Chapter 14: Ecoregion 8.4.4 Blue Ridge: Coweeta Hydrologic Laboratory, North Carolina

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Introduction

Research involving nutrients and biogeochemistry has a long history at the Coweeta Hydrologic Laboratory (CHL). The majority of nutrient research has focused on nitrogen (N), phosphorus (P), and dissolved organic carbon (DOC), and less so on other nutrients such as calcium (Ca). This chapter reviews research at the CHL on watershed biogeochemistry and stream organismal and ecosystem responses to nutrient enrichment, with primary attention to N and P. It also identifies future research at CHL that could fill science gaps that are of high priority for regulators and suggests ways that regulators might use existing science findings and datasets from CHL.

Site Description

CHL is located in southwestern North Carolina in the Blue Ridge Province of the southern Appalachians (Swank and Crossley 1988). CHL (lat. 35° 03′ 35” N, long. 83° 25′ 48” W) was established in 1934 near Otto, North Carolina, on 2185 ha of federal land that has been dedicated to research within the Nantahala National Forest (NNF). The CHL encompasses Shope Fork and Ball Creek basins, which together form the Coweeta Creek basin and also includes the adjacent Dryman Fork basin (fig. 14.1). Elevations range from 675 to 1592 m (Swank and Crossley 1988).

Forest types—

Vegetation at CHL includes northern hardwoods, cove hardwoods, xeric oak/pine, oak/hickory, and mixed-oak forests (Boring et al. 2014). Forests are diverse as is typical for southern Appalachian plant communities. Tree species are distributed predictably over the variable topography and follow a moisture gradient (Day et al. 1988). The plant communities at CHL are dynamic and change over time (Elliott et al 1999). Following the loss of American chestnut (*Castanea dentata* (Marshall) Borkh.) owing to chestnut blight beginning around 1925, CHL changed from an oak-chestnut-dominated community to a predominantly oak-hickory forest (Elliott and Swank 2008). The current forest is dominated by deciduous oaks (*Quercus*

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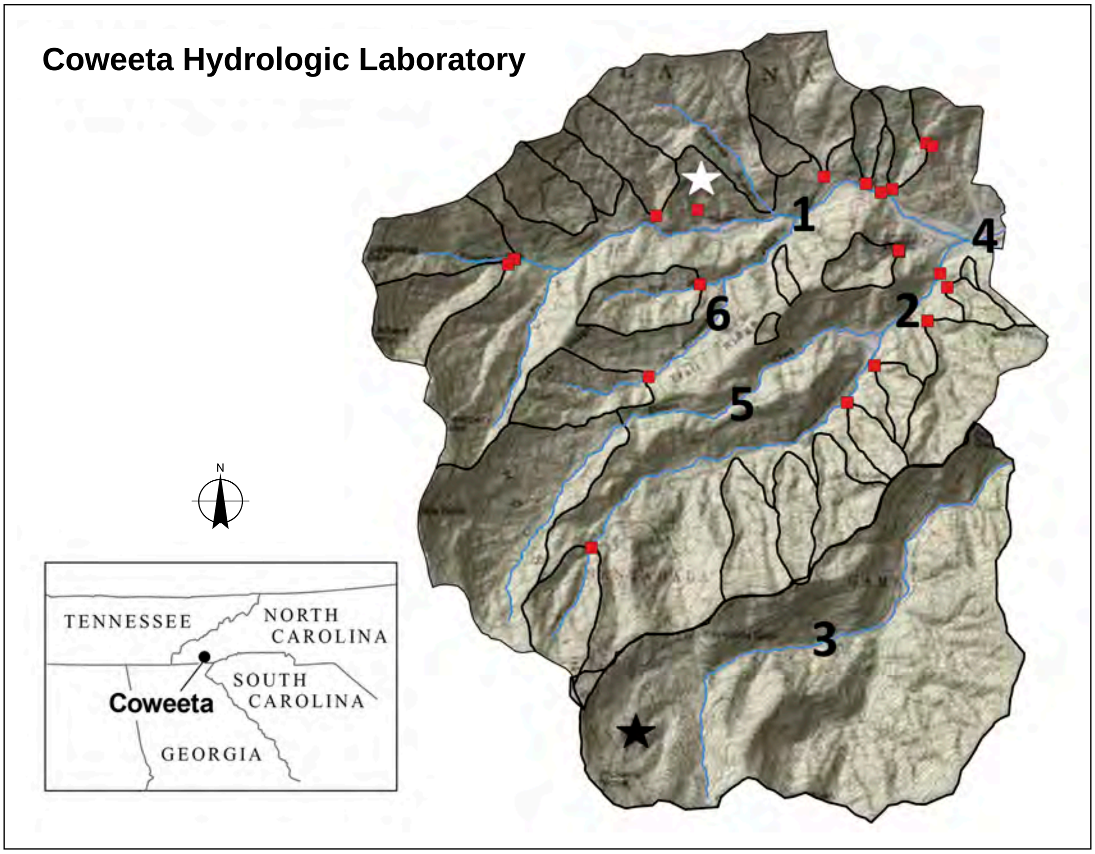

Figure 14.1—Coweeta Hydrologic Laboratory (CHL) in southwestern North Carolina with numbers indicating major streams: (1) Shope Fork, (2) Ball Creek, (3) Dryman Fork, (4) Coweeta Creek, (5) Henson Creek, and (6) Cunningham Creek. Red squares locate stream weirs. Black lines identify study watershed boundaries. Whole-stream nutrient additions were performed in Shope Fork watershed (white star), and Dryman Fork watershed (black star). Map courtesy of the Coweeta Long Term Ecological Research, KC Love, cartographer. Terrain imagery courtesy of ESRI Inc., under Creative Commons License CC BY-NC-SA 3.0.

spp.), tulip poplar (*Liriodendron tulipifera* L.), and maple (*Acer* spp.), with an evergreen understory of great laurel (*Rhododendron maximum* L.) and mountain laurel (*Kalmia latifolia* L.) (Boring et al. 2014).

The vicinity of CHL was lightly disturbed by American Indians prior to European-American settlement, primarily by seasonal understory burns. After the 1840s, European-American settlers burned and grazed uplands and cultivated crops in some valley bottoms (Douglas and Hoover 1988). Most of the basin was logged between 1900 and 1923 when 8 million board feet of timber were harvested (Elliott and Swank 2008). The heaviest cutting occurred at lowest elevations, in valleys, and accessible coves. Since establishment as an experimental site, human disturbances within CHL have been restricted to research purposes and have been well documented by the U.S. Forest Service (USFS) (Day et al. 1988, Elliott and Swank 2008).

Stream types—

First- through fifth-order streams drain 16 gaged catchments ranging in area from <5 to 760 ha (Benstead and Leigh 2012, Swank and Crossley 1988) (fig. 14.1). Most of the 73 km of streams within the CHL basin are first and second order (Meyer et al 1993). Ball Creek and Shope Fork, both fourth-order streams, join within the CHL boundaries to form Coweeta Creek, which flows east into the Little Tennessee River. Stream gradients are relatively steep, ranging from 15 to 30 cm/m (Meyer et al. 1993). Stream substrate varies along a longitudinal gradient with varying proportions of bedrock outcrops, boulders, cobble, gravel, pebble, sand, and silt (e.g., Wallace et al. 1999). Maximum average depth to bedrock below stream bottom is 10 cm. Low-order streams are shaded throughout the year by a dense understory of *R. maximum*. Large and small woody materials in the stream channel are abundant and form instream debris dams at all elevations. Headwater streams at CHL support a minimum of 290 plant and animal taxa, including 145 insect genera and roughly 50 diatom and algal species, making CHL streams moderately diverse habitats (Lowe et al. 1986, Meyer et al. 2007). Lower elevation streams have low to moderate densities of fish, including mottled sculpin (*Cottus bairdi* Girard), longnose dace (*Rhinichthys cataractae* Valenciennes), rainbow trout (*Oncorhynchus mykiss* Walbaum), and brook trout (*Salvelinus fontinalis* (Mitchill)) (Freeman et al. 1988).

Soils—

The underlying bedrock is dominated by metasandstone and schist (Velbel et al. 1988). Soils are immature Inceptisols and older Ultisols (Swank and Crossley 1988, Thomas 1996, USDA NRCS 2015). Soil depth decreases with increasing elevation.

Climate—

The climate is classified as marine, humid temperate (Cfb) based on Köppen's climate system (Swift et al. 1988). Average annual air temperature is 13 °C. Growing season is early May to early October. Average annual rainfall is 1700 mm at low elevations to 2500 mm at high elevations (Swank and Webster 2014). Average monthly precipitation is greatest in March and lowest in the fall, although tropical storms in autumn have produced record rainfalls.

Research History

Research at CHL originally tested theories in forest hydrology as put forth by C. R. Hursh in 1938 (Douglass and Hoover 1988). From 1934 to 1968, baseline data were collected to investigate effects of various land use practices, such as logging and cattle grazing, on water yield and water quality, such as turbidity. Later, these data provided a base on which to develop watershed-scale ecosystem studies. Research at CHL has been conducted under two main philosophies: (1) the quantity, timing, and quality of streamflow provide an integrated measure of the success or failure of land management practices; and (2) good resource management is synonymous with good ecosystem management (Swank and Crossley 1988).

In the early to mid-20th century, a suite of watershed management treatments was studied at CHL, consisting of several watershed timber cuttings, species conversions, and a prescribed burn. Swank and Crossley (1988) summarized the early watershed manipulations. Beginning in the 1970s, USFS scientists at CHL began collaborating with university scientists to address questions focusing on watershed nutrient cycling. This work was initially funded by the National Science Foundation (NSF) through the Institute for Broadening Participation program. In 1974 CHL scientists began an interdisciplinary study examining the effects of clearcut cable-logging to test hydrologic and ecological hypotheses and provide data relevant to forest land managers. In 1980, CHL became one of the original study sites in the NSF Long Term Ecological Research (LTER) program. In this program, investigator-led research projects, and USFS research cooperated to build an expanded ecological research program at CHL.

Stream ecosystem research began in the late 1960s at CHL, mostly in collaborations with universities, including the University of Georgia, Virginia Polytechnic Institute and State University, and North Carolina State University (Meyer et al. 1993, Tebo 1955, Woodall and Wallace 1975). During the 1980s, stream research focused on streams draining small catchments, including effects of drought on ecosystem structure and function (Wallace et al. 1991), clearcutting (Haefner and Wallace 1981, Swank and Webster 2014), stream macroinvertebrate removal (Cuffney et al. 1990, Lugthart and Wallace 1992), and debris-dam additions (Wallace et al. 1995). In the 1990s, research expanded spatially to include larger streams in the Coweeta basin. A study on Ball Creek examined the effects of gradients in geomorphology on ecosystem structure and function (e.g., Huryn and Wallace 1988). Research also shifted to focus on the controls of nutrient cycling and retention (Munn and Meyer 1990, Webster et al. 1991).

From the mid-1990s to the present, CHL streams became model systems to examine carbon (C) and nutrient limitation of detritus-based streams using whole-stream manipulations of nutrients and C inputs. Stream experimentation included litter exclusion, wood removal, leaf addition (Eggert and Wallace 2003a, Wallace et al. 1997a), riparian rhododendron removal (Yeakley et al. 2003), and stream nutrient additions (Cross et al. 2006, Rosemond et al. 2015). In the early 2000s, the focus of the LTER stream research program expanded beyond the Coweeta Creek basin to include a comprehensive study of drivers and effects of land use change across the southern Appalachians, focusing on the Little Tennessee River basin (Hagen et al. 2006).

Availability of Publications and Data

A complete CHL bibliography and searchable bibliographic database and a data file catalog can be found on the Coweeta LTER website (Coweeta LTER 2017a, 2017b). Long-term daily climate and streamflow datasets from CHL, formatted for ready comparisons with other experimental forests and ranges (EFR) and LTER sites, can be downloaded from the ClimDB/HydroDB website (LTER Network 2017). Long-term atmospheric deposition monitoring data from CHL are available via the National Atmospheric Deposition Program (NADP) data portal (NADP 2019).

Biological Responses to Stream Nutrients N and P

Issues of Concern

In the southern Appalachians, high-elevation, forested basins such as CHL have historically been regional sources of clean water. However, atmospheric deposition of N is increasingly a major source of N enrichment, especially in mountainous areas, which CHL represents. Furthermore, residential development and agriculture are both major sources of N and P to streams at low to mid elevations of the region, and although they do not occur within the Coweeta basin, where these types of land uses occur at higher elevations, they increase nutrient loading. Stream nutrient enrichment can negatively affect the beneficial uses of headwater streams and downstream water bodies. Beneficial uses at risk in North Carolina and surrounding states include (1) supporting aquatic life, (2) primary recreation (swimming, diving, water skiing), (3) secondary recreation (fishing, boating, fish consumption), (4) trout waters, (5) municipal water supply, and (6) outstanding resource waters. Excess N and P can degrade water quality to the degree that it does not meet numeric criteria for chlorophyll *a* (chl *a*), dissolved oxygen, or nuisance growth of algae. This concern applies to the streams and lakes downstream of CHL, such as the Little Tennessee River and Fontana Lake, and to streams and lakes in the surrounding states of Georgia, South Carolina, Tennessee, and Virginia, which have similar criteria to protect beneficial uses.

Nutrient addition experiments at CHL have used headwater streams as model systems to test the effects of nutrient enrichment that occur in human-modified landscapes on detritus-based processes in streams. Investigations at CHL have focused on effects of N and P on detritus-based pathways in aquatic systems, which have been less studied than these effects on algal-based pathways (Smith and Schindler 2009).

Findings From Studies

Ambient nutrient conditions—

Streams at CHL are generally nutrient poor, characterized by low concentrations of nitrate (NO_3^-), ammonium (NH_4^+), and phosphate (Swank and Crossley 1988, Swank and Vose 1997). The dominant form of N in CHL streams is NO_3^- because of rapid biological uptake of NH_4^+. Concentrations of NO_3^- range from ~10 to 200 µg/L but are typically <100 µg/L (Swank and Crossley 1988). Ammonium concentrations are typically <10 µg/L. Consequently, nutrient cycling in CHL streams exhibits high N uptake rates and thus tight nutrient cycling (Tank et al. 2000, Webster et al. 2003). Dissolved P concentrations in stream water are very low at CHL, typically <10 µg/L, thus streams also exhibit high P uptake rates (Mulholland et al. 1997). Mean annual rates of atmospheric deposition of inorganic N are ~6.1 and 7.2 kg N/ha/yr for low- and high-elevation watersheds, respectively. Annual deposition rates are increasing by ~0.084 kg N/ha/yr (Brookshire et al. 2011).

Effects of nutrients on stream carbon resources: detritus and algae—

As is common in closed-canopy forests, primary production by algae is light limited most of the year at CHL and contributes only a small fraction to the basal resources for consumers. Energy flow in streams at CHL is dominated by the decomposition of detritus, primarily plant leaf litter and wood, and is associated with heterotrophic bacteria and fungi (Hall et al. 2000, Wallace et al. 1997b). In these detritus-dominated systems, nutrient effects on detrital dynamics are more generally illustrative of effects on energy flow.

There have been two long-term whole-stream nutrient enrichment experiments conducted at CHL. The first study was conducted in watershed (WS) 53 and WS 54 using a paired-watershed approach (N + P experiment) (Suberkropp et al. 2010). N and P were added to one stream (WS 54) at an N:P ratio of 16:1 for 5 years (2000–2005) and responses compared to a reference stream (WS 53) (table 14.1). Both streams were sampled for 1 or 2 years pretreatment, depending on the response variable. The second study tested the relative importance of N and P on stream responses by adding nutrients to five streams in the Dryman Fork watershed for 2 years (2011–2013), with 1 year of pretreatment sampling (2010–2011; N × P experiment). Each of the five streams received different concentrations of N and P, resulting in a gradient of N:P ratios (Rosemond et al. 2015) (table 14.1). Other bioassays and short-term nutrient experiments have also been conducted in CHL streams (e.g., Tank and Dodds 2003).

Algal responses—

Although algal biomass is usually light limited at CHL, it may respond to nutrients under some circumstances. Nutrient enrichment experiments showed that responses in algal biomass occur during the spring months when irradiance is high or when riparian forest cover is reduced. For example, clearcutting of a watershed resulted in increased primary production, which led to increases in a grazing mayfly compared to a reference stream (Wallace and Gurtz 1986). However, a nutrient limitation study in the reference and clearcut stream found that although added N and P tended to increase algal biomass in the clearcut stream, differences observed were not significant (Lowe et al. 1986). This result corroborated that biofilms at CHL are primarily light limited (Lowe et al. 1986). Tank and Dodds (2003) found a similar nonsignificant increase in algal biomass in response to light in a separate study conducted during the fall in Ball Creek, which also found algal biofilms responded the most to P or N + P.

A 2-year continuous enrichment (N + P) of WS54 resulted in increased algal biomass chl *a* during the spring compared to a reference stream. However, another measure of algal biomass response, biovolume, did not significantly respond to enrichment, indicating higher chl *a*/cell (Greenwood and Rosemond 2005). In addition, enrichment increased algal growth rates, which is a proxy for productivity. The observed increase in chl *a*, even at peak biomass of 0.5 g ash-free dry-mass [AFDM]/m^2, still contributed only a very small portion to available resources compared to leaf litter standing crops (300 to 500 g AFDM/m^2) (Greenwood and Rosemond 2005). This study highlights the potential limits to the stimulation of primary production by nutrient enrichment at CHL and similar forested streams, although higher light availability would result in a greater response. Additionally, the study by Greenwood and Rosemond (2005) found that experimental enrichment did not alter the species composition of algae at CHL following 2 years of continuous enrichment.

Resources such as algal biofilms and detritus can change in their nutrient content as algae, bacteria, or fungi increase in biomass or acquire relatively more N or P vs. C in their tissues. Changes in the relative nutrient content (stoichiometry) of biofilms or detritus, with altered water column nutrient availability, can result in higher quality food for consumers, and can affect ecosystem functions. In studies at CHL, the nutrient content of algal biofilms (as C:N and C:P ratios) responded significantly to enrichment. The C:P ratio of biofilm changed the greatest compared to a reference reach (C:P = 845 vs. 1741), followed by reductions in N:P and C:N ratios. This finding indicated that biofilm resources become more nutrient rich in response to increased dissolved nutrient availability and that P content changed more than N content (Rosemond et al. 2008). Changes in biofilm nutrient content at CHL are consistent with several studies that show algal biofilms have relatively flexible stoichiometry (Stelzer and Lamberti 2002, Taylor et al. 2014) and increase in nutrient content when levels of water column nutrients rise.

Collectively, these studies suggest that when light is sufficient, such as during spring, streams at CHL appear to be nutrient limited and algae can respond to increased nutrient availability. Additionally, these studies show that the nutrient content of algal resources can respond to nutrient enrichment, which can have important implications for the quality of food to consumers.

Heterotrophic microorganisms and detrital dynamics—
Experimental nutrient enrichments at CHL have revealed strong effects on leaf litter breakdown and C dynamics. Enrichment of a stream with N and P at a target N:P ratio of 16:1 (table 14.1) increased breakdown of leaf litter two- to threefold compared to reference conditions for both red maple (*Acer rubrum* L.) and rhododendron (*Rhododendron* L.) litter (Greenwood et al. 2007, Gulis and Suberkropp 2003). The breakdown rate was greater for rhododendron, which has a lower initial

Table 14.1—Nutrient concentrations and years of treatment for the N + P and N × P enrichment experiments

		Year		SRP	DIN
	Stream[a]	(July-July)	Treatment[b]	(µg/L)	(µg/L)
N + P experiment	WS 53	1999–2000	PRE	6.8 ± 3.0	23.2 ± 8.5
		2000–2005	REF	8.0 ± 1.3	31.0 ± 3.4
	WS 54	1999–2000	PRE	9.5 ± 2.3	29.3 ± 4.9
		2000–2005	ENR	80.0 ± 5.6	506.2 ± 36.3
N × P experiment	2:1	2010–2011	PRE	2.9 ± 0.2	18.1 ± 1.5
		2011–2013	ENR	47.5 ± 4.3	75.4 ± 7.5
	8:1	2010–2011	PRE	2.5 ± 0.2	111.6 ± 17.3
		2011–2013	ENR	47.8 ± 8.0	180.8 ± 15.8
	16:1	2010–2011	PRE	3.0 ± 0.5	37.4 ± 5.7
		2011–2013	ENR	35.6 ± 3.8	307.5 ± 40.8
	32:1	2010–2011	PRE	3.1 ± 0.3	188.8 ± 14.4
		2011–2013	ENR	20.1 ± 2.6	314.5 ± 41.7
	128:1	2010–2011	PRE	2.5 ± 0.2	56.6 ± 7.8
		2011–2013	ENR	7.1 ± 0.8	303.0 ± 34.5

For the N × P experiment, stream numbers represent target N:P ratios. Values for WS53 and WS54 are from Davis et al. (2010a).

[a] Five streams in the Dryman Fork watershed were enriched for 2 years at different concentrations of N and P and N:P ratios. WS54 was enriched with nitrogen + phosphorus (N + P) at 16:1 N:P ratio from 2000 to 2005.

[b] Treatment indicates the concentration of soluble reactive phosphorus (SRP ± SE) or dissolved inorganic nitrogen (DIN ± SE) during pre-enrichment (PRE), reference conditions, or enriched (ENR) periods.

nutrient content. In the N × P experiment, breakdown rates increased for maple and rhododendron in all treatments 2.2- and 4.9-fold on average, respectively. Stream water N and P concentrations were roughly equivalent predictors of breakdown rate, and mechanistic pathways of nutrient effects occurred via both microbial biomass and shredder biomass (Manning et al. 2015). A ~sixfold increase in breakdown rate was also reported for standardized wood veneers in the N + P experiment, but this effect was less pronounced on maple twigs, which have a lower surface:volume ratio compared to veneers (Gulis et al. 2004). Overall, the magnitude of response of wood was greater than that of leaf litter.

As a result of increased breakdown rates, nutrient enrichment drastically reduced leaf litter standing crops at the reach scale in both enrichment experiments. Summer minima of standing crops were much lower and occurred much sooner than in reference conditions (Rosemond et al. 2015, Suberkropp et al. 2010). Standing crops were reduced in the summer to an extent (<50 g AFDM/m^2) which may have negative consequences for secondary production of macroinvertebrates in the long term (Eggert and Wallace 2003b). The rate of whole-stream litter loss increased by ~58 percent, and N and P concentrations had approximate additive effects on the loss of detrital standing crops (Rosemond et al. 2015). Moreover, the effect of enrichment on leaf litter standing crops was retained across a discharge gradient of <1 to 20 L/s. Related to these findings, Benstead et al. (2009) reported increased fine particulate organic matter (FPOM) export in the enriched stream compared to the reference stream in the N + P experiment. Increased FPOM export indicates that a higher proportion of particulate C is transported downstream instead of being used by organisms; and also reflects increased shredder activity. Ultimately, these studies show that nutrient enrichment accelerates reach-scale loss of detrital C owing to more rapid export of particulate C, which reduces storage of a vital energy resource.

The effects of nutrients on emergent stream functions, such as litter breakdown rates and retention of C, are due to the responses of heterotrophic bacteria and fungi to increased nutrients. These microorganisms are important components of food webs at CHL (Hall et al. 2000). Fungi colonize detritus when it enters a stream, alter detrital stoichiometry by taking up nutrients, and contribute to decomposition via mineralization of leaf C. Fungal biomass and production increased on leaf litter in response to added nutrients in the N + P experiment, which led to higher microbial respiration rates and thus contributed to increased rates of litter breakdown (Gulis and Suberkropp 2003, Suberkropp et al. 2010). Fungal biomass and respiration rates increased on leaf litter to a greater extent than bacteria increased on FPOM (Tant et al. 2013). At Hubbard Brook Experimental Forest (HBEF) (chapter 3), fungal biomass and respiration rates on leaves vs. wood showed a similar response to nutrient enrichment (Stelzer et al. 2003). Bioassays comparing responses of microbial biofilms in reference and litter-excluded streams at CHL found that fungal biomass was co-limited by N and P (Tank and Webster 1998), although another bioassay study found fungal biomass in Ball Creek to be primarily P limited (Tank and Dodds 2003).

Similar to algae, the nutrient content of detritus increased in response to experimental nutrient addition (Rosemond et al. 2008). The quality of detritus for consumers is largely driven by its nutrient content, particularly the ratio of C:N:P, which is important for both C loss rates and detritivores. Several studies indicate that nutrient enrichment generally reduces the C:N or C:P of detritus (Cross et al. 2003, Tant et al. 2013). In the N + P experiment at CHL, enrichment reduced bulk leaf litter C:P by 37 percent and N:P by 42 percent, but C:N showed little change over 2 years of enrichment (Rosemond et al. 2008, Tant et al. 2013). In the N × P experiment, enrichment altered litter stoichiometry, with the greatest effect again being reduced C:P of litter, although C:N was also reduced (Manning et al. 2015). Litter N content increased with fungal biomass, and litter P content increased with stream water P concentration. Effects of enrichment on litter stoichiometry were found to occur via subtly different mechanisms for N and P, and those mechanisms drove microbial and invertebrate responses to enrichment (Manning et al. 2015). Findings at CHL are consistent with studies that found strong positive linkages between dissolved P concentrations and detrital P content by examining landscape gradients in stream nutrient concentrations in the U.S. interior highlands and Costa Rican tropical streams (Scott et al. 2013, Small and Pringle 2010).

Collectively, results of studies at CHL indicate that nutrient enrichment stimulated breakdown rates of leaf litter, and reduced overall storage of organic matter. Litter that is available to consumers was of higher quality owing to lower C:nutrient ratios. N and P both contribute to increases in litter breakdown and fungal responses. However, stream water P created stronger responses in detrital P content. These responses have important consequences for stream biota as well as downstream nutrient and C dynamics.

Effects of nutrients on macroinvertebrate biomass and production—Experimental nutrient additions at CHL have shown clear effects on biomass and production of macroinvertebrates, altered assemblage size structure, and altered food web structure. After 2 years of experimental enrichment of N + P, secondary production of the entire macroinvertebrate assemblage approximately doubled relative to a reference stream (Cross et al. 2006). This response was lower for long-lived species because they likely faced resource limitation resulting from depletion of detritus and have longer generation times (Cross et al. 2005). Higher shredder biomass was found in leaf packs during this same experiment (Greenwood et al. 2007). The response was mediated by a near doubling of the flows of C, N, and P from basal resources to macroinvertebrates associated with an increased proportion of detrital C consumed (14 percent pretreatment vs. 35 percent during enrichment) (Cross et al. 2007).

In this study, increases in secondary production were primarily driven by reductions in the elemental imbalances between food resources and consumers. However, by the end of year 5 of enrichment, food web structure changed (Davis et al. 2010a): specifically, predator efficiency decreased in response to enrichment, as evidenced by a decreased proportion of primary consumers consumed. This occurred despite secondary production of primary consumers increasing 2.2-fold in the nutrient-enriched stream. The effect of increased primary consumer production did not result in increased production of macroinvertebrate predators over the long term. This was driven by increased dominance of a large-bodied shredding caddisfly (*Pycnopsyche gentilis*) that was largely invulnerable to predation because it builds stone cases in later instar stages. Additionally, long-term enrichment had a greater effect on larger bodied vs. smaller bodied primary consumers, shifting the size distribution of primary consumers. After 5 years of experimental enrichment, small-bodied primary consumer biomass was similar to pretreatment levels. Abundance of primary consumers also decreased to pre-enrichment levels, indicating that enrichment increased overall body size of consumers. Conversely, small-bodied predator biomass and abundance exhibited a positive long-term response to enrichment, while large-bodied predators did not (Davis et al. 2010b). Similar results were found across an urban nutrient gradient in which predator production did not track total primary production owing to the increase in large-bodied noninsect taxa that were invulnerable to predation (Johnson et al. 2013). Therefore, positive effects of enrichment on primary consumer production may not propagate to larger macroinvertebrate predators; instead "trophic dead ends" can be created if energy flow is diverted to a few dominant taxa.

Consumer nutrient content—

Experiments conducted at CHL were some of the first to show that the nutrient content of food resources can lead to changes in the nutrient content of consumers (Cross et al. 2003). In contrast to the flexible nutrient content in algae and detritus, consumers are theoretically and empirically less flexible in their body-nutrient content (Sterner and Elser 2002). Nevertheless, Cross et al. (2003) found that P content of some macroinvertebrates increased after 2 years of enrichment in the N + P experiment. The variation in invertebrate C:N:P was reduced by 30 to 40 percent in the enriched stream. Caddisflies (Trichoptera) as a group exhibited the greatest change in body C:P compared to other insect orders. Changes in consumer body nutrient content of macroinvertebrates may affect growth and production of higher trophic levels by reducing the consumer-resource imbalance between prey and their predators.

Macroinvertebrate assemblage structure—

Policy and monitoring associated with assessing stream health in regards to the Clean Water Act currently and historically have focused on macroinvertebrate assemblage structure and biotic indices (e.g., Barbour et al. 1999, Rosenberg and Resh 1993). Although most of the studies of biological responses to nutrient enrichment experiments at CHL have focused on food web production and system-level C and nutrient fluxes, some aspects of macroinvertebrate assemblage structure have been shown to respond. Size structure of macroinvertebrates was affected by enrichment, which affected both instream predators (Davis et al. 2010a) as well as riparian spiders (Davis et al. 2011). Analysis of the N + P experiment macroinvertebrate data indicated very little response of traditional bioassessment metrics to nutrient enrichment until year 5 of additions when the treatment stream began to exhibit a significant departure from reference. These metrics are, however, coarse measures of assemblage structure. A more sensitive, detrended correspondence analysis, showed that shifts in community structure were occurring as a result of experimental enrichment and that this shift increased in subsequent years of enrichment (Rosemond, n.d.).

Vertebrate predator response—

Effects of nutrient enrichment were also found to affect vertebrate predators. Larval salamanders are the dominant vertebrate predator in streams at CHL and the only vertebrate predators in high-elevation streams, which are inaccessible to fish. Both the longer term N + P experiment and the N × P experiment have shown that nutrient enrichment stimulated larval salamander growth and growth rates (Bumpers et al. 2015, Johnson et al. 2006). Larval *Eurycea wilderae* growth rates increased in response to added N and P after only 9 months of enrichment, indicating higher trophic levels can be affected by nutrient enrichment relatively rapidly (Johnson et al. 2006). In the N × P experiment, similar but more comprehensive studies found that larval *Desmognathus quadramaculatus* growth rates increased up to 40 percent in both an enclosure study and a mark-recapture study of free-roaming larvae. Average body size of free-roaming *E. wilderae* larvae increased up to 66 percent owing to experimental nutrient addition. For both species, higher growth rates and larger body sizes were positively correlated with stream water P concentration, but not N concentration (Bumpers et al. 2015). Analyses of salamander food webs in the N × P study found that *D. quadramaculatus* increased prey consumption, particularly of algivore prey relative to detritivores (Bumpers et al. 2017). Despite increased growth rates of *E. wilderae*, no significant diet response was detected in response to nutrient enrichment (Bumpers et al. 2017). The results of this study suggest that stream water P limited salamander growth in these systems. Together these studies indicate that nutrient effects can propagate through multiple trophic levels to affect vertebrate predators in largely P-limited streams such as those at CHL. Additionally, the positive nutrient effect on salamanders contrasted with the predaceous macroinvertebrate response, which showed no positive nutrient effect and became decoupled from prey. These results indicated that traits of individual predator species, such as life history and physiology, may strongly influence their response to nutrient enrichment.

Comparisons to other stream nutrient enrichment studies—
Few studies have been published of the responses of detritus-based stream systems to experimental nutrient additions with comparable spatial or temporal scales to the work done at CHL. Stelzer et al. (2003), for example, reported results of an ~9-week nutrient addition at HBEF. A long-term study by Slavik et al. (2004) investigated responses to 16 years of summer enrichment in the Kuparak River, an algal-based tundra river in Alaska. Energy flow in that river is dominated by instream algal primary production, which was initially stimulated by experimental P enrichment (Peterson et al. 1993). Macroinvertebrate responses were varied; several taxa responded positively via increased density or biomass, some taxa initially increased in density and then declined, and others were negatively affected by P enrichment (Peterson et al. 1993, Slavik et al. 2004). Growth rates of a vertebrate predator, adult arctic grayling (*Thymallus arcticus*), were stimulated by the addition of P (Slavik et al. 2004), which paralleled responses of larval salamanders in the CHL experiment. Unlike CHL, however, after 8 years of P enrichment, mosses replaced algae as the dominant primary producer, affecting insect abundances (Slavik et al. 2004), and a suite of ecosystem processes, including increased NH_4^+ uptake rates. A strength of the Kuparak study is that enrichment was studied long enough to capture complex and slowly developing responses to nutrient enrichment. Together with the work of Davis et al. (2010a) at CHL, these studies suggest that long-term responses of nutrients are difficult to predict from short-term experiments, highlighting the value of long-term (8+ years) experiments and monitoring. Additionally, the long-term enrichments at CHL and Kuparak River both revealed important biological consequences of nutrient enrichment, suggesting that approaches similar to those taken at these two sites have great potential to further understanding of biological and ecosystem responses to nutrient enrichment in other regions and stream types.

Other Factors Relevant to Biological Responses to Stream Nutrients N and P

Stream studies at CHL are part of an integrated ecosystem study based on collaboration between the USFS and universities and, as a result, many other long-term monitoring datasets and shorter term research results can provide a rich context for interpreting results, including how these factors interact with N and P in CHL streams. For example, long-term climate data (e.g., temperature and precipitation), streamflow, and water chemistry data exists for several study watersheds within CHL. See “Availability of Publications and Data” above for more information.

Effects of terrestrial organic matter inputs—

Terrestrially derived organic matter plays a critical role in ecosystem structure and function of CHL streams. In 1993, a long-term, large-scale experiment was initiated at CHL in which leaf litter and wood inputs were excluded from a stream draining WS55 to investigate how terrestrial carbon inputs influence stream processes. A mesh canopy eliminated organic matter inputs into the stream for a 13-year period and results have been compared with a nearby reference stream. In 1996, all small wood (<10 cm diameter) was removed from the treatment stream, followed by large-wood removal in 1998. “Artificial wood,” consisting of polyvinyl chloride pipes, was subsequently added in 2000, and leaf litter in 2001. These experiments allowed a step-by-step assessment of the role of detrital organic matter in headwater stream processes (Wallace et al. 1997a, 1999, 2015). Leaf standing crops declined to near zero during year 1 of the exclusion and remained low until leaf litter was experimentally added back to the stream (Eggert et al. 2012). Phosphorus uptake in the treatment stream was greatly reduced following leaf exclusion relative to the reference stream (Webster et al. 2000) and remained very low during the wood-removal periods. Ammonium uptake rates were reduced as well, as indicated by increased uptake lengths. Nutrient concentrations in stream water were unaltered by leaf exclusion and were not significantly different from the reference streams (Tank et al. 1998). When leaves were added back into the stream, P uptake increased but was still below pretreatment levels. Only after 3 years of leaf addition did phosphorus uptake return to reference levels (Webster et al., n.d.). There was also evidence that biofilms were enhanced in the treatment stream during the litter-exclusion period, likely owing to reduced uptake on detrital resources (Tank and Webster 1998). Long-term measurements of the response of stream processes to leaf litter and wood manipulations unequivocally demonstrate the coupling of nutrient processes with detrital standing crops and the crucial role that organic matter plays in regulating headwater stream ecosystem structure and function.

Effects of dissolved organic carbon—

Dissolved organic carbon (DOC) is an important energy resource for microorganisms (e.g., Hall et al. 2000) and can control nutrient dynamics in streams (Bernhardt and Likens 2002). Brookshire et al. (2005) found that the addition of NO_3^- increased DOC uptake in Hugh White Creek in CHL. Moreover, demand for dissolved organic nitrogen (DON), such as urea, increased with DOC demand. This study demonstrated the tight coupling of N and C dynamics at CHL. DON demand is mediated by DOC demand, and DOC demand is mediated by dissolved inorganic N (DIN) availability, suggesting changes in either DOC or DIN can affect the other (Brookshire et al. 2005). These findings are consistent with those at HEBF (see chapter 3) and suggest that DOC dynamics have important consequences for stream nutrient dynamics and vice versa. Additionally, Wilcox et al. (2005) experimentally added labile DOC to a stream and found that bacterial densities and microbial respiration rates increased by threefold, likely affecting DIN dynamics. Chironomid growth rates also increased as a result of DOC addition.

Effects of climate—

Increases in temperature appear to increase N export and accelerate ecosystem N loss (Brookshire et al. 2011). Long-term trends and seasonality of NO_3^- concentrations in stream water at CHL are largely explained by microbial responses to temperature. The effect of warming may have a much greater effect on N export than atmospheric deposition, suggesting that in the southern Appalachians, the direct effect of climate change may increase NO_3^- export in stream water more than expected export from N deposition (Brookshire et al. 2011). However, the potential interactions between stream nutrient enrichment and climate warming has not been well studied.

Reference Watersheds

The CHL maintains eight designated reference study watersheds: WS 2 (12 ha), WS 14 (61 ha), WS 18 (13 ha), WS 27 (39 ha), WS 31 (34 ha), WS 32 (41 ha), WS 34 (33 ha), and WS 36 (49 ha), which have had minimal onsite human disturbance since they were established in 1943 or earlier (Swank and Crossley 1988). These watersheds have served as references in many studies at CHL and have been continuously monitored and studied as model systems for reference conditions in headwater streams of the southern Appalachians. However, larger scale environmental changes have likely affected these reference basins, including increased atmospheric N deposition (Brookshire et al. 2011) and increasing mean annual temperature (Laseter et al. 2012). Exotic organisms have also impinged upon the Coweeta basin as a result of exurbanization (Scott and Helfman 2001). Hemlock woolly adelgid (*Adelges tsugae*), an exotic insect pest, has caused tree mortality that may potentially affect streamflow and stream chemistry at CHL (Brantley et al 2014), and cankerworm infestations partially defoliated WS 27 and WS 36 from 1972 to 1979 (Swank and Crossley 1988). Such exogenous perturbations are similar to what could be expected in other relatively undisturbed mountain watersheds in the region.

Baseline monitoring of stream water N (NO_3^-, NH_4^+) and P (soluble reactive phosphorus [SRP]) was initiated in CHL reference watersheds from 1971 to 1985, depending on the watershed, and has continued to the present. Monitoring of stream water total N and total P were added in 2005 and 2007, respectively (Miniat 2014).

A recent analysis of long-term trends in CHL stream chemistry (1972–2007) showed increasing NO_3^- and NH_4^+ concentrations in four reference watersheds of the CHL (Adams et al. 2014, Argerich et al. 2013). The increasing NO_3^- trend (mean increase of 0.2 μg N/L/yr for NO_3^- and 0.08 μg N/L/yr for NH_4^+) from minimally disturbed watersheds contrasts with the decreasing trend observed in the northern Appalachians where stream N concentrations are much greater than those found at CHL (see HEBF, chapter 3). The increasing trend in stream NO_3^- at CHL is likely partially driven by increasing atmospheric N deposition (Brookshire et al. 2011).

Cross-Site and Regional Studies

Nutrient dynamics—

Nutrient dynamics and transformations in CHL streams, such as uptake rates and denitrification rates, have been compared to streams in surrounding areas of the southeastern United States across a gradient of land use, and with other streams in North America (LINX collaborators 2014, Mulholland et al. 2008). These studies were part of a large continental-scale study of N dynamics in streams called the Lotic Intersite Nitrogen Experiments (LINX I and II). In these studies, isotopically labeled N was added to streams as ammonium (LINX I) or nitrate (LINX II). Compared to other LINX I study streams, Ball Creek at CHL exhibited very low rates of nitrification, accounting for only ~3 percent of NH_4^+ removal (Peterson et al. 2001). Webster et al. (2003) found that Ball Creek had very high NH_4^+ uptake velocity. These rates were higher than that of Walker Branch, a comparable but lower discharge forested headwater stream in Tennessee (Peterson et al. 2001). The high NH_3^+ uptake rates were likely due to seasonal differences between measurements. Ball Creek measurements were made during autumn and reflect heterotrophic demand from microbial colonization of newly fallen detritus; whereas Walker Branch measurements were made during spring (Mulholland et al. 2000). Additionally, Ball Creek measurements of NH_3^+ uptake rates in the LINX I studies were higher than that reported by Hall et al. (1998) for Hugh White Creek during the summer in Coweeta. Valett et al. (2008)

found strong and predictable seasonal patterns of N uptake in forested CHL streams (uptake lengths from 16 to 752 m). Demand was highest in the autumn, when allochthonous litter inputs peaked (uptake velocity four- to sevenfold higher than in other seasons). The autumn pulse of resources overwhelms thermal controls on N uptake, demonstrating the importance of organic matter in driving nutrient-uptake dynamics. Mulholland et al. (2008) compared NO_3^- removal dynamics in forest, urban, and agricultural streams across eight biomes, including three streams at CHL. They found that at low NO_3^- concentrations, biotic N removal is high and primarily occurs in small streams, such as those at CHL. Additionally, as NO_3^- increases, areal uptake rates of NO_3^- increase, but efficiency decreases.

Mulholland et al. (1997) compared P uptake between Hugh White Creek at CHL and Walker Branch in Tennessee. They found that the microbial community in Hugh White Creek exhibited high demand for P, as evidenced by rapid P uptake, and was likely a result of low ambient P concentrations and a greater supply of higher quality organic matter, compared to Walker Branch. The high rates of P uptake and short uptake lengths (~30 m) were similar to those reported by Webster et al. (1991) for other CHL streams. The hyporheic zone accounted for ~43 percent of P uptake in Hugh White Creek but was negligible in Walker Branch.

Regional studies of interacting factors with nutrients—
Forests at CHL are part of LTER-sponsored studies of human impacts along a gradient from forest to urban and agriculturally developed land in the Little Tennessee River watershed. These studies incorporate the effects of human disturbance and social dimensions of land use change on aquatic ecology (e.g., Brookshire et al. 2011, Cheever et al. 2012, Hagen et al. 2010). Nutrient concentrations, and the potential for greater primary production, increased with distance downstream from forested headwater streams (Gardiner et al. 2009, Scott et al. 2002). These regional studies have shown that co-occurring stressors from human disturbance created complex and variable ecosystem responses, such as mixed responses of litter breakdown to increased nutrients. Possible interacting factors include contaminants, altered bed substrate, altered temperature and flow regimes, and changes in macroinvertebrate assemblages. Hagen et al. (2006) found general increases in leaf litter breakdown rates along a gradient from forested (low-nutrient) to heavy agricultural (high-nutrient) streams in the Little Tennessee River basin near CHL. However, within the agricultural land use gradient, there were no significant relationships with nutrient concentrations. The lack of response to nutrients among agricultural streams was likely due to interacting factors related to land use, such as altered shredder abundance, temperature, or flow, that negated effects of increased nutrient availability.

Dose-Response Studies

Biological responses to a range of experimental additions of N and P to streams at CHL have been presented in the "Findings From Studies" section above and in table 14.1.

An additional nutrient-enrichment study at CHL was conducted in experimentally constructed streamside channels. This experiment used a greater range in concentrations of N and P than the whole-stream manipulations. Microbial breakdown of red maple and rhododendron leaf litter was tested across a gradient of 25 low to moderate N (32 to 550 μg N/L) and P (4 to 90 μg P/L) concentrations at N:P ratios ranging from 2 to 127. With enrichment, rates of breakdown of maple and rhododendron increased up to six- and twelvefold, respectively (Kominoski et al. 2015). Concentrations of both N and P were more closely related to breakdown rate than microbial biomass and respiration, which were more variable, but microbial biomass and respiration were also stimulated by N and P additions. This study suggests that concentrations of N and P that are common across the southeastern United States are stimulating microbial breakdown of leaf litter and, where both nutrients are high in streams, this effect is exacerbated (Kominoski et al. 2015).

Responses to Forest Management and Natural Disturbances

Studies at CHL evaluating the effects of various forestry practices were pivotal in the early development of best management practices (BMPs) (see Prud'homme and Greis 2002). Direct tests of BMPs at CHL have helped shape and revise those practices (e.g., Swift 1986). For example, stream responses to clearcutting of a watershed were studied in the late 1970s. Changes in Big Hurricane Branch, a second-order stream, following clearcutting of the entire watershed included increased streamflow, higher summer water temperatures, increased light, increased sediment load, and increased nutrient concentrations (Webster et al. 1983). Despite fertilizer application, NO_3^- levels did not increase significantly until 9 months after logging. This was largely attributed to biological uptake of nutrients before they reached the downstream weir where samples were taken. Peak NO_3^- concentrations were observed 1 year after logging, and increases in stream water concentration were attributed to increased N availability resulting from reduced forest vegetative uptake. During the next several years, NO_3^- concentrations decreased slightly owing to forest regrowth. However, concentrations then began increasing again, 12 years after cutting, peaking 20 years after treatment (Swank et al. 2001). These delayed N increases, long after treatment, were primarily due to insect infestation that killed a large stand of black locust (*Robinia pseudoacacia* L.), an N-fixing tree, and hydrologic variability. Decomposition of the dead trees contributed to NO_3^- enrichment more than a decade after the initial logging treatment. This response shows complex interactions between logging and forest succession related to instream nutrient dynamics and highlights the importance of long-term monitoring for interpretation of stream recovery from disturbances (Swank et al. 2014). Export of other ions and solutes besides NO_3^-, as well as streamflow, approached pretreatment levels 4 to 6 years after treatment (Swank et al. 2014).

Natural disturbances can also increase stream nutrient concentrations and alter detrital dynamics. For example, insect defoliation elevated stream N concentrations (770 µg NO_3^-/L in the disturbed stream vs. 6 µg NO_3^-/L in the reference stream) and increased leaf litter breakdown. (Meyer and Johnson 1983).

The effects of experimental near-stream rhododendron removal and naturally caused hurricane blowdown on nutrient export were compared for 3 years in WS 56. Nutrient losses from the soil water to the stream were significantly greater from the blowdown than from the rhododendron removal (Yeakley et al. 2003). The blowdown doubled hydrogen ions and increased NO_3^- in groundwater fourfold, and stream water NO_3^- concentration twofold, whereas the rhododendron removal increased NO_3^- concentration in streams 1.66-fold. Nutrient concentrations remained elevated 3 years following the blowdown (Yeakley et al. 2003). Chlorophyll *a* concentrations of instream primary producers increased downstream of both the rhododendron removal and blowdown areas and were related to increased light levels and nutrients (Eggert, n.d.).

Several studies at CHL show that riparian disturbances can create significant changes in DOC concentrations. Meyer and Tate (1983) found that DOC concentrations and export of DOC in a stream draining a clearcut watershed increased relative to a reference. Recent analysis 25 years after cutting indicated that DOC concentrations have since decreased, suggesting a net depletion of DOC sources as a result of clearcutting (Meyer et al. 2014). Meyer et al. (1998) found reduced DOC concentrations in the litter-exclusion project, which was primarily driven by reduced instream litter, illuminating the importance of leaf litter for DOC dynamics. Additionally, Yamashita et al. (2011) examined DOC quantity and quality in a reference stream compared to streams that underwent clearcutting and conversion to white pine (*Pinus strobus* L.) and found that concentrations of DOC in the disturbed watersheds were lower than in the undisturbed watershed. Collectively, these studies demonstrate how forest management and other human alterations to terrestrial habitats can affect stream water DOC. The tight coupling between DOC and nutrient dynamics suggests that perturbations that cause changes in DOC dynamics may alter nutrient dynamics and vice versa (e.g., Brookshire et al. 2005).

Reliability and Limitations of Findings

Results obtained at CHL generally represent southern Appalachian hardwood forest headwater streams that are relatively undisturbed or have received land use practices similar to those that have been implemented at CHL, such as timber harvesting and forest road construction. However, caution should be used when applying the findings of CHL to other stream systems. Validation studies may be needed in those areas to test how well CHL findings predict local conditions. Studies that use landscape-level gradients of nutrient concentrations owing to land use can provide insight into regional responses to nutrient enrichment (e.g., Evans-White et al. 2009). Finally, the long-term responses to enrichment in forested streams in the Southeast for periods longer than 8 years have not been studied and are not well understood.

Research Needs

From the perspective of the regional regulatory community, the highest priority research need that might be filled at CHL would be a better understanding of short-term vs. long-term nutrient enrichment effects and what thresholds of N and P enrichment produce biological responses. Filling this research need would be useful to water quality regulatory agencies for reducing scientific uncertainty in setting conservative nutrient criteria that consider effects of long-term chronic enrichment and avoid the negative consequences of nutrient enrichment in low-nutrient streams with high-quality water. Given biological responses to nutrients that were unexpected and manifested 3 years after enrichment at CHL (Davis et al. 2010a), it is critical to understand how streams in the southeastern United States will respond to chronic nutrient loading for periods longer than 8 years and how these long-term responses might differ from the 2- to 5-year studies that have been conducted.

Research conducted at CHL has shown that valuable insights into biological responses to stream nutrient enrichment can be obtained from stream-reach experimental nutrient additions, which are difficult to detect from landscape gradients because of confounding influences such as co-occurring additional stressors. A greater understanding of the long-term effects of nutrient enrichment could be gained at CHL by conducting long-term enrichment studies that compare and contrast acute (1-year) vs. chronic (10 years) nutrient enrichment to explore the relative influence of each, and, of particular interests to regulators, to identify what specific biological responses occur at threshold concentrations of N and P. Coweeta Hydrologic Laboratory could be used to conduct such studies because the relatively undisturbed streams would facilitate the isolation of nutrient effects. To capture long-term responses and feedbacks associated with N and P enrichment, experiments would need to be conducted for 8 years or longer. Studies should incorporate both structure (assemblage) and functional (process) measures and investigation of the effects of co-limiting factors, such as light and temperature, in their design. Specifically, researchers would need to test a replicated gradient of low to moderate N and P concentrations over this long-term period and measure responses of chl *a*, terrestrially-derived C, and biological metrics currently used in nutrient criteria and bioassessment. An additional element could include alternating the dosage frequency across streams to compare responses to short- to long-term exposures to the same overall nutrient load. This design could be replicated on other relatively undisturbed streams at EFRs in other regions to broaden the applicability of results. Lastly, recovery trajectories would need to be monitored in order to fully understand how systems respond to and recover from chronic nutrient loading. This experimental framework would deliver valuable information over a long time period.

A number of secondary questions might also be addressed within this kind of experimental framework. Although answering them may be of lower priority for meeting regulators' science needs, they do address issues of importance to water quality criteria for nutrients, such as the frequency of nutrient delivery, but also illustrate the potential that this research approach might have to broaden the range of biological responses that could be considered in water quality standards for nutrients.

- How do changes in N and P loading interact with changes in C inputs and other stressors such as temperature and hydrology to affect carbon exports from streams?
- How resilient are streams to nutrient enrichment? Unexpected results and changes that occurred after 5 years of nutrient addition found by Slavik et al. (2004) and Davis et al. (2010a) highlight the need for more long-term experimental studies and comprehensive long-term monitoring of all biological components of stream ecosystems.
- What ecosystem characteristics confer resistance to nutrient effects? The interactions between detrital carbon and nutrients suggest that protecting or enhancing carbon inputs will promote nutrient uptake and reduce negative ecological consequences.
- How long does recovery from nutrient enrichment take and how do responses differ among the different levels of organization within the ecosystem, such as at the organismal, population, community, and whole-ecosystem levels?
- How does nutrient enrichment compare with responses to other commonly co-occurring stressors, such as sediment, riparian removal, and geomorphic alteration? Are there specific nutrient-related response signatures that can be used to diagnose nutrient stress among multiple stressors? Do other stressors amplify or mitigate nutrient enrichment?

Potential Utility to Water Quality Regulatory Agencies

Research from CHL on effects of N and P contribute valuable insights into the way detritus-based streams respond to enrichment, especially highlighting that long-term stream food web responses are difficult to predict from short-term enrichments, and that stream carbon dynamics interact in complex ways with nutrients. In general, research at CHL can offer valuable insight into the management of nutrients and highlight the profound effect that nutrients have on terrestrially derived carbon resources, which are critical for the support of stream food webs.

Long-term studies at the minimally disturbed catchments of CHL contribute valuable data on expected concentrations and long-term trends of nutrients in Appalachian streams in the southeasern United States, as well as data on natural variability of those concentrations that are crucial to informing regulatory agencies about magnitude and frequency components of numeric criteria. The streams at CHL also still represent the lower stress load and higher resistance end of response curves, and the research there is providing important information on ecological response thresholds at that end of the gradient. For example, responses to enrichment at CHL have been identified at low to moderate, yet realistic, levels of nutrient enrichment relative to those that occur across the southeastern United States, nationally, and globally (Scott et al. 2002, US EPA 2013, Woodward et al. 2012). Thus, meaningful consequences to ecosystem processes and stream biota are likely to occur in detritus-based forest streams in the Southeast that are experiencing increases in nutrients as low as ~200 µg/L DIN and ~15 to 20 µg/L SRP (Kominoski et al. 2015, Rosemond et al. 2015).

Research at CHL is providing much needed experimental nutrient stressor-response data on underappreciated detrital pathways by identifying ecological response thresholds that could be used by regulatory agencies as critical and powerful lines of evidence in developing defensible numeric nutrient criteria that include the effects of both N and P. There are many publications and datasets based on research conducted at CHL that help determine baseline nutrient conditions and changes that have occurred over the past 20+ years in these relatively unaffected streams. The two whole-stream enrichment studies at CHL provide comprehensive findings on the effects of nutrient enrichment in southeastern U.S. forest stream ecosystems. This research shows clear responses of detritus to increased N and P availability, highlighting the need to maintain detrital inputs into streams from streamside (riparian) forests in addition to managing nutrient concentrations.

Research at CHL has found that both N and P are important in driving the detrital responses. Additionally, the relationship of larval salamander growth and P concentration suggest that P enrichment, or N and P enrichment, may have a more pervasive effect on the entire ecosystem than N enrichment alone. Furthermore, the altered food web pathways that included macroinvertebrate stream predators at CHL, and required more than 3 years of nutrient enrichment to emerge (Davis et al. 2010a), have highlighted the need for longer term enrichment studies for detection of complex biological responses.

Key points:

- Enrichment with N and P reduces leaf litter standing crops and increases export of particulate C, reducing the temporal and spatial availability of a critical resource for ecosystem processes and consumers.
- Carbon resources such as leaf litter are key in processes such as nutrient uptake.
- N and P enrichment affects nutrient content of algae and detritus, with effects that propagate through stream food webs to affect invertebrate and vertebrate predators.
- The effects of nutrients on food webs depend on species-specific traits such as body size, generation times, and habitat preferences, which together drive consumer responses to nutrients.
- The highest priority research gap to fill is to better understand long-term (8 + years) ecosystem responses to N and P enrichment, to identify the concentrations at which predictable changes in biological structure and function occur, and to identify the degree that concentrations can deviate from references conditions before aquatic uses are negatively affected. Long-term enrichment studies that compare short-term (1 year) vs. long-term (8+ years) nutrient loading across gradients of nutrient concentrations would help close this information gap.

Biological Responses to Stream Nutrients Other Than N and P

Issues of Concern

There are currently no immediate concerns for stream health related to nutrients other than N and P, although changes in development or land use in the southern Appalachians might lead to future issues related to these nutrients.

Findings From Studies

The study watersheds at CHL are monitored for a suite of nutrients other than N and P, including Ca^{2+}, magnesium (Mg^{2+}), potassium (K^{+}), sodium (Na^{+}), Chloride (Cl^{-}), sulfate (SO_4^{2-}), and silicon dioxide (SiO_2). However, there are only a few experimental studies involving nutrients other than N and P. For example, Woodall and Wallace (1975) measured total standing stocks of Ca, Mg, and K in CHL streams.

Baseline monitoring of stream water chemistry indicates that Na^+ makes up about 43 percent of total cations followed by Ca^{2+} and Mg^{2+} (~23 percent each). Bicarbonate (HCO_3^-) makes up 74 percent of anions. Major differences can exist between low- and high-elevation streams, largely driven by differences in precipitation and streamflow. Notably, in high-elevation streams, concentrations of HCO_3^- are much lower, and SO_4^{2-} concentrations are much higher than in low-elevation streams (Swank 1988).

Reference Watersheds

Nutrients Cl^-, Na^+, Ca^{2+}, K^+, and Mg^{2+} have been monitored in reference watersheds W 2, W 18, W 27, and W 36 since 1971; in WS 14 since 1980, in WS 31 since 1984; and in WS 34 since 1985. Additionally, SO_4^{2-} and SiO_2 have been monitored since 1973 in WS 2, WS 14, WS 18, WS 26, and WS 36 (Miniat 2014).

Effects of Management and Natural Disturbances

Following conversion of a hardwoods watershed to white pine, retention of K^+, Mg^{2+}, and Ca^{2+} increased by 50 to 70 percent (Swank and Vose 1994). This was largely attributed to greater primary production by white pines. A threefold increase in stream water sulfate was also observed. The pine forest was a more conservative system for base cations owing to lower discharge and retention of soil ions. After clearcutting Big Hurricane Branch watershed, stream water concentrations of dissolved ions Ca^{2+}, SO_4^{2-}, K^+, Cl^-, Mg^{2+}, Na^+, and SiO_2 all changed (Webster et al. 1983). Initial small increases in Ca^{2+} and K^+ were attributed to fertilizer applied to roads. Calcium concentrations and export continued to increase and peaked 3 years after logging. Calcium and K^+ concentrations remained elevated but stabilized in the long term. Golladay et al. (1992) evaluated the effects of high rainfall events on the export of nutrients in two watersheds that were clearcut and in two reference watersheds. They found no significant changes in the net export of dissolved Ca^{2+} or K^+ in response to disturbance, but generally disturbed streams exported more particulate Ca and K, although differences in underlying geology may have influenced these results.

Webster and Patten (1979) examined Ca^{2+} and K^+ dynamics in three streams, two of which were experimentally manipulated: one was maintained as an old field, one was planted in pine, and the third was a reference hardwood forest. Forest disturbances resulted in moderate changes to Ca^{2+} and K^+ dynamics. Additionally, Swank et al. (2014) summarized stream water chemistry responses to forest disturbances at CHL (see also Swank 1988) and reported generally modest changes in concentrations of nutrient other than N and P in response to forest disturbances at CHL.

Research Needs

Currently, there are no critical research needs regarding nutrients other than N and P at CHL.

Potential Utility to Water Quality Regulatory Agencies

Research at CHL on nutrients other than N and P has not been as high a priority. However, it has revealed that watershed disturbances experienced at CHL do lead to changes in several stream nutrients, but generally other nutrients are altered less than N and P. If future water quality issues related to nutrients other than N and P were to arise in the region, CHL monitoring datasets and research results might be of use to regulators addressing those issues.

Key points:

- Underlying bedrock geology may influence responses of nutrients such as Ca, Mg, and K.
- Forest management disturbances at CHL generally have effects on other nutrients that are smaller than the effects on N and P.

Overview and Synthesis

The body of research conducted at CHL can provide valuable insights for the regulatory community. Results of long-term monitoring and studies of streams in reference watersheds at CHL are available to provide numeric values from minimally disturbed landscapes for use in setting numeric criteria. Coweeta Hydrologic Laboratory and other EFRs are vital repositories of some of the last remaining minimally disturbed lands that are available for study and provide scientific data on stream conditions needed to help set reference-based numeric values that can serve as lines of evidence in developing regional numeric criteria. Moreover, nutrient datasets from the network of EFRs, including CHL, can help inform regulatory efforts to classify nutrient chemistry regionally and nationally by providing a basis for quantifying natural variability and trends in reference stream nutrient concentrations as well as incorporating time-varying data into the setting of nutrient criteria, especially patterns in the delivery of nutrients.

Variability in ecological responses to nutrients in streams is, in part, a function of co-occurring stressors and co-limiting factors that often obscure or antagonize nutrient stress and make it difficult to identify response thresholds. Stream-scale nutrient enrichment experiments, such as those conducted at CHL, are critical for understanding the variety of ecological responses to nutrient enrichment and to identifying response thresholds, as well as disentangling the effects of co-occurring stressors and co-limiting factors, as was evidenced by the citation of CHL research in national stressor-response guidance and numeric nutrient setting efforts (e.g., US EPA 2010). Results of CHL research have strong potential to improve the clarity of ecological response models and to help develop more defensible numeric criteria for protecting stream ecosystems.

Numeric nutrient effects have largely focused on primary producer response pathways and have insufficiently considered the effects of enrichment on detrital pathways, as was demonstrated by an almost complete absence of attention given to detrital response pathways in guidance (US EPA 2010). An underlying assumption has been that small, headwater systems take up and process nutrients and thereby protect downstream waters. Results from experimental research at CHL provide scientific evidence that this benefit from headwaters systems also entails a cost of altered ecological structure and function, including significantly decreased nutrient uptake efficiency, and changes in organic matter dynamics, secondary production, and macroinvertebrate assemblage composition. There is a need to explore more thoroughly such complex biological responses to stream nutrients and how they manifest over larger spatial and temporal scales.

Lastly, there is an ongoing national debate among states on the relative role of N vs. P limitation and, despite pervasive evidence of colimitation (Elser et al. 2007), some continue to argue for management of a single nutrient, primarily P. There is, therefore, a current need for improved scientific understanding of effects of N enrichment on stream ecosystems and of the interactions of N and P in co-limited water bodies. The water quality regulatory community would benefit from science produced at CHL and other EFRs that helped to resolve this question.

Key points:

1. Potential practical uses by the regulatory community of science products from CHL:
    - CHL data provide robust characterization of baseline nutrient concentrations and natural variability in nutrient concentrations for southern Appalachian forested streams.
    - CHL nutrient addition experiments have produced a comprehensive understanding of N and P effects on detritus-based headwater streams based on stream-scale nutrient manipulations.
    - The nutrient addition experiments suggest the need to maintain or restore detrital inputs into streams in addition to setting numeric criteria for N and P.
    - Both N and P are important in driving ecosystem responses. The effects of nutrient addition on CHL streams occurred at low-to-moderate

concentrations of N and P relative to what is occurring across most of the southeastern United States and the nation.

2. Important scientific gaps for regulators that might be filled at CHL:
    - Increase understanding of how responses differ between chronic and short-term nutrient loading and how far N and P concentrations can increase before designated aquatic uses are negatively affected. Additionally, a comprehensive understanding of short- vs. long-term responses will require understanding how nutrient loading interacts with multiple stressors (e.g., riparian disturbance, other contaminants, altered geomorphology), as commonly occurs in streams in human-modified landscapes.
3. How priority science gaps might be filled at CHL:
    - Filling the identified information gaps would require specifically designed nutrient addition experiments that test a gradient of N and P concentrations (e.g., low/low, low/high, high/low, and high/high) over multiple generation times of organisms. Aquatic life uses should be monitored to determine negative biological responses to provide regulators with scientific evidence on response thresholds.
    - Recovery trajectories of streams could also be measured to better estimate how streams might respond to restoration by nutrient reduction management.

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