

Effects of Succession on Nitrogen Export in the West-Central Cascades, Oregon

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ABSTRACT

This study examined impacts of succession on N export from 20 headwater stream systems in the west central Cascades of Oregon, a region of low anthropogenic N inputs. The seasonal and successional patterns of nitrate ($\text{NO}_3\text{-N}$) concentrations drove differences in total dissolved N concentrations because ammonium ($\text{NH}_4\text{-N}$) concentrations were very low (usually $< 0.005 \text{ mg L}^{-1}$) and mean dissolved organic nitrogen (DON) concentrations were less variable than nitrate concentrations. In contrast to studies suggesting that DON levels strongly dominate in pristine watersheds, DON accounted for 24, 52, and 51% of the overall mean TDN concentration of our young (defined as predominantly in stand initiation and stem exclusion phases), middle-aged (defined as mixes of mostly understory reinitiation and older phases) and old-growth watersheds, respectively. Although other studies of cutting in unpolluted forests have suggested a harvest effect lasting 5 years or less, our young successional watersheds that were all older than 10 years still lost significantly more N, primarily as $\text{NO}_3\text{-N}$, than did watersheds containing more mature forests, even though all forest floor

and mineral soil C:N ratios were well above levels reported in the literature for leaching of dissolved inorganic nitrogen. The influence of alder may contribute to these patterns, although hardwood cover was quite low in all watersheds; it is possible that in forested ecosystems with very low anthropogenic N inputs, even very low alder cover in riparian zones can cause elevated N exports. Only the youngest watersheds, with the highest nitrate losses, exhibited seasonal patterns of increased summer uptake by vegetation as well as flushing at the onset of fall freshets. Older watersheds with lower N losses did not exhibit seasonal patterns for any N species. The results, taken together, suggest a role for both vegetation and hydrology in N retention and loss, and add to our understanding of N cycling by successional forest ecosystems influenced by disturbance at various spatial and temporal scales in a region of relatively low anthropogenic N input.

Key words: Cascades; nitrate; dissolved organic nitrogen; dissolved organic carbon; logging; watersheds; forest succession; nitrogen export.

INTRODUCTION

Nitrogen excess is a significant issue in watershed ecology because of disruptions in nutrient cycling, increased acidification and decreased cation ex-

change capacity, increased emissions of greenhouse gases, deleterious effects on forest productivity, estuarine nutrient enrichment and algal blooms, toxic aquatic effects, and violation of receiving water nitrate standards. A large body of research documents elevated N deposition effects on forest biogeochemical cycling in eastern U.S. old-growth and successional forests (Magill and others 1996;

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Aber and others 1998; Fenn and others 1998). Research in unpolluted forest ecosystems has focused on old-growth forests (Sollins and others 1980; Edmonds and others 1998; Perakis and Hedin 2002) or on very recently clear-cut watersheds (Sollins and McCorison 1981; Martin and Harr 1989). Few data have been reported along a full successional gradient in regions experiencing little N deposition where 'natural' N cycling can be observed (Peet 1992), even though successional status is often cited as an important influence on N flux (Likens and Bormann 1995).

Vitousek and Reiners (1975) proposed a conceptual model of nutrient loss over successional time in which forest harvest produces an immediate flush of N, after which young aggrading systems tightly retain N as a limiting, essential nutrient and export low levels of N in stream water. This condition of very low N export persists until old-growth forests exhibit reduced N demand, and dissolved inorganic N (DIN) losses rise to approximately equal N inputs. This pattern has been observed in temperate forests, particularly in eastern U.S. forests that have received elevated N deposition (for example, see Likens and Bormann 1995; Goodale and others 2000). Vitousek and others (1998) modified this theory to take into account factors that may cause the persistence of N limitation, and thus low N exports, in older forests, including very low N inputs, disturbance, and gaseous and/or dissolved organic losses. Indeed, in many temperate forests, dissolved organic N (DON) can be a major component of stream N export (Edmonds and others 1995; Hedin and others 1995; Lajtha and others 1995; Vitousek and others 1998; Campbell and others 2000; Neff and others 2000; Coats and Goldman 2001; Perakis and Hedin 2002; Vanderbilt and others 2003). If these DON losses equal or are nearly equal to N inputs, DIN losses may remain low even when biotic demand for N has decreased. However, both biotic and hydrologic seasonality may affect N losses as well; N exports have been shown to increase when biotic activity is low (Likens and Bormann 1995; Williams and others 1995) or during snowmelt (Murdoch and Stoddard 1992; Sickman and others 2003) or at the onset of storms after drought (Fenn and Poth 1999; Bechtold and others 2003; Vanderbilt and others 2003). Similarly, Swank and others (2001) noted that species turnover during succession may result in pulses in nitrate export. Finally, Binkley and others (1982) pointed out that in systems with significant biological N₂ fixation, as may exist in early successional forests in the Pacific Northwest, water chemistry profiles may reflect N inputs that

change with successional status and thus not conform to patterns predicted by these other models.

This paper presents results of a study of west Cascades headwater stream systems where past natural and anthropogenic disturbance factors have been documented, resulting in a watershed forest cover successional mosaic. Twenty small catchments were monitored for stream N export over the course of two water years to better understand successional and other biophysical effects on N loss from managed forest ecosystems. We predicted that our young forests, all more than ten years in age, would exhibit very low DIN loss due to high biotic demand; long-term water chemistry records in the nearby H. J. Andrews Experimental Forest (HJAEF) indicate that the N-flush spike after harvest lasts for approximately 5 years (K. Lajtha and J.A. Jones unpublished data). Because the HJAEF water chemistry profiles do not show appreciable influence of red alder (*Alnus rubra*)-fixed N inputs and because our vegetation is similar, we did not expect to see a strong signal from biological N₂ fixation. We also predicted that DON losses would increase with succession as organic matter cycling increased and DIN losses would increase slightly as the rate of organic matter accumulation slowed in old growth forests. We also predicted that there would be few seasonal patterns of N export in any forest, as N export in general should be extremely low in these rapidly aggrading, unpolluted forests, and soils should have a sufficiently high C:N to immobilize any mineralized N.

METHODS

General Site Description

The study area is the upper 447 km² portion of the South Santiam River basin situated on the west slope of the Oregon Cascades (Figure 1). Most of the area lies within the Sweet Home Ranger District (SHRD) of the 6783 km² Willamette National Forest (WNF). Elevations range from 238 m at Cascadia in the west to 1671 m at the eastern edge of the basin, which is characterized by dense coniferous forests and steeply dissected slopes. The study area falls within the western hemlock (*Tsuga heterophylla*) vegetation zone at lower elevations and the Pacific silver fir (*Abies amabilis*) zone above 1250 m (Franklin and Dyrness 1988). The basin is typical of the Pacific Northwest coastal rain forest, some of the most productive forest lands in existence (Waring and Franklin 1979) and the source of a large share of the world's timber supply for many decades (Waddell and others 1989).

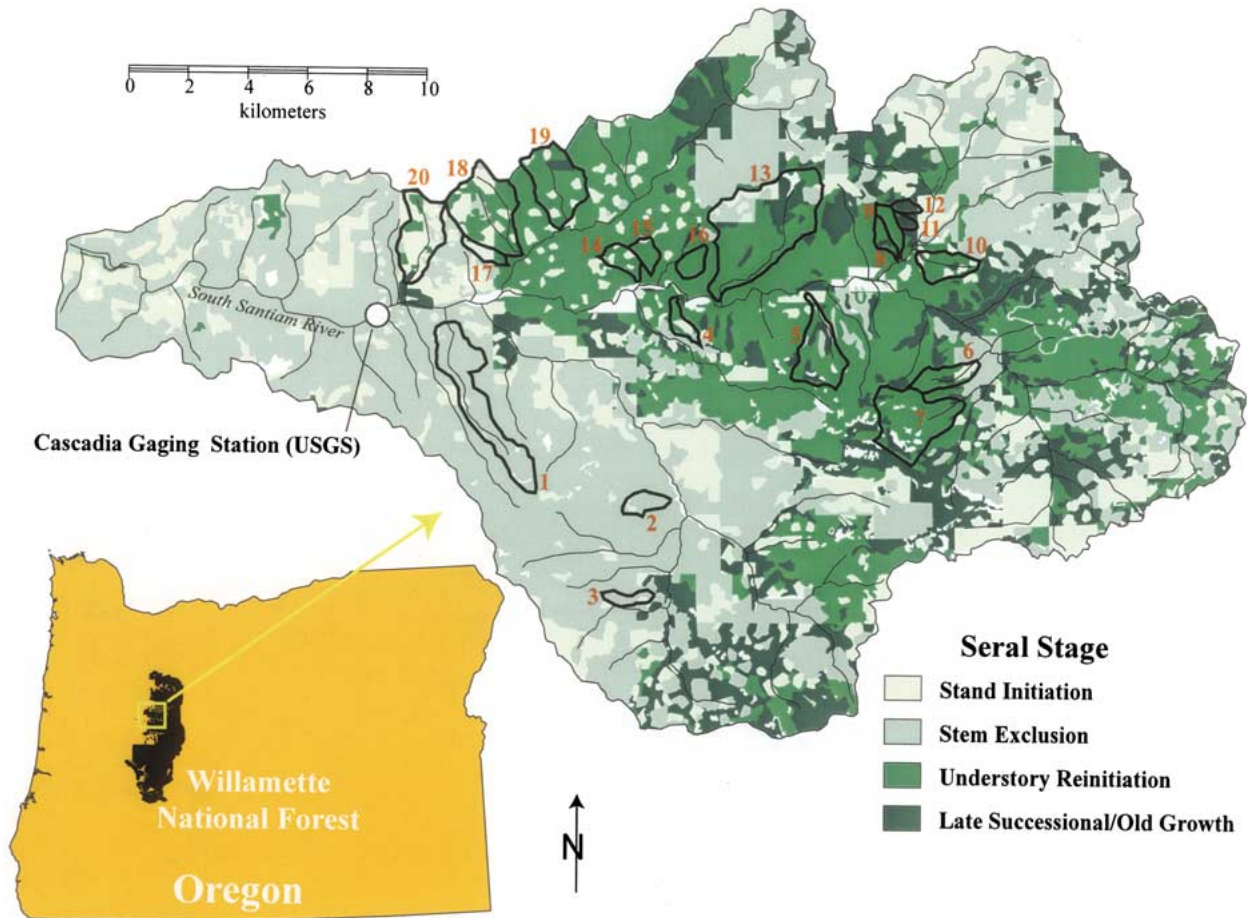


Figure 1. Location of study watersheds in the South Santiam River basin of Oregon's west central Cascades. The site of the USGS gaging station is shown, as well as the distributions of the four forest successional stages.

The upper South Santiam River basin is also representative of much of the west-central Cascade Mountains, including the HJAEF. The HJAEF is located approximately 20 km to the south in the WNF and has been the subject of much ecological research (for example, Dyrness 1973; Halpern 1989; Grant and Wolff 1990; Jones and Grant 1996; Vanderbilt and others 2003). Vegetation is dominated by Douglas fir (*Pseudotsuga menziesii*). Less common tree species include western hemlock, western redcedar (*Thuja plicata*), red alder, bigleaf maple (*Acer macrophyllum*) and Pacific silver fir. Common understory species include Pacific rhododendron (*Rhododendron macrophyllum*), vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), red huckleberry (*Vaccinium parvifolium*), oceanspray (*Holodiscus discolor*), *Rubus* sp., Oregon-grape (*Berberis* sp.), and golden chinquapin (*Castanopsis chrysophylla*).

The Pacific Ocean lies 160 km to the west and influences the area's climate. Mean monthly temperatures range from 2 to 18°C. Annual precipitation averages approximately 240 cm in the western

Cascades (Greenland 1994), with 80% of this amount falling in the November-April period (Jones and Grant 1996). Rain dominates below 400 m, and snow above 1200 m. A transient snow pack develops between these two elevations (Harr 1981), while a seasonal snow pack commonly develops above 1200 m.

Data from the nearby HJAEF indicate that the mean precipitation total nitrogen (TN) input was either 1.62 or 2.01 kgN ha⁻¹ y⁻¹, depending on the elevation of the bulk deposition collector (430 or 922 m, respectively) (Vanderbilt and others 2003). In general, N deposition to the west-central Cascades is low and impacted little by anthropogenic inputs.

Bedrock geology consists primarily of andesitic tuffs and breccias (James 1977), with some basalts and glacial deposits (Sherrod and Smith 1989). Soil depth to volcanic bedrock ranges from one to six meters and texture varies among fine to coarse loamy, loamy-skeletal, and fine-silty. Soil hydraulic characteristics have been described by Perkins

(1997). Infiltration, subsurface flow rates and hydraulic conductivity are high (Harr 1977). Mineral soil C:N ratios in the study area range from 11:1 to 34:1 and forest floor C:N ratios range from 54:1 to 126:1 (M.A. Cairns, unpublished data).

Forest History

Prior to permanent European settlement beginning in 1843, and to a lesser degree for the subsequent century, landscape dynamics in the western Cascades were constrained primarily by patterns of wildfire (Agee 1993). Morrison and Swanson (1990) reported that historic fire return intervals varied from 25 to 110 years for low-intensity ground fires, and 100–200 years or more for high-intensity stand-replacement fires. Large-scale wildfires have not been reported in the study watersheds since 1856 (SHRD 1995). Other disturbance factors include mass soil movement and associated channel debris torrents (Swanson and others 1990), insects (Waring and Running 1998), and volcanic activity (Yamaguchi 1993).

Beginning in the mid-20th century, clear-cut harvesting on National Forests (Harris 1984) joined clear-cutting on private lands, which had begun in the decades prior to 1900 (Robbins 1988). Reforestation with Douglas fir plantations follows clear-cutting to begin the process of forest succession. In this industrial forestry period, dispersed clearing of 10–20 ha patches, using a typical rotation length of 40–80 years, has resulted in forest fragmentation (Franklin and Forman 1987), with few watersheds containing stands all of the same seral stage.

Watershed Characteristics

This study used a simplified classification system of successional status (Oliver and Larson 1990) to assign each stand in the South Santiam basin to one of four seral stages. The WNF-Sweet Home Ranger District (SHRD 1995) reported that 17% of the study area is in the stand initiation (SI) stage, typically with trees less than 15 cm diameter at breast height (DBH) and less than 30 years of age. This stage represents the start of the forest succession process. Approximately 40% of the basin is in the stem exclusion (SE) stage, where natural crowding leads to self thinning. Trees are typically 10–25 cm DBH, and ages are 15–70 years. Stands in the understory reinitiation (UR) stage compose 27% of the forest cover. These stands are usually 50–200 years of age and trees are 20–90 cm DBH. The late successional/old-growth (OG) stage is typically reached after more than 150 years

have elapsed following stand-replacement disturbance. Trees in this seral stage exceed 61 cm DBH (current average is >76 cm) and OG forests cover approximately 16% of the upper South Santiam basin (SHRD 1995). Age and size ranges overlap among the four stages because successional status is based on forest structure and process (for example, self-thinning results in open canopies that allow for re-establishment of understory shrub species), rather than strictly on the basis of size or age (Oliver and Larson 1990).

Mapped seral stage data (SHRD 1995) were augmented with information from the basin's dominant private forest land manager, data from seven digital orthophoto quadrangles (USGS 1992–94), and field verification of forest cover classes. Stands in the two early seral stages were easily verifiable from stand history records. Stand ages in the two later stages were estimated from an analysis of tree increment cores and fire history maps (SHRD 1995).

The resulting Geographic Information System (GIS) map was used to select watersheds of variable successional status for stream sampling. All of the approximately 235 small (<10 km²), discrete, headwater streams were stratified by accessibility, size, elevation, and proportion of the catchment in each of the four seral stages. After eligible watersheds were grouped into similar age-classes, a stratified-random process was used to select a group of study watersheds that expressed the full range of forest successional development. Stream chemistry and hydrology data from the 20 chosen watersheds were sampled at sites near the stream mouths. There are no buildings, farms, or impoundments above the sampling sites. Only eight streams were officially named; the rest were assigned names by the project. GIS analyses revealed various biophysical characteristics of the study watersheds, including area, stream order, mean elevation, aspect, land ownership, slope, and drainage density. Geological data were obtained from a USGS source (Johnson and Raines 1995). Historical mean precipitation was interpolated from a 2-km resolution isohyetal map of modeled long-term (1961–1990) annual precipitation (PRISM model, Daly and others 1994). Hardwood forest cover was obtained from a dataset representing conditions in approximately 1990 (ISE 1999). Those data were derived from Landsat TM imagery with a spatial resolution of 30 × 30 m. We combined the closed hardwood and semi-closed hardwood land cover classes.

An age index for each watershed, composed of stands of varying seral status, was calculated by

area-weighting the four stand-level seral stages (SI = 1; SE = 2; UR = 3; OG = 4), and potentially ranged from 1 (entirely SI) to 4 (entirely OG). For comparisons of successional patterns, watersheds were grouped into young, middle-aged and old categories. The five watersheds with the lowest age indices (1.63–1.92) were grouped as young watersheds, and were dominated by stands in the SI and SE seral stages. The seven with the highest age indices (2.99–3.82) were dominated by stands in the UR and OG stages, and were grouped as old successional watersheds. The middle eight (2.28–2.86) were grouped as middle-aged watersheds and did not have high proportions of either SI or OG stages.

Sample Collection and Analysis

Stream water samples were collected from each of the watersheds during two water years, WY00 and WY01 (October 1999 to September 2001). Sampling was concentrated in fall and winter high-flow periods and included 23 separate sampling events. Two seasonal streams (#8 and #9) were dewatered except during times of high flow. One watershed (#7) was inaccessible on one occasion due to deep snow. Missing chemistry data for these watersheds were estimated using averages from previous and subsequent sampling events.

Water samples were collected in new polyethylene containers, after prerinsing with stream water, and placed on ice until processed. Samples were vacuum-filtered through 0.25 μm polycarbonate membrane filters (Whatman Inc., Newton, MA, USA) within 24 h of collection. Ammonium-N and nitrate-N were determined with flow injection analysis using an automated colorimetric auto analyzer method (Lachat Instruments, Milwaukee, WI, USA, Method 10-107-06-3-D for $\text{NH}_4\text{-N}$ and US EPA 1987, Method 353.2 for $\text{NO}_2 + \text{NO}_3\text{-N}$). Total dissolved nitrogen (TDN) samples were pre-digested with persulfate (Koroleff (1983) as modified by Qualls (1989); Motter 2000) and analyzed for $\text{NO}_3\text{-N}$. DOC was determined by acidification and sparging followed by uv/persulfate oxidation on a Tekmar-Dohrmann Phoenix 8000 Carbon Analyzer. DON was calculated by difference: $\text{DON} = \text{TDN} - (\text{NO}_3\text{-N} + \text{NH}_4\text{-N})$. Information concerning quality assurance protocols, QC checks, standard operating procedures, and hold times is available (Erway and others 2001).

Discharge and Nitrogen Export

None of the sampled streams were gaged, although a USGS gage at Cascadia on the South Santiam River was the source of stream flow data

throughout the study. During WY00, the gaged South Santiam discharge (Q) slightly exceeded the long-term average of 163 cm, while during WY01, the gaged Q was less than one-half the long-term average. Instantaneous discharge was measured with the velocity-area procedure (Kaufmann 2002) at the time of each sampling event. Stream flow was estimated for the periods between sampling events by applying a regression model developed for each stream based on the instantaneous tributary Q and the gaged South Santiam Q at that time. Daily N export (kg ha^{-1}) was estimated by multiplying N concentration by modeled daily Q, summed for monthly N export, and monthly fluxes totaled for each of the two water years. Annual TDN loss was calculated by multiplying Q per unit area by the flow-weighted average annual N concentration. Correlation coefficients and goodness-of-fit statistics were computed for the 20 stream Q models.

Precipitation

Precipitation was not collected in the study watersheds but we estimated precipitation using data from a nearby site. We used low elevation (430 m) HJAEF long-term mean precipitation (248 cm; Vanderbilt and others 2003), a model of precipitation for the 20 study watersheds (Daly and others 1994), and the deviation of annual gaged Cascadia Q during WY00 and WY01 from mean long-term annual Cascadia Q to estimate precipitation in the study watersheds.

Statistical Analyses

Differences in watershed N and DOC concentrations due to successional development stage (young, middle-aged, or old forest cover) were determined by analysis of variance (SAS 1996). Tukey's honest significant difference tests were used for post hoc pairwise comparisons. Effects of seral development and other biophysical attributes were assessed with regression analysis. Normal probability plots indicated that variables were normally distributed. All hypothesis tests utilized $\alpha = 0.05$.

RESULTS

Watershed Characteristics

Watersheds ranged in size from 30 to 966 ha (median = 90 ha) (Table 1). Mean watershed elevation varied from 578 to 1228 m and mean long-term precipitation varied from 161 to 224 cm y^{-1}

Table 1. Attributes of Study Watersheds, in Order of Increasing Average Successional Age

Watershed	Name	SI (%)	SE (%)	UR (%)	OG (%)	Age index ^a	Area (ha)	Mean elev. (m)	Mean Precip. (cm y ⁻¹) ^b	Hardwood (%) ^c
17	"Husted Creek"	68	0	31	0	1.63	61	578	162	3
20	Soda Creek	60	17	19	3	1.64	330	706	164	16
2	"Barringer Creek"	14	86	0	0	1.86	86	657	173	19
3	"Filtering Sun Brook"	13	87	0	0	1.87	61	779	171	5
1	Wolf Creek	5	94	0	0	1.92	533	681	166	7
18	Whiterock Creek	33	6	60	0	2.28	486	711	166	5
4	"Longbow Creek"	26	13	61	0	2.35	71	645	193	0
14	"Vinemaple Creek"	25	0	75	0	2.50	94	593	161	7
10	Taylor Creek	24	0	68	8	2.61	154	795	192	1
6	"Hidden Stream"	21	0	68	11	2.70	137	1008	207	2
19	Hensley Creek	13	0	79	8	2.82	366	663	171	2
15	"Little Pool Creek"	8	0	92	0	2.83	70	608	162	1
13	Trout Creek	10	11	60	17	2.86	966	859	191	7
9	"New Creek"	0	1	99	0	2.99	72	827	189	0
16	"Slide Creek"	0	0	100	0	3.00	76	653	193	2
5	Little Boulder Creek	2	13	64	19	3.02	305	964	224	2
7	W. Fork Three Creek	0	0	82	11	3.11	477	1228	224	6
8	"Nood Nook Brook"	0	0	87	13	3.13	54	714	194	0
12	"Falcon Nile Creek"	2	5	7	86	3.76	34	864	188	3
11	"Snake Creek"	0	0	18	82	3.82	30	776	187	1

^aArea-weighted (SI=1; SE=2; UR=3; OG=4). SI=stand initiation; SE=stem exclusion; UR=understory reinitiation; OG=late successional/old-growth.

^bHistorical area-weighted values estimated from PRISM map (http://biosys.bre.orst.edu/restore/datasets/view_detail.cfm?datasetID=6).

^cInstitute for a Sustainable Environment, University of Oregon. 1999. Willamette River Basin landuse and landcover, circa 1990, version 3a. www.oregonstate.edu/dept/pnw-ercl

(median = 188; SE = 4.3 cm y⁻¹). Hardwood tree cover ranged from 0–19% with a median value of 2% (Table 1). Other geophysical attributes of the study watersheds are shown in the Appendix.

The forest age index ranged from 1.63 to 3.82 (Table 1). The stands in the two early seral stages (SI and SE) originated from clear-cut harvest, while the stands in the later seral stages (UR and OG) originated from fires. All 20 watersheds experienced wildfires in approximately 1200. A series of large fires burned in the basin in about 1500 and another wildfire impacted much of the area in 1856 (SHRD 1995). Although small ground fires have most likely occurred in recent times, the last catastrophic fire was thus approximately 150 years before the present.

Stream Chemistry

Nitrate concentrations were seasonal in watersheds containing young forest cover, although not in middle-aged or older watersheds, with concentrations peaking in early December at the start of the wet season and low concentrations observed during the dry growing season (Figure 2). Young watersheds had higher NO₃-N concentrations than older watersheds, showing statistically significant

elevations on nearly all of the sampling dates. Although nitrate concentrations in old watersheds exceeded those in middle-aged watersheds on most sampling dates, the concentrations were significantly different on only one date. When mean NO₃-N concentrations for all watersheds were regressed against seral status, expressed as either % (SI + SE) or age index, correlations were highly significant ($R^2 = 0.66$, $P < 0.0001$ and $R^2 = -0.42$, $P < 0.01$, respectively).

Total dissolved N concentrations followed the seasonal and successional patterns of NO₃-N concentrations because NH₄-N concentrations were very low (0.000–0.015 mg L⁻¹, usually < 0.005 mg L⁻¹) and mean DON concentrations were much less variable. Young watersheds had higher DON levels than older watersheds, showing significant differences on most sampling dates (Figure 3). DON concentrations were generally the same in middle-aged and old watersheds on all sampling dates. When mean DON concentrations for all watersheds were regressed against seral status, expressed as either % (SI + SE) or age index, correlations were highly significant ($R^2 = 0.44$, $P < 0.01$ and $R^2 = -0.37$, $P < 0.01$ respectively). The overall annual mean DON concentration was 0.030 mg L⁻¹ and DON accounted for 24, 52, and 51% of the

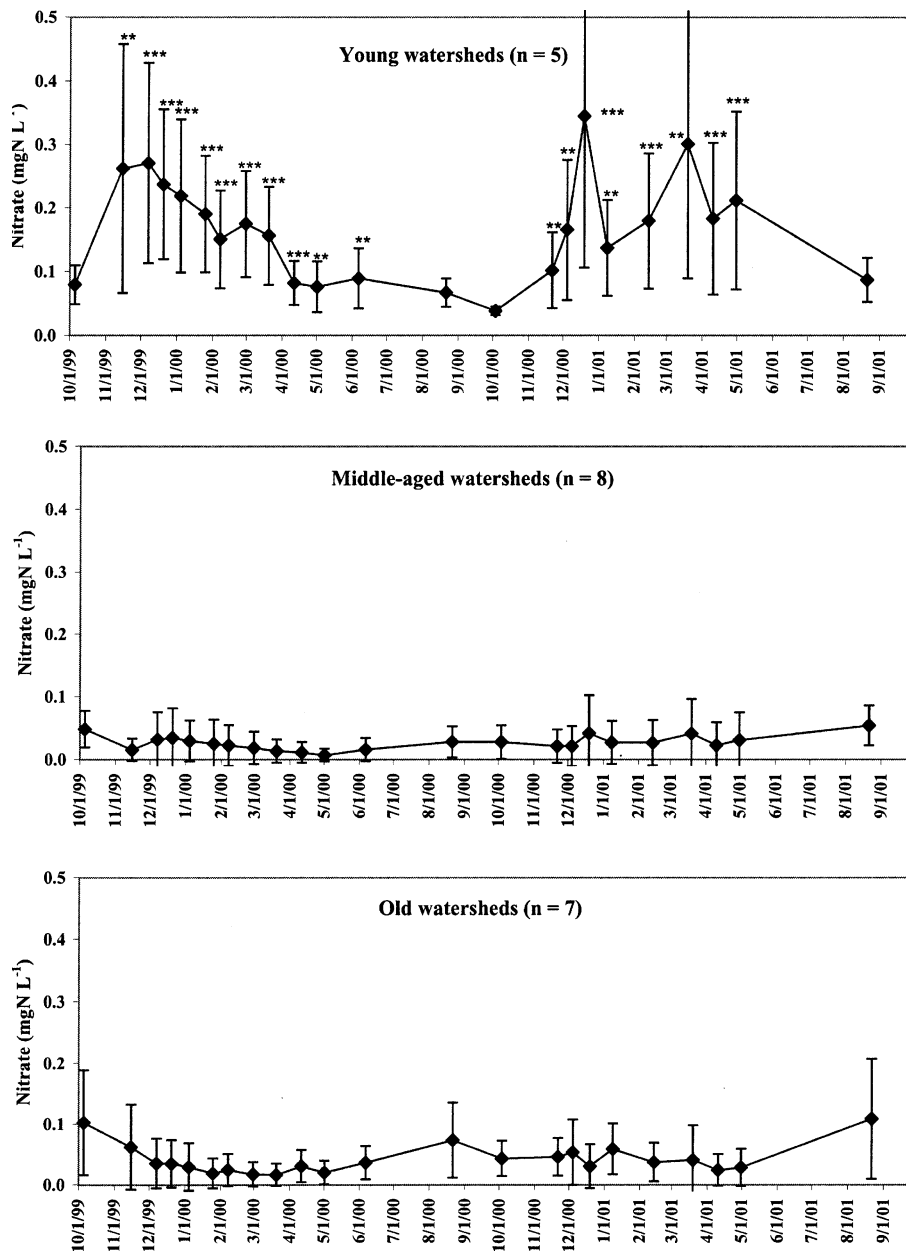


Figure 2. Seasonal $\text{NO}_3\text{-N}$ (mg L^{-1}) concentrations in watersheds covered with young, middle-aged, and old successional forests sampled over two water years. Plotted concentrations are the mean (± 1 SD) of the watersheds in that age class (n in parentheses). Asterisks (**, ***) indicate concentrations significantly elevated ($\alpha = 0.01, 0.001$) relative to the other age classes for that date.

overall mean TDN concentration of the young, middle-aged and old watersheds, respectively. The percentage for young watersheds was significantly lower than for middle-aged watersheds ($F = 3.9$; $P < 0.05$); the percentage for old watersheds was not different from either young or middle-aged watersheds.

Patterns of watershed DOC concentrations were similar to patterns of DON concentration. DOC levels peaked in the winter of WY00 and in May of

WY01, the latter following a very dry winter (Figure 4). DOC concentrations were higher in young watersheds than in older watersheds, showing statistically significant elevations on most of the sampling dates. DOC concentrations were usually between 0.5 and 2.0 mg L^{-1} , although concentrations exceeded 3.0 mg L^{-1} in several watersheds on several occasions. DOC concentrations did not differ significantly between middle-aged and old watersheds. When mean DOC concentrations for

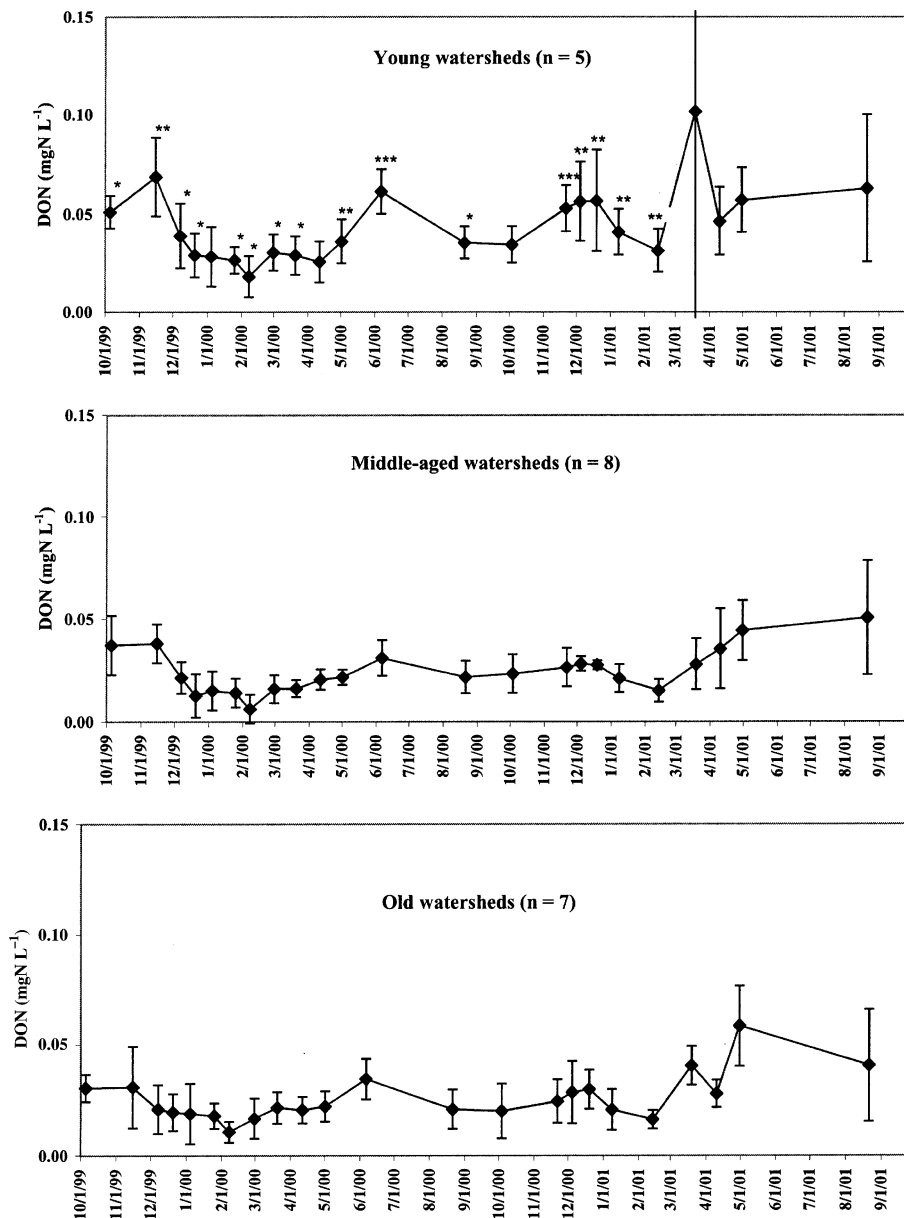


Figure 3. Seasonal DON (mg N L^{-1}) concentrations in watersheds covered with young, middle-aged, and old successional forests sampled over two water years. Plotted concentrations are the mean (± 1 SD) of the watersheds in that age class (n in parentheses). Asterisks (*, **, ***) indicate concentrations significantly elevated ($\alpha = 0.05, 0.01, 0.001$) relative to the other age classes for that date.

all watersheds were regressed against seral status, expressed as either % (SI + SE) or age index, results were non-significant ($P = 0.18$, $P = 0.23$, respectively).

Compared across all watersheds, mean DON concentrations were significantly correlated ($P < 0.01$) with mean DOC concentrations (Figure 5a). The best fit to this relationship suggested a stream water DOC:DON ratio varying from 21 to 52 within the range of the data, although goodness-of-fit decreased at higher DOC and DON concentrations.

Fluxes of Water, Nitrogen and DOC

The South Santiam basin hydrograph is typical of streams of the west-central Cascades (Figure 6). Long-term records from the low-elevation bulk deposition collector at nearby HJAEF reveal mean annual precipitation of 248 (SE = 45) cm, 208 (SE = 39) cm from the high-elevation bulk collector, and 200 (SE = 31) cm from the high-elevation wet-only collector (Vanderbilt and others 2003). Comparing these amounts with modeled mean

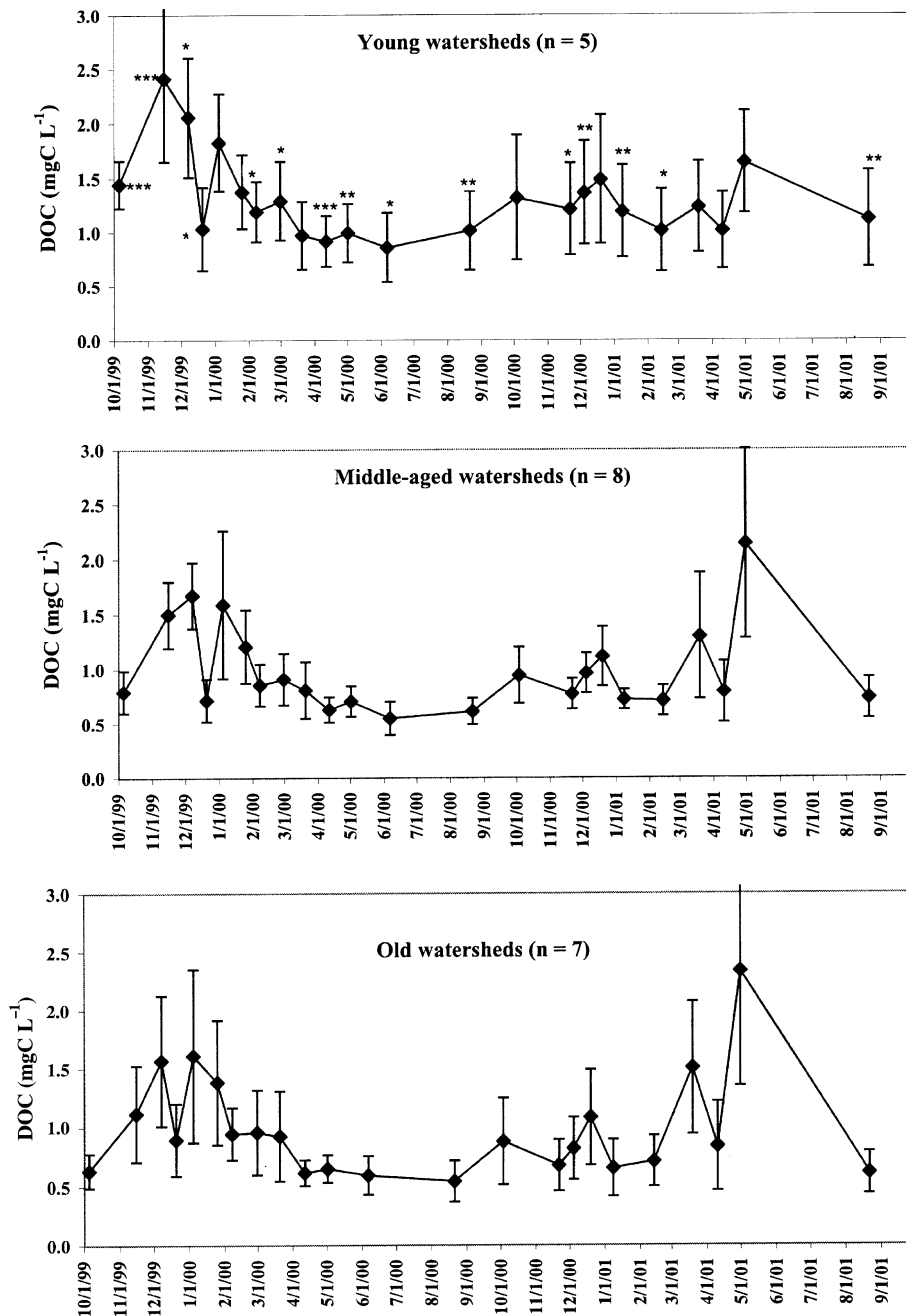


Figure 4. Seasonal DOC concentrations (mg L^{-1}) in watersheds covered with young, middle-aged, and old successional forests sampled over two water years. Plotted concentrations are the mean (± 1 SD) of the watersheds in that age class (n in parentheses). Asterisks (*, **, ***) indicate concentrations significantly elevated ($\alpha = 0.05, 0.01, 0.001$) relative to the other age classes for that date.

annual precipitation for South Santiam watersheds (Table 1) indicates that the South Santiam study watersheds are somewhat drier. Estimated long-term precipitation ranged from less than 165 cm y^{-1} at the lower watersheds to more than 220 cm y^{-1} at the higher watersheds (mean = 184 ; SE = 4 cm) (Table 1), 25% less than at the low-elevation

HJAEF site but within 8–12% of the two high-elevation HJAEF average values. Thus mean annual precipitation during WY00–01 for the 20 study watersheds ranged from 125 – 173 cm y^{-1} , (mean = 142 ; SE = 3 cm) (Table 2).

Discharge was modeled with regressions computed from Q measured in study watersheds and

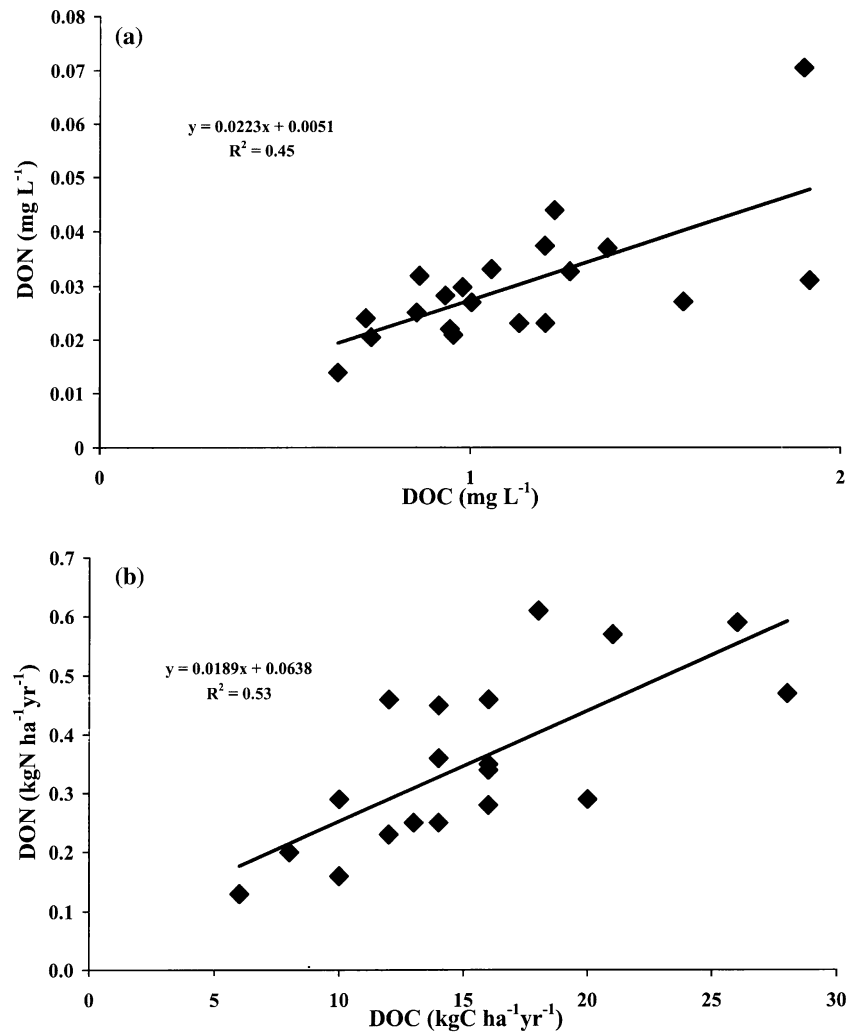


Figure 5. Relationships between (a) mean DON and DOC concentrations and (b) mean annual DON and DOC export values for all 20 watersheds over the course of the two-year study.

USGS gaging station Q values from the South Santiam River at Cascadia. All 20 regressions were highly significant and correlation coefficients were usually greater than 0.8. Daily Q was computed with these models, summed for annual Q, and expressed as the mean for the two water years. Resulting values ranged from 55 to 215 cm y⁻¹ (mean = 123; SE = 10 cm y⁻¹) (Table 2).

Differences among watersheds in mean annual N export resembled differences in mean N concentration. Variations in mean NO₃-N export were explained by the proportion of the watershed in young forest cover (SI + SE seral stages) ($R^2 = 0.69$, $P < 0.001$) (Figure 7). The median NO₃-N loss was 0.22 kg ha⁻¹ y⁻¹ (mean = 0.81; SE = 0.22 kg ha⁻¹ y⁻¹), with a range from 0.0 to 3.04 kg ha⁻¹ y⁻¹ (Table 2). Nitrate export from young watersheds was significantly greater than that from middle-

aged or old watersheds ($F = 13.2$; $P < 0.001$); export from old watersheds was not different from middle-aged watersheds.

Patterns of TDN export mirrored the patterns in TDN concentrations. TDN loss from the young watersheds was higher than that from the middle-aged and old watersheds ($F = 11.8$; $P < 0.001$), due to an order of magnitude difference in the contribution of NO₃-N (Figure 8). Across all watersheds, NH₄-N export averaged 0.06 kg ha⁻¹ y⁻¹ and varied little. DON export also varied much less than nitrate export. The median DON loss was 0.32 kg ha⁻¹ y⁻¹, with a range from 0.13 to 0.61 kg ha⁻¹ y⁻¹ (Table 2). On average, DON made up 47% of total N export and ranged from 12% to 89%. This proportion was significantly lower for young watersheds than for middle-aged or old watersheds ($F = 4.5$; $P < 0.05$); the proportion for old

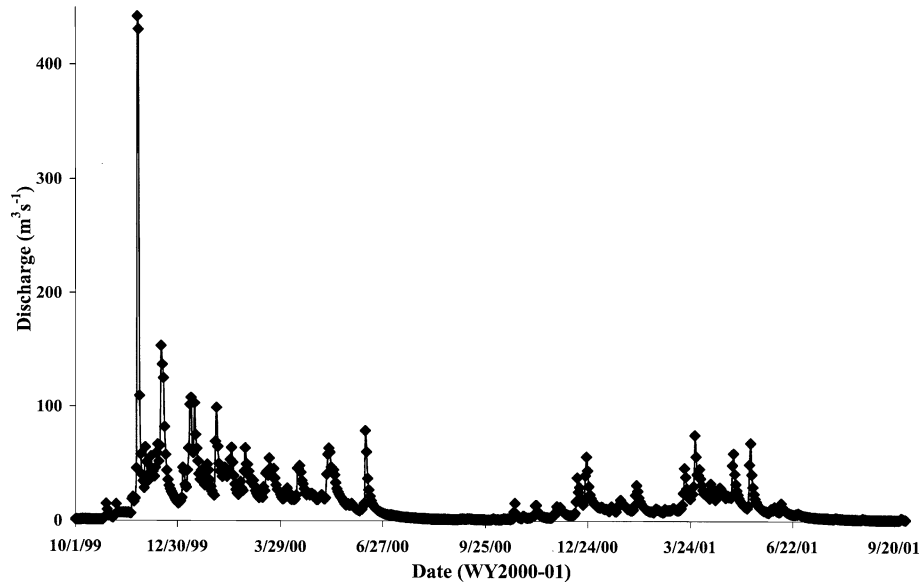


Figure 6. Two-year hydro graph from the USGS gaging station's daily average discharge measured on the South Santiam River near Cascadia, OR. Note the lack of a normal November – January peak Q in WY01.

watersheds was not different from middle-aged watersheds.

In contrast to patterns of DOC concentrations, DOC export rates were not different among young, middle-aged, and old watersheds ($F = 0.15$; $P = 0.86$). DOC export ranged from 6 to 28 kg ha⁻¹ y⁻¹ and the median was 14 kg ha⁻¹ y⁻¹. Compared across all watersheds, DOC flux was correlated ($P < 0.001$) with DON flux (Figure 5B). The best fit to this relationship suggested a DOC:DON export ratio varying from 36 to 47 within the range of the data. Both DON and DOC flux increased with discharge ($P < 0.01$), although neither varied with elevation nor precipitation.

Linear regression of TDN export against proportion of the study watersheds in the young seral stages, SI + SE, showed a highly significant ($F = 32.2$, $P < 0.0001$) relationship, similar to the relationship found for NO₃-N export. Multiple linear regression of (a) stream water DOC:DON export ratio and (b) successional status against NO₃-N export revealed that a model containing these variables was highly significant ($F = 27.9$, $P < 0.0001$) and that both variables were necessary to adequately explain the nitrate loss. The relationship with stream water DOC:DON was negative, and the relationship with % (SI + SE) was positive. When % hardwood cover was included in the model with the other two factors, it was a non-significant factor. Together the two variables explained 77% of the variation in NO₃-N export. Nitrate loss from all South Santiam basin study watersheds was best described by the following equation:

$$\begin{aligned} \text{Mean annual NO}_3\text{-N export (kg ha}^{-1}\text{y}^{-1}) \\ = 1.60 + 0.02A - 0.03B, \end{aligned} \quad (1)$$

where A = proportion of the watershed in young (SI + SE) seral stages and B = ratio of mean annual stream water DOC export to mean annual DON export.

DISCUSSION

Because of the ability of streams to integrate catchment responses to forest function changes, the use of stream water chemistry to detect watershed disturbance has been repeatedly demonstrated (for example, see Driscoll and others 1988; Likens and Bormann 1995). Our study, like most previous research, assumes that the stream nutrient concentrations reflect forest processes, and do not reflect in-stream processing. Although acknowledging that in-stream processes may exert significant control over N export by headwater streams (Peterson and others 2001; Bernhardt and Likens 2002; Valett and others 2002), such processes were beyond the scope of this study. It is also highly unlikely that in-stream processing would differ so significantly over our age gradient that our interpretation of the data would significantly change; the effect of in-stream processing is generally to lower N concentrations and thus moderate true differences in export from upland forests.

The results from the current study employing a range of successional stages showed wide

Table 2. Mean Annual Water, N, and DOC Flux

Watershed	Precipitation cm y ⁻¹	Discharge	Export				DON %	DOC kgC ha ⁻¹ y ⁻¹	DOC: DON
			TDN	NO ₃ -N	NH ₄ -N	DON			
			kgN ha ⁻¹ y ⁻¹						
17	125	94	0.78	0.38	0.04	0.36	46	14	39
20	127	100	2.55	2.06	0.05	0.45	18	14	31
2	133	123	3.57	3.04	0.08	0.46	13	16	35
3	132	122	2.85	2.47	0.04	0.34	12	16	47
1	128	88	3.32	2.66	0.05	0.61	18	18	30
18	128	115	1.63	1.12	0.15	0.35	21	16	46
4	149	68	0.43	0.27	0.02	0.13	30	6	46
14	125	195	0.75	0.10	0.06	0.59	79	26	44
10	148	111	0.35	0.08	0.04	0.23	66	12	52
6	160	199	0.64	0.11	0.07	0.47	73	28	60
19	132	100	0.48	0.16	0.04	0.28	58	16	57
15	125	80	0.32	0.09	0.03	0.20	63	8	40
13	147	124	0.40	0.12	0.04	0.25	63	13	52
9	146	120	0.34	0.00	0.05	0.29	85	20	69
16	149	89	0.98	0.65	0.03	0.29	30	10	34
5	173	215	2.22	1.69	0.07	0.46	21	12	26
7	173	191	1.56	0.91	0.08	0.57	37	21	37
8	150	55	0.18	0.00	0.02	0.16	89	10	63
12	145	157	0.49	0.15	0.11	0.23	47	12	52
11	145	104	0.39	0.10	0.04	0.25	64	14	56
Means	142	123	1.21	0.81	0.06	0.35	47	15	46
SD	15	46	1.10	1.01	0.03	0.14	25	6	12

variability among watersheds in both concentration and export of the various N forms. In contrast to our expectation that our youngest forests, all of which were greater than 10 years in age at the time of initial measurement, would be rapidly aggrading and would lose very little N, the young watersheds lost significantly more N, primarily as nitrate, than did watersheds containing more mature forests. We had predicted that the release of N from cutting would have disappeared after about 5 years as can be observed from long-term stream water chemistry records at the nearby H.J. Andrews Experimental Forest and elsewhere (Brown and others 1973; Sollins and McCorison 1981; Feller and Kimmins 1984; Harr and Fredriksen 1988; Swank and others 2001). Although DON concentrations and estimates of DON export were very similar between the South Santiam watersheds and the gaged watersheds of the HJAEEF, nitrate concentrations in our youngest watersheds seasonally exceeded the peak nitrate values observed in the clearcut watersheds at HJAEEF (WS 10 and 6, during the 5 years post-harvest). Another factor may be needed to help explain the elevated N export by the youngest watersheds. One possibility is biological N-fixation.

We considered the possibility that the presence of alder might contribute to N loading of streams, and that high N export from early successional streams might be due to significant N inputs from N₂-fixation. Nitrogen-fixing red alder has been shown to increase watershed N export in a number of studies (Binkley and others 1982; Van Miegroet and Cole 1984; Wigington and others 1998; Compton and others 2003). Alder has been reported to fix nitrogen at rates as high as 100–200 kg ha⁻¹ y⁻¹ (Binkley and others 1994), although rates in the range of 75–100 kg ha⁻¹ y⁻¹ are more likely (J Compton, personal communication). However, we initially did not expect alder to significantly affect N fluxes in streams of the South Santiam for several reasons. These previous studies were conducted in coast range forests with high rainfall and where alder is much more prevalent. Red alder occurs less frequently and is seldom seen as pure stands in the Cascades and Cascades watersheds have lower NO₃-N concentrations compared to Oregon coastal watersheds (Sollins and others 1980; Sollins and McCorison 1981; Harr and Fredriksen 1988; Martin and Harr 1988; Martin and Harr 1989; Wigington and others 1998). Red alder is generally found below 750 m elevation, and tree development is best

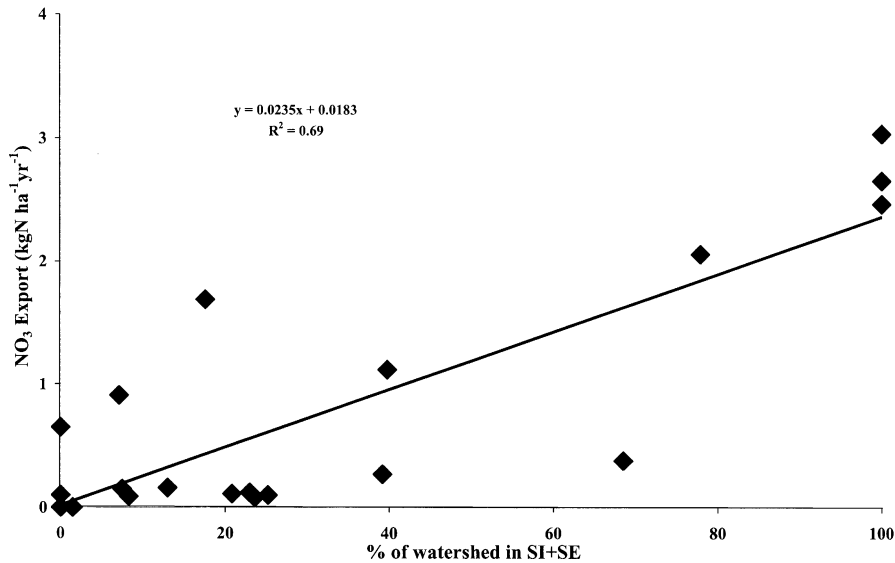


Figure 7. Relationship between watershed successional status, expressed as the proportion of the watershed covered by stand initiation and stem exclusion (SI+SE) stands, versus mean annual nitrate export rate.

below 450 m (Harrington and others 1994). Our study watersheds spanned elevations from 301 to 1590 m. Individual watersheds ranged from 578 to 1228 m in mean elevation with a median of 713 m. Although it was not possible to directly measure alder cover in our watersheds, broadleaf cover was estimated from a 30×30 m spatial resolution database (ISE 1999) and ranged from 0–19%. It is not clear how much of that cover is alder, but bigleaf maple tends to dominate broadleaf cover in the upland Cascades, whereas alder dominates broadleaf cover in the Coast Range. In the Compton and others (2003) Coast Range study, there was a positive relationship between broadleaf cover, estimated with a different methodology than we used, and N export, with elevated N export generally at a broadleaf cover exceeding 20%. Although two of our young watersheds with elevated N export had moderate broadleaf cover (16% and 19%), the other three young watersheds with elevated N export averaged only 5.5% broadleaf cover. Several older watersheds with elevated N export also had low broadleaf cover, and thus there is no clear link between abundance of hardwoods and elevated N export.

However, there is indirect evidence that the high N levels seen in the young watersheds were not produced in upland soils. In these rapidly growing forests, measured forest floor C:N ratios, ranging from 57 to 126, should be sufficiently high to immobilize any mineralized N; these values are above levels (22–30) reported for the onset of

nitrification and nitrate export (Dise and others 1998; Gunderson and others 1998; Goodale and Aber 2001; Ollinger and others 2002). In the Pacific Northwest, low N inputs coupled with high woody debris inputs leads to high soil C:N ratios in forests that do not experience chronic harvest. The high N immobilization capacity of such soils may account for the rapid recovery of stream N loss after harvest, and also for the absence of a significant signal of *Ceanothus*-fixed N in soil solutions or streams (Spears and others 2001). Similarly, Swank and others (2001) argued that the rapid recovery (~ 4 years) of N export to streams at Coweeta was due to high organic matter pools in upland soils. However, Cascades alder tends to occur predominantly in riparian areas and thus N from decomposing alder leaves or from root exudates and turnover could bypass the upland soils and enter streams during storms or during a rise in the water table. Inputs from small amounts of alder, then, could affect stream N levels, particularly against a backdrop of very low N export, irrespective of soil or plant retention mechanisms in the upland forest. Although we did not directly test this hypothesis, it is an avenue for further research.

Seasonal and Successional Patterns of Nitrate Loss

In many watersheds with elevated N inputs, seasonal patterns are driven by increased summer uptake by vegetation, producing lower stream

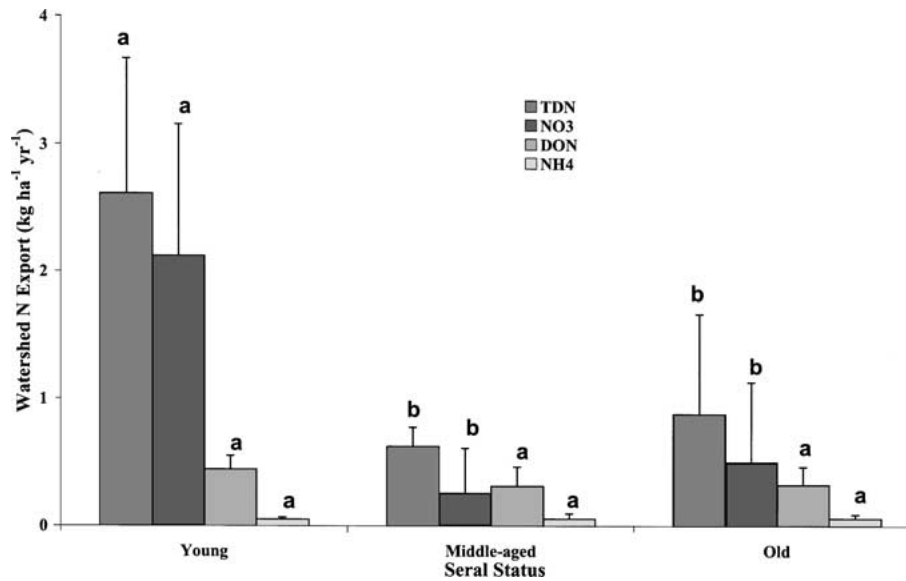


Figure 8. Mean watershed TDN, NO₃-N, DON, and NH₄-N export (kgN ha⁻¹ y⁻¹) by successional status. Error bars indicate the standard deviations among sites. Different letters indicate significantly different N fluxes.

NO₃-N concentrations and/or DIN exports (Lajtha and others 1995; Pardo and others 1995; Williams and others 1995; Stottlemeyer and Toczydlowski 1999). In several studies of watersheds with very low N exports, the exact opposite pattern has been observed (Swank and Vose 1997; Edmonds and others 1998; K Lajtha and JA Jones unpublished data), where N concentration increases slightly during summer months, perhaps due to a concentration effect when evapotranspiration is high. Other studies have demonstrated seasonal flushing at the onset of fall freshets when products of decomposition, accumulated during the dry season, are lost to stream water during the ascending arm of the hydrograph. Vanderbilt and others (2003) described a peak in DON concentrations, but not in NO₃-N, in HJAEF stream water prior to the peak of the hydrograph, similar to DOC patterns described by Boyer and others (2000) and Buffam and others (2001). Edmonds and others (1998) observed a fall flushing pattern for NO₃-N in the Olympic National Forest. In this study, we found that only the youngest watersheds with elevated NO₃-N levels showed seasonal patterns of lower nitrate during summer months, with concentrations increasing during the winter high water flow. This suggests that when vegetation is active, stream N exports decrease, and N is lost when hydrologic exports are high. However, reduced plant activity alone cannot explain the increased N exports during winter months, as the older stands also experience reduced uptake during the winter but do not show increased export. Patterns in the younger water-

sheds could be due to increased mineralization during the summer when hydrologic export is low followed by flushing of the mineralized N in winter, or possibly due to direct inputs of alder-fixed N, as discussed above.

Patterns of DOC and DON Loss

Stream DON concentrations were much less variable than NO₃-N concentrations and did not show the pronounced seasonal and successional trends that were observed for nitrate, a pattern commonly observed in many forested ecosystems (for example, Goodale and others 2000; Sickman and others 2003). We did not see the seasonal pattern described by Vanderbilt and others (2003) who observed a pronounced DON peak in the fall at the onset of the rainy season, before the peak of the hydrograph. This lack of clear variation with successional status or with season may reflect more of an abiotic control over DON levels than for nitrate. Although many plants do take up some DON compounds (Nasholm and other 1998), DON is not considered to be as biologically available as DIN, and thus summer lows in DON concentration are not necessarily expected. DON is sorbed in soils through abiotic reactions to a greater degree than are DIN species (Northup and others 1995), and thus often show seasonal variations more related to hydrology than biotic activity (Hagedorn and others 2000; Qualls 2000).

Our mean annual DOC export (15 kg C ha⁻¹) was less than predicted for similar forests using

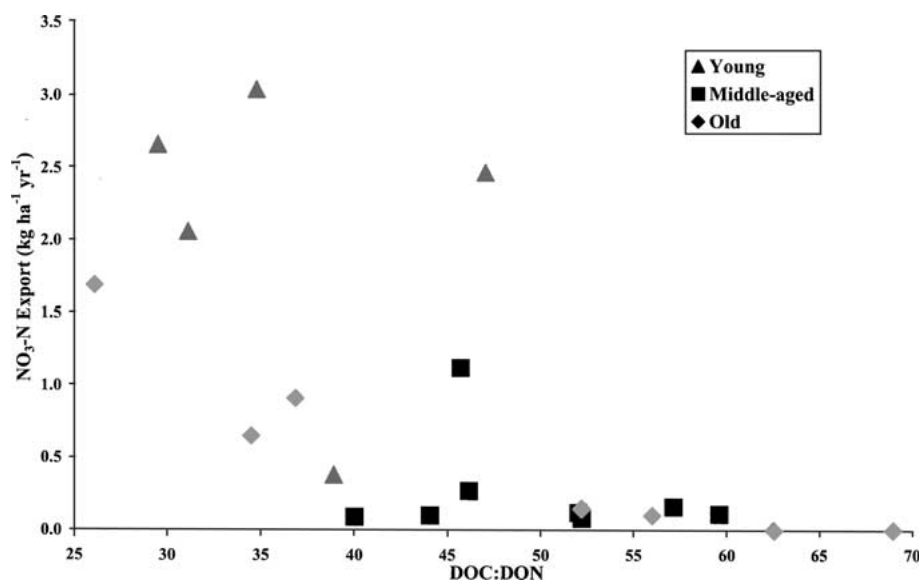


Figure 9. Scatterplot of mean annual $\text{NO}_3\text{-N}$ loss against stream water DOC:DON export ratio for 20 study watersheds in the South Santiam basin.

total soil C:N ratios (Aitkenhead and others 2000). Those authors summarized data from 30 cool conifer watersheds, reporting mean DOC export of 42 (SE = 3) $\text{kgC ha}^{-1} \text{y}^{-1}$. Our average DOC was similar to several Alaskan watersheds (Mulholland and Watts 1982) and the McKenzie River, OR (Moeller and others 1979). Our deviation from the global mean may simply be due to natural variation, or could reflect the fact that our watershed soils are Andisols, with a high DOC retention capacity.

Negative correlations between stream water DOC:DON ratios and nitrate export (Figure 9) are commonly found, and may reflect soil C availability and N immobilization potential. An increase in soil C availability relative to N can lead to a reduction in N export (Park and others 2002). Soil solution and stream water DOC:DON ratios have been used as integrated proxies of soil C:N ratios (Kortelainen and others 1997; Campbell and others 2000) and are used to predict watershed nitrate leaching (Harri-man and others 1998). A close examination of the data suggests that stream water DOC:DON ratios less than 40 result in high $\text{NO}_3\text{-N}$ export and that ratios greater than 50 result in very low export (Figure 9). Data from New Hampshire suggest a similar break point lying between a stream water DOC:DON ratio of 30 and 35 (Goodale and others 2000). A linkage between DOC and N availability was reported from Hubbard Brook where adding DOC to a stream reach led to stimulated bacterial growth, higher respiration rates, and an increased assimilative demand for N (Bernhardt and Likens 2002).

In conclusion, many interrelated factors affect N exports from these watersheds, including successional status and soil characteristics, and perhaps also the presence of alder in riparian areas. Only specific manipulations, such as watering or fertilization experiments (for example, Bechtold and others 2003) can help separate these factors.

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Appendix. Characteristics of Watersheds, in Increasing Order of Successional Development

Watershed #	Aspect	Slope (%)	Stream Order	Drainage Density (m ha ⁻¹)	Geological Formations ^a	Privately owned (%)	Road Density (km km ⁻²)
17	SE	43	1	28	Tu	70	2.0
20	S	35	2	15	Tu, Tub	95	3.5
2	E	38	1	17	Tu, Tus	100	3.3
3	E	26	1	19	Qls,Tu	67	3.3
1	NW	31	2	13	Qls,Tus,Tu,Tbaa	100	2.9
18	SE	37	2	14	Tu,Tub	63	1.5
4	NW	33	1	21	Tus,Tu,Tbaa	0	3.5
14	SE	28	1	16	Tu	0	4.1
10	W	46	1	14	Tu,Tus	5	1.3
6	E	51	1	14	Tus,Tbaa	0	0.7
19	S	54	2	15	Tu,Tub	1	1.0
15	S	36	1	15	Tu	0	2.3
13	SW	47	3	16	Tu,Tbaa,Tsv	17	1.0
9	SE	55	1	19	Tu	0	0.0
16	SW	43	1	15	Tu,Tbaa	0	0.0
5	N	49	2	17	Tus,Trb,Tbaa	2	0.0
7	NE	33	2	7	Tbaa,Trb,Tu	0	0.0
8	SE	61	1	23	Tu	0	0.0
12	E	65	1	22	Tu	7	0.0
11	SE	65	1	18	Tu	0	0.0

^aJohnson and Raines (1995) www.wrgis.wr.usgs.gov/open-file/of95-680/.

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