Riparian canopy type and management history control forest-to-stream plant litter fluxes

Trent M. Hoover, Xavier Pinto, and John S. Richardson

Department of Forest Sciences, 3041-2424 Main Mall, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4

Corresponding author: Trent M. Hoover
Telephone: 604-822-1845
Fax: 604-822-9102
Email: trent.hoover@gmail.com

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Abstract

Terrestrial plant litter is a key basal component of many forest stream food webs. We measured seasonal changes in plant litter fluxes to 20 small streams flowing through temperate rain forests in south-western British Columbia to determine how riparian forest type and riparian management history influence organic carbon dynamics in these systems. Plant litter fluxes varied among streams with recently clearcut riparian zones, riparian reserve strips, coniferous riparian forests, and deciduous-dominated riparian forests. In general, differences among riparian forest types were most pronounced in the summer, when fluxes of plant litter from clearcut riparian forests were significantly less than those from riparian reserve strips and coniferous riparian forests, and those from deciduous-dominated riparian forests were less than those from riparian reserve strips. Fluxes of plant litter also varied among seasons (spring < summer < autumn). Fluxes of leaf litter were similar in riparian reserve strips and conifer-dominated forests of similar age without adjacent logged areas, indicated that this forest management technique acts to maintain this ecosystem process. The removal of riparian forests (clearcutting) dramatically increased light availability while reducing leaf litter inputs, suggesting that these forest stream systems may shift from net heterotrophy to net autotrophy. However, subsequent and relatively rapid re-establishment of riparian canopies limited light availability and increased plant litter fluxes, indicating that these streams likely return to a state of net heterotrophy after only a few years. As riparian forest stand age increased, inputs shifted from broadleaf (angiosperm leaf) inputs to coniferous inputs, indicating a possible long-term decrease in the lability and value of the leaf litter resources available to stream consumers.

Introduction

Terrestrially-derived plant detritus is a critical resource upon which the food webs of forest streams are based (Fisher and Likens, 1973; Hall et al., 2001). Intense shading by riparian canopies limits autochthonous primary production (e.g. Hill, Ryon, and Schilling, 1995; Kiffney et al., 2003), while substantial inputs of plant litter from both trees and riparian understory plants ensure that forest stream systems are predominantly heterotrophic (Hall et al., 2001, Battin et al., 2008). As light and leaf litter are limiting resources for the algal-based and detritus-based components of stream food webs, the removal or reduction of riparian canopies can dramatically affect the structure and function of stream ecosystems (Kiffney et al., 2003; Gjerlov and Richardson, 2004). Thus quantifying the spatial and temporal dynamics of critical ecosystem processes such as the production and cross-system flux of plant litter is necessary to understand the food web dynamics and ecological functioning of these systems.

Structural attributes of forest stands – including tree species, the amounts of woody debris, leaf area, canopy density, and the distribution of live trees –
undergo a sequence of characteristic changes after a forest stand is established and develops after a disturbance (Frazer et al., 2000). Many of these stand attributes also determine the amount and type of leaf litter falling from the canopy. However, while litterfall from riparian forests generally exceeds that of upland forests (Xiong and Nilsson, 1997), successional changes in riparian forest-to-stream fluxes of plant detritus are poorly established (but see O'Keefe and Naiman, 2006). A combination of natural (e.g. forest fire) and human-induced (e.g. logging) disturbances have created substantial spatial variation in the age of riparian forests, especially those in north-western North America (Frazer et al. 2000). Although abiotic characteristics (e.g. light availability) that are critical determinants of stream food webs can change dramatically after riparian forests are removed by logging, it is less well known how long these effects persist. To understand how long-term, landscape-scale shifts in riparian canopy development and species composition influence the balance between autochthonous and allochthonous production in streams, information on successional changes in these ecosystem attributes is required.

Alder (Alnus spp.) is a common riparian hardwood tree species, especially along streams flowing through early- to mid-successional temperate rain forests of western North America (Richardson et al. 2005). Due to their low C:N content, alder leaves are readily colonised by bacteria and fungi upon entry into the stream, and are subsequently rapidly broken down by stream invertebrates (Webster and Benfield, 1986; Piccolo and Wipfli, 2002; Richardson et al., 2005). Furthermore, the leaves of hardwood tree species such as alder are retained rapidly in streams, especially where coarse bed material or woody debris is present (Hoover et al. 2006). As such, leaf litter of this type represents an accessible, labile, and valuable resource type. In contrast, many conifer needles are tough, have high C:N contents, contain protective chemical compounds (including waxy cuticles), and are less-readily retained than leaves (Webster and Benfield, 1986; Quinn et al., 2000; Lopez et al., 2001; Richardson et al., 2005; Trent Hoover, unpublished data), and thus represent a low-quality food resource to stream detritivores. However, little is known about the spatial and temporal (seasonal and successional time-scales) variation in the relative importance of deciduous and coniferous litter types in landscapes where both tree types are present in riparian canopies.

In this study we examined the extent to which riparian forest type (coniferous vs. broadleaf) and post-harvest riparian management strategy (riparian reserve vs. clearcut) influence the flux of terrestrial plant litter into the forest streams of a coastal mountainous region of south-western British Columbia, Canada. We measured the types, amounts, and seasonal changes in plant litter (PL) inputs to 20 streams and asked two distinct questions (1) does the amount or composition of forest-to-stream fluxes of PL vary among riparian forest types and among seasons, and (2) how does forest successional stage determine three critical ecosystem attributes – PL fluxes, PL composition, and availability of light – that
influence the food webs of small streams. These questions were addressed in a series of streams whose riparian canopies varied in age from 1 to 144 years old.

Methods

Study Area

Forest-to-stream fluxes of riparian plant material were measured in 20 small streams (first- to third-order) located in the southern half of the Malcolm Knapp Research Forest (MKRF, 49.272°N, 122.586°W), located north of Maple Ridge, British Columbia (Fig. 1). The MKRF lies within the coastal Western Hemlock forest which is typically dominated by western hemlock (Tsuga heterophylla (Raf.) Sarg.), Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) and western redcedar (Thuja plicata Donn). Forest harvesting activities have been ongoing in the MKRF since the 1920s, and the riparian zones of streams logged in recent decades are often dominated by stands of red alder (Alnus rubra Bong.). The study area has a characteristically wet mild climate, with wet winters, dry summers, and mean annual precipitation of 2194 mm. Mean annual air temperature is 9.6 °C, ranging from a mean monthly high of 22.7 °C (July) to a mean monthly low of -0.5 °C (January). Elevation at the study sites ranged from 60 – 350 m above sea level.

Forest-to-stream fluxes of plant litter

Spatial and temporal variation in forest-to-stream plant litter fluxes were measured seasonally (May, July, and October 2007) in 20 streams whose riparian zones differed with respect to dominant tree type and riparian management history.

Seasonal variation in forest-to-stream fluxes of plant litter were measured in four riparian canopy types (1) clear-cut logged (CC), with both deciduous and coniferous riparian trees removed, (2) older-successional stage coniferous forests within riparian reserve strips (RRS) between 10m and 30m wide, adjoining clear-cut areas, (3) dominated by deciduous trees (DEC), primarily red alder, and (4) older-successional stage coniferous forests (CON) dominated by a limited number of coniferous tree species, primarily Western Hemlock (Tsuga heterophylla), Douglas-fir (Pseudotsuga menziesii), and western red-cedar (Thuja plicata) (Table 1).

Clear-cut riparian areas were logged between 1 and 8 years prior to the study. As such the degree of riparian vegetation re-growth differed substantially among clearcut sites and ranged from those dominated by logging slash and limited re-growth of shrubs and grasses (CC3) to sites that had extensive re-growth of riparian plants including red alder and coniferous tree saplings (up to 4 m in height; CC1). Timber harvesting methods at two recently clearcut sites (CC4 and
CC5) had left shrubs and small riparian trees intact, preserving some of the canopy cover over those streams. All five RRS sites examined were created 9Y prior to the study as part of an extensive experiment designed to test the efficacy of riparian reserve strips in protecting headwater stream ecosystems (see Kiffney et al. 2003 for a description of the project). As such, riparian reserve strips varied in width from 10 to 30 m.

Due to existing variation in stand age, the stream sites included in the study also represent a chronosequence of riparian forest development. Riparian forest stand ages in the study area ranged from 1 – 144Y old (Table 1), permitting an examination of successional changes in forest type and plant litter fluxes to streams. Stand ages for all CC, RRS, and CON sites and four DEC sites were obtained from the MKRF GIS database (2009); data for DEC1 (South Creek) was not available on the MKRF database, and so stand data for this site was obtained by coring three alder trees at the site and recording the age of the oldest tree. Stand composition for all RRS and CON sites were obtained from the MKRF database, while stand composition data of CC and DEC sites were obtained by estimating the percent coverage of each tree species at each site using an upward-looking gridded quadrat (45° view angle).

Plant litter fluxes were measured at all 20 sites in spring (May 11 – 28), summer (July 10 – 27), and autumn (October 9 – 18) using leaf litter trays (26 cm x 52 cm plastic trays lined with 1 mm fibreglass screen) placed at the stream’s edge. During each sampling period, two trays were placed several meters apart within each 30 m study reach and left for either three or four days. The samples were then collected, and the contents of the two trays were combined to produce a single sample. Plant litter samples were collected twice each season at each site (20 sites x 2 replicates x 3 seasons = 120 samples). Data from the two within-season replicates were averaged to obtain a single seasonal value prior to analysis.

In the lab, litter collected in each sample was sorted into six different functional categories (1) coniferous needles (including western hemlock and Douglas-fir), (2) red-cedar fronds, (3) red alder leaves, (4) deciduous broadleaves other than red alder (including salmonberry (Rubus spectabilis Pursh) and vine maple (Acer circinatum Pursh)), (5) fruits and flowers, and (6) branches and wood fragments (includes bark, moss, and lichen from branches and boles). Sorted plant litter samples were then dried at 60°C for 24 hours to determine dry mass, which was then used to calculate the plant litter flux (mass m⁻² day⁻¹) of each of the six categories of plant litter for each site.

**Gap Analysis**

To quantify canopy structure hemispherical photos were taken above the stream surface at each site using a Nikon Coolpix equipped with a Nikon Fisheye Converter. Three photos were taken along the 30 m reach (at 0, 15, and 30 m)
at each site once in each season. For each photo the camera was mounted and
levelled on a tripod approximately 0.3 m above the water surface. Generally
photos were taken on overcast days to provide uniform lighting of the canopy.

Canopy images were analysed using the Gap Light Analyzer 2.0 developed by
Frazer, Canham and Lertzman (1999). The Gap Light Analyzer was used to
extracts canopy structure data for each photo, including percent canopy
openness. It is important to note that even in instances where canopies were
essentially completely open above the stream (as in the case of recent clearcuts
that removed all trees and shrub cover) canopy openness values of
approximately 60% were still obtained due to the presence of streamside
vegetation.

Statistical Analyses

Total PL fluxes were calculated were calculated by summing the daily PL fluxes
of all plant material types collected. Among-season variation in total PL flux was
examined using a 3 x 4 (season x riparian forest type) repeated-measures
ANOVA. Subsequent post-hoc between-season specific comparisons were
made using paired t-tests. One-way ANOVA was used to test for within-season
differences in total PL fluxes among riparian forest types, with Tukey’s HSD used
for specific post-hoc comparisons.

Within-season comparisons of among-treatment and among-PL type
comparisons of PL fluxes were made using 4 x 6 (riparian forest type x PL type)
ANOVA. The proportion of inputs composed of angiosperm leaves (pAL) was
calculated as (red alder leaf flux + other broadleaf flux) / (all non-wood PL fluxes).
Comparisons of pAL were made using a 3 x 4 (season x riparian forest type)
ANOVA. Within-season comparisons of pAL were made using one-way ANOVA,
with Tukey’s HSD used to test for specific post-hoc comparisons.

Piece-wise linear regression was used to evaluate the changes in red alder leaf
and total PL inputs that occur with stand age; due to the successional changes in
riparian tree assemblages that occur after logging (Hibbs and Bower 2001),
separate regression analyses were conducted for stand ages < 40Y and > 40Y
old. Non-linear regressions (fit to the three-parameter sigmoidal model y = a / (1
+ e ^ (-(x – x_0) / b))) were used to examine changes in coniferous inputs (both
conifer needles and redcedar fronds) with stand age. ANOVA was used to test
the significance of all regression analyses. Logging operations in two clearcut
sites (CC4 and CC5) did not remove riparian shrubs and small broadleaf trees
(e.g. vine maple, bigleaf maple); these two sites were not included in regression
analyses as these harvesting practices produce a different successional
trajectory and thus likely different types of PL inputs to streams.
Non-linear regression analyses (data fit to power model $y = ax^b$) were used to relate stand age to variation in canopy openness. Separate regression analyses were conducted for each season.

Analyses were conducted in Systat 10 (SPSS, Chicago, Illinois).

**Results**

The amount and type of PL entering streams varied substantially among streams with recently clearcut (CC), riparian reserve strip (RRS), red alder-dominated (DEC) and conifer-dominated (CON) riparian forests as well as among seasons (Fig. 2). Total forest-to-stream fluxes of PL (all types of PL summed) differed among the four types of riparian forests ($F(3,16) = 3.25, P = 0.05$) and among seasons ($F(2,15) = 50.86, P < 0.001$). Total PL fluxes in summer were significantly greater than those in spring (mean difference = 0.77 (SD ± 0.69) g m$^{-2}$ day$^{-1}$, $t(19) = 5.00, P < 0.001$), while total PL fluxes in autumn were significantly greater than those in summer (mean difference = 2.22 (SD ± 2.38) g m$^{-2}$ day$^{-1}$, $t(19) = 4.19, P < 0.001$) (i.e. spring < summer < autumn).

Interestingly, total PL fluxes were not significantly different among the four riparian forest types in spring ($F(3,16) = 1.73, P = 0.20$) or autumn ($F(3,16) = 1.65, P = 0.22$). In summer, however, total PL fluxes were significantly different among treatments ($F(3,16) = 12.49, P < 0.001$), where CC < CON ($P = 0.02$), CC < RRS ($P < 0.001$), DEC < RRS ($P = 0.004$), all other $P > 0.05$ (Fig. 2).

**Within-season comparisons**

In spring, there was no difference in PL fluxes among riparian forest types ($F(3,96) = 1.96, P = 0.13$), although there was a significant difference in input rates among the six PL types ($F(5,96) = 11.97, P < 0.001$) (Fig. 2). The interaction between riparian forest type and PL type was significant ($F(15,96) = 4.26, P < 0.001$). In spring, PL fluxes were low in all riparian forest types (Fig. 2). Inputs of PL to CON and RRS forest streams were similar and primarily consisted of conifer needles, while in DEC sites inputs were primarily flowers and fruits (Fig. 2). Conifer needle inputs were very limited in CC sites, while flower and fruit inputs were low in CON sites.

In summer, however, there were significant differences in PL fluxes among riparian forest types ($F(3,96) = 1.16, P < 0.001$), PL types ($F(5,96) = 5.38, P < 0.001$); the interaction between forest type and PL type was also significant ($F(15,96) = 9.93, P < 0.001$). Summertime inputs of PL to streams in CON and RRS forests were again primarily composed of conifer needles, while angiosperm leaves dominated inputs in CC sites (inputs primarily non-alder leaves) and DEC forests (inputs were both alder and non-alder leaves) (Fig. 2). Conifer needle inputs were again very limited in CC sites.
In autumn, as in spring, there was no difference in PL fluxes among riparian forest types (F(3,96) = 1.79, P = 0.16), although there was a significant difference in input rates among the six PL types (F(5,96) = 4.78, P = 0.001); the interaction between riparian forest type and PL type was significant (F(15,96) = 4.49, P < 0.001). Autumnal PL fluxes from CON and RRS forests were primarily composed of cedar fronds; fluxes of conifer needles from CON and RRS riparian canopies were notably less than in summer. Inputs of alder leaves dominated fluxes in DEC sites, while PL fluxes to CC streams were almost composted almost entirely of non-alder angiosperm leaves (e.g. vine maple, etc.).

Composition of plant litter fluxes

The proportion of inputs comprised of angiosperm leaves (pAL) varied among seasons (F(2,48) = 8.63, P = 0.001) and among riparian forest types (F(3,48) = 15.48, P < 0.001), with a significant interaction between season and forest type (F(6,48) = 2.57, P = 0.031). In spring, pAL was generally low (Fig. 3) but not significantly different among riparian forest types (F(3,16) = 1.01, P = 0.41). By summer, differences in pAL among riparian forest types had become significant (F(3,16) = 5.51, P = 0.009). Mean pAL had increased dramatically for DEC and CC riparian forests (Fig. 3); pAL of DEC forests was significantly greater than both RRS and CON forests (P = 0.048 and 0.024). By autumn, differences in pAL had become even more pronounced among riparian forest types (F(3,16) = 11.67, P < 0.001). PL entering streams in DEC forests was almost entirely composed of angiosperm leaves (Fig. 3); pAL of DEC and CC sites was significantly greater than both RRS (P = 0.003, 0.001) and CON forests (P = 0.043, 0.007).

Successional chronosequence, plant litter fluxes, and canopy openness

In the temperate rainforest streams examined in this study, the successional chronosequence of riparian forests influenced both the amount and composition of PL fluxes to streams (Fig. 4). In general, total PL fluxes (all plant litter types summed) increased with stand age (Fig. 4) until riparian forests were approximately 35Y old (R² = 0.75, F(1,5) = 11.9, P = 0.026). There was no consistent change in total PL flux as stand age increased further (R² = 0.042, F(1,6) = 0.021, P = 0.89). The general increase in PL fluxes in the first 35Y after clearcutting were largely attributable to an increase in red alder leaf inputs (R² = 0.88, F(1,5) = 31.9, P = 0.0048), followed by a subsequent decline in this PL type with stand age (Fig. 4). In contrast, fluxes of coniferous material (both conifer needles and redcedar fronds) were very low in young forests, and increased gradually until stand ages > 80Y (conifer needles R² = 86, F(2,12) = 31.5, P < 0.0001; redcedar fronds R² = 28, F(2,12) = 1.9, P = 0.20). In older stands (i.e. > 83Y), PL inputs were almost entirely composed of coniferous material, with the exception of Spring Creek (DEC3). Spring Creek was one of the widest streams examined in the study (mean channel width = 3.9 m), a factor which may have
permitted riparian red alder trees to persist despite the presence of dense stands of western hemlock adjacent to the stream.

Canopy openness declined rapidly with stand age (Fig. 5), regardless of season of measurement (spring $R^2 = 0.87$, $F(1,12) = 75.3$, $P < 0.0001$; summer $R^2 = 0.90$, $F(1,12) = 103.0$, $P < 0.0001$; autumn $R^2 = 0.91$, $F(1,12) = 115.0$, $P < 0.0001$). Canopy openness was consistently greater in the autumn in relatively young riparian forests (stand age < 40Y). This was likely due the greater proportion of broadleaf tree species (e.g. red alder, cottonwood) and thus seasonal leaf loss (Fig. 2) at these sites. Canopy openness in RRS remnants of 80 – 88Y old forests (Fig. 5, inset panel) that had been created during logging 9Y prior to the study was similar to that of other moderately old riparian forests (83 – 88Y old) that had not experienced recent timber harvesting.

Discussion

The amounts and composition of plant litter inputs to the temperate rain forest streams in this study varied substantially among seasons and among riparian forest types (clearcut, riparian reserve strip, deciduous-dominated, and coniferous-dominated). Forest-to-stream fluxes of plant litter were greatest in the autumn and lowest in the spring. This pattern of seasonal variation in litterfall is common to many temperate regions (e.g. O'Keefe and Naiman, 2006). However, due to high retention rates, fast breakdown, and relatively high nutritional value (Richardson 1991; Lopez et al., 2001; Richardson et al. 2005), leaf litter that enters streams during the spring and summer months is generally thought to contribute substantially to nutrient cycling in benthic consumer communities, especially as it represents a continuous energy source during a period of resource limitation (Richardson 1991). In this study, plant litter entering streams in conifer-dominated forests consisted primarily of conifer needles (western hemlock and Douglas-fir), while inputs to deciduous-dominated streams originated from a wide variety of sources (conifer needles, alder leaves, other broadleaves). The greater leaf litter resource diversity in deciduous-dominated streams may enhance food web stability (Huxel and McCann, 1998), especially if it leads to greater consumer diversity (Kominoski et al. 2009).

Fluxes of plant litter to the streams in this study varied among seasons (spring < summer < autumn). Some invertebrate macroinvertebrates have high reproductive rates and short generation times, indicating that the population dynamics of these taxa are capable of tracking resource supply (Richardson 1991). Populations of these taxa would be expected to reach yearly maxima during the autumn in the streams studied. However, other invertebrate taxa have annual life cycles; the population dynamics of these taxa will be constrained by periods of limited resources. The clearcut streams in this study have very low supplies of plant litter during the spring, creating a 'resource bottleneck' that may limit the abundance and/or diversity of the detritivore communities in these
reaches. Kiffney, Richardson, and Bull (2004) found that the increases in solar fluxes and reductions in detrital inputs that result from logging riparian forests increased primary production, further shifting the community structure of invertebrate and vertebrate consumers.

One of the main differences between the plant litter fluxes reported here and those reported elsewhere (e.g. Xiong and Nilsson 1997) is that the fronds of western red-cedar constitute the largest fraction of inputs to streams in conifer-dominated stands (both with and without adjacent logged areas) in autumn. This supports the findings of Richardson (1992) who showed that autumnally-shed redcedar frond litter is known to comprise a large proportion of the total inputs to Pacific temperate coastal streams where this tree species is present. As such, this litter type is likely an important food resource for detritivores in these streams. However, very little is known about how it is utilised by the benthic community. Richardson et al. (2004) showed that the mean breakdown rate of redcedar litter was intermediate between that of red alder and western hemlock, and found that redcedar fronds supported a discrete subset of the benthic invertebrate community, especially in autumn. Although information is limited, this seems to indicate that redcedar represents an important resource for some invertebrate species.

Riparian reserves are designed to protect the ecological integrity of small streams. The degree to which they do so is dependent, in part, on reserve strip width. Kiffney et al. (2003) showed that photosynthetically active radiation, periphyton, and water temperature increased as reserve width (and protection generally) decreased (i.e. clearcut > 10 m buffer > 30 m buffer > control forest). In our study, total plant litter inputs to streams flowing through conifer-dominated forests and riparian reserve strips of similar stand age and tree species composition were similar, indicating that riparian reserves generally maintains detrital resource dynamics in these systems. Plant litter inputs may actually moderately increase in riparian reserve strip streams for several years after adjacent logging due to an increase in the growth of understory herbaceous plants. An increase in broadleaf inputs of this type was evident in the composition of plant litter inputs in this study, especially in the autumn. Moderate increases in both herbaceous inputs and autotrophic production by algae (Kiffney et al., 2003) may result in a localized increase in consumer abundance and diversity in streams flowing through reserve strips. In this study, plant litter inputs shifted from broadleaf (angiosperm leaf) inputs to coniferous inputs with riparian forest age, indicating a possible long-term decrease in the lability of the leaf litter resources available to stream consumers (see Webster and Benfield, 1986). Net litter inputs to streams in the study area may decrease further as riparian forests continue to age, as significant changes in canopy structure occur in the later stages of canopy development (150 – 200Y; Frazer et al., 2000).

The removal of riparian forests (clearcutting) dramatically increased light availability while reducing leaf litter inputs, suggesting that these forest stream
systems may shift from net heterotrophy to net autotrophy for a short period following timber harvesting. However, in some systems an almost complete reduction of canopy cover is not sufficient to produce a shift to net autotrophy. Bott et al. (2006) found that while autochthonous primary production was greater in meadow streams than forested streams, both stream types remained heterotrophic in all seasons measured. Regardless, the subsequent re-establishment of riparian canopies in the current study indicates that light levels decline and plant litter fluxes increase in only a few years, indicating that these streams likely rapidly return to a state of net heterotrophy. Forest streams with regenerating riparian forests may switch from a state of net autotrophy to one of net heterotrophy earlier where nutrient concentrations (and thus in-stream primary production) are low (Dodds 2007), where the riparian plant community is comprised of rapidly-growing species (Richardson et al. 2005), or where stream width (and hence area-to-edge ratio) is low (Bott et al. 2006).

Predicted climate changes for the temperate coastal regions of western North America are expected to produce drastically different distributions of conifer tree species (Hamann and Wang, 2006). Some of the most important conifer species in British Columbia are expected to decrease in frequency through loss of suitable habitat (e.g. *Abies lasiocarpa*, *Picea glauca*, and *Pinus contorta*), while hardwoods and conifers that currently have a more southerly distribution are expected to gain suitable habitat at the northern end of their ranges and to increase in frequency where they already occur (e.g. *Abies grandis*, *Pseudotsuga menziesii*, and *Thuja plicata*; Hamann and Wang, 2006). When coupled with increased rates of tree death due to climate change (Battles et al. 2008), these changes will alter the seasonal timing, amounts, and resource value of forest-to-stream fluxes of plant litter (Richardson et al. 2005), which will in turn have important ecological consequences for stream biota and food web dynamics (e.g. Going and Dudley, 2008). Stream and forest managers attempting to preserve the ecological integrity of small stream systems will need to be aware of projected changes in tree species distributions (Hamann and Wang, 2006), especially as forest structure can be more directly addressed by management practices and silvicultural prescriptions than other aspects of forest ecology.

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References


List of tables

Table 1. Physical and riparian descriptions of all sites where terrestrial-to-stream plant litter fluxes were measured

<table>
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<tr>
<th>Canopy type</th>
<th>Stream</th>
<th>Canopy Openness (% (SD))$^a$</th>
<th>Mean Channel Width (m)$^b$</th>
<th>Year Riparian Forest estab.</th>
<th>Dominant Tree Species (spp(%), spp(%))$^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deciduous (DEC)</td>
<td></td>
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<tr>
<td>1</td>
<td>South</td>
<td>6.7 (2.3)</td>
<td>0.60</td>
<td>1978</td>
<td>rA(83), Cw(12)</td>
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<td>2</td>
<td>East</td>
<td>11.9 (1.4)</td>
<td>2.00</td>
<td>1975</td>
<td>rA(60), wH(30)</td>
</tr>
<tr>
<td>3</td>
<td>Spring</td>
<td>9.7 (1.6)</td>
<td>3.93</td>
<td>1924</td>
<td>rA(60), wH(30)</td>
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<tr>
<td>4</td>
<td>Blaney</td>
<td>6.3 (0.3)</td>
<td>4.57</td>
<td>1972</td>
<td>rA(50), blM(30)</td>
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<tr>
<td>5</td>
<td>Donegan i</td>
<td>6.5 (2.0)</td>
<td>1.47</td>
<td>1939</td>
<td>rA(80), wH(7)</td>
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<tr>
<td>Coniferous (CON)</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>South</td>
<td>11.3 (1.1)</td>
<td>1.73</td>
<td>1924</td>
<td>rC(60), dF(22)</td>
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<td>2</td>
<td>Upper Spring</td>
<td>9.4 (1.2)</td>
<td>2.47</td>
<td>1863</td>
<td>dF(90), wH(10)</td>
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<td>Elf</td>
<td>6.9 (0.5)</td>
<td>1.80</td>
<td>1924</td>
<td>wH(60), rC(30)</td>
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<td>East</td>
<td>8.7 (0.4)</td>
<td>2.57</td>
<td>1949</td>
<td>dF(90), wH(10)</td>
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<tr>
<td>5</td>
<td>Lower Mirror</td>
<td>10.0 (1.0)</td>
<td>1.97</td>
<td>1919</td>
<td>wH(70), dF(20)</td>
</tr>
<tr>
<td>Clear-cut (CC)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Upper Mirror</td>
<td>16.2 (10.4)</td>
<td>1.35</td>
<td>1998</td>
<td>n/a</td>
</tr>
<tr>
<td>2</td>
<td>Upper Millionaire</td>
<td></td>
<td></td>
<td>1995</td>
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<tr>
<td>3</td>
<td>Kazoo</td>
<td>51.5 (10.8)</td>
<td>1.03</td>
<td>2005</td>
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<tr>
<td>4</td>
<td>G10</td>
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<tr>
<td>5</td>
<td>G30</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Upper South</td>
<td>11.5 (1.6)</td>
<td>1.23</td>
<td>1927</td>
<td>dF(50), wH(40)</td>
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<td>Lower South</td>
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<td>1.37</td>
<td>1924</td>
<td>wH(40), rC(32)</td>
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<td>3</td>
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<td>10.8 (3.2)</td>
<td>2.37</td>
<td>1924</td>
<td>wH(60), dF(30)</td>
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<td>Lower Mirror 30</td>
<td>8.2 (0.7)</td>
<td>2.43</td>
<td>1919</td>
<td>wH(70), rC(30)</td>
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<td>5</td>
<td>F</td>
<td>11.3 (3.9)</td>
<td>1.02</td>
<td>1924</td>
<td>rC(60), dF(22)</td>
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(a) Canopy closure and channel width as measured in summer (July and August 2007)
(b) rA = red alder *Alnus rubra*, Cw = cottonwood spp., blM = bigleaf maple *Acer macrophyllum*, dF = Douglas-fir *Pseudotsuga menziesii*, wH = western Hemlock *Tsuga heterophylla*, rC = redcedar *Thuja plicata*
List of figures

**Figure 1.** Map of all sites in the Malcolm Knapp Research Forest (MKRF, in southwestern British Columbia, Canada) where terrestrial-to-stream plant litter fluxes were measured. Numbers correspond to the sites in Table 1.

**Figure 2.** Mean forest-to-stream plant litter fluxes for the four riparian forest types examined (CC = recently clearcut, RSS = riparian reserve strip, Decid. = deciduous-dominated, Conifer = coniferous-dominated). The composition of the plant litter inputs is shown for each riparian forest type; the sum of all plant litter components equals the total flux. Note that the vertical scales differ among plots. Data are shown for spring, summer, and autumn seasons.

**Figure 3.** Proportion of plant litter fluxes comprised of broadleaf litter (calculated as broadleaf flux / total plant litter flux) in each of the four riparian forest types examined (CC = recently clearcut, RSS = riparian reserve strip, Decid. = deciduous-dominated, Conifer = coniferous-dominated). Data are shown for spring, summer, and autumn seasons. Bars are means ± SE.

**Figure 4.** Average plant litter flux (average of spring, summer, and autumn values) versus stand age. For red alder leaves (top panel), and all plant litter inputs summed (bottom panel) early successional stand data (<35Y) are fit to a linear model ($R^2 = 0.88$ and 0.75, respectively); for conifer needles and redcedar fronds, data were fit to a three-parameter sigmoidal model ($R^2 = 0.86$ and $0.28$, respectively, curve is not shown for the redcedar data as the relationship is not significant). Data for the two recent clearcut sites (G10 and G30 Streams, logged in 2006 and 2004, respectively) where timber harvesting activities did not remove small riparian trees (e.g. vine maple and small bigleaf maple) are shown (hollow symbols) but not included in regression analyses.

**Figure 5.** Canopy structure (measured as percent canopy openness) versus stand age. Data for three seasons (spring, summer, and autumn) are shown. Data are fit to the power function $y = ax^b$; values of $b$ (slope) ranged from -0.41 (autumn, long dashes) to -0.53 (summer, solid line) and -0.57 (spring, short dashes). Excluded are the two recent clearcut sites (G10 and G30 Streams, logged in 2006 and 2004, respectively) where timber harvesting activities did not remove small riparian trees (e.g. vine maple and small bigleaf maple).
Figures

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Fig. 3
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![Graph showing percent canopy openness over years since forest established with data points for Spring, Summer, and Autumn]

Fig. 5