

Nitrogen Export from Forested Watersheds in the Oregon Coast Range: The Role of N₂-fixing Red Alder

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ABSTRACT

Variations in plant community composition across the landscape can influence nutrient retention and loss at the watershed scale. A striking example of plant species importance is the influence of N₂-fixing red alder (*Alnus rubra*) on nutrient cycling in the forests of the Pacific Northwest. To understand the influence of red alder on watershed nutrient export, we studied the chemistry of 26 small watershed streams within the Salmon River basin of the Oregon Coast Range. Nitrate and dissolved organic nitrogen (DON) concentrations were positively related to broadleaf cover (dominated by red alder: 94% of basal area), particularly when near-coastal sites were excluded ($r^2 = 0.65$ and 0.68 for nitrate-N and DON, respectively). Nitrate and DON concentrations were more strongly related to broadleaf cover within entire watersheds than broadleaf cover within the riparian area alone, which indicates that leaching from upland alder stands plays an important role in watershed nitrogen (N) export.

Nitrate dominated over DON in hydrologic export (92% of total dissolved N), and nitrate and DON concentrations were strongly correlated. Annual N export was highly variable among watersheds ($2.4\text{--}30.8 \text{ kg N ha}^{-1} \text{ y}^{-1}$), described by a multiple linear regression combining broadleaf and mixed broadleaf–conifer cover ($r^2 = 0.74$). Base cation concentrations were positively related to nitrate concentrations, which suggests that nitrate leaching increases cation losses. Our findings provide evidence for strong control of ecosystem function by a single plant species, where leaching from N saturated red alder stands is a major control on N export from these coastal watersheds.

Key words: nitrogen leaching; nitrogen fixation; red alder; nitrate; streams; Oregon Coast Range; nitrogen saturation; dissolved organic nitrogen; cation leaching.

INTRODUCTION

Human activities have more than doubled the supply of nitrogen (N) to terrestrial and aquatic ecosystems on a global scale, resulting in important

changes in ecosystem structure and function in many regions (Vitousek and others 1997). In areas where the N supply exceeds the ecosystem demand, a collection of processes termed “N saturation” can occur, by which nitrate accumulates in soils and is lost to groundwater, lakes, and streams (Aber and others 1998). High rates of N leaching can then lead to cation losses and nutrient imbalances in terrestrial ecosystems and eutrophication in aquatic eco-

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systems (Murdoch and Stoddard 1992; Likens and others 1996; Vitousek and others 1997).

Although the concept of N saturation originated in the context of human-accelerated N deposition, biological processes can also alter N availability and losses at several scales. Plant community composition influences nutrient cycling and soil fertility (Hobbie 1992; Binkley and Giardina 1998), and these effects on cycling rates can translate into differences in ecosystem nutrient retention and watershed-scale losses (Lovett and others 2000). One dramatic example of species effects on terrestrial ecosystem function is the role of symbiotic N₂-fixing species. Tree species with symbiotic N₂-fixing *Frankia* or *Rhizobium* bacteria can fix 50–200 kg N ha⁻¹ y⁻¹ in pure stands (Boring and others 1988; Binkley and others 1994). These fixation inputs can be greater than atmospheric N loading in industrial regions (Wright and Rasmussen 1998), and result in leaching losses that exceed rates from N-saturated forests of polluted regions (Van Miegroet and others 1992; Gundersen and Bashkin 1994).

In the Pacific Northwest of North America, N₂-fixing red alder (*Alnus rubra*) colonizes areas of infrequent but intense disturbance, such as clear-cuts, landslides, and burned areas, as well as repeatedly disturbed riparian areas (Harrington and others 1994). This native tree forms stands that are pure or mixed with conifers and has a relatively short life span (less than a century). Red alder can increase soil N content and cycling rates in pure stands or in mixtures with conifers (Binkley and others 1992, 1994). The high rates of nitrification and organic matter cycling under alder generally accelerate cation leaching and soil acidification when compared to native conifer stands (Van Miegroet and Cole 1984, 1985; Bormann and others 1994). Red alder can also impart a legacy of lower cation and phosphorus (P) availability for future stands of both alder and conifers (Brozek 1991; Compton and others 1997). Although alder stands can influence N concentrations of adjacent streams and lakes (Goldman 1961; Binkley and others 1982; Stottlemeyer and Toczydlowski 1999), the landscape-scale influence of alder distribution on stream chemistry has not been clearly demonstrated.

Here we examine the influence of upland and riparian alder stands on dissolved N and cations in Oregon Coast range streams. We conducted monthly sampling of 26 small-watershed (less than 3000 ha) streams to test the hypothesis that stream nitrate and dissolved organic nitrogen (DON) are influenced by the areal cover of red alder stands within the watershed. Riparian alder could be an important source of N to streams; for this reason,

we compared stream N concentrations with vegetation cover of both riparian areas and the entire watershed. Because soil nitrate leaching may accelerate cation leaching (Aber and others 1989; Vitousek and others 1997), nitrate losses associated with alder stands might result in increased cation levels in stream water. Losses of N and cations from forested watersheds have important implications for long-term terrestrial and aquatic ecosystem function.

METHODS

Basin Description

The study was conducted in the Salmon River basin, which drains from the Oregon Coast Range Mountains westward into the Pacific Ocean, approximately 5 km north of Lincoln City, Oregon, USA. This 200-km² basin is 95% forested, with a mosaic of private industrial conifer plantations, mixed and pure alder stands, and patches of older forests originating after the Nestucca fire in 1845–49 (Greene and others 1992). Ownership in the lower watershed is dominated by private non-industrial and federal landholders (for example, Cascade Head Experimental Forest, Siuslaw National Forest). Private industrial forest plantations occupy most of the upper basin. There are very few buildings or other developments above our sampling sites. Dominant soils within the basin are moderately deep to deep Inceptisols and Andisols (Humitropepts, Fulvudands, and Haplocryands) formed in colluvium from Miocene and Eocene age sedimentary or volcanic rocks (USDA 1997). The basin covers an area from less than 1 km to approximately 20 km from the ocean and ranges in elevation from sea level to 910 m.

The forests are dominated by sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) near the coast, shifting to western hemlock and Douglas-fir (*Pseudotsuga menziesii*) further inland. Red alder is the dominant broadleaf canopy tree within approximately 40 km of the coast, with big leaf maple (*Acer macrophyllum*) increasing further inland and at higher elevations (Ohmann and Gregory 2002). At low elevations, red alder stands can blanket entire hillsides of the Coast Range (Franklin and Dyrness 1988), particularly in areas that were clear-cut or burned in the 20th century.

Stream Sampling, Flow Measurements, and Chemical Analyses

Within the Salmon River basin, we sampled 26 first- to third-order streams with a range of watershed areas and runoff (Table 1). Sampling sites were

Table 1. Study Watershed Characteristics and Stream Chemistry, Salmon River Basin

Stream Code	Name	Watershed Area (ha)	Distance to Coast (km)	Runoff (mm/y)	Broadleaf Cover (%)	Broadleaf percent Alder ^a	Mixed Cover (%)
SM 45	Teal Creek	77	0.6	1300	14	98	44
SM 44	^b	26	1.0	965 ^c	10	92	56
SM 32	Crowley Creek	391	1.3	1284	19	96	39
SM 43	^b	45	1.8	1114 ^c	70	99	8
SM 11	^b	90	2.6	1200 ^c	74	98	8
SM 40	Baxter Creek	46	3.8	2061 ^c	21	95	72
SM 31	Calkins Creek	129	4.0	1338	32	98	30
SM 46	Salmon Creek	69	4.6	1360 ^c	3	99	40
SM 39	^b	35	4.7	2200 ^c	53	98	28
SM 38	Willis Creek	361	5.9	1909 ^c	39	98	11
SM 37	^b	115	6.2	1281 ^c	27	96	26
SM 36	Curl Creek	141	6.8	1218 ^c	32	93	22
SM 27	Toketa Creek	212	7.0	1132	25	98	14
SM 28b	N. Fork Deer Creek	111	7.3	1090	33	94	17
SM 28a	S. Fork Deer Creek	97	7.3	1031	23	91	18
SM 22	Morton Creek	128	8.3	2009	27	97	21
SM 10	Bear Creek	1250	8.4	2000	25	94	20
SM 21	Panther Creek	447	9.1	1006	37	95	25
SM 23	Callow Creek	54	9.5	3053	12	81	30
SM 35	Widow Creek	807	11.5	1491	45	92	17
SM 34	Alder Brook	289	12.2	1487	25	93	27
SM 33	Treat Creek	748	12.5	2285	19	89	14
SM 24	Slick Rock	1861	14.5	2469	3	95	12
SM 7	Deer Creek 2	644	14.7	1449	17	96	26
SM 25	Sulphur Creek	302	15.2	1440	26	92	49
SM 25b	Prairie Creek	310	15.5	1451	17	91	39
SM 26	Salmon River	2617	17.6	1431	7	89	17
Mean		422	7.9	1558	27%	94%	27%
SD		608	4.9	516	18%	4%	15%

^aPercent of basal area occupied by alder in this cover type (J. Ohmann and M. Gregory personal communication)

^bUnnamed stream

^cEstimated flows

generally at the lower end of the watershed above a major confluence or road crossing. We sampled stream water for chemical analysis monthly from January through December 2000. Watersheds were not nested, except for Callow Creek, a small tributary of Bear Creek, where discharge differs by an order of magnitude. Discharge was estimated on each sampling date at a subset of 16 sites by the velocity area method, with a stream velocity meter and top-setting wading rod (Swoffer Instruments, Seattle, WA, USA).

Stream water was collected in 1-L containers and stored on ice until returning to the lab. Samples were filtered within 24 h of sampling (0.25- μ m polycarbonate membrane filters; Whatman, Newton, MA, USA). Water samples were analyzed for ammonium and nitrite plus nitrate using auto-

mated colorimetric continuous flow autoanalyzer (Lachat method 10-107-06-3-D for ammonium and USEPA [1987] method 353.2 for nitrate+nitrite; Lachat Instruments, Milwaukee, WI, USA). Nitrite-N ranged from 0 to 1.4% of nitrate-N concentrations in a subset of samples from all sites ($n = 50$); therefore, nitrite plus nitrate was considered equivalent to nitrate. Total dissolved N was determined using persulfate digestion (Cabrera and Beare 1993), followed by automated colorimetric analysis for nitrate as described above. DON was calculated as total dissolved N minus nitrate and ammonium. If DON was negative by less than 0.005 mg N L⁻¹, the value was set to zero. Samples were reanalyzed if DON was negative by more than 0.005 mg N L⁻¹. Dissolved calcium, magnesium, sodium, and potassium were determined in HNO₃ acidified

aliquots using flame atomic absorption spectrophotometry (Perkin-Elmer Instruments, Norwalk, CT, USA) (USEPA 1987). Chloride concentrations were determined by ion chromatography (Dionex Corporation, Sunnyvale, CA, USA). Cation concentrations were adjusted for sea salt contributions using sea salt chloride ratios (Hedin and others 1995).

Watershed and Riparian Zone Vegetation Cover

Land cover within the Salmon River basin was obtained from the Coastal Lands Assessment and Monitoring Study (CLAMS) (<http://www.fsl.orst.edu/clams/index.htm>, obtained June 2001). This raster vegetation layer integrates field plots, environmental data, and 1996 Landsat TM imagery (Ohmann and Gregory 2002) to produce forest classes based on land cover (forest, open, and woodlands), forest type (broadleaf, conifer, and mixed broadleaf-conifer), and size of conifer and mixed forests (small, medium, large, and very large).

To categorize watershed area above the sampling point, we checked perimeters using the 10-m digital elevation model and 1:24,000 hydrology layer and clipped out the vegetation layer. In addition to creating data layers of land cover, Ohmann and Gregory (2002) also modeled stand characteristics for large areas of the Coast Range. In our study watersheds, red alder averaged 94% (range, 81%–98%) of the basal area in the portion of the watershed categorized as broadleaf (Table 1). For this reason, we conclude that broadleaf cover within the watersheds is dominated by red alder stands and that red alder is the major broadleaf species occurring in mixed broadleaf-conifer stands. To examine the relationship between riparian zone land cover and stream chemistry, we used the vegetation cover data to create three riparian buffers from the center of the stream channel (30, 60, or 120 m on both sides). Distance to the ocean for each watershed was measured from the stream sampling location.

Calculations and Statistical Analyses

Flow-weighted annual average concentrations were calculated from the instantaneous discharge measurements and water chemistry at each sampling date. To determine annual runoff, we used linear regressions between the instantaneous flow measurements for individual streams and for a continuously gauged site on the Salmon mainstem near Otis, Oregon. These linear regression relationships were used in combination with the average daily discharge at the gauged site ($L s^{-1}$) (obtained from

Oregon Water Resources Department) and then divided by watershed area to generate an annual water flux per unit area. On sampling dates or streams where discharge was not measured, water flux was calculated using the specific yield ($L s^{-1} ha^{-1}$) for adjacent watersheds with similar soils and precipitation. Annual dissolved N export per unit area was calculated by multiplying the runoff by the flow-weighted average annual N concentration for each stream.

Initial examination of the data indicated that stream nitrate concentrations were highest within 5 km of the coast, coincident with high chloride concentrations, suggesting that sea salt inputs may directly affect stream nitrate concentrations in the near-ocean watersheds (M. R. Church and others unpublished). Therefore, to examine the broader landscape role of red alder, a subset of streams more than 5 km from the coast was used for some analyses ($n = 18$). All linear regressions were performed using the General Linear Model in SYSTAT for Macintosh v. 10 (SPSS., Chicago, IL, USA). Normal probability plots indicated that all variables were normally distributed. Because there is little evidence that N_2 -fixation rates vary systematically with stand age (Binkley and others 1994), all four mixed-cover classes were summed to create the mixed category for analysis. Mixed and broadleaf covers were not correlated.

RESULTS

Flow-weighted average annual nitrate concentrations ranged from 0.074 to 2.043 mg N L^{-1} (Table 2). Nitrate was the dominant N form, with annual average concentrations ranging from 76% to 96% of total dissolved N. Ammonium concentrations were very low, often near the detection limit of 0.002 mg L^{-1} . N losses among the watersheds were highly variable, ranging from 2.4 to 30.8 kg N $ha^{-1} y^{-1}$ (Table 1). The average loss was 13.6 kg N $ha^{-1} y^{-1}$.

The proportion of broadleaf cover in each watershed was positively related to stream N concentrations, explaining approximately 51% of the variation in nitrate and 45% of the variation in DON. Nitrate concentrations were highest within 5 km of the coast (Tables 1 and 2); therefore, we also conducted the analysis after excluding these sites. Broadleaf cover explained approximately 66% of the variation in nitrate (Figure 1a) and 68% of the variation in DON (Figure 1b) after excluding the sampling sites within 5 km of the ocean. Including mixed stands in a multiple regression increased the

Table 2. Stream Chemistry

Stream Code	NH ₃ -N (μg/L)	NO ₃ -N (mg/L)	DON (mg/L)	NO ₃ -N:TDN (%)	Cl (μeq/L)	Ca (μeq/L)	Mg (μeq/L)	Na (μeq/L)	K (μeq/L)
SM 45	4	1.352	0.052	96	635	363	207	638	18
SM 44	7	1.424	0.088	94	580	261	175	553	22
SM 32	6	1.388	0.103	93	396	316	193	459	18
SM 43	7	2.043	0.090	95	290	273	163	415	23
SM 11	6	2.429	0.129	95	332	222	190	359	18
SM 40	7	1.203	0.063	95	135	71	85	162	12
SM 31	5	1.358	0.083	94	255	205	172	287	15
SM 46	3	0.359	0.020	94	174	159	109	196	9
SM 39	3	1.240	0.065	95	118	132	65	166	11
SM 38	3	0.726	0.046	94	116	211	132	185	8
SM 37	4	0.852	0.061	93	169	376	211	308	6
SM 36	5	0.875	0.048	94	163	356	200	291	6
SM 27	5	0.498	0.037	92	223	159	94	240	11
SM 28b	5	0.758	0.057	92	216	315	141	273	11
SM 28a	5	0.830	0.044	94	205	487	273	329	10
SM 22	5	0.762	0.056	93	167	374	237	289	11
SM 10	5	0.652	0.047	93	138	274	192	243	11
SM 21	6	0.978	0.055	94	184	401	253	319	9
SM 23	4	0.452	0.030	93	157	292	163	234	12
SM 35	5	0.771	0.087	89	114	371	167	203	8
SM 34	4	0.502	0.040	92	114	210	128	166	6
SM 33	3	0.314	0.028	91	66	174	101	130	5
SM 24	4	0.074	0.020	76	83	133	65	110	4
SM 7	5	0.406	0.034	91	113	338	143	202	8
SM 25	5	0.877	0.053	94	139	291	119	211	11
SM 25b	4	0.529	0.043	92	131	251	123	197	9
SM 26	4	0.167	0.033	82	102	151	92	140	4
Mean	5	0.882	0.056	92	204	265	155	271	11
SD	1	0.544	0.026	4	139	100	56	127	5

DON, dissolved organic nitrogen; TDN, total dissolved nitrogen; Cl, chlorid; Ca, calcium; Mg, magnesium; Na, sodium; K, potassium
Concentrations are flow-weighted averages of monthly samples during 2000.

explanatory value to 77% of the variation in nitrate and 72% of the variation in DON (Table 3).

In watersheds with more than 20% broadleaf cover, stream nitrate concentrations were relatively high throughout the year; the lowest values occurred in late summer, followed by broad peaks in the fall (Figure 2; three streams shown as an example). Stream DON concentrations were lower and less temporally variable than nitrate (Figure 2). Both nitrate and DON concentrations were positively related to broadleaf cover, and nitrate concentrations increased more dramatically with broadleaf cover, based on the regression slopes (Figure 1).

To examine the influence of riparian alder on stream chemistry, we compared broadleaf cover–N relationships for the riparian areas of varying width and for the entire watershed. Linear regressions of nitrate and DON as a function of broadleaf are

shown in Table 4. Broadleaf cover within the entire watershed explained a much greater proportion of the variability in nitrate (66%) and DON (69%) than broadleaf cover in any of the riparian buffer widths (less than 42%).

Of the cations, calcium (Ca) and sodium (Na) had the highest concentrations (Table 2). Total magnesium concentrations (unadjusted for sea salt contribution) were intermediate, and total potassium concentrations consistently were very low. Total sodium concentrations were much higher in the near-coastal streams, with the highest values (more than 10 mg Na L⁻¹) occurring in sites within 2 km of the ocean. Other cations were slightly higher near the coast. For sites more than 5 km from the ocean, non-sea salt calcium and sodium concentrations were significantly related to the proportion of broadleaf cover ($P < 0.10$ and $P < 0.05$, respectively), but r^2 values were low (less than 0.25).

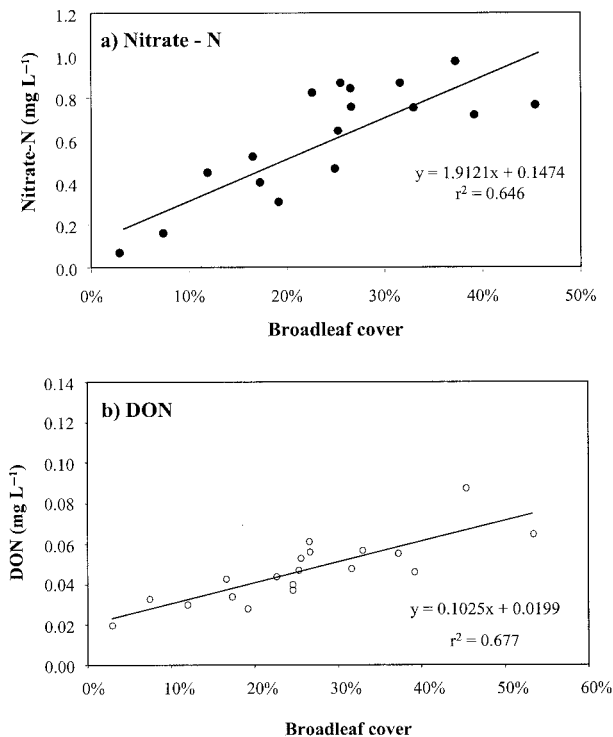


Figure 1. Relationship between broadleaf cover and flow-weighted average annual stream nitrate and dissolved organic nitrogen (DON) concentrations for sites more than 5 km from the ocean. Stream concentrations are flow-weighted averages of monthly samples during 2000.

Non-sea salt calcium, magnesium, and sodium concentrations were strongly related to nitrate concentrations ($r^2 \geq 0.50$) (Figure 3).

Annual N export ($\text{kg N ha}^{-1} \text{y}^{-1}$) from all study watersheds in the Salmon River basin was strongly related to broadleaf cover within the watershed (Figure 4a). Annual N export was best described by the following equation:

$$\text{Annual N export} = -4.8 + 39.0 (\text{broadleaf}) + 29.0 (\text{mixed}) \quad r^2 = 0.74 \quad (1)$$

where "broadleaf" and "mixed" represent the proportion of the watershed in each cover type. The intercept is not significantly different from zero (Table 3). Because we sampled few sites with less than 15% or more than 90% combined alder and mixed cover, the intercept and maximum estimates are highly uncertain. Figure 4b shows the relationship between broadleaf plus mixed cover and total N export from the study watersheds. N export was described as a polynomial relationship, where export is low in watersheds with few alder stands and

increases rapidly as alder and mixed cover increases.

DISCUSSION

Does the Landscape Distribution of Alder Influence Stream N?

Stream nitrate and DON concentrations were strongly positively related to broadleaf cover in individual watersheds. The broadleaf cover category was dominated by red alder in our study watersheds, averaging 94% of the basal area (Table 1). Leaching of N from alder and mixed alder-conifer stands clearly has the potential to influence stream chemistry. Most published rates of N_2 fixation range from 100 to 200 $\text{kg N ha}^{-1} \text{y}^{-1}$ for pure stands (Binkley and others 1994). Soil N and soil solution N leaching are much higher in pure and mixed red alder stands than under associated pure conifer stands (Van Miegroet and Cole 1984; Bormann and others 1994). The highest export in the Salmon basin was 30.8 $\text{kg N ha}^{-1} \text{y}^{-1}$ from a watershed with 74% broadleaf cover, which suggests that N inputs by red alder can result in very high rates of N export.

Because red alder is associated with particular disturbances and management practices, it is important to consider whether the relationship between alder cover and stream N is causal or indirect as a result of other influences, such as disturbance history. Areas that have experienced more intense disturbances (intense fires, log skidding) may be more likely to be dominated by alder. Although it is difficult to reconstruct the long-term disturbance history of a given site, large areas of the study watershed were burned in the Nestucca fire (between 1845 and 1849), and 150-year-old Sitka spruce and western hemlock forests currently occupy much of this burned area (Greene and others 1992). There does not appear to be a strong spatial link between broadleaf cover and the extent of this historic fire. In addition, the long-term legacy of fire is expected to be less dissolved N export as compared to unburned areas (Silsbee and Larson 1982; Hornbeck and others 1997) rather than increased export, as is the trend with alder. Studies in the Oregon Coast Range have not identified a dramatic effect of clear-cut logging on watershed-scale N export (Brown and others 1973; Miller and Newton 1983). For these reasons, disturbance alone would not be expected to contribute large amounts of N to streams. In the Salmon River basin, watershed export can be very high, ranging from 2.4 to 30.8 $\text{kg N ha}^{-1} \text{y}^{-1}$. Although disturbance factors may drive

Table 3. Regressions of Stream Nitrogen (N) Concentrations and Fluxes as Related to Watershed Broadleaf and Mixed Cover

Dependent Variable	Intercept ^a	Broadleaf Coefficient	SE	Mixed Coefficient	SE	r ²
Nitrate (mg L ⁻¹)	-0.349	2.824 ^d	0.379	1.716 ^d	0.434	0.70 ^d
DON (mg L ⁻¹)	0.003	0.125 ^d	0.021	0.069 ^c	0.024	0.59 ^d
TN loss (kg ha ⁻¹ y ⁻¹)	-1.8	39.0 ^d	4.9	29.0 ^d	5.6	0.74 ^d
Nitrate (mg L ⁻¹)	-0.077	1.977 ^d	0.297	0.929 ^b	0.331	0.77 ^d
DON (mg L ⁻¹)	0.010	0.118 ^d	0.019	0.030	0.021	0.72 ^d
TN loss (kg ha ⁻¹ y ⁻¹)	1.5	22.7	7.2	13.2	8.1	0.44 ^b

DON, dissolved organic nitrogen; TN, total nitrogen

Significance values for coefficients and slopes are the results of two-tailed t-tests. The significance of the overall regressions accompanies the r² value.

^aIntercept values were not significantly different from zero.

^bP ≤ 0.05 for coefficients and overall regression

^cP ≤ 0.01 for coefficients and overall regression

^dP ≤ 0.001 for coefficients and overall regression

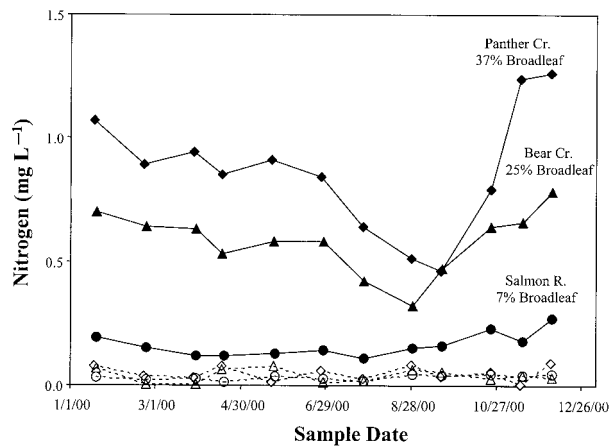


Figure 2. Seasonal trends in stream nitrate (solid symbols) and dissolved organic nitrogen (open symbols) concentrations for three streams within the Oregon coastal Salmon River basin. Distance to the coast for each stream is given in Table 1.

the distribution of alder stands, it is the exceptionally high rates of N fixation and leaching from alder stands that appear to yield high rates of N export at the watershed scale.

Red alder could supply N to aquatic ecosystems via several pathways: direct inputs of particulate organic matter via litterfall in riparian zones (Volk and others 2003), movement of soluble nutrients from riparian alder stands through groundwater and hyporheic zones (Goldman 1961; Wondzell and Swanson 1996), and leaching and lateral transport from upland stands of pure alder and alder-conifer stands. In contrast to the common view of riparian zones as filters (Peterjohn and Correll 1984; Hill 1996), Naiman and others (2000) suggested that riparian forests in the Pacific Northwest

Table 4. Regressions of Stream Nitrogen (N) and Broadleaf Cover within Riparian Buffers More than 5 km from the Ocean

Buffer Width (m)	Broadleaf Cover (mean ± SE, %) ^a	Nitrate r ²	DON r ²
30	34 ± 18	NS	0.30 ^c
60	33 ± 17	0.23 ^c	0.31 ^c
120	30 ± 15	0.34 ^c	0.41 ^d
Watershed ^b	25 ± 15	0.66 ^c	0.69 ^c

DON, dissolved organic nitrogen

^aMean (±) SD given for percentage of the buffer area occupied by broadleaf forest

^bEntire area for each watershed sampled

^cP < 0.05

^dP < 0.01

^eP < 0.001

could act as either N sources or sinks, depending on the distribution of alder and hyporheic connections. Nitrate and DON concentrations were much more strongly related to areal cover of alder in the entire watershed than to cover in any of the riparian buffer widths by themselves (Table 3). The N leaching from upland stands reaches ground and surface waters and apparently is not removed by biological uptake or denitrification along the flowpath. Based on the high stream nitrate concentrations and the strong positive relationship of nitrate with alder stands in the Salmon River basin, we believe that leaching and lateral transport from upland red alder is the major source of N to our study streams.

Red alder may play a keystone role in N biogeochemistry, where the presence of alder in mixed alder-conifer stands can also result in high rates of N leaching. Most of the variation in stream nitrate and DON concentrations among our study water-

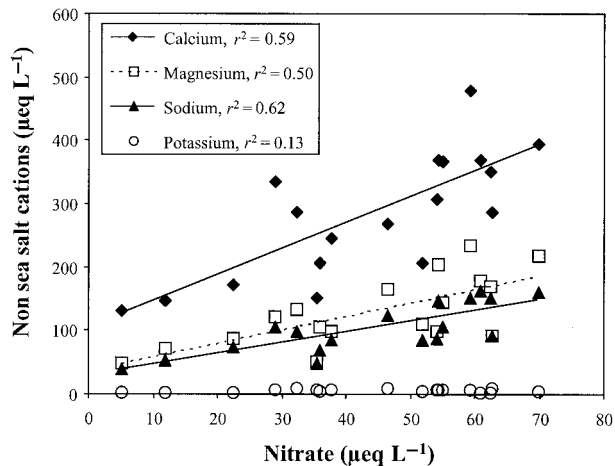


Figure 3. Stream cations as a function of nitrate in sites more than 5 km from the coast. Concentrations are flow-weighted averages of monthly samples during 2000, corrected for sea salt-derived cations. All regressions are significant ($P < 0.001$), except for potassium.

sheds was explained by the relationship with pure alder stands (Figure 4a), but including mixed stands improved the relationship by approximately 10% (Table 2). Using Eq. (1) we estimated that a watershed with 100% alder cover might have a loss rate of $39 \text{ kg ha}^{-1} \text{ y}^{-1}$ ($\text{SE} \pm 5$), and watersheds with 100% mixed cover might export $29 \text{ kg N ha}^{-1} \text{ y}^{-1}$ ($\text{SE} \pm 7$). Although these rates are highly uncertain because we sampled no watersheds with these cover characteristics, they are clearly within the range of leaching losses observed for stand-level studies of pure and mixed alder stands. For example, losses were $39 \text{ kg N ha}^{-1} \text{ y}^{-1}$ from a pure alder stand at Cedar River, Washington (below 0.4 m soil depth) (Van Miegroet and others 1992). Binkley and others (1992) found total N leaching of $26 \text{ kg N ha}^{-1} \text{ y}^{-1}$ below 0.8-m soil depth in mixed alder-conifer stands at Wind River, Washington, and $50 \text{ kg N ha}^{-1} \text{ y}^{-1}$ in mixed alder-conifer stands at Cascade Head, Oregon (within the Salmon River basin). The nonlinear relationship in Figure 4b suggests that in watersheds with low alder cover (less than 20%), rates of N removal may match the rates of N supply from upland alder stands, when the supply is less than $5 \text{ kg ha}^{-1} \text{ y}^{-1}$. For watersheds with high proportions of alder, we suggest that N inputs reach a level exceeding the capacity for removal by plant and microbial uptake, abiotic retention, and denitrification.

Influences on Stream Cation Levels

Sea salt contributions to sodium, magnesium, and potassium were high within 5 km of the ocean

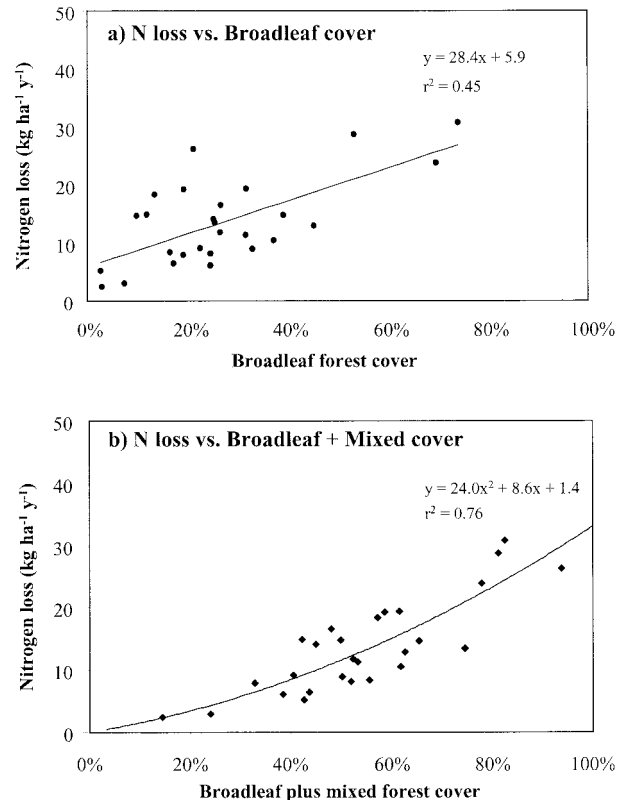


Figure 4. Watershed nitrogen (N) export as a function of a broadleaf and b broadleaf plus mixed (conifer-broadleaf) cover. Data are from all study watersheds within the Salmon River basin in 2000.

(85%, 55%, and 45%, respectively), but they were very low for calcium across all sites (less than 10%). Systematic variations in bedrock and sea salt inputs can influence stream cations, making it difficult to identify the direct effects of red alder on stream cation concentrations within the basin. Precipitation inputs of sodium were highest near the ocean on the Olympic Peninsula (Blew and Edmonds 1995), and stream sodium concentrations were highest in near-coastal sites in the Salmon River (Table 1). By removing the sea salt contributions, we attempted to more directly isolate the relationship between stream cations derived from soil weathering or mineralization processes and those derived from nitrate-driven leaching.

Stream nitrate concentrations were positively related to non-sea salt concentrations of calcium, magnesium, and sodium in the study streams (Figure 3), suggesting that nitrate leaching may be an important control on watershed-scale cation losses. Although bicarbonate and sulfate dominate the anion charge in these streams (unpublished data), variations in nitrate appear to play a role in cation

leaching. In a study of Coast Range streams, Stednick and Kern (1992) suggested that alder-derived nitrate increased stream cation fluxes, particularly since bicarbonate concentrations were similar among watersheds. Mineral weathering may be enhanced under alder (for example apatite) (Compton and Cole 1998), and cation uptake, cycling, and losses are clearly enhanced where alder is present (Binkley and others 1992; Homann and others 1992). Although broadleaf and mixed cover were only weakly related to watershed cation losses, the strong relationships between stream nitrate and dominant cations suggest that nitrate leaching from red alder stands could help drive cation losses at the watershed scale.

N Accumulation and Export in Oregon Coast Range Watersheds

In temperate forests with low atmospheric N inputs, the predominant form of N export is DON (Sollins and others 1980; Hedin and others 1995; Perakis and Hedin 2002). In contrast, nitrate often dominates N export in watersheds impacted by accelerated N deposition (Ohrui and Mitchell 1997). As N inputs shift ecosystems from N limitation to saturation, nitrate may become a more important component of the N cycle (Aber and others 1989). Nitrate accounted for an average of 92% of total dissolved N export from all study watersheds of the Salmon River basin and accounted for more than 85% when broadleaf cover was greater than 10%. The dominance of nitrate and high, relatively aseasonal nitrate concentrations (Figure 2) indicate that many of our study watersheds are N-saturated (Stoddard 1994).

Increased N availability may also increase DON export. Although N additions enhanced DON leaching from the forest floor at the Harvard Forest chronic N study (McDowell and others 1998), DON leaching from the deeper mineral soil did not respond (Currie and others 1996). Sorption or biotic uptake was hypothesized to maintain a constant flux of DON in response to N additions (McDowell and others 1998). In the Salmon River basin, DON export increased with watershed-scale nitrate export (Figure 5). Alder stands could increase DON losses directly through root or symbiont exudation or indirectly by increasing soil N availability. Long-term N additions via N_2 fixation increased the export of DON, but the resulting DON losses do not offset the high rates of N inputs and associated patterns of nitrate leaching.

Oregon Coast Range streams have high nitrate concentrations relative to other small forested watersheds in the Pacific Northwest and other temper-

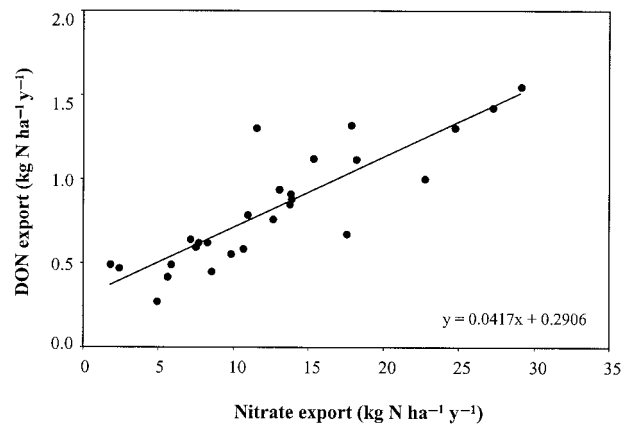


Figure 5. Relationship between nitrate and dissolved organic nitrogen (DON) export for all study watersheds within the Salmon River basin. Pearson correlation coefficient is 0.89.

ate regions. The average N export from watersheds within the Salmon River ($13.6 \text{ kg N ha}^{-1} \text{ y}^{-1}$) is nearly an order of magnitude greater than the export from a small coniferous watershed in the Oregon Cascades ($1.5 \text{ kg N ha}^{-1} \text{ y}^{-1}$) (Sollins and others 1980). In a survey of streams across the Coast Range during a fall storm, the variation in nitrate concentrations (from less than 0.005 to 2.4 mg NL^{-1}) was hypothesized to be controlled by forest vegetation and specifically N_2 fixation by red alder (Wigington and others 1998). Small watersheds within the Alsea basin of the western Coast Range had losses of up to $20 \text{ kg nitrate-N ha}^{-1} \text{ y}^{-1}$ (Stednick and Kern 1992); and Flynn Creek, with approximately 68% alder cover, exported $25\text{--}35 \text{ kg nitrate-N ha}^{-1} \text{ y}^{-1}$ (Brown and others 1973). In contrast, forested watershed streams in the western Cascades and Olympics have very low dissolved N concentrations and loss rates of less than $2 \text{ kg N ha}^{-1} \text{ y}^{-1}$, where DON dominates N losses (Triska and others 1989; Edmonds and others 1995). Variations in red alder cover across the region may explain the patterns of nitrate leaching across the Oregon Coast Range. In the Cascade and Olympic mountains of western Oregon and Washington, red alder generally is restricted to riparian areas and does not play the same broad landscape role as in the Coast Range. Rates of N export from Salmon River watersheds ($2.4\text{--}30.8 \text{ kg N ha}^{-1} \text{ y}^{-1}$) generally are greater than those from small forested watersheds in more polluted regions of the northeastern United States [$1\text{--}2.5 \text{ kg N ha}^{-1} \text{ y}^{-1}$ in New Hampshire (Goodale and others 2000); $3.8 \text{ kg N ha}^{-1} \text{ y}^{-1}$ in the Catskills (Lovett and others 2000)] and are more similar to N-saturated forests in Eu-

rope and Asia [$10\text{--}31 \text{ kg N ha}^{-1} \text{ y}^{-1}$ (Gundersen and Bashkin 1994; Ohrui and Mitchell 1997)].

Coast Range soils also have particularly high N content relative to other areas of western Oregon (Cromack and others 1999; Remillard 2000). In the Salmon River basin, soil N content was $13,720 \text{ kg ha}^{-1}$ in mixed alder–conifer stands and $9,800 \text{ kg ha}^{-1}$ in pure conifer stands (Binkley and others 1992). These are among the highest values of forest soil N content globally (Cole and Rapp 1981). Export from watershed SM-11, with 74% alder cover, was $30.8 \text{ kg N ha}^{-1} \text{ y}^{-1}$. If pure alder stands fix $100\text{--}200 \text{ kg N ha}^{-1} \text{ y}^{-1}$ (Binkley and others 1994), then at least 55% of the fixed N was retained within the watershed, since denitrification is a relatively small vector of N loss in alder stands (less than $0.3 \text{ kg N ha}^{-1} \text{ y}^{-1}$) (Binkley and others 1992). Although alder-dominated watersheds are relatively open with respect to N cycling (high inputs and outputs), substantial N accumulation does occur within these ecosystems. The mechanisms for maintaining this continued ecosystem N retention and accumulation over the long term are not understood, but they are probably linked to the high carbon storage under alder (Cole and others 1995). Although extremely high N export may be related to the present-day distribution of red alder stands, large-scale fires with a frequent rotation time (approximately 200 years) (Long and others 1998) could have enabled alder to colonize these disturbed areas during the last several thousand years. Fire may be an important vector of short-term N loss, and the long-term effect may be to increase ecosystem N content by promoting alder colonization. The widespread and shifting distribution of red alder could leave a legacy of high soil and stream N across much of the Oregon Coast Range.

Implications of Large N Export for Terrestrial and Aquatic Ecosystems

Due to their long growing seasons, relatively low drought stress, and abundant N availability, the forests of the Oregon Coast Range are among the most productive conifer forests on Earth (Waring and Franklin 1979). Rapid colonization and high rates of N_2 fixation by red alder after disturbance may be in large part responsible for the high N availability in these forests. However, the rapid accumulation of N beyond ecosystem demands can lead to N saturation, and the consequences of alder-driven N saturation are not widely recognized or understood.

It is not clear whether N leaching associated with red alder will manifest itself in widespread cation deficiencies or declining forest productivity, as pro-

posed and observed in polluted regions of the northeastern United States and Europe (Aber and others 1989, 1998; Likens and others 1996). In alder-dominated watersheds, biological inputs drive N saturation rather than the anthropogenic deposition inputs specified in the original model (Aber and others 1989). The processes associated with N saturation appear to be similar, in that N supply exceeds the watershed capacity to retain or remove this N, leading to nitrate losses that can in turn accelerate cation losses and soil acidification. The expansion of *Alnus* approximately 8000 years ago in southwestern Alaska has been linked to increased N availability in lakes and their watersheds and with increased aquatic productivity and soil acidification at this time (Hu and others 2001). There is recent evidence linking high soil N to increased severity of fungal pathogens and reduced needle retention in the Oregon Coast Range (Maguire and others 2000). Increases in fire, logging, and land clearance since European settlement may have allowed red alder to expand across the disturbed landscape during the 20th century (Heusser 1964; Davis 1973; Carlton 1988). Given its influence in regulating N and possibly cation supply, it is important to consider the role of alder when assessing the long-term impact of human activities on forest ecosystem productivity.

N export from alder-dominated watersheds may also affect aquatic ecosystem function. N or P can limit autotrophic production in Pacific Northwest streams and rivers (Hill and Knight 1988; Welch and others 1998); therefore, high inorganic N loads could produce high N:P ratios and P limitation. In the highly shaded headwater streams of the Salmon River basin, instream processing retained only a small proportion of nitrate inputs (S. T. Larned unpublished). Because coastal waters are N-limited for at least part of the year (Bernhard and Peele 1997; Wheeler and Björnsäter 1992), nitrate loading to coastal areas from alder-dominated watersheds could influence estuarine algal blooms, community composition, and other symptoms of eutrophication (Cloern 2001).

In the Pacific Northwest, human activities have altered watershed-level nutrient budgets in relatively unique ways. Although declining salmonid returns have reduced inputs of marine-derived N to Pacific coastal watersheds by approximately an order of magnitude (Finney and others 2000), changes in land cover in the 20th century could have accelerated terrestrial-derived N inputs from red alder. A positive feedback has been suggested for Pacific coastal streams, where the N and P supplied by returning Pacific salmon increase the pro-

ductivity of riparian forests, freshwater ecosystems, and juvenile salmon (Johnston and others 1990; Bilby and others 1996; Helfield and Naiman 2001). The relative role of alder versus salmon inputs to stream productivity is not known. However, even if the amount of N delivered is similar, watershed-derived nitrate and DON are not expected to play the same role in aquatic ecosystems as the protein-rich particulate organic N derived from the decay of returning salmon. The role of terrestrial versus marine-derived nutrients is of particular interest since stream amendments are being suggested as a fisheries management practice in this region (Stockner and Ashley 2003). The effects of such amendments superimposed on the inherently high levels of watershed N export in the Oregon Coast Range are unknown. Clearly, more attention needs to be paid to the collective influence of human activities on watershed-scale nutrient cycling and aquatic productivity in the Pacific Northwest coastal region.

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