilization in decaying root systems and litter, we cannot directly link changes in the streamflow chemistry to plant uptake after clear-cutting. Likewise, it would be frivolous to predict losses had uptake been suppressed, as it may have been in 1976–1977, a very dry year (Table 6). However, we can gauge the relative significance of vegetation uptake by comparing it with element fluxes into and out of the watershed over the same time, with uptake of the preharvest old-growth forest, and with results of other studies of nutrient cycling.

Comparisons of vegetation uptake to atmospheric input can be misleading. Sollins *et al.* (1980), using a mass balance approach to analyze preharvest stands on WS-10, determined that most Na, K, Ca, and Mg input was a result of mineral weathering, the weathering input similar in magnitude both to losses from the root zone and to amounts taken up by and cycled through the vegetation. We have no estimates of nitrogen fixation, although we assume that this input on WS-10 was small because of the absence of N-fixing species. In the preharvest stands, fixation amounted to $0.3\text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$, mainly by the lichen *Lobaria oregana* (Tuck.) Müll. Arg. in the old-growth canopy (Sollins *et al.* 1980). The lichen was decimated during clear-cutting. Where a Douglas-fir forest was clear-cut and slash burned, N_2 fixation was estimated to be $10\text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ in a succeeding 17-year-old stand of *C. velutinus* (McNabb and Cromack 1983).

We found no direct correspondence between reduced vegetation uptake after clear-cutting and increased streamflow losses (except the unexplained correspondence of Na). Sollins *et al.* (1980), in the preclear-cut stands, found that fluxes of the

elements we studied decreased markedly from root zone to subsoil solution to stream, changes not completely explained but which could also account for the lack of correspondence in our study. However, we have no data comparable to those of Sollins *et al.* (1980) for quantitative losses of nutrients out of the root zone after clear-cutting. Several other studies have indicated that processes other than plant uptake may control losses soon after clear-cutting (e.g., Likens *et al.* 1978; review by Vitousek and Melillo 1979), although vegetation recovery may indirectly affect these processes. Sollins and McCorison (1981) indicated that although N concentrations were greater in the soil solution after the clear-cutting of WS-10 than before, total quantities of N lost from the root zone were small in either case. Ratios of WS-10 uptake for 1975 through 1978 to losses from the root zone on old-growth stands before clear-cutting (Sollins *et al.* 1980) were similar to ratios of uptake to losses in streamflow after clear-cutting (Table 6). This again indicates that the postclear-cutting N cycle through the vegetation was well developed after only 3 years, but that it may have had little effect on other portions of the ecosystem N cycle.

An important mechanism for obtaining the nutrients that support primary production, in addition to uptake from the soil solution, is reabsorption from senescing foliage. During the 3 years after clear-cutting, the proportions of such internal redistribution of mobile elements were generally small relative to those of the original stands (Table 6) and of other intact, mature forest vegetation (Cole *et al.* 1977; Sollins *et al.* 1980; Ryan and Bormann 1982), mainly because annual species were dominant. Internal redistribution for individual perennial species varied and was sometimes substantial (H. L. Gholz, unpublished data), but in spite of some exceptional species, it is clear that most nutrient demands on the watershed over the 3 years were met by uptake from the soil solution.

In comparison to rates on WS-10 during the first 2 years, rates of nutrient accumulation were very high on a clear-cut North Carolina watershed dominated by the nitrogen-fixer *Robinia pseudo-acacia* (Boring *et al.* 1981). Clear-cuts in Oregon dominated by *Ceanothus* have also shown high accumulation of N and biomass (Youngberg and Wollum 1976; Cole *et al.* 1977). At Hubbard Brook, stands of *Prunus pensylvanica*, not a nitrogen fixer, were also more productive in the first 1 to 2 years (Marks and Bormann 1972). (Both aboveground and belowground components were included in the latter study.) The rates of recovery on WS-10 are similar to those without *Prunus* invasion on WS-2 at Hubbard Brook (Bormann and Likens 1979). We conclude from these comparisons that revegetation over WS-10 as a whole occurred more slowly than after similar disturbances elsewhere. However, rates of recovery in the mesic downslope habitats on WS-10 were similar to the higher rates elsewhere.

Finally, the magnitude of vegetation uptake and watershed solution losses must be compared with the removal of elements in tree boles by clear-cutting. For example, N removed in boles was $57\text{ g}/\text{m}^2$ (Cromack *et al.* 1979); uptake for 1976–1978 was 0.2, 0.5, and $1.3\text{ g}/\text{m}^2$; and streamflow losses for the same years were 0.13, 0.08, and $0.21\text{ g}/\text{m}^2$. Clearly, in the Pacific Northwest, the impact of harvesting and revegetation uptake on solution losses is of small consequence compared with the one-time removal of elements during clear-cutting.

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