ABSTRACT: The Crown of the Continent is one of the premiere ecosystems in North America containing Waterton-Glacier International Peace Park, the Bob Marshall-Great Bear-Scapegoat Wilderness Complex in Montana, various Provincial Parks in British Columbia and Alberta, several national and state forest lands in the USA, and Crown Lands in Canada. The region is also the headwater source for three of the continent’s great rivers: Columbia, Missouri and Saskatchewan that flow to the Pacific, Atlantic and Arctic Oceans, respectively. Headwaters originate in high elevation alpine environs characterized by high snow accumulations in winter and rainstorms in summer. Most headwaters of the region contain high quality waters with few ions in solution and extremely low nutrient concentrations. Alpine streams have few species of aquatic organisms; however, they often possess rare species and have hydrogeomorphic features that make them vulnerable to climatic change. Subalpine and valley bottom streams of the Crown of the Continent Ecosystem (CCE) flow through well forested watersheds. Along the elevation gradient, the streams and rivers of the CCE flow through series of confining and nonconfining valleys resulting in distinct canyon and floodplain reaches. The alluvial floodplains are characterized by high species diversity and bioproduction maintained by the hydrologic linkages of habitats. The streams and rivers of the CCE have low nutrient concentrations, but may be significantly affected by wildfire, various resource extraction activities, such as logging or mining and exurban encroachment. Wildfire has been shown to increase nutrient loading in streams, both during a fire and then following the fire for as much as 5 years. Logging practices increase nutrient loading and the algal productivity of stream periphyton. Logging and associated roads are also known to increase sediment transport into Crown of the Continent streams directly affecting spawning success of native trout. The CCE is one of the fastest growing regions in the USA because of the many recreational amenities of the region. And, while the region has many remarkably pristine headwater streams and receiving rivers, there are many pending threats to water quality and quantity. One of the most urgent threats comes from the coal and gas fields in the northern part of the Crown of the Continent, where coal deposits are proposed for mountain-top removal and open-pit mining operations. This will have significant effects on the waters of the region, its native plants and animals and quality of life of the people.

(KEY TERMS: Crown of the Continent; Northern Rocky Mountains; Canadian Rocky Mountains; alpine streams; subalpine streams; rivers nutrients; sediment; logging; mining.)

INTRODUCTION

The Rocky Mountains in northern Montana and southern Alberta and British Columbia hold the geographic headwaters of a significant portion of the North American Continent. Indeed, within Glacier National Park resides a single spire, Triple Divide Peak, where three great river systems of the continent converge at the intersection of the Continental and Hudson Divides. Water flowing to the west enters the Columbia River basin (Pacific Ocean), water flowing to the northeast flows into the Saskatchewan River basin (Arctic Ocean), and water flowing southeast enters the Missouri River basin (Atlantic Ocean). Thus, the montane landscape and its headwaters quite literally form the water tower of the continent. This region has been referred to as the Northern Continental Divide Ecosystem (Salwasser et al., 1987), the Northern Rocky Mountain Province (Bailey, 1995), and the Crown of the Continent Ecosystem (Hayden, 1989). Although the first two names are most commonly used in scientific literature, they disregard the substantial portion of the contiguous montane system and headwaters in Canada. The term Crown of the Continent is more inclusive and representative of the importance of the region and is far and away the earliest title given recognizing the regional hydrologic and geographic uniqueness and appeared in an article written by George Bird Grinnell (1901) describing his travels in the region (Figure 1). Throughout the remainder of this paper we refer to the area as the Crown of the Continent Ecosystem (CCE).

The CCE is characterized by high heterogeneity of landscape and hydrology. To the east is the steppe of the Great Plains and the Rocky Mountain Front. Interior to the CCE are the belt series mountain ranges dominated by sedimentary geologic formations of mountains and valleys with elevation differentials extending from 1000msl at the valley floors to over 3000msl along the mountain peaks. The climate on the west slope of the Continental Divide is dominated by Pacific Maritime weather patterns flowing from west to east. Local climatic conditions are highly heterogeneous with some higher elevations receiving more than 2 m of snow water equivalent in winter. At the other extreme, some of the valley bottoms in the western portion of the CCE receive less than 20 cm of moisture per annum. Along the eastern slope of the Rocky Mountain Front the weather is highly variable, particularly in winter with cold, continental air masses flowing from northern Canada interrupted by warm air flow from the south, referred to as Chinook winds.

The core of the CCE is Waterton-Glacier International Peace Park, which holds a United Nations designation as an International Biosphere Reserve and World Heritage Site. Central to this designation is the role of aquatic biodiversity and the quality and quantity of water as it interacts with the mountain-valley landscape. Indeed, the distribution and abundance of biota and the way people use the landscape are closely interconnected to the region’s headwaters. Some of the best evidence for climatic change globally is found here. The glaciers of Glacier National Park (GNP) have been shrinking rapidly since the founding of the park in 1910. A recent analysis estimated an ≈40% reduction in glacier volume since 1950 and simulation modeling has projected that the glaciers of GNP will be gone by 2050 (Hall and Fagre, 2003). This will have a significant effect on headwater hydrologic regimes and the organisms that are dependent on continuity of flow in alpine running water habitats (Hauer et al., 1997).

The CCE is experiencing rapid growth in human population, particularly in the Flathead River basin in the western part of the Ecoregion. Natural wilderness, recreation and scenic attributes, epitomized by Glacier National Park and Flathead Lake, are the long-term primary drivers of economic growth for the region. Water quality, the support of aquatic organisms, and the integrity of aquatic and riparian habitats are essential to maintaining the renewable goods and services (sensu Costanza et al., 1991) that characterize the quality-of-life enjoyed by residents and visitors from around the world. The CCE is critically important to the biodiversity and ecological integrity of the entire continent. Indeed, the CCE holds one of the highest accumulations of diversity of plants and animals in North America (Stanford and Schindler, 2005), including the full array of native carnivores and ungulates. For example, valley bottoms and the river floodplains of the CCE are critical habitat for most of the large animals of the ecoregion, including several species listed as sensitive, threatened or endangered, including bull char, westslope cutthroat trout, wolves, grizzly bear, lynx, and wolverine.

The objectives of this review paper are to (1) introduce the importance of water resources in the CCE to continental scale biodiversity of complexity, (2) illustrate hydrogeomorphic, biogeochemical, and organismal linkages between CCE alpine, subalpine and valley bottom headwater streams and their coupling to water quality and quantity and regional biocomplexity, (3) present supporting studies that demonstrate the various sources and processes associated with both natural and man-caused disturbance and their effects within the CCE, and finally (4) discuss pending threats to headwaters that will likely affect the larger river systems that flow from this ecoregion, as well as direct impact to ecosystem integrity within the CCE itself.
HYDROLOGIC AND ECOLOGICAL LINKAGES IN THE CCE

Alpine Streams

Alpine streams throughout the world have varied hydrologic and biogeochemical characteristics, as well as variation in biota. Despite the worldwide distribution of alpine stream systems, studies of their biota and biogeochemistry are limited (Ward, 1994). There are three main types of alpine streams developed from descriptions in the European literature of the Alps; kryal, krenal and rhithral, each with distinct biotic and abiotic characteristics (Illies and Botosaneanu, 1963). Kryal streams are fed by year-round melt water directly from snowfields, icefields and glaciers and are characterized by high heterogeneity within and between streams of this type. Krenal streams arise as springbrooks hydrologically maintained by ground water. Krenal streams generally have relatively stable chemical, hydrological and thermal conditions. Rhithral streams are driven by seasonal snowmelt, and have wide temperature fluctuations, as well as diverse biota. Krenal streams in particular transition into rhithral streams as distance from the ground-water sources increase and waters coalesce from first order streams (sensu Strahler, 1964). Alpine streams often have high gradients with waters flowing over bedrock and cobble-boulder substrate, high dissolved oxygen levels, high variation in temperature regimes due to open canopies and summer solar radiation, and low nutrient concentrations.

Elgmork and Saether (1970) defined different zones of the streams based on genera of chironomids. The chironomid genus Diamesa dominated the upper, perennial snowmelt regions. The upper thermal limit of many of these species was 5°C. Again, based on chironomid community composition, Steffan (1971) defined the hypokryal and metakryal as distinct zones within kryal (glacial) streams in Scandinavia. Species assemblages within these zones were related to temperature. Hypokryal habitats were the most extreme in glacial streams, and supported very low numbers of individuals and species. Three species of Diamesa were the only invertebrates reported from the foot of glaciers in Sweden. These sites were isothermal, having mean temperatures from 0.5°C to 1.5°C, as well as very low daily temperature fluctuations.

Alpine streams of the CCE occur abundantly along the continental divide in Glacier and Waterton Parks. Waters of these alpine springs were generally supplied by permanent snowfields or small icefields isolated behind mounds of colluvium. We found stream temperatures remaining at 0-0.5°C at the springhead and to vary less than 2°C within 0-10 m of the source. However, solar radiation in mid-summer can quickly elevate the temperature of these streams. We found mid-afternoon temperatures as high as 21°C in alpine streams within only a few hundred meters of their source. Although these streams can become quite warm during the day, often night temperatures at these sites ranged from 0-3°C. Thus, diel temperature flux in the alpine, at distances of a few hundred meters from the source, varied as much as 18°C.

Analyses of snow samples taken from 52 snow survey locations, mostly in the alpine and subalpine of Glacier Park, revealed very low nitrate concentration in snow water (mean = 4.36 μg/l; std. dev. = 1.31; Hauer et al., 2003b). In a separate study, we found biologically available phosphorus (PO₄) concentrations to range between 0.5 and 0.7 μg/l in kryal and krenal stream types (Figure 2a). In alpine streams with very low NO₃ concentrations, algal communities were frequently dominated by blue-green algae near the source. Diatoms replaced the blue-green algae even short distances downstream following incorporation of nitrogen into the stream system by the blue-green algae (Hauer and Giersch, 1999a).

Fauna of the alpine streams of the CCE is dominated by aquatic insects. Generally within 100 m of their source, krenal streams are dominated by several species of Simuliidae (black flies) and Heptageniidae (mayflies) (Hauer et al., 2000). The stonfly, Lednia tumana, known only from alpine streams in Glacier Park, can be found in snowmelt streams and in springs with maximum summer afternoon temperatures exceeding 15°C. Generally, species assemblages increase in complexity downstream to include numerous mayfly nymphs from the families Heptageniidae and Ephemerellidae, several species of the predatory caddisfly larvae Rhyacophila spp., and the large predatory stonfly Megarcys watertoni (Hauer and Giersch, 1999b).

Both kryal and krenal streams reflect these low concentrations of NO₃ and PO₄ with the marked exception of the development of alpine fens, which form one of the most ecologically interesting associations in alpine streams. Fen development is under hydrogeomorphic control and occurs where ground water supplied by waters from a permanent snowfield are forced to the surface by bedrock (Figure 2b). Where the water source is diffuse, alpine vegetation grows and annually adds to an accumulation of undecomposed organic matter. The fen is characterized by permanently wet organic soils and a peat layer that is generally 10-20 cm thick. The fen, with its abundant alpine vegetation and peat, attracts populations of the heather vole, Phenacomys intermedium. The heather voles feed on the vegetation of the fen and...
produce small burrows and food caches throughout the fen. They also produce latrine sites that are often placed in or near open water (Figure 2c). The deposits of frass and fecal pellets in the latrine sites contribute significantly to the nitrogen and phosphorus loading of the krenal stream. We found NO$_3$ concentrations in the springheads associated with heather vole populations ranging from 100-250 µg/l (i.e., 20-50 times the snow source concentrations) and PO$_4$ concentrations of 3-5 µg/l (i.e., 5-10 times the snow source concentrations). These high concentrations of nutrients, especially NO$_3$, found in the krenal springheads, generally declined rapidly downstream. We found both NO$_3$ and PO$_4$ concentrations to decline 70-80% in $\approx$100 m of stream length. The fauna of these fen related krenal streams is also remarkable. The aquatic insect community of alpine fen streams is isolated to the caddisfly larvae Allomyia bifosa. This small caddisfly from the family Apataniidae, is extremely rare only known from high alpine krenal streams along the continental divide from Alberta and British Columbia to Montana. The Allomyia larvae feed on diatoms in the stenothermal krenal streams. We found these larvae to disappear from the stream when temperatures rise above 5°C. Thus, this very rare species appears to be restricted to krenal streams near the springhead with elevated NO$_3$ support of diatoms, but where temperatures remain near 0°C. This condition also appears to occur most readily where there is the presence of an alpine fen supporting a heather vole population.

The significance of these alpine aquatic environments, their low nutrient concentrations and the complex interactions described between hydrogeomorphic setting, terrestrial organisms such as heather voles, and very rare stream species, is manifold. First, these systems are the water towers of our continent. A large percentage of the water volume discharged each year from rivers such as the Columbia, Missouri, and Saskatchewan, or other river systems with origin in the Rocky Mountains, is generated as snow or rainfall within the mountain complex at higher elevations. Elevation and colder temperatures of the region extend the rate of snowmelt. Water, stored as snow, melts throughout the summer maintaining stream flow in the valleys and plains. This is critically important to maintaining both the ecological goods and services of the region (e.g., fisheries, wildlife, and recreation), but also agricultural uses and hydropower. Typically, the water quality is high with few nutrients and low concentrations of sediment. But, these aquatic systems are also fragile and highly vulnerable to climatic change as well as exploitation of the water resources. Although stream systems are connected through their dendritic network (Ward, 1997) the organisms of alpine segments may be isolated by thermal or habitat criteria making transfer from one stream to another difficult. This has led to regionally endemic species that are very vulnerable to extirpation. For example, the fen modified krenal
streams are highly dependent on their hydrogeomorphic setting and are sustained by snowmelt over the summer. Late summer loss of the snowfield that supports the fen-krenal stream system, perhaps due to climatic change resulting in either less annual snow accumulation or earlier spring melting of the snow could lead to a loss of the wetland complex. This in turn could result in a radical change in state of the stream system from perennial to ephemeral (Hauer et al., 1997).

Pristine Subalpine Streams

The subalpine of the CCE are highly variable, but tend to have similar unifying characteristics and species compositions. Hydrologically, these streams receive most of their flow from rain and snow deposited at high elevation of the alpine and within the subalpine zone of the mountain slopes. Abundant ground waters enter these streams following discharge into small springs along the toe of side slopes. Stream discharges in the CCE closely follow that of a snowmelt regime (Poff and Ward, 1989). In our study of McDonald Creek in Glacier National Park (Hauer et al., 2000 and Hauer et al. 2003b), we observed interannual variation in the magnitude and timing of maximum discharge, but this occurred each year of an 8-year study between mid-May and mid-June. Discharge typically increased >10 times the autumn base flow. Nutrient concentrations were always very low, but both nitrogen and phosphorus dynamics followed a positive, clockwise hysteresis demonstrating an accumulation of materials poised to flux through the stream system at the onset of spring runoff (Figure 4). Over 90% of the total nitrogen flux from the McDonald Creek basin occurred as NO₃ with maximum concentrations approaching 450 µg/l, but minimum concentrations less than 100µg/l. These low concentrations predominate throughout the fall and winter base flow period and increase very rapidly at the onset of spring runoff. The rate of increase in NO₃ concentrations is significantly greater than the rate of increase in spring discharge. This suggests that nitrate is accumulated and concentrated in the ground water over the winter near the valley floor where the first snow melt that initiates the flood period occurs in the spring and discharges high NO₃ water from side slope aquifers into the stream. Nitrogen concentration decreases after the initial pulse in the early spring; and although discharge increases, primarily driven by high elevation snowmelt as the spring warming progresses, nitrogen concentration decreases. This is most likely the result of dilution of the ground water by melting snows from high elevation. Although we have no direct evidence, we strongly suspect that the high concentration of Alnus spp. in avalanche chutes and high slope wetlands maybe play a significant role in the loading of NO₃ to subalpine shallow aquifers. Many studies have shown that soils directly surrounding stands of Alnus are rich in nitrogen allowing for increased production by neighboring species. Postgate (1978) showed how Alder communities can increase soil nitrogen as much as 100 kg-N/hectare/year through the mineralization of leaf litter alone. On a floodplain in the Alaskan interior, Alder communities are believed to have increased total soil nitrogen accumulation by a factor of four over a twenty year span (Walker, 1989).

We have observed a very different response in phosphorus concentration from that of nitrogen. During base flow soluble reactive phosphorus (SRP as PO₄) constitutes approximately 50% of the total phosphorus (TP) flux in McDonald Creek. However, during spring snowmelt TP increases in concentration in a linear fashion with increased discharge achieving maximum concentrations of ≈ 20µg/l (Figure 3). The majority of this phosphorus is associated with sediment particles, especially fine silts and clay (Ellis and Stanford, 1988). At peak discharge, biologically available SRP makes up less than 10% of the total phosphorus flux from the basin. Regardless of whether it is TP or SRP, phosphorus concentrations remain extremely low in McDonald Creek, which is typical of the undisturbed subalpine and valley bottom streams of the CCE.

In the pristine forest streams of the CCE, we observe very predictable temperature regimes closely

![FIGURE 3. Regression of Total Nitrogen (Tn) and Total Phosphorus (Tp) Against Discharge in McDonald Creek, Glacier National Park. Hysteresis is caused by concentrations during the rising limb of the hydrograph being greater than concentrations during the falling limb of the hydrograph given the same discharge. Note that TN (mostly as NO₃) increases during early spring runoff at a greater rate than does TP (modified from Hauer et al. 2003).](image)
correlated with elevation (Hauer et al., 2000). This has a direct effect on the distribution of stream organisms and is particularly demonstrated among the stream benthic macroinvertebrate community. In this study (Hauer et al., 2000), we quantitatively collected benthos samples at regularly scheduled intervals throughout the year over a several year period. Although we collected over 100 species of the three dominant orders of aquatic insects occurring commonly in CCE streams (i.e., Ephemeroptera, mayflies; Plecoptera, stoneflies; and Trichoptera, caddisflies), we observed the 27 taxa illustrated in Figure 4 to occur in abundances that permit comparison of spatial distribution. We found an interesting phenomenon that can be directly explained by species specific energetics (Hall et al., 1992). Taxa within the same order and possessing similar trophic relations had abundance patterns demonstrating statistically normalized distribution curves along the elevation (and thus temperature) gradient. For example, the net-spinning caddisfly Parapsyche elsis achieved maximum abundance in the upper reaches of

FIGURE 4. Distribution and Abundance of Commonly Occurring Benthic Macroinvertebrates Along the Elevation and Stream Gradient. Stream invertebrates are distributed along the elevation and longitudinal gradient within well-defined reaches having close correlation with maximum summer temperatures (modified from Hauer et al., 2000).
McDonald Creek, but were replaced in abundance by a similar net-spinning caddisfly, *Arctopsyche grandis* in the lower reaches of the creek, just above Lake McDonald. Physiological experiments in the laboratory have clearly demonstrated metabolic response of these species to change in temperature such that *P. elsis* larvae appear to be unable to sustain an energy and metabolic balance above 15°C and prefer reaches with temperatures having maximum summer temperatures <12°C whereas *A. grandis* larvae tolerate temperatures as high as 20°C and achieve maximum abundance in reaches with summer maximum temperatures between 17-19°C (Lowe and Hauer, 1999). Indeed, the vast majority of stream macroinvertebrates in the CCE have remarkably predictable distributions along the elevation and temperature gradient (Stanford et al., 1988, Hauer et al., 2000; Figure 4).

Valley Bottom Streams and Rivers

Valleys of the CCE were modified by Pleistocene alpine glaciers that carved through the landscape. Valley bottom, alluvial streams and rivers are characterized by broad and active alluvial floodplains, with highly complex physical and biological interactions between main river channels, surficial backwaters, springbrooks, and buried paleo-channel networks (Stanford and Ward, 1993; Hauer et al., 2003a; Stanford et al., 2005). These complex interactions within and between habitats are driven by strong lateral and vertical flux of water and materials including flood-caused cut and fill alluviation, routing of river water and nutrients above and below ground, channel avulsion, and dynamics of large wood (Figure 6). The

![Diagram of floodplain structure](image)

**FIGURE 5.** (a) Idealized View of the 3-D Structure of Alluvial the Floodplains of the CCE, Emphasizing Dynamic Longitudinal, Lateral, and Vertical Dimensions and Recruitment of Wood Debris. Arrows indicate ground- and surface-water exchange (vertical), channel and flood plain (lateral) interactions, and upstream to downstream or longitudinal (horizontal) connectivity on the floodplain. The floodplain landscape contains a suite of structures produced by the legacy of cut and fill alluviation. The hyporheic zone is defined by penetration of river water into the alluvium. Phreatic ground water from the hillelope or other aquifers may underlie and/or be adjacent to the hyporheic zone. Alluvial aquifers usually have complex bed sediments with interstitial zones of preferential ground-water flow as illustrated by the buried river channel substrata (modified from Stanford et al., 2005). (b) Aerial view of the Nyack floodplain in the CCE. Yellow arrows mark the geomorphic knickpoints where the valley transitions from a canyon reach to the floodplain reach and then back to another canyon reach.

![Satellite image of floodplain](image)

**FIGURE 6.** (a) Satellite Multi-Spectral Image of the Nyack Floodplain (Middle Flathead River, Montana 2004). The flood plain extends laterally to both valley walls. Much of the gallery forest of cottonwood and spruce has been cleared for hay farming. Owing to the porous nature of the valley bedsediments, a legacy of river deposition since glaciation, river water downwells into the alluvial aquifer beginning at the upstream knickpoint where the river becomes unconstrained. The downstream knickpoint defines entry into another canyon which impounds the alluvial aquifer allowing it to intersect the surface creating springbrooks and wetlands as water flows from the aquifer back into the river. (b). Here the position of the main channel during a sequence of years from 1945-2004 color coded to emphasize the dynamic nature of the river. Figure from Stanford et al. (2005).
strong forces are driven by the river hydrologic regime and sediment dynamics to form and maintain a complex, dynamic distribution of resource patches and associated biota: the shifting habitat mosaic (SHM; Stanford et al., 2005). These characteristics are critically important in maintaining water quality, bioproduction, and biodiversity of the river system. The SHM is maximized on expansive river floodplains producing inherently high biodiversity and biocomplexity. This is particularly well illustrated on the Nyack Floodplain of the Middle Fork of the Flathead River where over a 60 year interval river dynamics and the processes of cut and fill alluviation result in a shifting channel eroding old surfaces and creating new surfaces (Figure 7).

Floodplains composed of coarse sediments engaged in the processes embodied by the SHM are penetrated by river waters creating complex three-dimensional mosaics of surface and subsurface habitats (Stanford and Ward, 1988; Brunke and Gonser, 1997; Poole, 2002). Ground water-surface water interactions are critical characteristics of these streams and their floodplain corridors. Alluvial aquifer water returning to the surface is generally higher in NO₃ and PO₄ than surrounding surface flows, resulting in patches of high algal productivity (Bansak, 1998; Wyatt et al., 2006). In the river, hyporheic return flow also results in increased macroinvertebrate growth and productivity (Pepin and Hauer, 2002) and growth rates of riparian vegetation (Harner and Stanford, 2003). Native species of fish, particularly the salmonids (bull char, west slope cutthroat trout, mountain whitefish) focus on the complexity of floodplains and spawn in habitats dominated by extensive ground water-surface water interaction (Baxter and Hauer, 2000).

The riparian floodplains of montane alluvial rivers are extremely ecologically diverse. The river valley floodplains of the CCE have extremely high biodiversity, from riparian plant species and aquatic food webs (Stanford et al., 2005) to large carnivores (Demarchi et al., 2003). The continuity of these highly diverse components of the CCE landscape is highly dependant on hydrologic linkages and the high water quality associated with the geology as well as the pristine character of large areas of the CCE (Stanford and Ellis, 2002).

**Disturbance to Streams of the CCE**

Whether started by natural causes, such as lightening, or intentionally by the native peoples, wildfire has been an integral component of forests in the CCE for thousands of years. During the period from the 1920s to the 1990s fire suppression efforts contributed to significant accumulations of fuel and dramatically changed the population structure of the forest. When forests have burned, forest policy and post-fire activities have often contributed to, rather than ameliorated, the disturbance to soil, water and reforestation (Karr et al., 2004). Forest wildfires occur, almost universally, during extended periods of dry-hot weather in mid to late summer. During this period, stream discharge is generally at base flow and stream temperatures at near maximum for the annual cycle. Study of the effects of wildfire on stream systems in the CCE have shown that during the fire streams flowing through burning riparian forest receive elevated temperatures directly from radiant heat and temperatures may increase sharply as the fire passes through the stream corridor (Hauer and Spencer, 1998). Although we have seen dead resident cutthroat trout in depositional pools of fire affected streams, many fish survive the short duration of elevated temperatures by seeking thermal refugia in areas receiving hyporheic ground water (Spencer and Hauer, 1991). Likewise, there is strong evidence that macroinvertebrates also seek thermal refugia by crawling or borrowing into the interstitial space of the cobble substrata (Gangemi, 1991).

Phosphorus and nitrogen dynamics in streams during and following a wildfire are particularly interesting and play a significant role in nutrient loading of streams in the short term and downstream lakes in the longer term. During the fire, ash from the fire is carried into the air and settles on the water surface of the stream. Ash accumulates in backwater areas and sinks to the stream bottom where it is entrained.
in the gravel substratum. The ash has high phosphorus content, but low nitrogen content. The phosphorus leaches from the ash particles and raises the concentration of soluble reactive phosphorus. In the CCE, studies have shown SRP to increase >200 times background levels during the fire as ash is loaded into the stream (Spencer and Hauer, 1991). As phosphorus is leached from the ash, phosphorus concentrations in the stream generally return to background levels within a few days. Although occurring because of the same fire event, fire-related nitrogen enters streams through the dissolution of smoke gases into the water. Both NO$_3$ and NH$_4$ increase in concentration during a wildfire by as much as 50 times as smoke drifts across the water surface. Thus, unlike ash, the delivery of nitrogen compounds to a stream may be highly variable over time and spikes in nitrogen concentration may occur repeatedly as smoke is carried by winds that shift direction carrying smoke to or away from a particular stream. Studies have further shown that NO$_3$ sources of nitrogen are produced by well-ventilated fires and NH$_4$ sources are produced when fires are poorly ventilated or have incomplete combustion, such as smoldering fires (Spencer and Hauer, 1991). Watersheds of the CCE are known to continue leaching phosphorus and nitrogen above background levels, particularly during spring snowmelt, for as much as 5 years after the fire (Hauer and Spencer, 1998). There are also significant problems associated with postfire management, particularly the unintended consequences to salvage logging on forested public lands throughout the western United States, such as increased road building and sediment loading into streams, hardening of stream banks, and introduction of exotic species (Bestcha et al., 2004).

Although forest logging practices have greatly improved as “best management practices” have been adopted by most of the federal and state forests, watershed studies in the CCE clearly show effects of logging and associated activities on stream water quality. A paired watershed study showed the effects of logging on nutrient dynamics and algal growth as a first-order ecological response to increased nutrient loading (Hauer and Blum, 1991). This study was conducted on 9 paired watersheds draining national forest lands of the Flathead National Forest within the USA of the CCE. Watersheds were paired into three groups of three streams each. One group was composed of second-order streams, one group of third-order streams, and the third group was composed of fourth-order streams. In each group there was one stream that drained a watershed with no timber management and no roads, the other two streams of each group drained watersheds with timber harvest and associated logging roads. The stream pairings, the watershed size, percentage of the watershed logged and the total distance of roads within each watershed are summarized in Table 1.

The study showed that soluble reactive phosphorus (SRP), nitrate (NO$_3$), total phosphorus (TP), and total nitrogen (TN) were all higher among streams flowing from watersheds with timber harvest and roads than streams flowing from undisturbed (control) watersheds (Table 1). Employing an ANOVA for repeated measures, the study found that although the relationship was significant for both SRP and NO$_3$, it was highly significant for TP (Figure 8) and TN (Figure 9). The ecological significance of this can be explained by the relationship between these highly labile forms of nutrients (SRP and NO$_3$) compared to the addition of more refractory forms of these nutrients (TP and TN) as they appear in particulate organic matter. The labile nutrients (SRP, NO$_3$) are generally transported distances measured in meters before they are taken up by periphyton in the process of stream nutrient spiraling (sensu Webster and Patten, 1979; Elwood et al., 1983). Thus, both SRP and NO$_3$ are rapidly incorporated into stream algae before being re-released or semi-permanently bound in algal biomass (Mulholland et al., 1985; Mulholland et al., 2000). In contrast, TP and TN while including SRP and NO$_3$, include organically bound molecules, such as sloughed algae, that is transported by the stream.


<table>
<thead>
<tr>
<th>Watershed Group</th>
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<th>Area Logged (ha)</th>
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</table>
In this field experiment, much higher concentrations of TP and TN were observed in streams from logged (treatment) watersheds. These findings were corroborated by algal biomass and Chlorophyll a in each of the nine study streams (Hauer and Blum, 1991; Figure 9).

The results of this study clearly demonstrate the effect of logging on streams in the CCE. Streams of watersheds with logging have increased nutrient loading, first as SRP and NO₃, which is rapidly taken up by stream periphyton. This leads to increased algal growth that is directly correlated with the quantity of logging within the watershed. The increased periphyton increases particulate organic matter in transport as the algal biomass is sloughed into the stream. We observed this as increased TP and TN in logged watershed streams. Other studies in the CCE have shown that increased sediment loading and an incorporation of fines into spawning gravel, especially during the summer and fall base flow period, has a dramatic effect on the success of spawning by bull trout (Salvelinus confluentus). Experiments have shown that as the percentage of fines increases from 20% to 40% there is >80% decrease in successful fry emergence (Weaver and Fraley, 1991).

While there are numerous sources of disturbance to CCE subalpine and valley bottom streams, logging and wildfire being two primary examples, exurban development along stream corridors is becoming an increasingly common occurrence. If recent trends continue, exurban encroachment into stream and river corridors will be a significant factor affecting ecological integrity of CCE headwaters and interact with other disturbance, both natural and human, in what frequently have unintended consequences. For example, as people build second homes for recreation in the headwater basins of the CCE, they frequently place a demand for fire protection on local, state and federal agencies, such as the US Forest Service. This, in turn, affects management decisions by the regulatory agencies as they make decisions prior to fire or manage post-fire landscapes (Beschta et al., 2004; Karr et al., 2004).

FUTURE AND IMPENDING THREATS

The Crown of the Continent Ecosystem is one of the fastest growing areas in the USA, particularly in the Flathead and Mission Valleys. Flathead County has grown over 25% in the past 10 years. The rate of building second homes on the private lands of the North Fork of the Flathead River has increased by nearly 10 fold in the past 20 years. Clearly, exurban development and encroachment into the headwater basins of the CCE will increase at an increasing rate over the next 10-20 years as the baby-boom generation begins to retire and seek the amenities of a clean and picturesque environment. However, there remain many other economic and resource extraction pressures on the headwater systems of the CCE.

During the 1970s high grade coal deposits were proposed for development in the Canadian portion of the North Fork of the Flathead River adjacent to the already active mining occurring in the Elk River Basin to the north. Considerable ecological work was done to evaluate North Fork water quality, biological
integral, and air quality. The original mining proposal, referred to as the Cabin Creek Site, was denied in 1988 following evaluation by the International Joint Commission (IJC 1988). The IJC ruled that the potential threats to downstream water quality were unacceptable.

Integral to this decision by the IJC was the North Fork's status in the USA as the west boundary of Glacier National Park from the US – Canadian border to the North Fork's confluence with the Middle Fork, near West Glacier and Glacier National Park's designation as an International Biosphere Reserve by the United Nations. Also, the North Fork, designated a Wild and Scenic River in the USA, contributes approximately 25% of the total annual flow entering Flathead Lake, considered as one of the "Crown Jewels" of the US Northern Rockies EcoRegion.

Since the mid-1980's, various resource development plans in the Canadian North Fork (CNF) have appeared. Numerous haul and access roads have been built into the tributary drainages of the CNF. The Flathead Coalfields, located south of the Crowsnest Coalfields near Fernie, BC, are part of the Kootenay Group Outcrop. More recent resource exploration has identified new coal mining sites, potential for coalbed methane development, and possible oil and natural gas reserves.

Coal mining, coal-bed methane extraction, and oil and gas exploration require a vast network of roads, which have been shown as significant sources of silt and nutrients contributing to water pollution (Hauer and Blum, 1991), directly impact native fisheries (Baxter et al., 1999), and have strongly negative consequences for large predators, such as grizzly bears (McLellan and Shackleton, 1988). Thus, there are highly likely negative impacts resulting from increased motorized access, noise and water quality changes associated with proposed coal or coal-bed methane extraction, and the additive relations to other forms of human mediated landscape change.

As is true of almost any protected area in the world, political boundaries in this region have little to do with ecological realities. The plants and animals in the CCE move freely across international, park or private ownership boundaries. Furthermore, Glacier National Park, by itself, is probably not large enough to support viable populations of many of its far-ranging predatory animals like wolves, grizzly bears, wolverine and mountain lions (Stanford and Schindler 2006).

While the headwaters of the Crown of the Continent have remained in remarkably good ecological condition, the pressures to exploit natural resources or develop lands near streams and rivers have direct impact on water quality and ecological integrity of these headwaters vitally important to human populations and ecological integrity of both the USA and Canada. As we seek to appropriately manage the waters of the CCE, we must keep in mind that human activities are pervasive and can have unintended consequences both for people and the biota throughout the region and beyond. It will also be imperative for future sound management of the CCE to recognize that neither the Ecoregion nor the various direct effects that have been the focus of this review are isolated from both human and environmental externalities. Coal and gas are part of an international market. People immigrate from one part of both the USA and Canada to another part. And finally, global climate change will have its own suite of effects that will in some cases alleviate some direct impacts and exacerbate others.

**LITERATURE CITED**


