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Influence of clearcut logging, flow duration, and season on emergent aquatic insects in headwater streams of the Central Oregon Coast Range

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Abstract. We measured the effects of timber-harvest condition (clearcut and forested) and flow duration (perennial and intermittent) on emergent aquatic insect assemblages at 20 headwater streams in the Central Oregon Coast Range. Clearcut streams had been logged to the stream banks within 2 y prior to the start of our study. Adult aquatic insects were sampled from a 40-m reach at each study stream in 3 seasons: summer, autumn, and spring. Emergent insects were strong indicators of harvest condition and, regardless of flow duration or season, more aquatic insects emerged from streams in clearcut catchments than in forested catchments. Plecoptera had higher emergence rates from intermittent streams than from perennial streams in spring. Functional feeding group composition was not apparently affected by harvest condition or flow duration. Taxon richness was slightly higher at clearcut than at forested streams, primarily because of the occurrence of rare taxa at clearcut streams. Nonmetric multidimensional scaling (NMS) ordination of emergent aquatic insect assemblages showed community patterns that varied by season and harvest condition, but little by flow duration. Stream canopy % cover, stand age, logging debris (% slash), and substrate composition differed between clearcut and forested streams and were strongly correlated with NMS axes. Taxa that responded to conditions created by logging, such as % slash or canopy opening, contributed to differences in assemblages between headwater streams flowing through clearcut and forested catchments.

Key words: logging, headwater streams, emergence, macroinvertebrates, perennial, intermittent, Oregon.

Headwater streams make up a major proportion of channel length within stream networks and serve important ecological and biological functions by delivering water, sediment, and organic material to downstream reaches (Sidle et al. 2000, Gomi et al. 2001, Meyer and Wallace 2001, Wipfli and Gregovich 2002). Small streams are either perennial or seasonally intermittent, depending on location in the catchment, annual climatic cycles, and modifications of hydrological patterns by human activities (Harr et al. 1975, Whiles and Wallace 1995, Price et al. 2003). During droughts or periods of low rainfall, intermittent streams cease flowing when the level of the water table falls below the streambed. In forested ecosystems, narrow channel widths of perennial and intermittent headwater streams interact with adjacent overhanging riparian vegetation to create tight linkages between the terrestrial and lotic systems (Vannote et al. 1980, Gregory et al. 1991). Macroinvertebrate communities in these small streams are strongly influenced by changes in the riparian vegetation because of their dependence on a food base derived from allochthonous inputs (Cummins and Klug 1979, Vannote et al. 1980, Hawkins et al. 1982).

Work focused on perennial, fish-bearing streams has shown that the composition and function of benthic macroinvertebrate communities can be influenced by timber harvest. When riparian areas are logged, the energy base of small streams can shift from allochthonous to autochthonous sources (Stockner and Shortreed 1976, Murphy and Hall 1981, Noel et al. 1986). Macroinvertebrates can respond to the altered food base in a variety of ways, including changes in densities and shifts in functional feeding group

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predominance (Newbold et al. 1980, Murphy et al. 1981, Hawkins et al. 1982, Noel et al. 1986, Cole et al. 2003, Haggerty et al. 2004). Shredders and collectors are dependent on riparian-derived resources and are the dominant functional feeding groups in headwater streams with intact riparian canopies (Cummins and Klug 1979, Vannote et al. 1980, Price et al. 2003). When autochthonous resources increase, functional feeding group composition in macroinvertebrate communities is expected to shift from dominance by shredders to dominance by scrapers.

Headwaters provide resources to downstream reaches, subsidies to the terrestrial food web, and colonizers to other streams. Adult insects emerging from headwaters often enter the terrestrial riparian corridor where they can become prey for streamside communities and serve as important energy subsidies to terrestrial fauna (Nakano and Murakami 2001). Intermittent headwater streams can harbor species adept at colonizing recently disturbed or temporary habitats (Progar and Moldenke 2002). Thus, reductions of forest cover that alter community dynamics in headwater streams can change linkages between upstream and downstream reaches (Wipfli and Gregovich 2002) and between terrestrial and aquatic systems (England and Rosemond 2004). Small headwater streams are vulnerable to anthropogenic alterations of the landscape that affect the catchment, riparian zone, or stream channel. Tree harvest that impacts macroinvertebrate communities in intermittent stream sections potentially can alter downstream perennial communities or the resilience of stream assemblages (Brown et al. 1997, Progar and Moldenke 2002).

Timber harvest is done with a variety of techniques and occurs on both public and private lands throughout the Oregon Coast Mountains of the Pacific Northwest, USA. The current Forest Practices Act, which establishes forestry guidelines for all properties in Oregon, classifies small, nonfish-bearing headwater streams as *Type N*, and does not require riparian buffers around these streams (ODF 2004). Current forest-management proposals call for increased protection of small nonfish-bearing streams (Adams 2007). Given the extent of the landscape potentially affected by increased protection, headwater streams have become a research priority (Naiman et al. 1993, Moore and Richardson 2003), and several recent studies in the Pacific Northwest have investigated the impact of land-management practices on the macroinvertebrate communities of either perennial or intermittent headwater streams (Haggerty et al. 2002, 2004, Progar and Moldenke 2002, Wipfli and Gregovich 2002, Cole et al. 2003, Herlihy et al. 2005). The goal of our study was to compare the taxonomic and functional feeding group composition of assemblages of emergent aquatic insects among perennial and intermittent headwater streams in recently clearcut and in forested catchments.

Methods

Study design and stream treatments

All study streams are 0- to 1st-order headwater streams in the Central Oregon Coast Range. The Oregon Coast Range has a temperate marine climate with cool, rainy winters and mild, drier summers (Taylor and Hannan 1999). Most of the streams feed tributaries to the North Fork of the Alsea River. Only 1 stream, a headwater of Greasy Creek, ultimately drains into the Willamette River (Fig. 1). The benthic community of this stream was similar to the perennial forested streams within the Alsea catchment (Banks 2005). Sampling sites were located on Weyerhaeuser Company timberlands and public lands administered by the US Bureau of Land Management.

Our study had a crossed 2-factor design with 2 levels of each factor: harvest condition (clearcut and forested) and flow duration (perennial and intermittent). The 20 streams chosen for sampling were as similar as possible with respect to parental geology, active channel width, and estimated drainage area. Ten streams were in catchments that had been clearcut within 2 y prior to the start of sampling. The remaining 10 streams had riparian zones with a developed canopy layer and were in catchments that had not been logged in ≥34 y. Prior to logging, clearcut streams were in forest stands that were similar in age and canopy composition to the stands around the forested streams. Clearcut and forested streams were further classified as perennial or intermittent (completely dry at the surface during summer months).

Logging of the clearcut catchments complied with the regulations of the Oregon Forest Practices Act for small streams within the Oregon Coast Range that are nonfish-bearing and not used for domestic water use (ODF 2004). In 2001 (3 sites) or 2002 (7 sites), catchments of clearcut streams were logged to the stream banks; no riparian buffers were required for stream protection. Thus, 98 to 100% of all trees were harvested in clearcut catchments (Fig. 1). Clearcut areas were cable logged, and trees were yarded uphill to a landing for final processing and loading. Harvesting rules for Type N streams permit dragging of trees across the stream channel; however, no evidence of this practice was observed in our study streams, and skid trails generally were ≥15 m from the edge of the stream channel. Our study sites were not completely covered with logging debris; however, slash (large and small wood remaining after logging) was present in

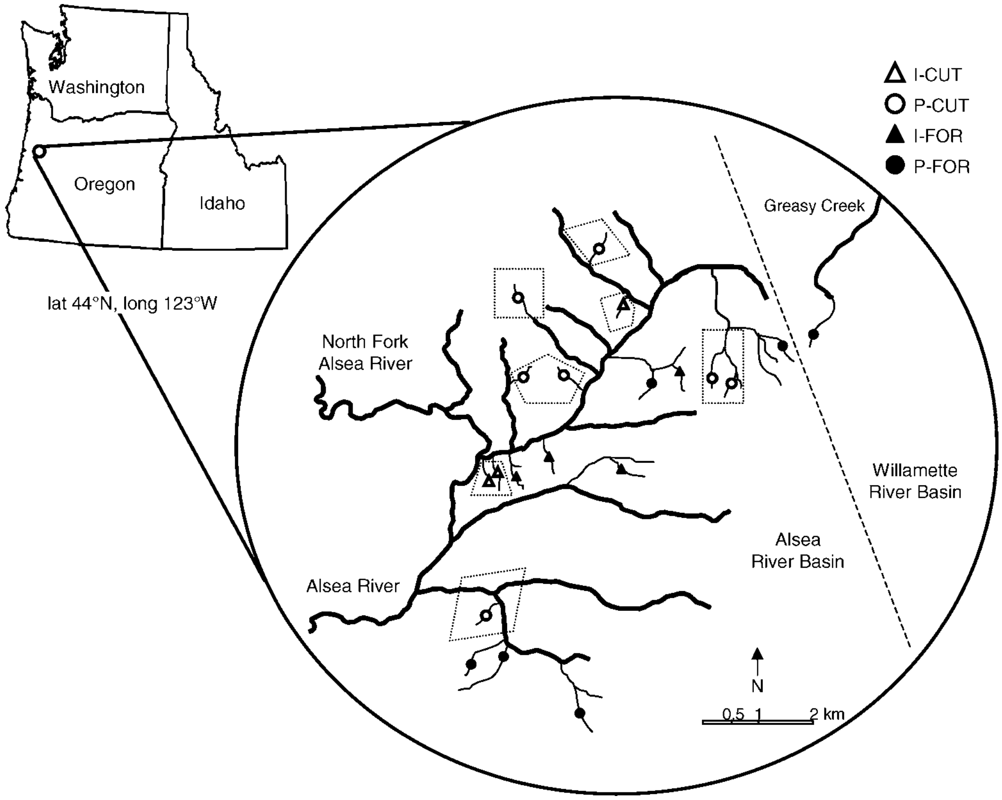

FIG. 1. Locations of the 20 study streams in the Central Oregon Coast Range. Thick lines depict streams and were derived from a 10-m digital elevation model geographical information system layer. Thin lines depict headwater streams and were sketched. Dashed-line polygons mark the approximate size and shape of clearcuts based on aerial photographs. I-CUT = intermittent-clearcut sites, P-CUT = perennial-clearcut sites, I-FOR = intermittent-forested sites, P-FOR = perennial-forested sites.

the stream channel, over the stream, or on the stream banks in every reach of the clearcut streams.

Our study originally was designed with equal replication of 5 streams for each combination of harvest condition and flow duration. However, flow duration was predicted based on a visual assessment of stream conditions in spring 2003, before the start of sampling in summer 2003, and before stream channels lost surface flow. Final characterization of flow duration was determined at the end of summer when surface flow upstream of and throughout the reach had ceased (intermittent) or the reach had retained surface flow (perennial) during summer months. Differences between predicted and observed flow duration resulted in an unbalanced study design with 3 intermittent-clearcut (I-CUT), 4 intermittent-forested (I-FOR), 7 perennial-clearcut (P-CUT), and 6 perennial-forested (P-FOR) streams.

Aquatic-insect and stream-habitat sampling

A 40-m study reach was delineated in each stream (Banks 2005). Adult aquatic macroinvertebrates were sampled with 4 emergence traps/stream. Emergence traps were set for 4 wk in each of 3 seasons: summer (4 August–7 September 2003), autumn (16 October–16 November 2003), and spring (5 April–7 May 2004). Not all streams could be visited in 1 day, so the beginnings and ends of sampling periods were staggered to accommodate stream locations and field conditions. Differences among starting dates (traps set in the stream channel) or ending dates (final collections) among the 20 streams was $\leq$4 d in all seasons.

Each emergence trap covered 0.19 m^2 of streambed (Fig. 2), and the area was completely enclosed by netting (~150-μm mesh size) draped over the trap and anchored along the streambed with natural materials from the stream (e.g., cobbles, woody debris; Banks 2005). The capture wells in the traps were filled with a 50:50 mixture of ethylene glycol and water to capture and preserve emergent insects. Well contents were collected 2 wk after initial trap deployment to prevent sample loss. The traps were reset at that time, and emerging adults were collected for an additional 2 wk. Well contents were sieved through a 500-μm screen, preserved in 90% ethanol, and returned to the laboratory for identification.

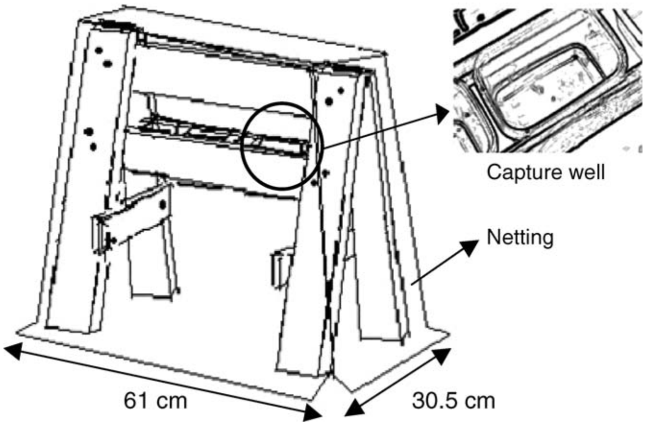

FIG. 2. Schematic representation of emergence traps used to collect aquatic insects.

Ephemeroptera and Plecoptera were identified to genus with the keys in Merritt and Cummins (1996). Trichoptera were identified to family with the keys in Merritt and Cummins (1996) and to genus with a variety of keys (Denning 1956, Ross 1956, Gordon 1974, Blickle 1979, Ninmo 1987, Armitage and Hamilton 1990). Coleoptera were identified to family with the keys in Borror et al. (1989). With the exception of Empididae, which were identified to genus, Diptera were identified to family with the keys in McAlpine et al. (1981). Functional feeding groups were assigned based on Merritt and Cummins (1996) and McAlpine et al. (1981). The family Chironomidae includes taxa with many different feeding modes, and this family could not be assigned to a definitive functional feeding group. Taxa with members belonging to multiple or unknown functional feeding groups were not considered in analyses of functional feeding group composition.

A modified version of the US Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP) protocol, Quantifying Physical Habitat in Wadeable Streams, was used to characterize the physical habitat of each reach during summer low flows in August 2003 (Kaufmann et al. 1999, Banks 2005). During each sampling period, stream cover provided by vegetation and topography was measured with a spherical densiometer read at midstream in the 4 cardinal directions and converted to % cover. Water temperature was recorded every 30 min from August 2003 to May 2004 using StowAway TidbiT^{TM} loggers (Onset Computer Corporation, Pocasset, Massachusetts). Mean seasonal water temperature for summer (August–September), autumn (October–November), winter (December–February), and spring (March–April) was calculated for each stream by averaging the mean daily water temperatures of each season. Intermittent streams were either drying or completely dry at the surface during both summer and autumn sampling periods, but it was possible to derive water temperatures for these streams because loggers were submerged for at least a portion of each season.

Data analysis

Physical-habitat variables that were measured once during the summer were compared among harvest-condition and flow-duration treatments with 2-way factorial analyses of variance (ANOVAs). Differences among treatment means were judged significant when $p < 0.002$ (Bonferroni correction of $p < 0.05$). Physical-habitat variables that were measured several times during the study (water temperature, stream % cover) were compared among harvest-condition and flow-duration treatments with separate 2-way ANOVAs for each season. Dependent variables were tested for normality and arcsine($\sqrt{[x]}$)- or $\log_{10}(x)$-transformed as necessary.

The tallies for every 2-wk collection were standardized to emergence rates (ind. m^{-2} d^{-1}). Mean daily emergence rate was calculated as the mean of the rates during the two 2-wk collection periods per season to give a single emergence rate per stream per season. The final data set consisted of 60 samples and was used in all analyses of emergent aquatic insect assemblages and functional feeding group composition.

Emergence rates of all aquatic insects, Ephemeroptera only, Plecoptera only, Trichoptera only, and Diptera only were compared among harvest-condition and flow-duration treatments with repeated-measures 2-way ANOVAs with Type III sum of squares. Differences among treatment means were judged significant when $p < 0.005$ (Bonferroni correction of $p < 0.05$). The covariance structure of the data was tested for sphericity. When the data did not have Type H covariance structure, p-values were adjusted using the Huynh–Feldt's estimator. The few aquatic insects that belonged to orders other than Ephemeroptera, Plecoptera, Trichoptera, and Diptera were not considered separately. Terrestrial insects were collected during sampling but were excluded from our analyses of aquatic insects. Emergence rates of collector-gatherers, collector-filterers, shredders, scrapers, and predators also were compared among harvest-condition and flow-duration treatments with repeated-measures 2-way ANOVAs. Transformations of the functional feeding group data were not necessary.

Taxon richness, evenness, and Shannon–Wiener diversity (H′) were tested for sphericity and compared among harvest-condition and flow-duration treatments with repeated-measures 2-way ANOVAs. H' accounts for both evenness and taxon richness using the formula $H' = -\Sigma p_i \ln(p_i)$ (Magurran 1988), where p_i is the proportion of individuals found in the i^{th} taxon. Evenness was calculated as $E = H'/\ln(S)$, where S is the number of taxa collected (Magurran 1988).

Assemblage composition of emergent aquatic insects was examined with nonmetric multidimensional scaling (NMS) with a random starting configuration (PC-ORD, version 4.20; MjM Software Design, Gleneden Beach, Oregon). The Sorenson distance measure was used to calculate dissimilarity between sites. Taxa that occurred in <3 of the 60 samples were excluded from the analysis to enable us to discern relationships in community assemblages more readily (McCune and Grace 2002). This practice reduced the total number of taxa from 76 to 57. Emergence-rate data were $\log_{10}(x + 1)$-transformed prior to analyses. We used Spearman rank correlations to examine strength of the associations of environmental gradients and taxa with ordination-axis scores. The environmental matrix included data from physical-habitat surveys, and elevation, catchment area, and stand-age data that were derived from topographic maps, current land-management maps provided by land managers, and communication with landowners.

Indicator Species Analysis was used to determine whether any taxon was indicative of a harvest condition or flow duration within each season. Indicator values for each taxon were calculated as a product of % faithfulness (all sites in treatment contain the taxon) and % exclusiveness (taxon should be in that treatment only and not others). Indicator values for a taxon can range from 0% (no indication) to 100% (perfect indication; Dufrene and Legendre 1997). Within a season, a taxon would receive the highest possible % indication (100) if it was consistently and exclusively present in streams within a particular harvest condition or flow duration. The statistical significance of indicator values was tested by the Monte–Carlo method with 1000 randomized runs (PC-ORD). Taxa with indicator values with $p < 0.05$ were considered good indicators for a particular harvest condition or flow duration.

Results

Physical habitat

Catchment areas of all streams were <1 km^2 (Table 1). Channel dimensions, elevations, and reach slopes were variable among streams and showed no consistent differences related to flow duration or harvest condition. Mean seasonal water temperature was coldest in winter and spring, and warmest in summer in all streams. Mean seasonal water temperatures did not differ among flow-duration or harvest-condition treatments within seasons (Table 1). Perennial streams tended to have larger substrates than intermittent streams; and P-FOR streams had the highest % coarse substrate (Table 1). Intermittent streams, by definition, had no surface water in summer, but flowed continuously in autumn. At the beginning of spring sampling, surface water was flowing in intermittent streams, but wetted width decreased during the spring collection period. Flow was discontinuous in some reaches by the end of the spring sampling period.

Percent canopy provided by both big and small trees was lower at clearcut than at forested streams. Clearcut streams had no riparian buffer strips and had been replanted with Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) seedlings in 2002 or 2003. Clearcut streams had less stream % cover than forested streams in any season (Table 1). Slash was abundant at all clearcut streams and often covered portions of the stream channel. Sparse vegetation and topographic features provided stream shade at some sites. Six forested sites had canopies with a mixture of deciduous and coniferous trees composed of red alder (*Acer rubrus* Bong.), big-leaf maple (*Acer macrophyllum* Pursh.), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and Douglas-fir. Three of the forested sites had riparian canopies dominated by coniferous trees, and 1 forested site had a canopy consisting of deciduous trees. Understory vegetation was composed of tree saplings, and salmonberry (*Rubus spectabilis* Pursh) and thimbleberry (*Rubus parviflorus* Nutt.) shrubs. Ground cover included salal (*Gaultheria shallon* Pursh), sword fern (*Polystichum munitum* Kaulfuss), and many different herbaceous plants.

Emergence rates of aquatic insect orders and functional feeding groups

Total insect emergence rates were significantly higher from clearcut than from forested streams through all seasons (Table 2, Fig. 3). Total insect emergence rates were not significantly affected by flow duration (Table 2, Fig. 3). Emergence rates for Diptera varied significantly with harvest condition, but emergence rates for other orders did not differ between clearcut and forested streams (Table 2). Diptera, of which 87% were chironomids, had significantly higher emergence rates from clearcut than from forested streams through all seasons, with the highest overall emergence rates in summer and autumn (Fig. 4A–C). Emergence rates for Ephemeroptera and Plecoptera were significantly higher in spring than in other

TABLE 1. Median (minimum, maximum) of habitat variables for the 40-m stream reaches classified by harvest condition and flow duration. Superscripted letters next to variable names indicate results from 2-way analyses of variance showing significant differences between or among groups ($p < 0.002$). ^{A} = perennial > intermittent, ^{B} = forested > clearcut, ^{C} = clearcut > forested. I-CUT = intermittent-clearcut sites, P-CUT = perennial-clearcut sites, I-FOR = intermittent-forested sites, and P-FOR = perennial-forested sites.

Physical-habitat variables	I-CUT ($n = 3$)	P-CUT ($n = 7$)	I-FOR ($n = 4$)	P-FOR ($n = 6$)
Stream				
Elevation (m)	173 (146, 294)	332 (132, 571)	328 (181, 564)	285 (145, 615)
Catchment area (ha)	3.0 (2.3, 6.0)	4.6 (3.7, 33.0)	3.4 (1.9, 6.0)	16 (4.1, 55.0)
Reach slope (%)	15 (14, 33)	21 (4, 34)	10 (4, 42)	19 (6, 40)
Active channel width (m)	1.2 (0.3, 2.0)	1.2 (0.7, 3.0)	1.2 (1.0, 2.3)	2.3 (1.4, 3.3)
Bankfull width (m)	1.5 (1.0, 2.0)	2.5 (1.0, 3.5)	1.6 (1.5, 4.0)	2.8 (1.5, 4.0)
% sand and fines	86 (64, 90)	52 (20, 90)	80 (65, 92)	33 (14, 56)
% small gravel, sand, and fines	90 (64, 92)	69 (33, 90)	86 (81, 92)	55 (33, 64)
% coarse substrate^{A}	4 (0, 4)	13 (0, 34)	8.5 (0, 15)	40 (29, 65)
% organic matter	6 (4, 36)	13 (2, 47)	6 (3, 8)	4 (2, 7)
Summer stream % cover^{B}	48 (2, 48)	17 (0, 52)	97 (95, 99)	93 (89, 96)
Autumn stream % cover^{B}	24 (11, 42)	21 (3, 57)	97 (90, 100)	95 (92, 99)
Spring stream % cover^{B}	17 (0, 26)	11 (0, 52)	94 (91, 99)	94 (83, 99)
% fast-water habitat type	56 (33, 100)	80 (11, 100)	40 (0, 100)	77 (55, 100)
% slow-water habitat type	11 (0, 11)	18 (0, 89)	20 (0, 50)	23 (0, 36)
Summer water temperature (°C)	11.9 (11.0, 12.6)	12.3 (11.2, 13.0)	12.8 (10.9, 13.0)	12.5 (11.4, 13.0)
Autumn water temperature (°C)	10.3 (8.7, 10.4)	10.0 (8.5,10.0)	9.6 (9.2, 10.9)	9.2 (7.6, 9.7)
Winter water temperature (°C)	9.8 (8.9, 10.3)	9.7 (6.4, 9.7)	8.5 (7.5, 9.5)	8.0 (7.1, 8.9)
Spring water temperature (°C)	9.9 (8.7, 10.1)	9.6 (7.8, 10.3)	9.2 (7.5, 9.5)	8.9 (7.8, 9.4)
Riparian				
Stand age^{B} (y)	1 (0, 1)	0 (0, 1)	62 (52, 62)	36 (34, 62)
% big-trees canopy^{B}	0 (0, 5)	0 (0, 2.5)	15 (5, 25)	25 (5, 25)
% small-trees canopy^{B}	2.5 (0, 2.5)	0 (0, 15)	25 (25, 58)	25 (25, 88)
% nonwoody understory	25 (25, 25)	25 (5, 58)	73 (25, 88)	88 (0, 88)
% woody understory	5 (2.5, 5)	5 (5, 15)	15 (5, 25)	15 (0, 25)
% nonwoody ground cover	58 (25, 88)	25 (15, 58)	88 (73, 88)	88 (5, 88)
% woody ground cover	5 (5, 15)	5 (5, 25)	5 (5, 25)	5 (0, 25)
% slash^{C}	73 (58, 88)	58 (25, 88)	0 (0, 0)	0 (0, 15)

seasons, whereas emergence rates for Trichoptera were significantly higher in summer than in other seasons (Table 2, Fig. 4A–C). Emergence rates of Plecoptera were significantly higher from intermittent than from perennial streams in spring, when 6× more individuals emerged from I-FOR than from P-FOR streams and 1.5× more individuals emerged from I-CUT than from P-CUT streams (Table 2, Fig. 4A–C).

Emergence rates of functional feeding groups tended to be highly variable within flow durations and harvest conditions, but differed significantly among seasons (Table 2). Emergence rates of collector-filterers, dominated by the caddisfly *Wormaldia* in every season, were significantly higher in summer than in other seasons (Fig. 5A–C), as were emergence rates of collector-gatherers, dominated by *Paraleptophlebia* and *Diphetor* (Fig. 5A–C), and the predator Ceratopogonidae (Diptera). Emergence rates of the predator *Sweltsa* (Plecoptera) were highest in spring. Emergence rates of shredders, primarily Plecoptera in the families Leuctridae and Nemouridae, were highest from intermittent streams in the spring (Fig. 5A–C). Very few scrapers were collected, and no seasonal differences in emergence rates of scrapers were detected (Table 2, Fig. 5A–C).

Taxon richness, evenness, and H′ were significantly lower in autumn than in any other season (Tables 2, 3). Taxon richness was significantly higher at clearcut than at forested streams in every season (Tables 2, 3), primarily because of the presence of rare species at clearcut streams. Only 4 of the 17 taxa that were unique to clearcut streams were found at ≥5 clearcut streams (Ephydridae, *Neoplasta* and *Dolichocephala* [Empididae], *Homoplectra* [Hydropsychidae]). Of the 8 taxa that were unique to forested sites, *Calliperla* (Perlodidae) appeared most frequently in spring samples at 4 of the 10 forested streams. Evenness was slightly higher at forested than at clearcut streams in all seasons and in both flow durations (Table 3), but the difference was not significant (Table 2). H′ did not differ between harvest conditions or between flow durations (Tables 2, 3).

TABLE 2. F-values with $p < 0.005$ from repeated-measures 2-way analyses of variance of taxon metrics and emergence rates (ind. m^{-2} d^{-1}) of all aquatic macroinvertebrates, orders, and functional feeding groups. H′ = Shannon–Wiener diversity, n.s. = $p > 0.005$.

Variable	Season	Harvest	Flow	Interactions
Taxon metrics				
Richness	24.98	17.13	n.s.	n.s.
Evenness	25.43	n.s.	n.s.	n.s.
H′	34.84	n.s.	n.s.	n.s.
Emergence rates				
Total	n.s.	37.48	n.s.	n.s.
Ephemeroptera	21.15	n.s.	n.s.	n.s.
Plecoptera[a]	26.77	n.s.	n.s.	9.26 (season × flow)
Trichoptera[a]	20.73	n.s	n.s.	n.s.
Diptera	n.s.	40.79	n.s.	n.s.
Collector-filterer	10.57	n.s	n.s.	n.s.
Collector-gatherer	26.98	n.s.	n.s.	n.s.
Shredder	8.26	n.s.	n.s.	n.s.
Scraper	n.s.	n.s.	n.s.	n.s.
Predator[a]	12.29	n.s.	n.s.	n.s.

[a] Adjusted by the Huynh–Feldt's estimator

Insect assemblages

Stress for the 3-dimensional NMS ordination solution was 11, and the solution explained 89.3% of the variability in the insect assemblage data. Insect assemblages were separated on the basis of season along NMS axes 1 and 3 (Fig. 6A). Spring assemblages were separated from summer and autumn assemblages along axis 3, and summer and autumn assemblages were separated along axis 1. Insect assemblages were separated on the basis of harvest condition along NMS axis 2 (Fig. 6B). NMS did not separate assemblages on the basis of flow duration along any of the 3 axes.

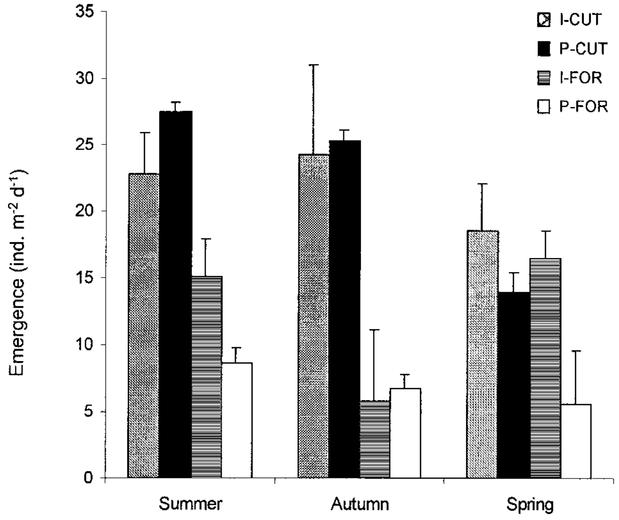

FIG. 3. Mean (+1 SE) emergence rates of all aquatic insects in summer, autumn, and spring sampling. Treatment abbreviations are given in Fig. 1.

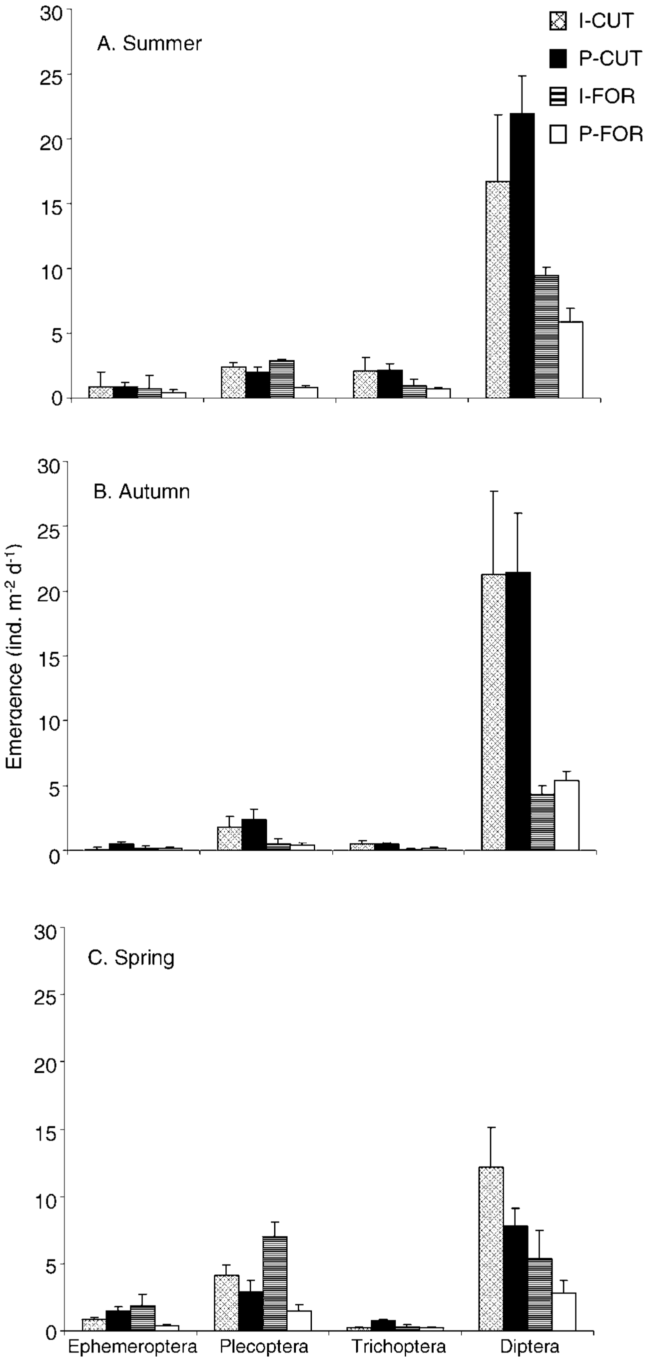

FIG. 4. Mean (+1 SE) emergence rates of Ephemeroptera, Plecoptera, Trichoptera, and Diptera during summer (A), autumn (B), and spring (C) sampling. Treatment abbreviations are given in Fig. 1.

Many habitat variables were strongly correlated

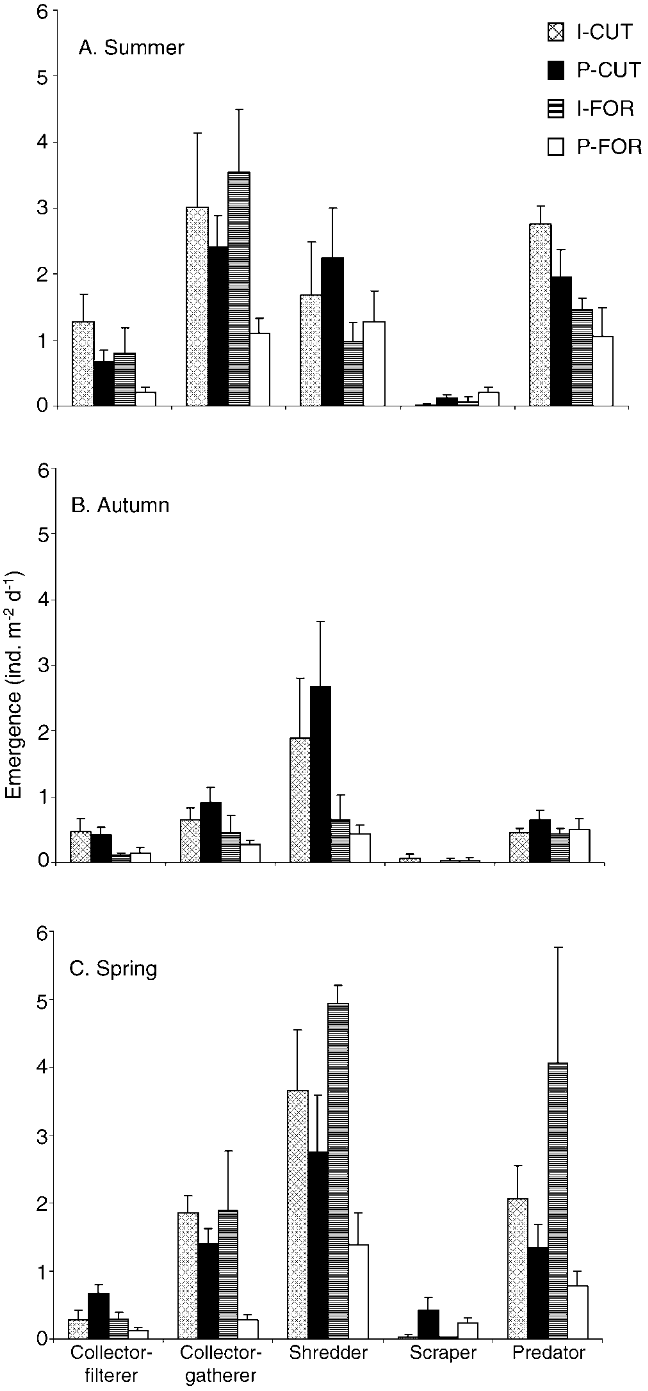

FIG. 5. Mean (+1 SE) emergence rates of collector-filterer, collector-gatherer, shredder, scraper, and predator functional feeding groups during summer (A), autumn (B), and spring (C) sampling. Treatment abbreviations are given in Fig. 1.

TABLE 3. Mean (±1 SD) taxon richness, evenness, and Shannon–Wiener diversity (H′) of emerging macroinvertebrates for each season classified by harvest condition and flow duration. I-CUT = intermittent-clearcut sites, P-CUT = perennial-clearcut sites, I-FOR = intermittent-forested sites, and P-FOR = perennial-forested sites.

Variable	Summer	Autumn	Spring
Taxon richness			
I-CUT	18 ± 3	12 ± 4	17 ± 4
P-CUT	18 ± 1	15 ± 5	20 ± 3
I-FOR	16 ± 3	9 ± 3	15 ± 4
P-FOR	13 ± 2	9 ± 1	12 ± 4
Evenness			
I-CUT	0.54 ± 0.19	0.31 ± 0.07	0.57 ± 0.15
P-CUT	0.42 ± 0.14	0.33 ± 0.10	0.59 ± 0.10
I-FOR	0.60 ± 0.08	0.42 ± 0.11	0.68 ± 0.09
P-FOR	0.57 ± 0.13	0.31 ± 0.06	0.65 ± 0.15
H′			
I-CUT	1.57 ± 0.63	0.78 ± 0.26	1.59 ± 0.36
P-CUT	1.22 ± 0.40	0.89 ± 0.33	1.77 ± 0.29
I-FOR	1.64 ± 0.26	0.92 ± 0.39	1.83 ± 0.30
P-FOR	1.42 ± 0.24	0.66 ± 0.14	1.57 ± 0.38

with the NMS ordination axes and clearly showed seasonal and logging effects. Stream variables, such as active channel width, bankfull width, and catchment area, were not significantly different among flow durations and harvest conditions (Table 1), but were positively correlated with axis 1 (Table 4). Percent big- and % small-tree canopy were significantly higher at forested than at clearcut streams and were positively correlated with axis 1, whereas % slash was significantly greater at clearcut than at forested streams and was negatively correlated with axis 1 (Tables 1, 4). Riparian variables that were higher at forested than at clearcut streams were negatively correlated with axis 2 and included % big- and % small-tree canopy, stand age, and stream % cover. In contrast, % slash was positively correlated with axis 2 (Tables 1, 4). Mean seasonal water temperature was negatively correlated with axis 1 and was positively correlated with axis 3 (Table 4).

Indicator species analyses identified taxa that were indicators of particular harvest conditions or flow durations within each season. Of the 12 indicator taxa for the clearcut condition, 1 was Ephemeroptera, 4 were Trichoptera, 2 were Plecoptera, and 5 were Diptera; however, only Chironomidae and Psychodidae were common indicators across all seasons (Table 5). No taxa were indicators for the forested condition in any season (Table 5). In general, flow duration was not a strong influence on the composition of insect assemblages, but *Wormaldia*, Scirtidae, *Ostrocerca*, and *Sweltsa* had high % perfect indication for intermittent flow duration in both summer and spring (Table 5). Only *Dolophilodes* was an indicator of perennial flow duration in autumn.

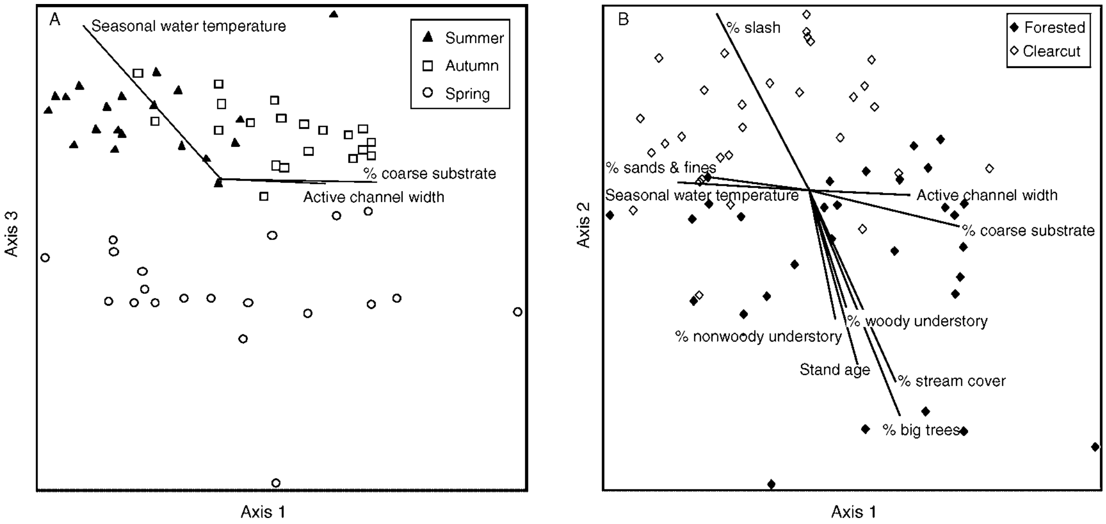

FIG. 6. Nonmetric multidimensional scaling (NMS) ordination biplots of emergent aquatic insect assemblages sampled from 20 headwater streams. Plots include vector overlays of environmental variables significantly correlated with NMS axes. A.—Axes 1 ($R^2 = 0.34$) and 3 ($R^2 = 0.24$), with sites coded by season (summer, autumn, and spring). B.—Axes 1 and 2 ($R^2 = 0.31$), with sites coded by harvest condition (forested vs clearcut).

Discussion

Effect of harvest condition on insect emergence rates

Clearcut logging of headwater stream catchments appeared to increase total insect emergence rates and to alter assemblage composition of aquatic insects emerging from both perennial and intermittent streams in the Central Oregon Coast Range. Logging activities that reduce canopy shading in streams with light-limited primary production increases algal biomass and ultimately leads to higher densities of benthic macroinvertebrates (Murphy et al. 1981, Hawkins et al. 1982, Noel et al. 1986). A 2- to 6-fold increase in benthic invertebrate density has been observed when autochthonous production increases (Murphy et al. 1981, Noel et al. 1986). Taxa that respond quickly after the food base is altered often have short generation times that facilitate rapid population increases when conditions are ideal (Newbold et al. 1980, Wallace and Gurtz 1986), and these changes are reflected in higher emergence rates of adults. Thus, the greater number of adult aquatic insects emerging from clearcut than from forested streams was consistent with patterns observed in benthic collections from other low-order streams.

Multivoltine taxa generally have short generation times and are efficient colonizers. Thus, they can increase quickly in abundance when conditions are favorable. Multivoltine insects, like Chironomidae and *Baetis*, commonly respond quickly to canopy reduction with increased density (Wallace and Gurtz 1986, Brown et al. 1997). In our study, emergence rates of Chironomidae were greater from clearcut than from forested streams. However, *Baetis* was encountered infrequently and emergence rates did not differ between harvest conditions.

Emergence rates of univoltine insects also were greater from clearcut than from forested streams. Univoltine insects develop within 1 year, but they can have highly flexible life cycles. Factors such as photoperiod, food quantity, food quality, water temperature, O_2 concentration, and stream drying can change the durations of life cycles of univoltine Plecoptera and Ephemeroptera (Dieterich 1992, Dieterich and Anderson 1995, Williams 1996). In our study, emergence rates of univoltine *Zapada* and *Moselia infuscata* were greater from clearcut than from forested streams in autumn and spring, respectively. Emergence rates of univoltine *Wormaldia* were greater from clearcut than from forested streams in all seasons.

Effects of harvest condition on assemblage composition

In many studies of the effects of logging, richness of benthic insect assemblages was not affected by the reduction in canopy cover (Duncan and Brusven 1985, Carlson et al. 1990). Changes in diversity were driven primarily by increases in abundance rather than by loss of species as long as channel morphology and sediment loads did not change substantially following logging (Carlson et al. 1990, Brown et al. 1997). However, in our study, taxon diversity was greater at clearcut than at forested streams in all seasons. Most of the taxa contributing to the differences in diversity

TABLE 4. Spearman's correlation coefficients (r) for correlations between physical-habitat variables and ordination axes derived from nonmetric multidimensional scaling of macroinvertebrate emergence data. Only relationships with $|r| > 0.3$ are shown. $^{A} = p < 0.01$, $^{B} = p < 0.0001$.

Physical-habitat variable	Axis 1	Axis 2	Axis 3
Stream			
Active channel width	0.482^{B}		
Bankfull width	0.389^{A}		
% sand and fines	-0.472^{B}		
% small gravel, sand, and fines	-0.416^{A}		
% coarse substrate	0.571^{B}		
% organic matter	-0.478^{B}		
Stream % cover	0.383^{A}	-0.551^{B}	
Catchment area	0.459^{B}		
Mean seasonal water temperature	-0.549^{B}		0.618^{B}
Riparian			
% big-trees canopy	0.428^{B}	-0.688^{B}	
% small-trees canopy	0.456^{B}	-0.590^{B}	
% nonwoody understory		-0.392^{A}	
% woody understory		-0.480^{B}	
% nonwoody ground cover		-0.487^{B}	
% slash	-0.412^{A}	0.623^{B}	
Stand age		-0.607^{B}	

were rare and somewhat unique to particular streams; i.e., they were found at only 1 or 2 of the clearcut streams. Four of the taxa that were unique to clearcut streams were found at ≥5 of the 10 clearcut sites. However, many of the taxa that emerged only from clearcut streams were present in the benthos at forested streams despite their absence from the emergence traps (Banks 2005). Thus, it is likely the taxa contributing to higher taxon richness at clearcut streams were present in the clearcut streams before logging and might be emerging at different times from clearcut than from forested streams because of changes in habitat conditions following logging.

Previous studies of logging impacts reported a shift in the predominant functional feeding group from shredders to scrapers within a year after tree harvest reduced shading from the riparian canopy (e.g., Wallace and Gurtz 1986, Stone and Wallace 1998). However, very few scrapers emerged during our study, and we found no evidence of the expected shift in functional feeding group composition based on harvest condition. Several explanations exist for these unexpected results. First, scrapers might not have been collected in the emergence traps because our sampling periods did not coincide with scraper emergence periods. Dieterich et al. (1997) found a distinct sequence of emergence in laboratory rearing studies and in field collections of aquatic insects from Oregon Coast Range headwaters. Emergence of shredders peaks in April, emergence of scrapers occurs in late April and early May, and collector emergence peaks in June. Progar and Moldenke (2002) found similar temporal sequences in functional feeding group composition of aquatic insects emerging from headwater streams in the Cascade and Coast ranges of western Oregon. Based on patterns in these studies, we think it unlikely that the absence of scrapers from our collections was an artifact of sampling period because our sampling periods encompassed the times during April and early May when highest peaks in scraper emergence had been documented in our geographic area (Dieterich et al. 1997, Progar and Moldenke 2002). Second, slash that remained in or around the streams after logging might have provided sufficient shade to

TABLE 5. Taxa that were significant indicators for particular harvest-condition or flow-duration treatments ($p < 0.05$). Indicator values (in parentheses) are % indication of high faithfulness and exclusivity for a particular harvest condition (clearcut or forested) or flow duration (perennial or intermittent). C = Coleoptera, D = Diptera, E = Ephemeroptera, P = Plecoptera, T = Trichoptera.

Order	Taxon	Summer	Autumn	Spring
E	*Ameletus*	Clearcut (60)		Clearcut (71)
D	Psychodidae	Clearcut (68)	Clearcut (70)	Clearcut (61)
D	Chironomidae	Clearcut (61)	Clearcut (63)	Clearcut (61)
T	*Lepidostoma*	Clearcut (78)		
D	*Dolichocephala*	Clearcut (60)		Clearcut (70)
C	Scirtidae	Intermittent (43)		
T	*Wormaldia*	Intermittent (72)		Clearcut (64)
P	*Despaxia augusta*		Clearcut (65)	
D	Ceratopogonidae		Clearcut (66)	
T	*Dolophilodes*		Clearcut (50)	Perennial (57)
P	*Zapada*		Clearcut (75)	
D	Tipulidae		Clearcut (71)	
T	*Homoplectra*			Clearcut (50)
P	*Sweltsa*			Intermittent (84)
P	*Ostrocerca*			Intermittent (66)

suppress scraper responses to riparian tree harvest. This effect has been noted in other studies of headwater streams in the Pacific Northwest (Cole et al. 2003, Haggerty et al. 2004). Last, finer-level taxonomic resolution in our identifications of adult Chironomidae would have allowed us to assign them to functional feeding groups and might have revealed more subtle differences in functional feeding group composition between flow durations or harvest conditions.

Effect of flow duration on assemblage composition

Progar and Moldenke (2002) reported that more insects emerged from flowing intermittent streams than from perennial streams. However, we found no differences in total insect emergence between intermittent and perennial streams during periods when intermittent channels retained surface flow, e.g., autumn sampling. Community assemblages at I-CUT streams were similar to assemblages at P-CUT streams. Moreover, numerous aquatic insects emerged from the study streams even when intermittent channels were dry on the surface in summer months. The streams probably retained substantial subsurface flow that kept substrates moist. Muchow and Richardson (2000) also collected true aquatic insects emerging from small streams during periods with no perceptible flow on the coast of British Columbia. After collecting year-round samples from Oregon Coast Range headwater streams, Dieterich (1992) concluded that the fauna of intermittent headwater streams resembles that of perennial headwater streams when duration of continuous flow is >4 to 5 mo during the year. Our study streams were dry for ≤4 mo and retained continuous surface flow for ≥8 mo. Thus, the results of our study corroborate the conclusions of Dieterich (1992).

Emergence rates of Plecoptera were higher at intermittent than at perennial streams in the spring. Muchow and Richardson (2000) observed that emergence rates of Plecoptera from summer-dry streams were as much as 2× greater than the emergence rates from perennial streams. Like Muchow and Richardson (2000), we collected more *Despaxia augusta*, a stonefly with a 2-y life cycle, at intermittent streams than at perennial streams even during summer, when channels were surface-dry. The occurrence and life-history pattern of *D. augusta* suggest that wetted sediments in intermittent streams with predictable drying cycles provide sufficient refugia from desiccation for some taxa even when there is no discernable surface flow.

Channel dimensions, substrate composition, and riparian vegetation probably were important controls on emergent aquatic insect assemblages in both intermittent and perennial headwater streams in each season. Sedimentation and reduced shade consequent to clearcut logging have strong effects on abundances and feeding guild structure of benthic macroinvertebrates (Murphy et al. 1981, Hawkins et al. 1982). Canopy reduction had a stronger effect on total abundance and guild structure than substrate character in Cascade Range streams (Murphy et al. 1981, Hawkins et al. 1982). The results of our NMS-ordination correlations indicate that both canopy reduction (i.e., lower stream % cover and % cover from big and small riparian trees at clearcut than at forested streams) and sedimentation (i.e., slightly higher % fines and sands at clearcut streams than at forested streams, higher % coarse substrate at P-FOR streams) were probably important influences on the composition of emergent insect assemblages in the headwaters of the Oregon Coast Range.

Harvest condition had more influence than flow duration on the composition of emergent insect assemblages. Our data indicate that assemblages from intermittent streams do not differ from assemblages at perennial streams, and assemblages from summer-dry clearcut streams are similar to assemblages at clearcut streams with continuous flow. Emergence of aquatic insects from intermittent streams when the streams were dry at the surface suggests that subsurface flow provided refugia for certain taxa under both clearcut and forested timber-harvest conditions. Taxa dependent on site-specific conditions created by logging, such as % slash or canopy opening, and taxa supported by subsurface habitats contributed to differences in assemblages between headwater streams flowing through clearcut and forested catchments.

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Literature Cited

Adams, P. W. 2007. Policy and management for headwater streams in the Pacific Northwest: synthesis and reflection. Forest Science 53:104–118.

ARMITAGE, B. J., AND S. W. HAMILTON. 1990. Diagnostic atlas of the North American caddisfly adults. Caddis Press, Athens, Alabama.

BANKS, J. L. 2005. Influences of clearcut logging on macroinvertebrates in perennial and intermittent headwaters of the Central Oregon Coast Range. MS Thesis, Oregon State University, Corvallis, Oregon.

BLICKLE, R. L. 1979. Hydroptilidae (Trichoptera) of America north of Mexico. New Hampshire Agricultural Experiment Station Bulletin 509. New Hampshire Agricultural Experiment Station, University of New Hampshire, Durham, New Hampshire.

BORROR, D. J., C. A. TRIPLEHORN, AND N. F. JOHNSON. 1989. An introduction to the study of insects. 6th edition. Saunders College Publishing, Orlando, Florida.

BROWN, A. V., Y. AGUILA, K. B. BROWN, AND W. P. FOWLER. 1997. Responses of benthic macroinvertebrates in small intermittent streams to silvicultural practices. Hydrobiologia 347:119–125.

CARLSON, J. Y., C. W. ANDRUS, AND H. A. FROEHLICH. 1990. Woody debris, channel features, and macroinvertebrates of streams with logged and undisturbed riparian timber in northeastern Oregon, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 47:1103–1111.

COLE, M. B., K. R. RUSSELL, AND T. J. MABEE. 2003. Relation of headwater macroinvertebrate communities to in-stream and adjacent stand characteristics in managed second-growth forests of the Oregon Coast Range mountains. Canadian Journal of Forest Research 33:1433–1443.

CUMMINS, K. W., AND M. J. KLUG. 1979. Feeding ecology of stream invertebrates. Annual Review of Ecology and Systematics 10:147–172.

DENNING, D. G. 1956. Trichoptera. Pages 237–271 *in* R. L. Usinger (editor). Aquatic insects of California. University of California Press, Berkeley, California.

DIETERICH, M. 1992. Insect community composition and physico-chemical processes in summer-dry streams of western Oregon. PhD Thesis, Oregon State University, Corvallis, Oregon.

DIETERICH, M., AND N. H. ANDERSON. 1995. Life cycles and food habits of mayflies and stoneflies from temporary streams of western Oregon. Freshwater Biology 34:47–60.

DIETERICH, M., N. H. ANDERSON, AND T. M. ANDERSON. 1997. Shredder-collector interactions in temporary streams of western Oregon. Freshwater Biology 38:387–393.

DUFRENE, M., AND P. LEGENDRE. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345–366.

DUNCAN, W. F. A., AND M. A. BRUSVEN. 1985. Benthic macroinvertebrates in logged and unlogged low-order southeast Alaskan streams. Freshwater Invertebrate Biology 4:125–132.

ENGLAND, L. E., AND A. D. ROSEMOND. 2004. Small reductions in forest cover weaken terrestrial–aquatic linkages in headwater streams. Freshwater Biology 49:721–734.

GOMI, T., R. C. SIDLE, M. D. BRYANT, AND R. D. WOODSMITH. 2001. The characteristics of woody debris and sediment distribution in headwater streams, southeastern Alaska. Canadian Journal of Forest Research 31:1386–1399.

GORDON, A. E. 1974. A synopsis and phylogenetic outline of the Neartic members of *Cheumatopsyche*. Proceedings of the Academy of Natural Sciences of Philadelphia 126: 117–160.

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

HAGGERTY, S. M., D. P. BATZER, AND C. R. JACKSON. 2002. Macroinvertebrate assemblages in perennial headwater streams of the Coastal Mountain range of Washington, U.S.A. Hydrobiologia 479:143–154.

HAGGERTY, S. M., D. P. BATZER, AND C. R. JACKSON. 2004. Macroinvertebrate response to logging in coastal headwater streams of Washington, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 61:529–537.

HARR, R. D., W. C. HARPER, AND J. T. KRYGIER. 1975. Changes in storm hydrographs after road building and clear-cutting in the Oregon Coast Range. Water Resources Research 11:436–444.

HAWKINS, C. P., M. L. MURPHY, AND N. H. ANDERSON. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. Ecology 63:1840–1856.

HERLIHY, A. T., W. J. GERTH, J. LI, AND J. L. BANKS. 2005. Macroinvertebrate community response to natural and forest harvest gradients in western Oregon headwater streams. Freshwater Biology 50:905–919.

KAUFMANN, P. R., P. LEVINE, E. G. ROBISON, C. SEELIGER, AND D. V. PECK. 1999. Quantifying physical habitat in wadeable streams. EPA/620/R-99/003. Office of Research and Development. US Environmental Protection Agency, Washington, DC.

MAGURRAN, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey.

MCALPINE, J. F., B. V. PETERSON, G. E. SHEWELL, H. J. TESKEY, J. R. VOCKEROTH, AND D. M. WOOD. 1981. Manual of Nearctic Diptera. Volumes 1 and 2. Biosystematics Research Institute, Ottawa, Ontario, Canada.

MCCUNE, B., AND J. B. GRACE. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

MERRITT, R. W., AND K. S. CUMMINS, (EDITORS). 1996. An introduction to the aquatic insects of North America. 3rd edition. Kendall/Hunt Publishing, Dubuque, Iowa.

MEYER, J. L., AND J. B. WALLACE. 2001. Lost linkages and lotic ecology: rediscovering small streams. Pages 295–317 *in* M. C. Press, N. J. Huntley, and S. Levin (editors). Ecology: achievement and challenge. Blackwell Scientific, Oxford, UK.

MOORE, R. D., AND J. S. RICHARDSON. 2003. Progress towards understanding the structure, function, and ecological significance of small stream channels and their riparian zones. Canadian Journal of Forest Research 33:1349–1351.

MUCHOW, C. L., AND J. S. RICHARDSON. 2000. Unexplored diversity: macroinvertebrates in coastal British Columbia headwater streams. Pages 503–506 *in* L. M. Darling (editor). Proceedings of a Conference on the Biology and

Management of Species and Habitats at Risk, Kamloops, British Columbia, 15–19 February 1999. Volume 2. British Columbia Ministry of Environment, Lands and Parks, Victoria, British Columbia, and University College of the Cariboo, Kamloops, British Columbia, Canada.

MURPHY, M. L., AND J. D. HALL. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 38:137–145.

MURPHY, M. L., C. P. HAWKINS, AND N. H. ANDERSON. 1981. Effects of canopy modification and accumulated sediment on stream communities. Transactions of the American Fisheries Society 110:469–478.

NAIMAN, R. J., H. DECAMPS, AND M. POLLOCK. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3:209–212.

NAKANO, S., AND M. MURAKAMI. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences of the United States of America 98:166–170.

NEWBOLD, J. D., D. C. ERMAN, AND K. B. ROBY. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. Canadian Journal of Fisheries and Aquatic Sciences 37:1076–1085.

NINMO, A. P. 1987. The adult Arctopsychidae and Hydropsychidae (Trichoptera) of Canada and adjacent United States. Quaestiones Entomologicae 23:1–189.

NOEL, D. S., C. W. MARTIN, AND C. A. FEDERER. 1986. Effects of clearcutting in New England on stream macroinvertebrates and periphyton. Environmental Management 10: 661–670.

ODF (OREGON DEPARTMENT OF FORESTRY). 2004. Forest Practices Administrative Rules and Forest Practices Act, Chapter 629. Forest Practices Administration, Oregon Department of Forestry, Salem, Oregon. (Available from: http://egov.oregon.gov/ODF/PRIVATE_FORESTS/docs/fp/FPArulebk.pdf)

PRICE, K., A. SUSKI, J. MCGARVIE, B. BEASLEY, AND J. S. RICHARDSON. 2003. Communities of aquatic insects of old-growth and clearcut coastal headwater streams of varying flow persistence. Canadian Journal of Forest Research 33:1416–1432.

PROGAR, R. A., AND A. R. MOLDENKE. 2002. Insect production from temporary and perennially flowing headwater streams in western Oregon. Journal of Freshwater Ecology 17:391–407.

ROSS, H. H. 1956. Evolution and classification of the mountain caddis flies. University of Illinois Press, Urbana, Illinois.

SIDLE, R. C., Y. TSUBOYAMA, S. NOGUCHI, I. HOSADA, M. FUJIEDA, AND T. SHIMIZU. 2000. Stormflow generation in steep forested headwaters: a linked hydrogeomorphic paradigm. Hydrological Processes 14:369–385.

STOCKNER, J. G., AND K. S. SHORTREED. 1976. Autotrophic production in Carnation Creek, a coastal rainforest stream on Vancouver Island, British Columbia. Journal of the Fisheries Research Board of Canada 33:1553–1563.

STONE, M. K., AND J. B. WALLACE. 1998. Long-term recovery of a mountain stream from clear-cut logging: the effects of forest succession on benthic invertebrate community structure. Freshwater Biology 39:151–169.

TAYLOR, G. H., AND C. HANNAN. 1999. The climate of Oregon: from rain forest to desert. Oregon State University Press, Corvallis, Oregon.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130–137.

WALLACE, J. B., AND M. E. GURTZ. 1986. Response of *Baetis* mayflies (Ephemeroptera) to catchment logging. American Midland Naturalist 115:25–41.

WHILES, M. R., AND J. B. WALLACE. 1995. Macroinvertebrate production in a headwater stream during recovery from anthropogenic disturbance and hydrological extremes. Canadian Journal of Fisheries and Aquatic Sciences 52: 2402–2422.

WILLIAMS, D. D. 1996. Environmental constraints in temporary fresh waters and their consequences for the insect fauna. Journal of the North American Benthological Society 15:634–650.

WIPFLI, M. S., AND D. P. GREGOVICH. 2002. Invertebrates and detritus export from fishless headwater streams in southeastern Alaska: implications for downstream salmonid production. Freshwater Biology 47:957–970.

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