J. N. Am. Benthol. Soc., 2009, 28(4):941–954

DOI: 10.1899/07-160.1
Published online: 27 October 2009

Urbanization alters litterfall rates and nutrient inputs to small Puget Lowland streams

Mindy L. Roberts[1]

Department of Civil and Environmental Engineering, University of Washington, Box 352700, Seattle, Washington 98195-2700 USA

Robert E. Bilby[2]

Weyerhaeuser Company, 33663 Weyerhaeuser Way S., Federal Way, Washington 98003 USA

Abstract. Terrestrial allochthonous inputs represent the primary energy source for small stream ecosystems, and activities that alter those inputs produce cascading effects through multiple trophic levels. Urban development affects riparian forests through direct removal or through modifications to species composition and structure. Our study evaluated stand composition and litterfall inputs to small streams across a range of urbanization. Heterogeneity was high, but a consistent pattern of deciduous dominance was observed in more-disturbed areas and a mosaic of conifer, mixed, and deciduous forest patches in less-disturbed areas. Such mosaics are a region-dependent pattern that results from Pacific Northwest forest succession. Riparian vegetation disturbance level increased as total impervious area in the watershed increased. Annual mean daily litterfall rates ranged from 0.0 to 2.5 g m^{-2} d^{-1} in 128 trap locations distributed over 13 stream reaches that represent the range of riparian vegetation conditions currently present in the Puget Lowland. Conifer, mixed, and deciduous plots in watersheds with disturbance produced 12.5 to 19.3 mg N m^{-2} d^{-1} and 0.9 to 1.3 mg P m^{-2} d^{-1}. Deciduous riparian forests associated with moderate urban development produced organic matter loads similar to those of conifer forests, but the greater prevalence of leaf material produced 54% higher N loads and 40% higher P loads from litter inputs compared to conifer-dominated riparian areas. Conversion from coniferous to deciduous vegetation also produced subtle shifts in timing of inputs. Anthropogenic activities shape and maintain the current vegetation regime in the Puget Lowland, and this regime has profound implications for nutrient processes and aquatic productivity.

Key words: urbanization, nutrients, organic matter, litterfall, allochthonous inputs, Puget Lowland, conifer, deciduous, disturbance.

Riparian zones are unique transitions between terrestrial and aquatic ecosystems (Gregory et al. 1991) and are characterized by strong physical, chemical, and biological gradients between upland and lotic conditions (Naiman et al. 2005) that enhance biodiversity. Natural processes and anthropogenic activities that alter riparian zones affect many ecological functions. Recent studies on urbanization and urban streams worldwide have identified a suite of structural and functional changes that are termed the *urban stream syndrome* (Meyer et al. 2005). The syndrome includes changes in hydrology, water chemistry, geomorphology, biota, and general ecosystem processes (Walsh et al. 2005). Direct modification of riparian vegetation from urban activities is another structural change that probably affects functioning of small urban streams.

Urbanization effects share characteristics with other anthropogenic and natural disturbances, and studies of other disturbances can be applied to urbanization. For example, riparian vegetation removal resulting from natural disturbance, such as floods, or human activities, such as logging or agriculture, drastically reduces allochthonous inputs and often enhances production of autochthonous organic matter, and fundamentally restructures stream trophic dynamics (Bilby and Bisson 1992, Delong and Brusven 1994,

[1] Present address: Department of Ecology, Environmental Assessment Program, P.O. Box 47710, Olympia, Washington 98504-7710 USA. E-mail: mindyr@myuw.net

[2] E-mail address: bob.bilby@weyerhaeuser.com

Oelbermann and Gordon 2000). Furthermore, some agricultural activities can suppress regeneration of native vegetation, a potential effect of urbanization as well.

The influence of riparian vegetation on stream ecosystems has been well documented. Vegetation shades streams and maintains cooler water temperatures during the summer months (Beschta et al. 1987, Chen et al. 1998). Large trees provide instream wood that protects banks, creates pools, and traps sediment and organic matter (Bilby and Bisson 1998). Both live trees and instream wood provide habitat for riparian species (Naiman et al. 2005). Riparian forests play important roles in the cycling of nutrients and buffer the effect of upland activities on stream ecosystems (Naiman et al. 2005). In addition, terrestrial allochthonous inputs provide the fundamental nutrient and energy sources for small stream ecosystems (Anderson and Sedell 1979, Triska et al. 1982, Wallace et al. 1997). In studies where litterfall inputs were physically excluded, instream nutrient concentrations increased as uptake and storage declined and strongly affected benthic organic matter (Webster et al. 2000) and multiple trophic levels (Wallace et al. 1997). Urbanization potentially alters each of these processes.

After removal of riparian vegetation in the Pacific Northwest, sites typically are colonized by native deciduous vegetation, which can persist for up to a century before shade-tolerant conifers replace the hardwood trees (Franklin and Dyrness 1973). Litterfall rates and nutrient concentrations vary by species, and this regional forest succession pattern produces allochthonous inputs that vary over time. Pacific Northwest litterfall rates are similar to those found in cool temperate forests in North America, Europe, and Asia (reviewed in Bray and Gorham 1964, mean = 0.9 g m^{-2} d^{-1} for 162 studies, range = 0.3–1.9 g m^{-2} d^{-1}).

At first, the absence of riparian vegetation produces very low organic matter inputs (Bilby and Bisson 1992). Red alder (*Alnus rubra*), the only common native tree or shrub species with N-fixing bacteria in the root nodules, and other deciduous vegetation typically become established in disturbed riparian areas and dominate forest composition for a period of decades to a century. This forest condition typically produces litter with high nutrient content (Zavitovski and Newton 1971, Gessel and Turner 1974). However, litterfall-based nutrient loads decrease as the forest composition shifts to conifers, such as Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) (Abee and Lavender 1972, Murray et al. 2000). Thus, to the extent that urban development affects stand structure, urbanization also fundamentally alters allochthonous inputs. However, no litterfall studies have evaluated the effect of urbanization on organic matter contributions to small streams.

Historically, riparian and valley bottom forests in the Puget Lowland area of western Washington were dominated by conifer forests in the cool temperate climate. Under preEuropean conditions, reconstructed from 1873 General Land Office survey notes, conifers represented 61% of the basal area of nearby riparian stands, but by 2000, deciduous species dominated (Collins and Montgomery 2002). Historical conifer abundance also was shown by pollen analyses from nearby lake sediment cores that demonstrated a shift from hemlock, cedar, and fir to red alder around 1900, near the time that logging had removed most of the timber from the Seattle area (Davis 1973). Very little pristine forest remains in the Puget Lowland, but old-growth communities occur at moderate elevations in the Cascade Mountains. These remnants maintain conifer dominance on terraces and hillslopes, whereas red alder dominates active floodplains (Rot et al. 2000). Thus, the natural riparian composition should be dominated by conifer species.

Urban and suburban land cover has grown in the Puget Lowland in response to rising population. The 40% increase between 1980 and 2000 in the 3 western Washington counties included in our study (Washington State Office of Financial Management 2006) increased the amount of land in urban/suburban land cover. Development pressures are strong within riparian zones, and these areas offer high economic and aesthetic value, in addition to ecological value. Tree cover in Seattle has decreased from 40% in 1972 to 18% in 2006 (City of Seattle 2006). No studies have systematically quantified changes to regional riparian forests, but changes are likely to be similar or more dramatic within riparian zones.

The purpose of our study was to determine how urban development affects allochthonous inputs to small streams. Specifically, the study quantified how urbanization affects riparian stand composition and subsequent changes to terrestrial organic matter and nutrient inputs to small streams in the Puget Lowland.

Methods

Study site selection

Hundreds of small streams flow through the Puget Lowland ecoregion of western Washington, which is bounded to the east and west by 2 mountain ranges, the Olympics and Cascades. The Lowland was formed during repeated glaciations that produced plateaus of glacial till and outwash deposits ranging

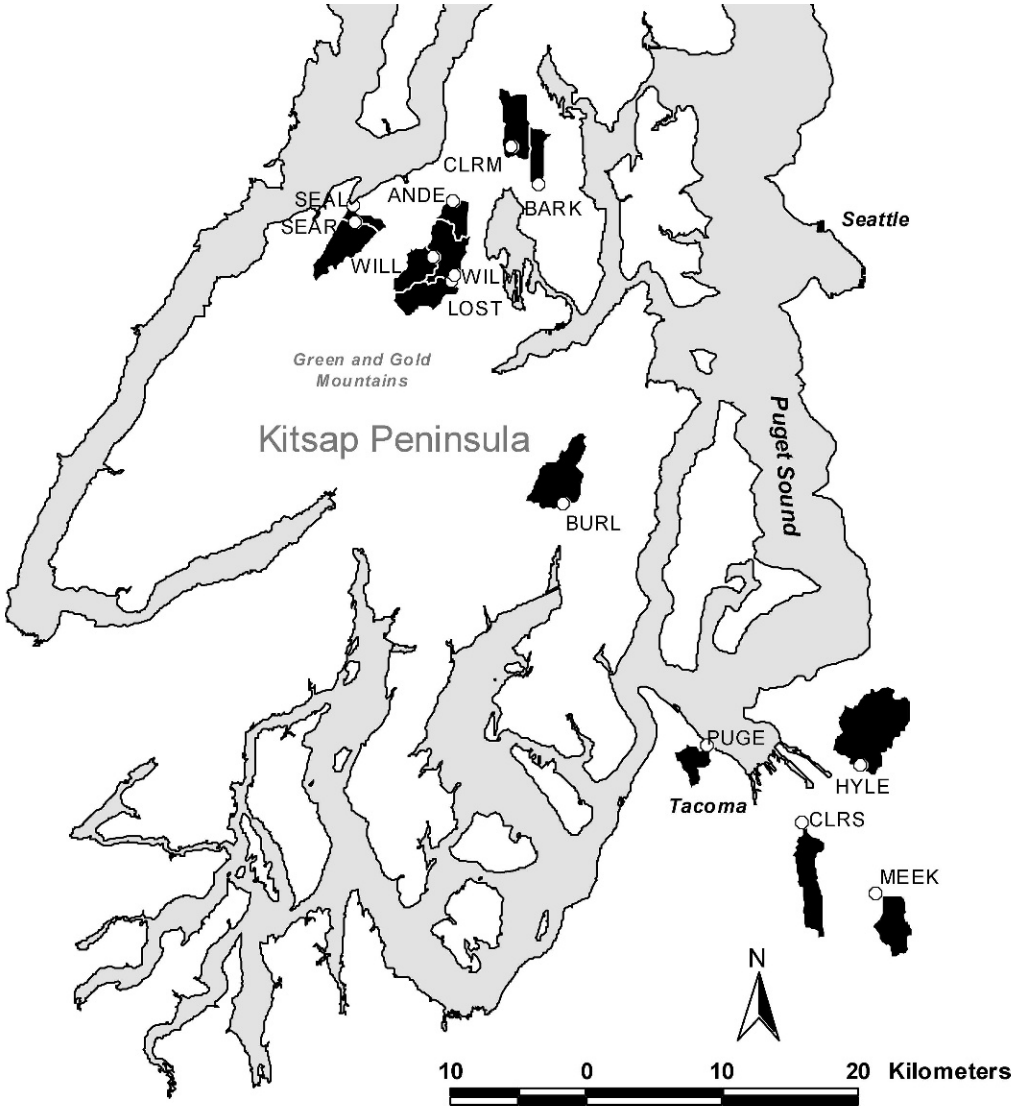

FIG. 1. Sites in the Puget Lowland at which litterfall was studied. Circles indicate study sites, and shading indicates upstream watersheds.

from 50 m to 150 m above sea level. The Green and Gold Mountains of the Kitsap Peninsula rise to 540 m and consist of volcanic bedrock and upland deposits of glacial till. Streams generally trend north/south as a result of glacial fluting and typically exhibit a pool/riffle morphology. Annual precipitation varies from 800 to 1300 mm.

Study sites (Fig. 1) were selected using a stratified-random approach. Small streams with watershed areas between 4 and 24 km^2 were identified (30-m digital elevation model) and stream centerlines were segmented at 100-m intervals. Only accessible points, defined as those within 1 km of a road or trail, were retained (59% of the original 2006 locations). Each point was coded with the initial riparian vegetation disturbance level, determined from orthophoto interpretation supplemented by qualitative field observations. Reference vegetation (REF) included both mature conifer-dominated and mixed riparian forests. Although not pristine, these areas represent the least-disturbed riparian condition in the Puget Lowland. Low-disturbance sites (LOW) included mature, deciduous-dominated vegetation with some conifers. Medium-disturbance sites (MED) included a range of vegetation characteristics, from very young natural vegetation to residential landscaping to restoration sites with native vegetation plantings. High-disturbance sites (HIGH) generally lacked overstory trees, and herbaceous vegetation dominated. Ten sites were identified randomly within each category. Access requests were made to property owners, and qualitative observations confirmed the orthophoto-based

TABLE 1. Watershed and site characteristics. Sites CLRM and PUGE were part of active restoration efforts that included riparian plantings. DEV = developed land, FOR = forested land, TIA = total impervious area, DBH = tree diameter at breast height.

Site	Riparian vegetation disturbance level	Wetted width (m)	Watershed characteristics (%)			Mean plot basal area (m^2/ha)		Mean DBH (m)		Stem density (no./ha)		Canopy cover (%)
			DEV	FOR	TIA	Total	Conifer	Total	Conifer	Total	Conifer	
ANDE	Reference	0.4	18.3	44.2	7.3	88.3	73.4	0.32	0.34	271	184	95.7
LOST	Reference	2.3	2.4	36.8	4.2	146.3	112.6	0.26	0.30	688	404	93.6
SEAR	Reference	2.0	5.4	45.3	4.3	96.3	83.5	0.14	0.22	1482	557	87.6
WILM	Reference	0.8	8.8	44.7	5.2	73.6	50.0	0.23	0.24	458	284	94.6
BURL	Low	5.4	18.4	29.5	7.9	60.9	30.9	0.23	0.35	356	81	85.7
SEAL	Low	1.8	5.4	44.2	4.4	105.0	38.6	0.18	0.28	1006	158	80.9
WILL	Low	0.2	8.3	38.5	5.3	52.9	24.9	0.14	0.12	830	525	93.8
BARK	Medium	2.2	19.9	32.1	8.8	37.9	1.1	0.14	0.13	648	21	90.0
CLRM	Medium	1.7	23.4	30.0	10.2	59.7	0.0	0.07	0.0	3380	0	85.9
CLRS	Medium	4.2	20.1	11.2	9.5	30.0	0.0	0.27	0.0	133	0	53.8
PUGE	Medium	1.4	60.2	4.9	29.5	15.2	0.7	0.04	0.03	3082	308	89.4
HYLE	High	5.4	39.8	19.7	19.2	0.6	0.0	0.08	0.0	31	0	3.6
MEEK	High	1.6	43.9	8.3	22.4	0.0	0.0	0.0	0.0	0	0	0.4

vegetation classification. Quantitative plot characteristics (described below) were used to finalize the plot type and site disturbance classification. The final study design included 4 REF sites, 3 LOW sites, 4 MED sites, and 2 HIGH sites. Originally 4 sites in each category were selected, but work at 2 HIGH and 1 LOW site was discontinued because of persistent vandalism.

Classified satellite imagery (30-m resolution) was used to quantify watershed characteristics. Percent forest (FOR) combined conifer and mixed forest classes, whereas % developed land (DEV) combined high- and low-density development and bare ground (Hill et al. 2003). Total impervious area (TIA) was estimated using impervious factors typical of the Puget Lowland (Dinicola 1990). Table 1 summarizes watershed land cover and study site characteristics.

Field methods

Ten litterfall traps were placed at each of the study sites (see below for description). A 10-m radial plot was used to characterize vegetation around each trap. Active channel area and roadways were subtracted. This step was a modification of traditional mensuration techniques necessitated by the developed study area. Wetted widths ranged from 0.2 to 5.4 m. Trees $\geq$1-cm diameter were identified to species (Pojar and MacKinnon 1994) and diameter at breast height was measured to determine basal area.

Each plot was assigned an overall type: 1) conifer (CON) (>70% of basal area occupied by conifers), 2) deciduous (DEC) (>70% of basal area occupied by deciduous species), 3) mixed (MIX) (neither conifers nor deciduous species occupied >70% of basal area), and 4) NONE (no trees). The characteristics of the 10 individual plots were compiled for each site to verify the initial riparian vegetation disturbance classification. Sites had heterogeneous plot characteristics (Fig. 2), and few sites had a uniform plot type throughout. REF sites were defined as those with $\geq$5 CON plots and $\geq$50 m^2/ha of conifer basal area. LOW sites had $\geq$3 CON or MIX plots and 0 NONE plots. MED sites had <3 CON or MIX plots and conifer basal area <2 m^2/ha. HIGH sites had few or no trees, total basal area <1 m^2/ha, and most plots designated as NONE. When these definitions were applied to plot data, the disturbance classifications of 2 sites changed.

Canopy cover was determined using a densiometer oriented over the center of each litterfall trap and at 10-m intervals along the stream centerline. The riparian canopy cover measured at trap locations on streambanks was highly correlated with the canopy cover measured over the stream channel ($R^2 = 0.93$, $p < 0.001$) but was 3% higher. This difference was statistically significant but was within the error range of densiometer measurements. Therefore, this small difference was judged not to be ecologically meaningful, and the litterfall estimates from the streambank traps was considered to be representative of stream inputs.

Litterfall traps were rectangular baskets (surface area = 0.2 m^2, height = 26 cm) lined with fine-mesh netting (<1 mm). Traps were placed on either right or left banks as close to the wetted channel as possible and at 10-m intervals measured along the stream

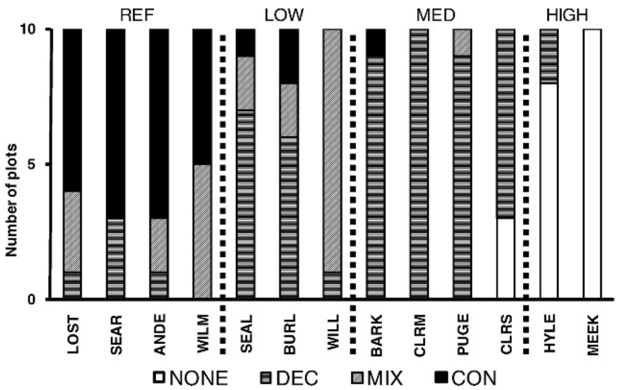

FIG. 2. Distribution of plot types, determined from basal area within radial plots around each of 10 litterfall traps at 10 study sites. Conifer (CON) plots had >70% coniferous basal area, deciduous (DEC) plots had >70% deciduous basal area, and mixed (MIX) plots were those where neither CON nor DEC basal area $\geq$70%. Where no trees occurred within the plots, the type was NONE. Vertical lines differentiate sites in different riparian vegetation disturbance classes. REF = reference, LOW = low disturbance, MED = medium disturbance, HIGH = high disturbance (see *Study site selection* for explanation).

centerline. A pebble was added to weight the netting and to indicate whether the trap had been disturbed since the previous collection. Samples with evidence of tampering were excluded from the calculations.

Litterfall samples were collected monthly between March 2004 and February 2005, and twice monthly during October and November 2004. Materials were placed in paper bags and dried $\geq$48 h at 60°C to ensure all moisture had been removed prior to storage.

Laboratory methods

Materials in litterfall samples were separated into base components to facilitate nutrient analyses and then summed into 4 categories. Leaves (LVS) included red alder, bigleaf maple (*Acer macrophyllum*), and other species. Needles and red cedar (NDRC) included red cedar (*Thuja plicata*), western hemlock, and Douglas fir. Wood (WD) was quantified separately. All other materials (OTH; catkins, cones, moss and lichen, grass, other components) were separated by size ($\geq$1 mm or <1 mm) and combined within size category (OTH > 1, OTH < 1). After sorting, each subsample was redried at 60°C to constant mass and weighed to the nearest 0.001 g.

Sorted samples collected in March, May, and October were combusted at 500°C for 5 h to determine ash-free dry mass (AFDM). Percent organic matter (OM) determined for each component varied little among sites and traps, except for OTH > 1 and OTH < 1. For all but these components, the mean %OM determined from the March, May, and October collections was used to estimate %OM for the remaining collections. All OTH > 1 and OTH < 1 components and any subsamples with visible sediment accumulated on the organic matter were combusted from each sample. Leaves were combusted by species in July, September, and November to determine %OM for the most common types. Green materials were not separated from senesced vegetation because Murray et al. (2000) found that green needles were 3% of the total needle litterfall and the contribution was minor. All OM loading rates are presented as AFDM.

Annual mean daily OM loading rates (plot means) were determined for 128 litterfall collection locations, and were summarized by category by adding the mass over all collections and normalizing by the number of days. Mean OM loading rates were calculated from the plot means and presented as site means, means by plot type (CON, MIX, DEC, and NONE), and means by riparian vegetation disturbance class (REF, LOW, MED, HIGH). Watershed TIA was compared with riparian vegetation disturbance class to evaluate effects of urban development on vegetation characteristics.

Nutrient content was analyzed in litterfall samples collected in October and November to represent peak organic matter inputs. Base component samples were ground using a Wiley mill (no. 40 screen). N and C levels were determined with a CHN analyzer (Perkin Elmer Model AD-4; Perkin Elmer, Waltham, Massachusetts). Total P concentrations were determined with inductively coupled plasma (Thermo Electron Corporation Model 61E argon plasma, Thermo Fisher Scientific, Inc., Waltham, Massachusetts). Samples were digested in high-grade concentrated nitric acid and stored in acid-washed vials.

Statistical analyses

Single-factor analysis of variance (ANOVA) was used to test for differences among riparian vegetation disturbance classes and plot types. Student–Newman–Keuls (SNK) tests were used for multiple comparisons. Statistical significance was determined at $\alpha \leq 0.05$.

Results

Urbanization affects stand composition

The level of watershed development was clearly reflected in the condition of the riparian vegetation at

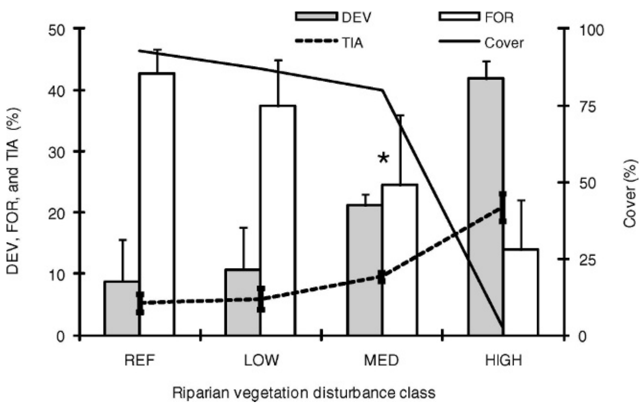

FIG. 3. Mean (+1 SD, among site) watershed characteristics (% developed land [DEV], % forested land [FOR], total impervious area [TIA]), % canopy cover [%Cover] at sites in each riparian vegetation disturbance class. Means shown by bars do not include data from the PUGE site. * indicates TIA for the PUGE site. REF = reference, LOW = low disturbance, MED = medium disturbance, HIGH = high disturbance (see *Study site selection* for explanation).

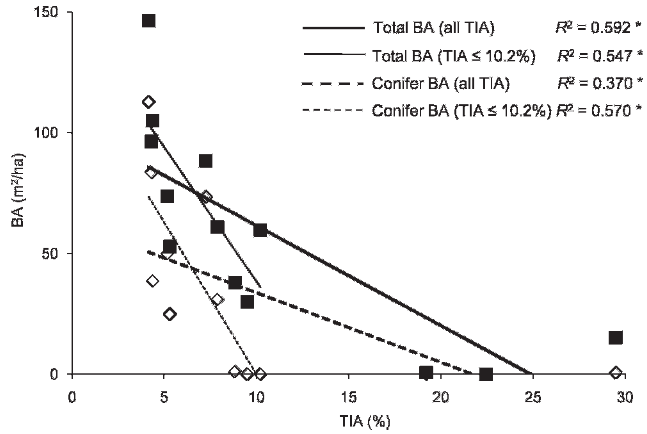

FIG. 4. Regressions for total and conifer basal area (BA) at sites as functions of watershed total impervious area (TIA). Regression lines are shown for all sites and for sites in watersheds with TIA $\leq$ 10.2%. * indicates statistically significant regressions ($p < 0.05$).

the study sites (Fig. 3). The proportion of a watershed in forest cover decreased consistently from REF to HIGH sites, as did site riparian canopy cover. Conversely, the proportion of developed land within the watershed increased consistently across these riparian vegetation disturbance classes. Conifers were abundant only at sites in watersheds with $\leq$7.9% TIA.

In the riparian zone, urban activities disrupted the natural successional processes, as evident in site characteristics presented in Table 1. REF and LOW sites had higher mean basal area (total and conifer) and larger mean tree diameter at breast height (total and conifer) than did MED and HIGH sites ($p <$ 0.002). Stem density was highest at 2 MED sites (CLRM and PUGE) where riparian restoration projects had occurred, reflecting recent planting rather than natural regeneration.

Both total and conifer basal area decreased with increasing TIA (p = 0.002 and 0.026, respectively; Fig. 4). The 3 most urbanized watersheds had the lowest plot basal areas, which influenced the regression. However, the decrease in basal area with increasing TIA also was significant for watersheds with $\leq$10.2% TIA (p = 0.002 and 0.031).

Overall canopy cover was high, as is typical for small streams with closed canopies. Canopy cover was lowest where basal area was minimal, but high canopy cover occurred even where basal area was low. Even the youngest stands that had developed from natural regeneration or enhanced restoration had a closed canopy.

Modified stand composition affects litterfall rates and nutrient loads

Annual mean daily litterfall rates ranged from 0.0 to 2.5 g m^{-2} d^{-1} in 128 traps distributed over 13 small stream sites that represent the range of riparian vegetation conditions currently present in the Puget Lowland. A weak but significant positive relationship was found between plot basal area and plot mean litterfall rates (R^2 = 0.149, $p <$ 0.001), and basal area differed significantly among riparian vegetation disturbance classes.

When the 10 plot means were combined into a single site mean, OM inputs (after combustion) ranged from 0.2 to 1.5 g m^{-2} d^{-1} (Fig. 5A). Within-site variability was high (Fig. 5A–C). Mean OM input rates increased from REF to MED riparian vegetation disturbance class, but rates were not significantly different among classes (Fig. 6A). CON and DEC plots had similar OM inputs (1.3 g m^{-2} d^{-1}). Inputs at MIX plots were significantly lower than those at DEC plots, but were not distinguishable from inputs at CON plots (Fig. 6B).

Nutrient loads were developed by multiplying OM mass loads for each base component by the nutrient content of the component (Table 2). Table 3 summarizes OM and nutrient loading rates by site. N loads were significantly lower for HIGH and REF than for LOW and MED disturbance classes (ANOVA, p = 0.001), which were not distinguishable (Fig. 6C). N loads were highest at DEC sites because of the higher nutrient content and OM loads of LVS compared with those of NDRC (Fig. 6D). N loads from WD were uniform across site types. OTH materials contributed

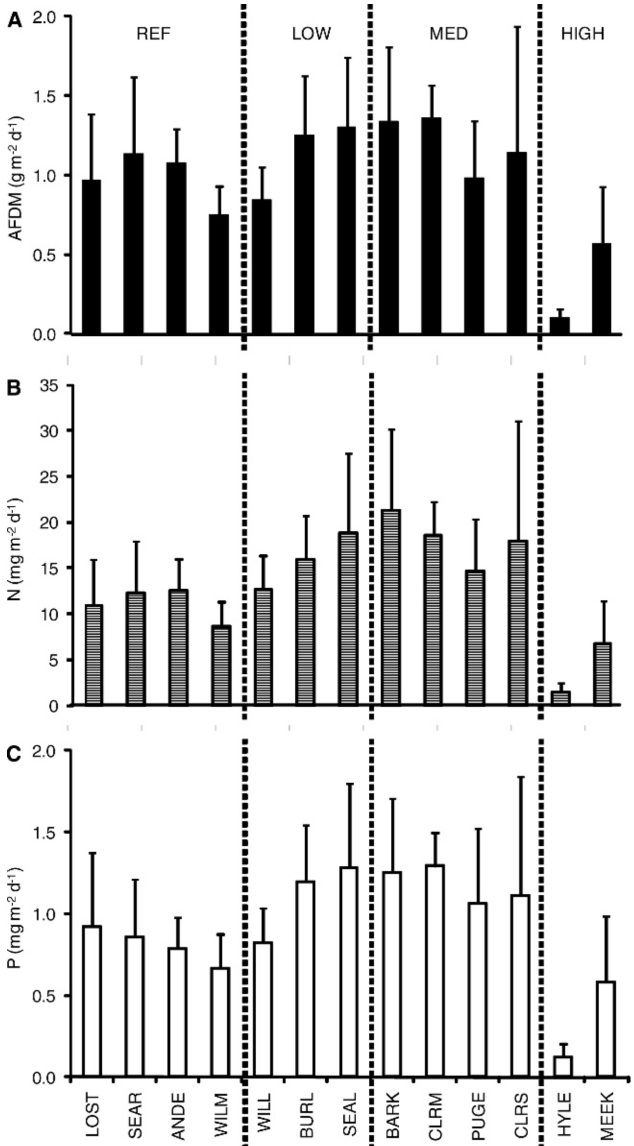

FIG. 5. Mean (+1 SD, within site) daily organic matter load expressed as ash-free dry mass (AFDM) (A), N (B), and P (C) loading rates at 10 study sites. Vertical lines differentiate sites in different riparian vegetation disturbance classes. REF = reference, LOW = low disturbance, MED = medium disturbance, HIGH = high disturbance (see *Study site selection* for explanation).

more N than did NDRC, even in CON plots and REF sites.

Phosphorus (P) loads were lowest at HIGH sites, and REF sites had lower P loads than did MED sites (Fig. 6E, $p = 0.003$). P loads at LOW sites could not be distinguished from those at REF and MED sites. DEC plots had higher P loads than did CON or MIX plots because of the higher nutrient content of LVS than of NDRC. P loads from WD were low and uniform among vegetation types, and OTH materials contributed P loads similar to those of LVS.

Very low litterfall was expected in sites with no trees, but some plots produced 0.5 to 1.0 g m^{-2} d^{-1} of organic matter, almost entirely from clumps of grass periodically deposited in the traps by municipal and residential mowing activities. OM, N, and P loads were lower at NONE plots than at DEC, CON, or MIX plots, but mass and nutrient inputs were still measurable at NONE plots (Fig. 6B, D, F), and mowing reduced but did not eliminate allochthonous inputs.

CON plots produced the highest NDRC inputs (0.50 g m^{-2} d^{-1}) and lowest LVS inputs (0.27 g m^{-2} d^{-1}) among CON, DEC, and MIX plots (Fig. 6B). The lack of NDRC inputs in DEC plots was more than offset by an increase in LVS inputs. NDRC inputs could be predicted from plot conifer basal area ($R^2 = 0.549$, $p < 0.001$). LVS inputs could be predicted weakly from plot deciduous basal area ($R^2 = 0.310$, $p < 0.001$). Variation in these relationships was caused by several plots with low basal area that produced high inputs of LVS and NDRC and some plots with high basal area that produced low inputs.

Local riparian vegetation structure determined the amount and quality of litterfall inputs at the reach scale, and the relationship between overall watershed urbanization and local riparian vegetation suggested a subsequent effect of urbanization on litterfall. However, the relationships were complicated. Litterfall rates were lower for watersheds with TIA >10.2% than for watersheds with lower TIA ($p = 0.008$; Fig. 7) because of the much lower canopy cover at the most urban sites. The relationships of OM ($p = 0.018$) and P ($p = 0.047$) with watershed TIA were significant when the 2 restoration sites were excluded. Among the watersheds with ≤10.2% TIA, N loads increased significantly with TIA ($p = 0.044$) because of the increasing prevalence of deciduous vegetation. However, when the restoration sites were excluded, the relationship was not significant ($p = 0.073$).

Seasonal litterfall rates vary with stand composition

Litterfall seasonality varied among vegetation types (Fig. 8). DEC plots produced higher inputs in late spring and summer than did CON plots, and the mass was similar to the difference in annual totals. Autumn produced the highest litterfall rates when trees were present, and >½ of the annual inputs occurred in October and November. At NONE plots, most inputs occurred during the spring and early summer. Inputs at CON plots were more concentrated in the late summer and autumn than were inputs at DEC and

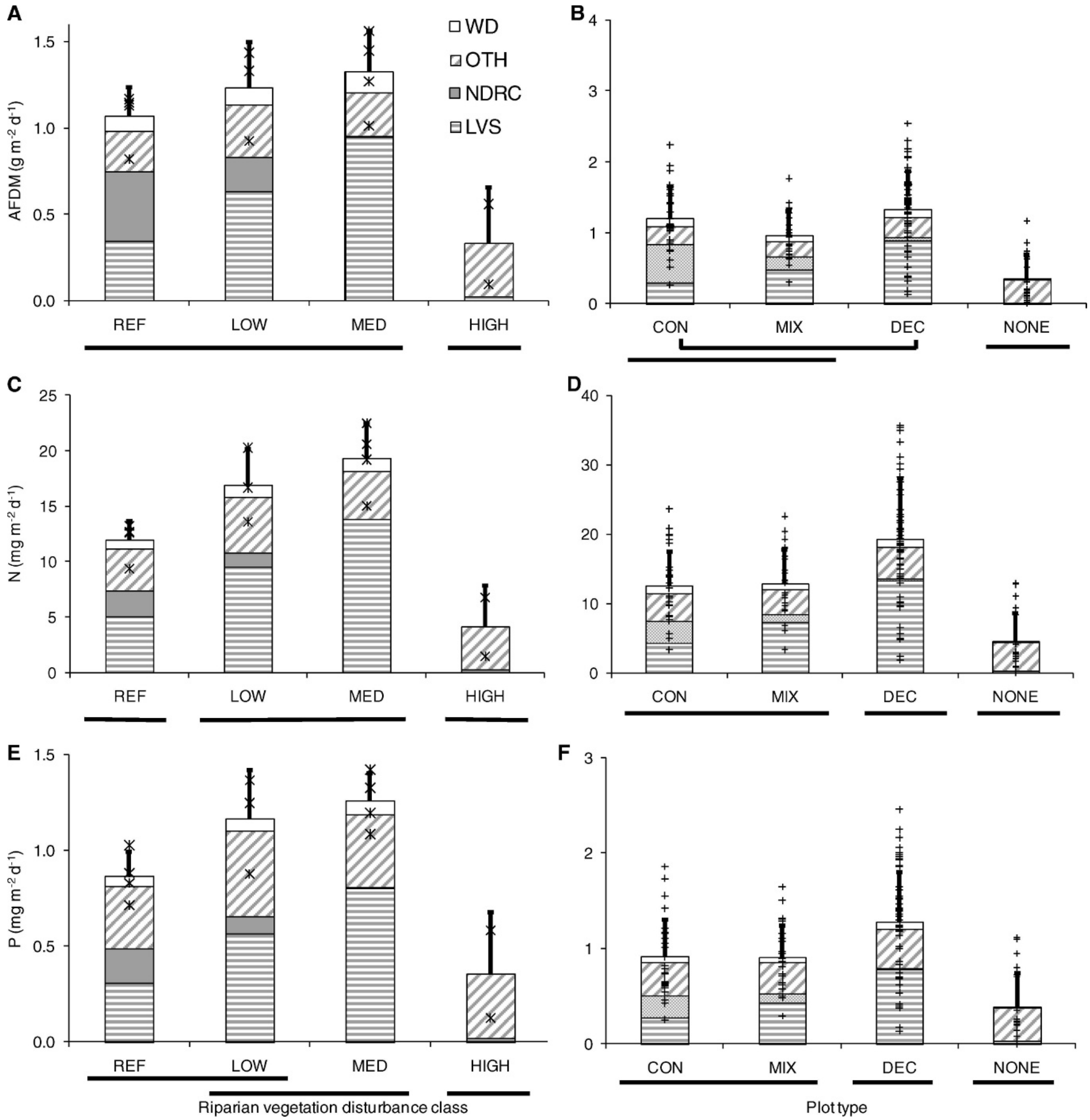

FIG. 6. Mean daily organic matter as ash-free dry mass (AFDM) (A, B), N (C, D), and P (E, F) loading rates by litterfall category (LVS = leaves, NDRC = needles and red cedar, WD = wood, and OTH = other plant materials) at sites classified by riparian disturbance level (A, C, E) and by individual plot type (B, D, F). REF = reference, LOW = low disturbance, MED = medium disturbance, HIGH = high disturbance (see *Study site selection* for explanation). Conifer (CON) plots had >70% coniferous basal area, deciduous (DEC) plots had >70% deciduous basal area, and mixed (MIX) plots were those where neither CON nor DEC basal area ≥70%. Where no trees occurred within the plots, the type was NONE. * indicates site means for total organic matter, + indicates plot means for total organic matter. Bars underlined by the same line are not significantly different.

TABLE 2. Nutrient content by litterfall component.

Component	C (%)	N (%)	P (%)
Red alder leaves (*Alnus rubra*)	47.8	1.87	0.091
Bigleaf maple leaves (*Acer macrophyllum*)	45.8	1.10	0.087
Other leaves (mean of 7 species)	45.4	1.22	0.080
Needles (*Tsuga heterophylla* and *Pseudotsuga menziesii*)	50.1	0.62	0.060
Red cedar needles (*Thuja plicata*)	50.5	0.59	0.042
Wood	48.6	1.02	0.062
Catkins (*Alnus rubra*)	48.3	0.84	0.045
Cones (*Tsuga heterophylla* and *Pseudotsuga menziesii*)	48.3	0.84	0.045
Moss and lichen	43.7	1.74	0.171
Grass	43.1	1.51	0.129
Other > 1	47.9	2.12	0.200
Other < 1	47.9	2.12	0.200

MIX plots, which received significant summer inputs. The date by which plots received 50% of the annual load was slightly later for CON plots (October 11) than for DEC plots (October 3).

Discussion

Urbanization affects riparian stand composition and litterfall inputs

Urbanization affects riparian vegetation stand structure through direct removal or modification of the forest cover or through suppression or selective enhancement of the natural regeneration processes. In the Pacific Northwest, natural forest succession following a disturbance leads to temporally variable allochthonous inputs that are very low immediately after removal of the forest canopy. Inputs increase considerably as red alder and other deciduous vegetation regenerate. The shift to long-lived conifers eventually produces a decrease in OM input, compared to that produced by the earlier, deciduous forest. The conifer-dominated riparian forest can persist for centuries or until another disturbance affects the forest composition. Because of historical and continuing landscape modifications in the Puget Lowland, vegetation in most riparian areas is being constrained to either the deciduous-dominated phase in natural succession or immediate post-removal phase where all OM inputs are very low.

TABLE 3. Litterfall organic matter (OM; ash-free dry mass), N, and P by study reach.

Site	OM (g m^{-2} d^{-1})	N (mg m^{-2} d^{-1})	P (mg m^{-2} d^{-1})
ANDE	1.08	12.6	0.79
LOST	0.96	10.8	0.92
SEAR	1.13	12.3	0.86
WILM	0.75	8.6	0.67
BURL	1.25	15.9	1.20
SEAL	1.30	18.9	1.28
WILL	0.84	12.7	0.82
BARK	1.34	21.3	1.26
CLRM	1.36	18.6	1.29
CLRS	1.14	17.9	1.12
PUGE	0.98	14.6	1.06
HYLE	0.10	1.5	0.12
MEEK	0.56	6.8	0.58

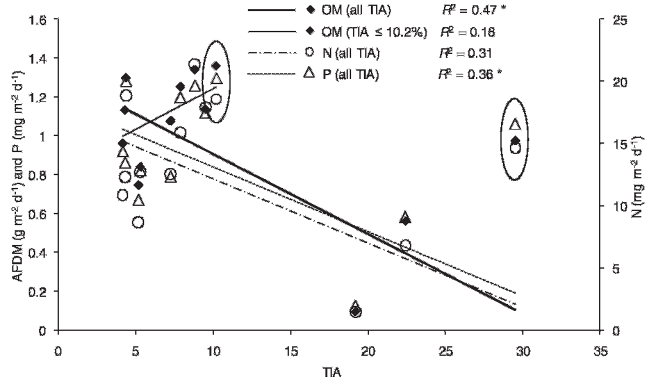

FIG. 7. Regressions for litterfall organic matter (OM) as ash-free dry mass (AFDM), N, and P loads as functions of watershed total impervious area (TIA) at each site. Values for the 2 restoration sites are enclosed in ovals and were not included in the statistical analysis. Regression lines for total OM are shown for all sites and for sites in watersheds with TIA ≤ 10.2%. Other regression lines are for all sites. * indicates statistically significant regressions ($p < 0.05$).

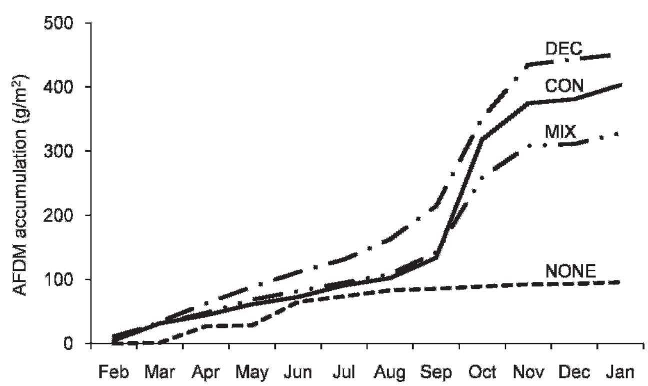

FIG. 8. Cumulative litterfall inputs summarized by month expressed as cumulative ash-free dry mass (AFDM) for each plot type. Conifer (CON) plots had >70% coniferous basal area, deciduous (DEC) plots had >70% deciduous basal area, and mixed (MIX) plots were those where neither CON nor DEC basal area ≥70%. Where no trees occurred within the plots, the type was NONE.

We found a very clear association between watershed development level and riparian vegetation condition. We also observed a decrease in both mean tree diameter and plot basal area as the proportion of developed land within a watershed increased, results indicative of a young regenerating riparian forest. Mature conifer stands were found only at sites with the lowest levels of urbanization in the watershed. As development increased, conifers were less prevalent and deciduous vegetation dominated. Last, sites in the most urbanized watersheds produced the lowest inputs because of nearly complete canopy removal.

Where forest cover remained or was restored, REF, LOW, and MED sites all produced similar annual litterfall. The primary difference among these sites was in the type of litter delivered to the stream. Leaf inputs increased with urbanization and dominance of deciduous vegetation. Deciduous riparian forests produced significantly higher N (+54%) and P (+40%) loads than did conifer or mixed forests.

Regional differences (Brown et al. 2009) clearly influence conditions in urban streams, but the pattern is not common to all ecoregions. Specifically, where native deciduous vegetation predominates, species shifts alone might not influence litterfall nutrient contributions. In regions with naturally open canopies, urbanization might not alter inputs at all.

Walsh et al. (2005) proposed 3 conceptual models for relationships between ecological condition and increasing urbanization: A) linear decrease, B) a threshold effect with a distinct drop in ecological function, and C) linear decrease to a threshold. The relationships between urbanization and stand characteristics (basal area, mean tree diameter, and canopy cover) suggest that model C applies to the study streams. We found decreases in these attributes up to a TIA of 10.2%, but values changed little with further increases in TIA. However, only 3 sites were in watersheds with TIA $>$10.2%, and further studies at higher levels of TIA might indicate that model A is a more appropriate fit and that no specific threshold exists.

Local litterfall inputs reflected overall watershed urbanization, with some complications induced by the 2 restoration sites. These sites produced greater inputs than would be expected based on watershed development, a result suggesting that restoration practices might reestablish at least some functional processes. The relationships between TIA and OM and P loads were significant only when the restoration sites were excluded and follow model A. The relationship between TIA and N was significant only among the watersheds with TIA $\leq$10.2%, and within these sites, the N loads increased with increasing TIA. Sites in the 3 watersheds with highest TIA produced significantly lower OM, N, and P inputs than did sites in watersheds with TIA $\leq$10.2%. This pattern is similar to model B of Walsh et al. (2005), except that loads increased from the lowest levels of development before declining. The restoration sites complicated statistical analyses for the overall study, but they indicate that efforts to restore stream functions might counteract the influence of watershed development on litter production.

Puget Lowland urban litterfall rates differ from related studies

Stand composition and litterfall rates reported in our study generally were within ranges reported previously for the Pacific Northwest and for cool temperate forests in general (Zavitovski and Newton 1971, Abee and Lavender 1972, Gessel and Turner 1974, Bilby and Bisson 1992, Murray et al. 2000), although subtle differences occurred. However, no other studies in the Pacific Northwest have evaluated the effect of urban activities on either stand composition or litter input. Our results suggest that OM input rates in urban areas are not dramatically different from those seen in forested areas except at very high levels of disturbance where few trees occur, but that differences in stand composition affect N and P in urban Puget Lowland litterfall.

OM loads from CON plots were within the range of those reported previously, which varied from 0.64 g m^{-2} d^{-1} in Bilby and Bisson (1992) for western Washington to 1.61 g m^{-2} d^{-1} in Abee and Lavender (1972) for western Oregon. However, N loads in Puget Lowland CON plots (12.5 mg m^{-2} d^{-1}) were higher than those reported previously for old-growth forest, which generally ranged from 5.3 (Murray et al. 2000) to 7.5 mg m^{-2} d^{-1} (Abee and Lavender 1972). Our reference locations were not pristine old-growth conifer sites, which are extremely rare in low-elevation riparian zones in the Puget Lowland. Mature red alder and bigleaf maple trees interspersed with conifers were common, and the higher observed N loads were a consequence of the abundant N input contributed by leaf litter (4.3 mg m^{-2} d^{-1}). P loads from CON plots were similar to those previously reported for old-growth sites (0.46 to 1.29 mg m^{-2} d^{-1}; Gessel and Turner 1974 and Abee and Lavender 1972, respectively). Therefore, even the lowest levels of development in the Puget Lowland produced higher N inputs than were measured in previous studies of conifer-dominated sites.

Mean OM loads from DEC plots were lower than the overall means reported previously for red alder

(1.5–$2.1\ g\ m^{-2}\ d^{-1}$) but were within the range of interannual and intersite variability (Abee and Lavender 1972, Murray et al. 2000). Species in our DEC plots were not entirely red alder, and the presence of other deciduous species in the Puget Lowland sites could have contributed to lower OM input rates than have been reported for pure stands. N concentrations in red alder in our study (1.87%) were similar to concentrations reported by Zavitovski and Newton (1971), but the higher overall organic matter loads in the study by Zavitovski and Newton (1971) produced N loads (22.9 and $39.1\ mg\ m^{-2}\ d^{-1}$) higher than those in the Puget Lowland ($19.3\ mg\ m^{-2}\ d^{-1}$). P loads reported by Gessel and Turner (1974) ($0.46\ mg\ m^{-2}\ d^{-1}$) were lower than P loads in the Puget Lowland sites ($1.27\ mg\ m^{-2}\ d^{-1}$) because of the lower P concentration of red alder leaves in the study by Gessel and Turner (1974) (0.030%) than in ours (0.091%).

Plots with no trees in our study produced more litterfall than did plots at a nearby clear-cut site at ~800 m elevation evaluated in a previous study (Bilby and Bisson 1992). In our study, even sites with no adjacent trees produced measurable terrestrial organic matter inputs, primarily grass clippings from mowing in urban areas. This distinctly urban alteration has no direct corollary in previous studies.

Stand composition was more heterogeneous within forested Puget Lowland sites (our study) than in previous studies that targeted more uniform stands. However, we found few relationships between stand characteristics and litterfall inputs. This result corroborates the findings of Zavitovski and Newton (1971) and Abee and Lavender (1972) for natural systems. In contrast, O'Keefe and Naiman (2006) found a strong relationship between litterfall rates and stand characteristics in coastal riparian forests along a pristine river west of the Olympic Mountains. Litterfall inputs in an old Douglas fir stand increased to a peak of $2.8\ g\ m^{-2}\ d^{-1}$ after 100 y before declining to $1.4\ g\ m^{-2}\ d^{-1}$ (O'Keefe and Naiman 2006). N loads followed a similar pattern, and peaked at $82\ mg\ m^{-2}\ d^{-1}$ before declining to $55\ mg\ m^{-2}\ d^{-1}$ (O'Keefe and Naiman 2006). This successional effect on litter production was more pronounced in the coastal rainforest than our Puget Lowland sites because of the spatial patterns of the disturbance regime. Along the coastal river, channel meanders and avulsions created patches of uniform stand age. In the Puget Lowland, successional shifts are not as clearly defined because urban effects might not be intense enough to reset the stand completely. Furthermore, complicated urban stand composition results from spatially and temporally variable activities by land managers at the scale of small parcel ownership rather than from a single intense event that resets riparian forest succession uniformly and completely. Thus, although previous studies provide a general indication of litterfall patterns expected in urban areas, heterogeneity in stand structure confounds direct extrapolation.

Implications of changing vegetation on long-term nutrient loads

Natural conditions for vegetation inferred from both reconstruction from historical survey notes (Collins and Montgomery 2002) and pollen cores from nearby lakes (Davis 1973) indicate that conifers dominated much of the Puget Lowland, including within riparian zones. Riparian areas supporting predominantly deciduous trees do occur naturally in the Puget Lowland, especially on active floodplains (Rot et al. 2000), but deciduous stands are vastly overrepresented currently relative to historical conditions. Our data, and the previous litterfall studies in nonurban Pacific Northwest areas compiled in our paper, suggest that higher nutrient loads to many streams are likely to result where human activities in riparian areas in the Puget Lowland promote the replacement of conifer trees with deciduous species.

Stream nutrient concentrations were not part of our study, but evidence from 2 nearby studies indicates that nutrient concentrations are enhanced in streams flowing through deciduous-dominated riparian areas. Volk (2004) and Osborne (2006) found higher nutrient concentrations in streams draining red alder and other deciduous forests than in streams draining conifer forests, and Brett et al. (2005) suggested alders as an overlooked enrichment factor in urban streams. Stream nutrient processes are highly complex and heterogeneous, but the nutrient subsidy represented by the alteration of riparian vegetation in urban areas might translate to measurable nutrient increases in downstream water bodies that are not influenced by other urban activities (Volk 2004, Osborne 2006). Other urban stressors, including land cover patterns (Brett et al. 2005) and septic system density (Walsh and Kunapo 2009), enhance both the generation and transport of nutrients in urban streams.

The effect of this nutrient subsidy from deciduous species on downstream aquatic ecosystems could be deleterious. The influence of large-scale changes in watershed vegetation on nutrient delivery and freshwater and marine productivity is the subject of ongoing research in the region. Interest in this topic has been spurred by episodes of low dissolved O_2 in parts of Puget Sound. N typically limits primary productivity in Puget Sound (Albertson et al. 2002), so increased N loading caused by conversion of conifer to deciduous forests could be contributing to this phenomenon.

Some analyses of the potential effect of vegetation alteration on N loading have been completed in the region. Rivers and wastewater treatment plants contributed 2700 and 2800 kg N/d as dissolved inorganic N on an annual basis to South Puget Sound, south of Tacoma, Washington (USA) (Roberts et al. 2008a). Extrapolation of litterfall loading rates per unit area to comparable nutrient loads requires knowledge of the total stream surface area within a system. No estimates of stream width, length, or total surface area are available for Puget Lowland streams. However, if we estimate that stream surface area constitutes 1% of the total South Puget Sound watershed area, then direct litterfall N loads of 9 to 21 mg N m^{-2} d^{-1} would deliver between 390 and 910 kg N/d to the drainage network. Similarly, if the watershed loads currently represent loads as much as 54% higher than natural because of vegetation shifts, then deciduous vegetation could be contributing as much as 950 kg N/d beyond what would be delivered from conifer forests. Both estimates are comparable in magnitude to the efflux of N calculated from stream concentration and flow estimates but are not as high as wastewater contributions. Peak vegetation inputs occur in autumn, but deciduous vegetation also produces considerably higher nutrient inputs in spring and summer than does conifer vegetation. Therefore, we think that the fundamental shift in vegetation has had a measurable effect on stream nutrient levels, as was found in studies of nearby nonurban watersheds (Volk 2004, Osborne 2006), and might be contributing to increasing water-quality problems in some areas of Puget Sound.

Further along the urban gradient, plots with no tree cover produced lower OM and nutrient inputs than did either CON or DEC forested plots. Canopy removal in urban areas probably causes a shift from allochthonous to autochthonous production (Bilby and Bisson 1992), and activities, such as mowing, suppress natural regeneration. In forested regions, food webs in small streams rely predominantly on allochthonous inputs. Thus, changes to these inputs could affect food webs and overall system productivity, and the decreased nutrient inputs might not produce beneficial effects.

Restoration strategies and management implications

Enhanced litterfall from restoration activities indicates that the effects of urbanization on riparian vegetation can be mitigated, and at least some ecological functions, such as shade, can be restored. Even young sites can have a closed canopy over small streams, and the 2 restoration sites included in our study produced litterfall comparable to that of a young, regenerating deciduous riparian forest. Where riparian restoration enhances conifer generation, such as at PUGE, nutrient inputs might decline as the conifers mature.

Regional management activities should focus on enhancing conifer regeneration rather than removing abundant red alder. Removing red alder would produce deleterious effects, such as increased heating from solar radiation and increased erosion by destabilizing streambanks. Riparian restoration that does not account for native vegetation composition might not restore the natural litterfall patterns under which stream biota have evolved. Differences in nutrient composition or timing could alter organic matter breakdown rates and food availability within these systems.

Further research is necessary to isolate the effects of changing litter inputs on nutrient levels and food webs in urban streams. For example, increases in urbanization increase the magnitude and frequency of high-flow events (Konrad and Booth 2002) and enhance leaf litter transport (Roberts et al. 2008b). Decreases in allochthonous inputs decrease benthic OM storage, reduce instream nutrient uptake (Webster et al. 2000, Roberts et al. 2007), and increase nutrient concentrations in stream water. Decreased litterfall inputs coupled with enhanced OM transport would reduce allochthonous materials available for biotic processes drastically, with profound changes to the benthic community (Wallace et al. 1997, Webster et al. 2000) and possibly decomposition processes (Roberts 2007).

Urban development clearly influences the composition of Puget Lowland riparian forests, and leads to changes in the quantity and quality of terrestrial inputs to small streams. These structural changes affect many ecological processes that rely on allochthonous inputs in the streams and in downstream water bodies, and further complicate management challenges. Results from the restored and forested plots in our study suggest that allochthonous OM contributions to the aquatic food web can be maintained in urban environments, provided that a native forest canopy is allowed to become reestablished. However, delivery of N and P to Puget Lowland streams is considerably higher than occurred historically because of the dominance of deciduous riparian areas in the region. Achieving a distribution of riparian conditions closer to historical conditions in the Puget Lowlands might be accelerated by protecting areas that currently support conifers and by restoration efforts to establish conifer trees in riparian areas.

Acknowledgements

This work was funded in part by a grant from the US Environmental Protection Agency Region 10 and the Puget Sound Action Team. The manuscript benefited from reviews by Derek Booth, Michael Brett, and 2 anonymous referees. Laura Nokes, Tim Strickler, Paolo Cruz, and Azhar Nizar provided field and laboratory assistance. The University of Washington (UW) Tacoma Environmental Science program provided laboratory equipment. Nutrient analyses were provided by Dongsen Xue, Chemical Analysis Service Center, UW College of Forest Resources.

Literature Cited

ABEE, A., AND D. LAVENDER. 1972. Nutrient cycling in throughfall and litterfall in 450-year-old Douglas-fir stands. Pages 133–144 *in* J. F. Franklin, L. J. Dempster, and R. H. Waring (editors). Proceedings of the Symposium on Research on Coniferous Forest Ecosystems: First Year Progress in the Coniferous Forest Biome. Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Portland, Oregon.

ALBERTSON, S. L., K. ERICKSON, J. A. NEWTON, G. PELLETIER, R. A. REYNOLDS, AND M. L. ROBERTS. 2002. South Puget Sound water quality study, phase 1. Washington State Department of Ecology Publication No. 02-03-021. Washington State Department of Ecology, Olympia, Washington. (Available from: www.ecy.wa.gov/biblio/0203021.html)

ANDERSON, N. H., AND J. R. SEDELL. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Annual Review of Entomology 24:351–377.

BESCHTA, R. L., R. E. BILBY, G. W. BROWN, L. B. HOLTBY, AND T. D. HOFSTRA. 1987. Stream temperature and aquatic habitat: fisheries and forestry interactions. Pages 191–232 *in* E. O. Salo and T. W. Cundy (editors). Streamside management: forestry and fishery interactions. Institute of Forest Resources Publication No. 59. University of Washington, Seattle, Washington.

BILBY, R. E., AND P. A. BISSON. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Canadian Journal of Fisheries and Aquatic Sciences 49:540–551.

BILBY, R. E., AND P. A. BISSON. 1998. Function and distribution of large woody debris. Pages 324–346 *in* R. J. Naiman and R. E. Bilby (editors). River ecology and management. Springer-Verlag, New York.

BRAY, J. R., AND E. GORHAM. 1964. Litter production in forests of the world. Advances in Ecological Research 2: 101–157.

BRETT, M. T., G. B. ARHONDITSIS, S. E. MUELLER, D. M. HARTLEY, J. D. FRODGE, AND D. E. FUNKE. 2005. Non-point-source impacts on stream nutrient concentrations along a forest to urban gradient. Environmental Management 35: 330–342.

BROWN, L. R., T. CUFFNEY, J. F. COLES, A. H. BELL, J. T. MAY, F. FITZPATRICK, G. MCMAHON, AND J. STEUER. 2009. Urban streams across the United States: lessons learned from studies in nine metropolitan areas. Journal of the North American Benthological Society 28:1051–1069.

CHEN, Y. D., R. F. CARSEL, S. C. MCCUTCHEON, AND W. L. NUTTER. 1998. Stream temperature simulation of forested riparian areas: II. Model application. Journal of Environmental Engineering 124:316–328.

CITY OF SEATTLE. 2006. Urban forest management plan, Seattle, Washington. City of Seattle, Seattle, Washington. (Available from: www.seattle.gov/environment/documents/Draft_Forest_Plan-Final.pdf)

COLLINS, B. D., AND D. R. MONTGOMERY. 2002. Forest development, wood jams, and restoration of floodplain rivers in the Puget Lowland, Washington. Restoration Ecology 10:237–242.

DAVIS, M. B. 1973. Pollen evidence of changing land use around the shores of Lake Washington. Northwest Science 47:133–148.

DELONG, M. D., AND M. A. BRUSVEN. 1994. Allochthonous input of organic matter from different riparian habitats of an agriculturally impacted stream. Environmental Management 18:59–71.

DINICOLA, R. S. 1990. Characterization and simulation of rainfall-runoff relations for headwater basins in western King and Snohomish Counties, Washington. U.S. Geological Survey Water-Resources Investigations Report No. 89-4052. US Geological Survey, Tacoma, Washington.

FRANKLIN, J. F., AND C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. Oregon State University Press, Portland, Oregon.

GESSEL, S. P., AND J. TURNER. 1974. Litter production by red alder in western Washington. Forest Science 20:325–330.

GREGORY, S. V., F. J. SWANSON, W. A. MCKEE, AND K. W. CUMMINS. 1991. An ecosystem perspective of riparian zones. BioScience 41:540–551.

HILL, K., E. BOTSFORD, AND D. BOOTH. 2003. A rapid land cover classification method for use in urban watershed analysis. University of Washington Department of Civil and Environmental Engineering Technical Report No. 173. University of Washington, Seattle, Washington. (Available from: water.washington.edu/Research/Reports/WRS173.pdf)

KONRAD, C. P., AND D. B. BOOTH. 2002. Hydrologic trends associated with urban development for selected streams in the Puget Sound Basin, Western Washington. U.S. Geological Survey Water-Resources Investigations Report 02-4040. US Geological Survey, Tacoma, Washington.

Meyer, J. L., M. J. Paul, and W. K. Taulbee. 2005. Stream ecosystem function in urbanizing landscapes. Journal of the North American Benthological Society 24:602–612.

Murray, G. L. D., R. L. Edmonds, P. M. Kiffney, and C. J. Volk. 2000. Ecosystem and watershed studies in Olympic National Park: 1999 annual report. Technical Report NPS/CCSOUW/NRTR-2000/04 submitted to National Park Service. College of Forest Resources, University of Washington, Seattle, Washington. (Available from: www.cfr.washington.edu/research.oar/Annual-Reports/1999%20Annual%20Report.pdf)

Naiman, R. J., H. Décamps, and M. E. McClain. 2005. Riparia. Ecology, conservation, and management of streamside communities. Elsevier Academic Press, Burlington, Massachusetts.

Oelbermann, M., and A. M. Gordon. 2000. Quantity and quality of autumnal litterfall into a rehabilitated agricultural stream. Journal of Environmental Quality 29:603–611.

O'Keefe, T. C., and R. J. Naiman. 2006. The influence of forest structure on riparian litterfall in a Pacific Coastal rain forest. Canadian Journal of Forest Research 36: 2852–2863.

Osborne, S. 2006. Influence of catchment characteristics on stream nitrogen transport and hypoxic conditions in south Hood Canal. MS Thesis, University of Washington, Seattle, Washington.

Pojar, J., and A. MacKinnon. 1994. Plants of the Pacific Northwest Coast. Research Program, British Columbia Forest Service, Vancouver, British Columbia. Lone Pine Publishing, Redmond, Washington.

Roberts, B. J., P. J. Mulholland, and J. N. Houser. 2007. Effects of upland disturbance and instream restoration on hydrodynamics and ammonium uptake in headwater streams. Journal of the North American Benthological Society 26:38–53.

Roberts, M. L. 2007. Sources, transport, and fate of terrestrial organic matter inputs to small Puget Lowland streams: effects of urbanization, floods, and salmon. PhD Dissertation, University of Washington, Seattle, Washington.

Roberts, M. L., R. E. Bilby, and D. B. Booth. 2008b. Hydraulic dispersion and reach-averaged velocity as indicators of enhanced organic matter transport in small Puget Lowland streams across an urban gradient. Fundamental and Applied Limnology 171:145–159.

Roberts, M. L., J. Bos, and S. Albertson. 2008a. South Sound water quality study, phase 2: dissolved oxygen, interim data report. Publication No. 08-03-037. Washington State Department of Ecology, Olympia, Washington. (Available from: www.ecy.wa.gov/biblio/0803037.html)

Rot, B. W., R. J. Naiman, and R. E. Bilby. 2000. Stream channel configuration, landform, and riparian forest structure in the Cascade Mountains, Washington. Canadian Journal of Fisheries and Aquatic Sciences 57: 699–707.

Triska, F. J., J. R. Sedell, and S. V. Gregory. 1982. Coniferous forest streams. Pages 292–332 *in* R. L. Edmonds (editor). Analysis of coniferous forest ecosystems in the western United States. Hutchinson Ross Publishing Company, Stroudsburg, Pennsylvania.

Volk, C. J. 2004. Nutrient and biological responses to red alder (*Alnus rubra*) presence along headwater streams: Olympic Peninsula, Washington. PhD Dissertation, University of Washington, Seattle, Washington.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102–104.

Walsh, C. J., and J. Kunapo. 2009. The importance of upland flow paths in determining urban impacts on stream ecosystems. Journal of the North American Benthological Society 28:977–990.

Walsh, C. J., A. H. Roy, J. W. Feminella, P. D. Cottingham, P. M. Groffman, and R. P. Morgan. 2005. The urban stream syndrome: current knowledge and the search for a cure. Journal of the North American Benthological Society 24: 706–723.

Washington State Office of Financial Management. 2006. April 1 intercensal and postcensal estimates of the total resident population by year for the state, counties, cities, the unincorporated areas, and incorporated areas: 1968 to 2006. Office of Financial Management, Olympia, Washington. (Available from: www.ofm.wa.gov/pop/cociseries/default.asp)

Webster, J. R., J. L. Tank, J. B. Wallace, J. L. Meyer, S. L. Eggert, T. P. Ehrman, B. R. Ward, B. L. Bennett, P. F. Wagner, and M. E. McTammany. 2000. Effects of litter exclusion and wood removal on phosphorus and nitrogen retention in a forest stream. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 27:1337–1340.

Zavitovski, J., and M. Newton. 1971. Litterfall and litter accumulation in red alder stands in western Oregon. Plant Soil 35:257–268.

Received: 5 December 2007
Accepted: 19 June 2009