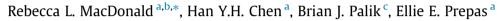
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Influence of harvesting on understory vegetation along a boreal riparian-upland gradient



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ABSTRACT

Management of riparian forests, and how they respond to disturbance, continues to be a focus of interest in the literature. Earlier studies on riparian plant community assembly following harvesting in the boreal forest have focused merely on highly contrasting microhabitats within a landscape, for example, streambank riparian habitat or upland habitat. Sustaining biodiversity and evaluating the success of riparian management requires an understanding of plant community assembly following overstory harvesting across the landscapes, e.g., along the entire riparian-upland gradient, and how they recover over time. Using pre- and post-harvest data, we quantified how riparian harvesting along a disturbance gradient affects understory plant species diversity, abundance, turnover, and composition. We also asked how these disturbance-response relationships vary from stream edge to uplands. We expect changes in the plant community will be greater and recovery to be slower with increased disturbance severity. Based on the ecology of riparian versus upland, we also expect harvesting to exert a stronger control with increasing distance from the stream channel through the colonization of early successional species and extirpation of extant species. We found that disturbance severity (i.e., from cut-to-shore) from harvesting exerted strong controls on the dynamics of understory vegetation in boreal riparian forests, which was still evident seven years after the disturbance event. However, the dynamic responses strongly differed with the distance from the stream channel. Specifically, streamside communities harvested with or without a 30 m riparian buffer, were maintained to a condition similar to uncut forests. However, upland communities were less resistant to overstory harvest and subsequently colonized by early successional species present in pre-harvest riparian plots. Furthermore, vascular and non-vascular plants exhibited contrasting responses in their richness, abundance, turnover, and composition. Our results indicate that streamside understory vegetation is inherently more resistant to stand-replacing disturbance than upland assemblages.

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1. Introduction

Managing ecological services provided by riparian ecosystems continue to be a focus of interest and debate. Inclusion of riparian buffers in forest management plans is a standard practice across North America, albeit with variations among provinces, states, and agencies. Although riparian buffers were devised initially to protect aquatic organisms and habitat, they have more recently been included as an element in terrestrial conservation initiatives. The application of riparian buffers have created artificial, linear patterns of mature forests along lakes, rivers and streams (Buttle, 2002; Kreutzweiser et al., 2012; Sibley et al., 2012), which has led to concerns about the lack of heterogeneity across the landscape and its effect on biodiversity. This concept has stimulated research into the use of disturbance (e.g., harvesting) in riparian habitats as a management tool (Sibley et al., 2012; Zenner et al., 2012). Earlier studies on riparian plant community assembly following harvesting in the boreal forest (e.g., Lamb et al., 2003; Biswas and Mallik, 2010; Braithwaite and Mallik, 2011) have focused merely on highly contrasting microhabitats within a landscape, for example, stream-bank riparian habitat or upland habitat. If a goal of riparian management is to sustain biodiversity, then understanding responses of understory plant community to overstory harvesting across the landscapes, e.g., along the entire riparian-upland gradient, is paramount to evaluating the longterm success of riparian management with respect to conservation.

Hydrological disturbance events (i.e., erosion of the soil surface and abrasion by suspended sediment and debris) and the ability of fluvial systems to act as conduits for the dispersal of propagules, structure streamside communities in space and time (Naiman







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and Décamps, 1997). Laterally, frequency and severity of flood disturbance typically decline with increased distance from the active channel, paralleled by an increase in ground-water depth. Along the same gradient, understory light availability generally decreases as tree density increases (Nierenberg and Hibbs, 2000; Lamb and Mallik, 2003; Palik et al., 2003). In sum, the overall effect of disturbance, resource quantity and quality of streamside habitats—which generally shape the structure and functioning of understory plant communities—may not be uniform across the stream-bank riparian – upland gradient. Thus, it is very likely that understory plant communities in stream-bank riparian forests may not respond to logging in the same manner as those in upland forests.

Overstory harvesting and associated ground disturbance alters understory plant communities directly through increasing mortality of individuals, propagules sources, local populations or groups of species, or indirectly by varying microclimatic conditions, habitat heterogeneity, and resource availability (Halpern and Spies, 1995; Roberts and Gilliam, 1995; Bergeron and Harvey, 1997; Scheller and Mladenoff, 2002). Both direct and indirect processes result in directional shifts in the plant community affecting both species diversity and composition. As a reflection of increased resource quantity, vascular species diversity often increases following canopy removal, whereas intolerant non-vascular species decrease (e.g., Halpern, 1988; Reich et al., 2001; Hart and Chen, 2008). In the boreal forest, understory streamside communities are usually highly productive and comprised of a variety of species and functional groups, including generalist plant species, specialized species adapted to streamside habitats (riparian obligates), and early successional species occurring in productive habitats at the trade-off of being less competitive in resource stressed environments (Lamb et al., 2003; Dynesius et al., 2009; Biswas and Mallik, 2010). In contrast, boreal upland understory communities are primarily driven by light availability and thus dominated by shade tolerant species that are unable to compete in early successional environments, such as ericaceous shrubs (e.g., Rhododendron groenlandicum, Vitis spp., and Gaultheria hispidula) and feathermoss (e.g., Pleurozium schreberi, Hylocomnium splendens, and Ptilium crisa-castrensis) (Nilsson and Wardle, 2005; Hart and Chen, 2008). Since vascular and non-vascular richness and cover is expected to increase and decrease, respectively, we predict that changes in the understory community will be more marked with increasing distance from the stream channel.

Community assembly following disturbance occurs within a temporal scale, and is a reflection of biotic (e.g., regional species pool) and abiotic (nutrient availability) processes. As such, time since disturbance is a critical factor when evaluating the effects of forest management on biodiversity and community composition (Roberts and Gilliam, 1995). A few studies have reported on the early impacts on understory vegetation to harvesting disturbance following partial harvesting (i.e., gap creation) (Zenner et al., 2012; Mallik et al., 2013), and adjacent clear-cutting (i.e., buffer strips) (Lamb et al., 2003; Biswas and Mallik, 2010). Yet, to our knowledge, there are no studies that have followed riparian plant communities through a disturbance event, although the need for these data is recognized (Mallik et al., 2013). Based on shifts in the life-history strategies of the extant plant community along the stream bank riparian-upland gradient, we expect recovery to be slower with increasing distance from the stream channel as changes in more upland communities are more likely to be sustained through the colonization of early successional species and extirpation of extant species.

Through a controlled field experiment using pre- and postharvest data, we quantify how harvesting treatments (i.e., cutto-shore, riparian buffers and uncut) affect understory species diversity, composition, and turnover over seven years. We also test if the treatment effects shift with distance from the stream channel (i.e., along a stream edge to upland gradient).

2. Materials and methods

2.1. Study area

The study is located in the Lower Foothills sub-region of the Boreal Plain, approximately 20 km northwest of Whitecourt, Alberta. The climate is sub-humid with a mean annual precipitation of 577 mm recorded at a weather station at Whitecourt (elevation 782 m) (Environment Canada, 2010). Rolling topography is a common feature of the study area. Soils originated from moderately fine to fine-textured till or glaciolacustrine parent material. The characteristic canopy is dominated by lodgepole pine (*Pinus contorta*Dougl. ex Loud. var. latifolia Engelm), white spruce (*Picea glauca* (Moench) Voss), trembling aspen (*Populus tremuloides* Michx) and balsam poplar (*Populus balsamifera* L.) in well-drained sites, and black spruce (*Picea mariana* (Mill.) BSP) and tamarack (*Larixlaricina* (*DuRoi*) K. Koch) in poorly drained sites.

2.2. Experimental design and data collection

Headwater stream sites, ranging in 0.5–1 m in width, were randomly selected in the study region to receive the following treatments listed in order of increasing disturbance severity; uncut (reference), riparian buffer, and cut-to-shore, each with four replicates, for a total of 12 sites. All selected sites originated from stand replacing fire in 1940. Uncut sites were undisturbed (i.e., no forestry activity in the adjacent upland). Buffer sites were clearcut with a 30 m wide un-harvested forest strip adjacent to the stream channel. Cut-to-shore sites were clearcut to the edge of the stream channel. Tree-length harvesting, i.e., trees were felled, topped, and delimbed at the stump before being dragged to roadside, was conducted during January to March 2004.

At each site, three randomly located, 30-m long transects were established running perpendicular from the stream to the upland. Along each transect, two 1-m² understory vegetation plots were randomly located within each of the following distance ranges from the stream bank: 0-5 m, 5-10 m, 10-15 m, 15-20 m, 20-25 m and 25–30 m, for a total of 12 plots per transect and 36 plots per site. Percent cover (0-100%) of each vascular and non-vascular plant species in each plot was estimated by eye (Mueller-Dombois and Ellenberg, 1974). All plants were identified to species with an exception of a few that were identified to genus, since it was not feasible to identify them to species in the field without flowers or fruits (e.g., Carex spp., Salix spp. and Viola spp.). Vegetation sampling was conducted during the periods of peak vegetation cover in the summer (July through August) prior to treatment, i.e., Yr 0 (2003) and the summers of Yrs 1 (2004), 5 (2008) and 7 (2010) after treatment. Within each site, species cover data of the 6 plots at each distance range were averaged to derive a mean.

2.3. Statistical analyses

2.3.1. Species richness, abundance and turnover

Species richness (*S*) was used as a measurement of diversity, which is the total number of species in each sample plot. Species richness is related to sampling area (Rosenzweig, 1995). We used a species accumulation curve (SAC) to assess adequacy of sampling efforts and to compare richness among treatments. The mean SAC and its standard deviation are computed from random permutations of the data (Gotelli and Colwell, 2001). SAC was carried out using specaccum function in the vegan package (Oksanen et al., 2013) using R version 3.0.1 (R core team, 2013). Abundance was

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