

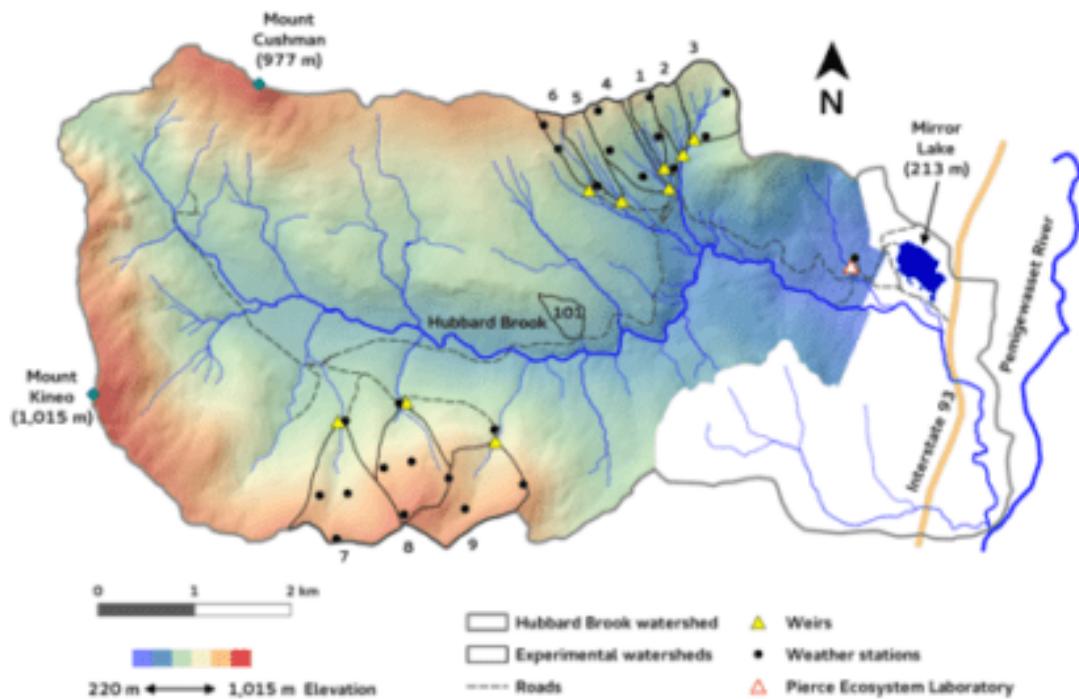
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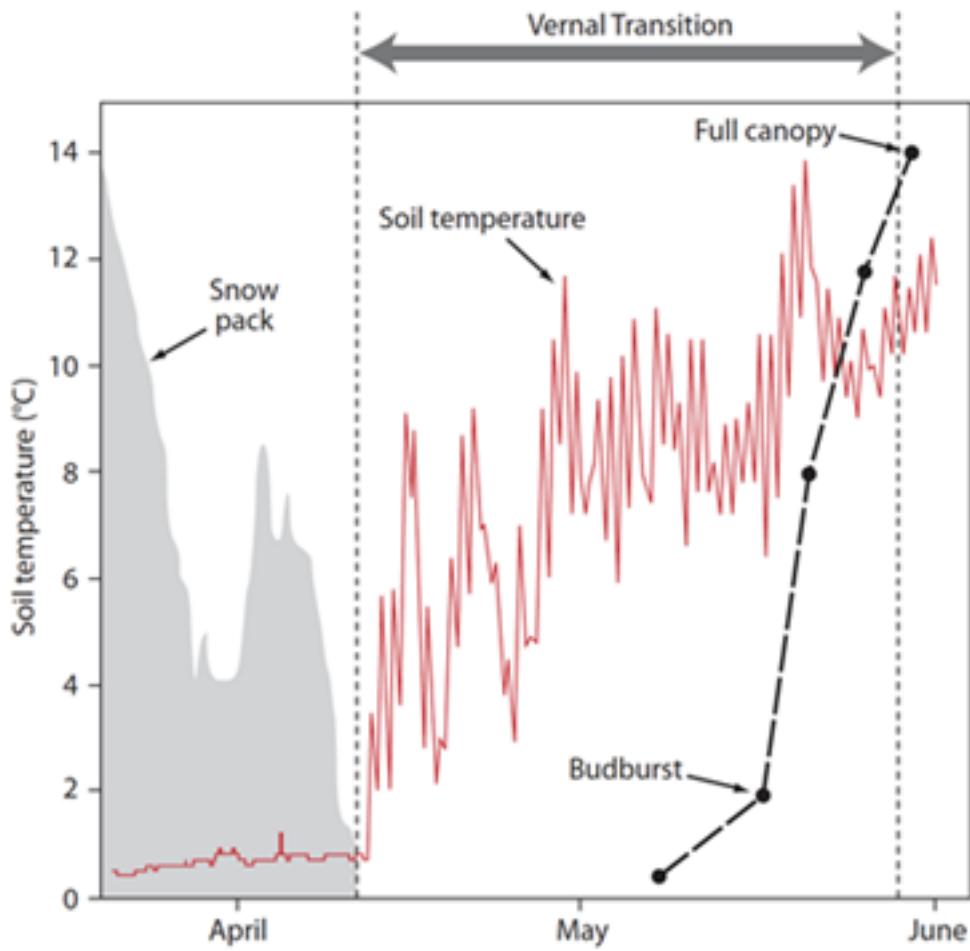
Introduction

This online book is designed as a concise but comprehensive synthesis of the HBES. Many readers will be interested to see the award-winning book by Richard Holmes and Gene Likens entitled, Hubbard Brook: The Story Of A Forest Ecosystem, a synthesis of the HBES for a general audience. Advanced readers are directed to the book, Biogeochemistry of a Forested Ecosystem (2013) by Gene Likens as well as the series of detailed element monographs published in the journal Biogeochemistry (Likens et al. 1994 (K), 1998 (Ca), 2002 (S); Fahey et al. 2005 (C); and Lovett et al. 2005 (Cl)). The synthesis is presented at the level of a graduate or advanced undergraduate student audience. The primary objective of the book is to introduce students and other prospective researchers to the current state of knowledge about the Hubbard Brook ecosystem. The chapters have been developed by scientific experts on each of the topics studied in the HBES, and they will be updated and expanded as new knowledge and data are generated by the HBES – it is meant to be a living volume. Links to the broader literature and to HBES data sets are provided to facilitate more detailed explorations. Teaching and learning exercises that utilize data from the HBES will be added as they are developed by our experts for academic use.



1. Site, History, and Research Approaches

For over 60 years scientists have been studying the dynamics of forests and linked aquatic ecosystems in the Hubbard Brook Experimental Forest, New Hampshire, USA. The Hubbard Brook Ecosystem Study (HBES) is an ongoing effort to understand the ecology, hydrology, energetics and biogeochemistry of this temperate forest ecosystem. The synthesis that follows provides an overview of several components of the HBES interpreted in light of current understanding at the level of the advanced student.



2. Climate Change

The Hubbard Brook Experimental Forest (HBEF) was established well before the issue of climate change emerged. However, many of the long-term measurements collected at the site have become valuable climate change indicators (Table 1). Perhaps any of these records would not be all that informative on their own, but combined they provide fairly convincing evidence of climate change at the HBEF that is compatible with regional trends in the northeastern U.S. (Hayhoe et al. 2007; Milillo et al. 2014).



3. Hydrology

The HBEF was established in 1955 for the purpose of studying the effects of forest management on streamflow and water quality, building upon pioneering work from other sites that established the efficacy of the paired small watershed approach (Bates and Henry 1928). The principle underlying the small watershed approach is that for a catchment with relatively watertight bedrock (thus minimal subsurface loss), water can leave the watershed only by stream discharge or evapotranspiration (ET).::

What's New

February 2026

- Lany et al. Foliar N - N chapter
- Possinger et al. Soil respiration - Soil biology chapter
- Bernhardt et al. Enhanced P weathering on WS5 - P chapter
- Green et al. IWUE and increased transpiration - Hydrology chapter
- Cleavitt et al. Sugar maple on WS5 - Vegetation chapter

1 Site, History, and Research Approaches

Chapter Editor(s): Timothy Fahey

For over 60 years scientists have been studying the dynamics of forests and linked aquatic ecosystems in the Hubbard Brook Experimental Forest, New Hampshire, USA. The Hubbard Brook Ecosystem Study (HBES) is an ongoing effort to understand the ecology, hydrology, energetics and biogeochemistry of this temperate forest ecosystem. The synthesis that follows provides an overview of several components of the HBES interpreted in light of current understanding at the level of the advanced student. The objective is to provide interested researchers with a succinct summary that will be helpful for guiding research and education efforts.

1.1 Site Description

The Hubbard Brook Experimental Forest (HBEF) is located in the southern part of the White Mountain National Forest (WMNF) in central New Hampshire (Figure 1.1). The HBEF is characteristic of much of the White Mountain National Forest (Fahey et al. 2015) The National Forest has hilly, occasionally steep topography; coarse, acidic, glacially-derived soils; bedrock dominated by metamorphic rock of igneous and sedimentary origin; northern hardwood forests on lower slopes and spruce-fir forests at higher elevations (above ca. 800 m).

1.2 Climate

The continental climate at the HBEF features long, cold winters and mild to cool summers (see Climate chapter). Major air flow over the forest is either (1) continental polar air from subarctic North America (the predominant direction), (2) maritime tropical air from the Caribbean and Gulf of Mexico from the south or southwest, or (3) maritime air from the North Atlantic out of the east or northeast. In spite of the proximity of Hubbard Brook to the ocean (116 km), the climate is predominantly continental.

Annual precipitation averages about 1,400 mm, of which about one third to one quarter is snow. A snowpack usually persists from mid-December until mid-April, with a peak depth in March of about 1,000 mm, having about 250 to 300 mm of water content.

Hubbard Brook Experimental Forest

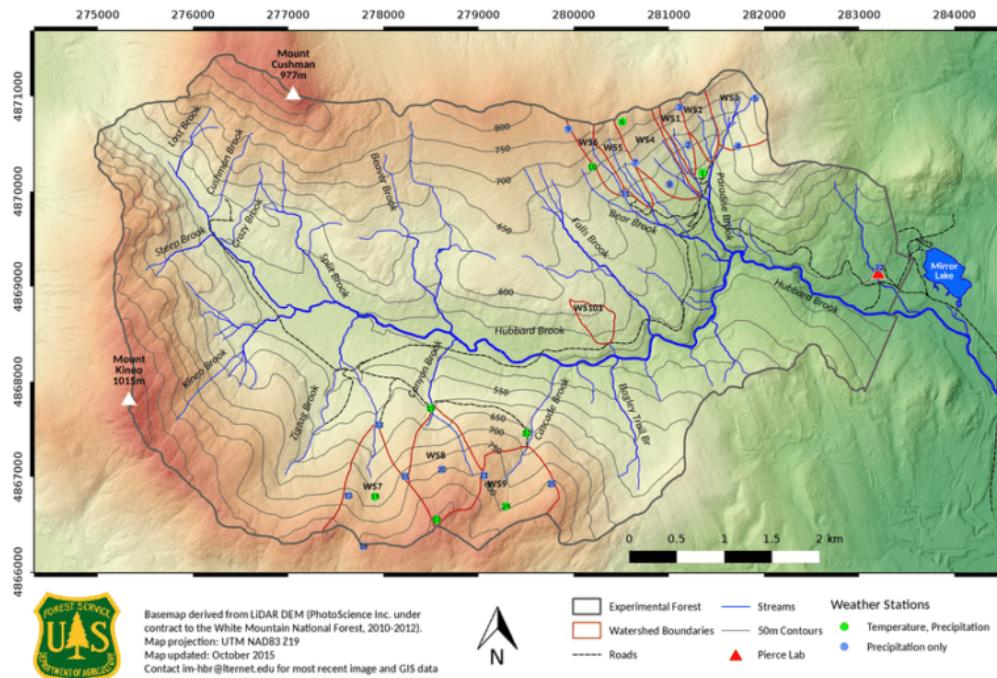


Figure 1.1: Hubbard Brook Experimental Forest Map

Winters are long and cold. January averages about -9°C, and long periods of low temperatures from -12 °C to -18 °C are common. Even though temperatures are low most of the time, occasional midwinter thaws result in elevated streamflow. Short, cool summers are the rule. The average July temperature is 18°C.

The average number of days without killing frost is 145; however, the growing season for trees is considered to be from 15 May, the approximate time of full leaf development, to 15 September, when the leaves begin to fall.

The estimated annual evapotranspiration (ET) is about 500 mm, determined by difference between precipitation and streamflow. This calculation is a reasonable approach for Hubbard Brook because of the apparent minimal deep seepage and annual removal of summer soil-water deficits by autumnal rains and spring snowmelt.

1.3 Geology

The eastern portion of the Experimental Forest (watersheds 1-6, and 9 included; Figure 1) is underlain by a complex assemblage of metasedimentary and igneous rocks. The major map unit is the Silurian Rangeley Formation, consisting of quartz mica schist and quartzite interbedded with sulfidic schist and calc-silicate granulite. Originally deposited as mudstones, sandstones and conglomerates, these rocks have been metamorphosed to sillimanite grade and have undergone four stages of deformation. Deformation style evident in outcrops is primarily tight isoclinal folds. However joints, slickensides and mylonites indicate brittle deformation as well. The metamorphic rocks were later intruded by a variety of igneous rocks including the Devonian Concord Granite, pegmatites, and Mesozoic diabase and lamprophyre dikes. The western portion of the forest (portions of watersheds 7 and 8 included) is underlain by the Devonian Kinsman Granodiorite, a foliated granitic rock with megacrysts of potassium feldspar.

Continental glaciers, which blanketed the region during the Pleistocene and retreated some 13,000 years ago, removed most preexisting soils. Glacial movement was primarily in a south-easterly direction as indicated by striations on bedrock surfaces, and by fragments of rocks in the till which are typical of bedrock to the northwest of the Hubbard Brook Valley. Materials deposited by the glacier are highly variable in degree of sorting and grain size, ranging from clays to 10m diameter boulders. The depth of glacial deposits ranges from zero on ridgetops and in stream valleys (resulting in bedrock outcrops) to 50m in the vicinity of Mirror Lake. Poorly sorted glacial till, commonly 2m thick, covers the bedrock in most of the valley. Ice contact terraces in the lower valley, consisting of well sorted sands and gravels, are typically tens of meters thick.

1.4 Soils

In the HBEF soils are predominantly well-drained Spodosols, more specifically, Typic Haplorthods derived from glacial till, with sandy loam textures. There are no residual soils, (i.e., derived from weathered bedrock). Principal soil series are the sandy loams of the Berkshire series, along with the Skerry, Becket, and Lyman series. These soils are acidic (pH about 4.5 or less) and relatively infertile (Table 1.1). A 20- to 200-mm thick forest floor layer is usually present. Soils on the ridgetops may consist of a thin accumulation of organic matter, resting directly on bedrock.

Table 1.1: Summary soils data for Watershed 5 at the HBEF (after Johnson et al. 1991a,b).

Soil Type	Typic Haplorthod; Typic Dystrochrept	
Soil Series	Berkshire; Skerry; Becket; Lyman; Tunbridge	
Property	Surface / Organic Layer	Mineral Soil
Avg. Depth (cm)	6.9	50.3
Mass (kg/m ²)	8.8	317.0
Soil Organic Matter (%)	60.0	10.0
pH in Water	3.9 (Oa Horizon)	4.3
Cation Exchange Capacity (cmol/kg)	18.0 (Oa Horizon)	5.0
Base Saturation (%)	50.0 (Oa Horizon)	12.0

The separation between the pedogenic zone and the virtually unweathered till and bedrock below is distinct. Depth to the C horizon averages about 0.6 m. At various places in the Forest, the C horizon exists as an impermeable pan. These layers restrict root development and water movement. Rocks of all sizes are scattered throughout the soil profile. In many locations boulder fields are prominent features.

A prominent feature of the surface topography throughout the HBEF is the rough pit-and-mound appearance caused by the uprooting of trees. Uprooting mixes mineral soil from lower mineral horizons with nutrient-rich organic surface layers or it can deposit the lower mineral layers directly on top of the forest floor humus layers without mixing, creating buried horizons. This natural disturbance changes seedbed conditions for regenerating species, and affects weathering and biogeochemical cycles.

1.5 Streams

Although stream channels occupy only 1% of the land area, the streams play an important role in many processes throughout the HBEF. The numerous streams in the HBEF range from small ephemeral channels that often dry up during summer to a large perennial 5th-order stream (Hubbard Brook). Because of the shallow soil depths and high soil porosity, the stream channels quickly swell during large storms (e.g., 80 mm or more). As much as 60 to 80% of storm precipitation can pass through the stream as storm flow.

Streamwater is usually characterized by low concentrations of suspended materials due to the coarse-grained texture of the soil. Mineral and organic particulate material is suspended and carried in storm periods, but once the flow recedes these materials quickly settle, leaving the stream with low concentrations of suspended solids. About 28 kg/ha of particulate matter (both inorganic and organic) are transported out of the watershed by streams each year.

Most of the stream channels have exposed bedrock at some locations. However, the first to third order streams have channels primarily made up of mineral and organic particulate matter lodged behind organic debris dams. These dams form a stair-step pattern in stream channels, and they play important roles in regulating many physical, chemical, and biological processes in the streams.

1.6 Historical Perspective

The Hubbard Brook Experimental Forest was established by the U.S. Department of Agriculture (USDA) Forest Service in 1955 as a major center for hydrologic research in New England. The initial size delineated for research was a 3,037-ha, bowl-shaped Valley (Figure 1).

During the first eight years following the establishment of the HBEF, the Northeastern Research Station of the USDA Forest Service developed a network of precipitation and stream-gauging stations, and installed weather instrumentation, as well as soil and vegetation monitoring sites on small experimental watersheds. Data from these installations combined with several initial studies formed the hydrometeorologic foundation for much of the future research at the HBEF. The major emphasis in these early studies was to determine the impact of forest land management on water yield, water quality, and flood flow.

The Hubbard Brook Ecosystem Study originated in 1960 with the idea of using a small watershed approach to study element flux and cycling. The initial development of the HBES was slow and deliberate. The entire effort during the first two years, 1963-1965, was conducted by three scientists and one technician at Dartmouth College and three scientists and one technician from the USDA Forest Service (USDA-FS). At that time, there were no precedents to follow since comprehensive studies of ecosystems had not been initiated. Using the small watershed approach, studies of element-hydrologic interactions were conducted to form a basis for subsequent process-level and experimental research. In this regard, the investigators were

fortunate to rather quickly develop quantitative element budgets for replicated ecosystems. These results provided insight into the function of natural ecosystems and helped focus future lines of research. It was agreed that slow growth would be more manageable and would allow for interaction among all senior investigators, ensuring proper coordination and development of the overall study. Research problems that were timely and particularly pertinent to the overall research goals of the study were identified. From the beginning, the HBES has emphasized the value of knowledge derived from cooperative research. At the same time, individual research freedom has always been encouraged among both cooperating scientists and graduate students. This policy has been largely responsible for the intellectual growth of the HBES, as well as its role as a center for undergraduate and graduate education in ecosystem science.

HBES has developed into a relatively complex matrix of projects involving a large number of scientists from diverse disciplines. Beginning in 1987, core funding for the HBES has been provided through the Long-term Ecological Research (LTER) network of the National Science Foundation. Together with support from the USDA Forest Service, the LTER program provides base funding for most monitoring activities in the HBES. Individuals or groups of researchers are supported by competitive grants to pursue a variety of specific research studies in the HBES in cooperation with the LTER program. From 1963, over 1750 publications have been produced through the HBES, providing a wealth of information on the structure, function and development of forest, stream and lake ecosystems.

For more history of Hubbard Brook Experimental Forest: Events Leading to the Establishment of the HBEF, written by Jim Hornbeck, May 2001 (pdf)

1.7 Conceptual Background

The mission of the Hubbard Brook Ecosystem Study is to improve understanding of the response of northern forest ecosystems to natural and anthropogenic disturbances. In the overall conceptual model underlying the Study (Figure 1.2), three types of disturbances - changing atmospheric chemistry, climate, and biota - drive changes in the interacting components of the ecosystem, including vegetation, biogeochemistry, hydrology, and food webs. These changes play out on a template that includes the biogeophysical characteristics of the landscape. The ecosystem responses may feedback to modify the template and alter biotic change. The template and the functional responses change through time in response to the disturbances and internal drivers.

In Figure 1.3 we illustrate measured and hypothesized changes in ecosystem concentrations and fluxes in response to long-term decreases in S and N atmospheric deposition and increases in CO₂ concentrations. Up and down arrows indicate increases and decreases. Gold arrows reflect measured changes, purple arrows show hypothesized changes. Gray arrows indicate major ecosystem processes driving other responses in the ecosystem. We have observed increases in soil pH and base saturation in response to declining S and N deposition and expect these changes to increase soil P availability. We have also observed increases in soil microbial biomass,

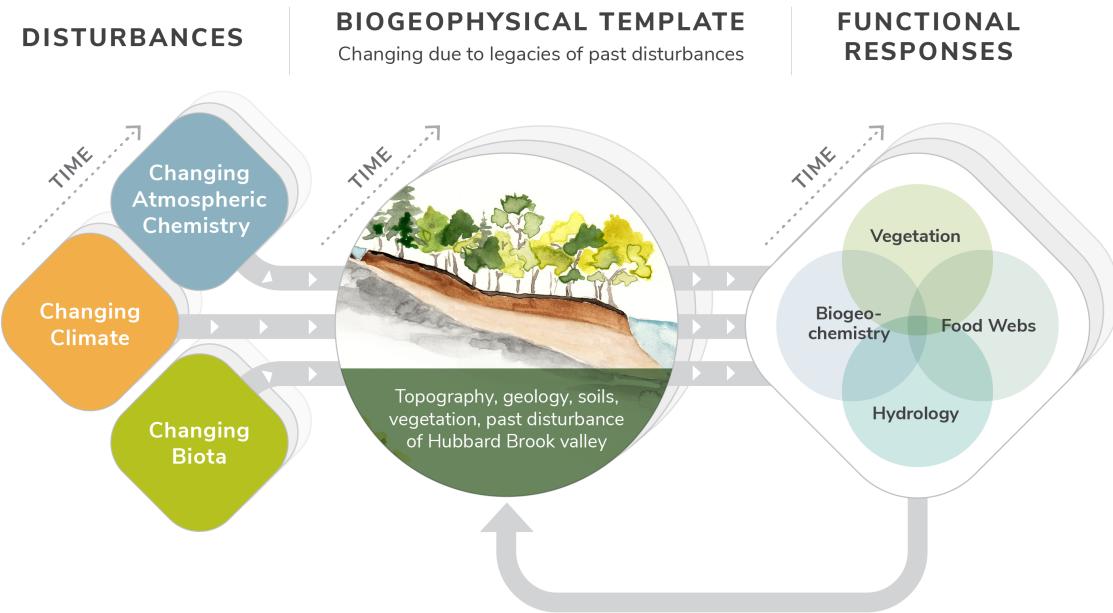


Figure 1.2: Conceptual model underlying the Hubbard Brook Ecosystem Study

decreases in forest floor organic matter stocks, and shifts in solution N losses from inorganic to organic forms. We hypothesize that rising atmospheric CO₂ contributes to these changes by stimulating plant CO₂ uptake and nutrient demand for growth, which in turn drives an increase in plant N and P uptake from solution, increased nutrient resorption from litter and decreased litter C/N ratios, as well as increases in allocation of plant C belowground to spur organic matter mineralization and soil respiration.

Climate change disturbance has myriad effects on forest ecosystem dynamics. Here we highlight (Figure 1.4) a conceptual framework for diagnosing the cause of the recent observed increase in rates of evapotranspiration (ET) at Hubbard Brook (see Hydrology Chapter). We are investigating how atmospheric conditions and vegetation interact nonlinearly to affect ET. Orange arrows indicate observed trends in the long-term data. Question marks show where there is uncertainty in our understanding. The green arrow shows how the coupling of canopy and aerodynamic resistance affects rates of evapotranspiration.

Our conceptual model of the hierarchical response of ecosystem function to chronic stressors and episodic events is illustrated in Figure 1.5. (A) Initial responses to stress trigger species-specific responses with limited system-wide impact. (B) With continued exposure, species abundances begin to re-order, resulting in reduced ecosystem function. (C) This slow loss of function can be accelerated by an (D) episodic disturbance. (E) If the stress persists, further changes in the biota are expected. These disturbance-driven shifts in biodiversity will have profound consequences on species additions and losses, species demography and evolution, and

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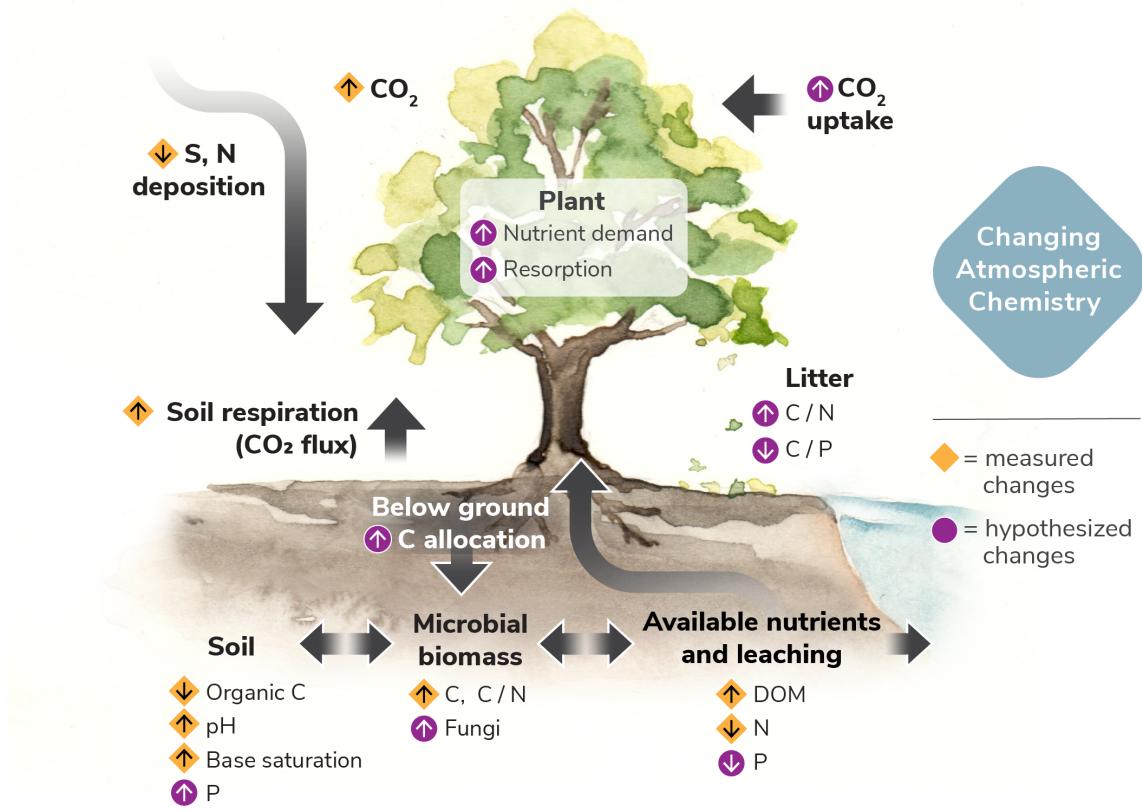


Figure 1.3: Illustration of measured and hypothesized changes in ecosystem concentrations and fluxes in response to long-term decreases in S and N atmospheric deposition and increases in CO_2 concentrations.

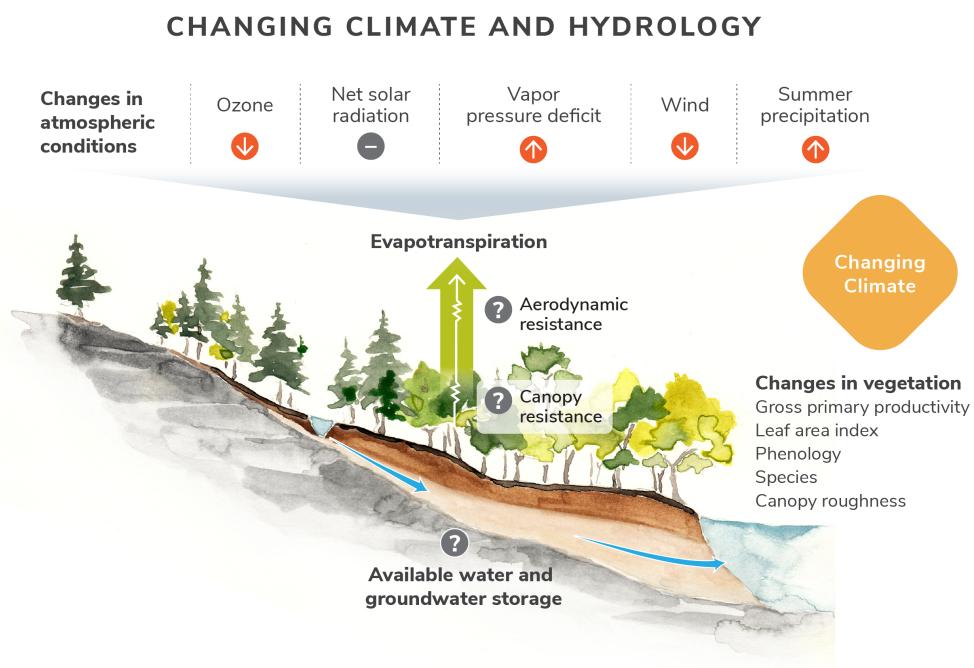


Figure 1.4: A conceptual framework for diagnosing the cause of the recent observed increase in rates of evapotranspiration (ET) at Hubbard Brook.

energy flow (inset).

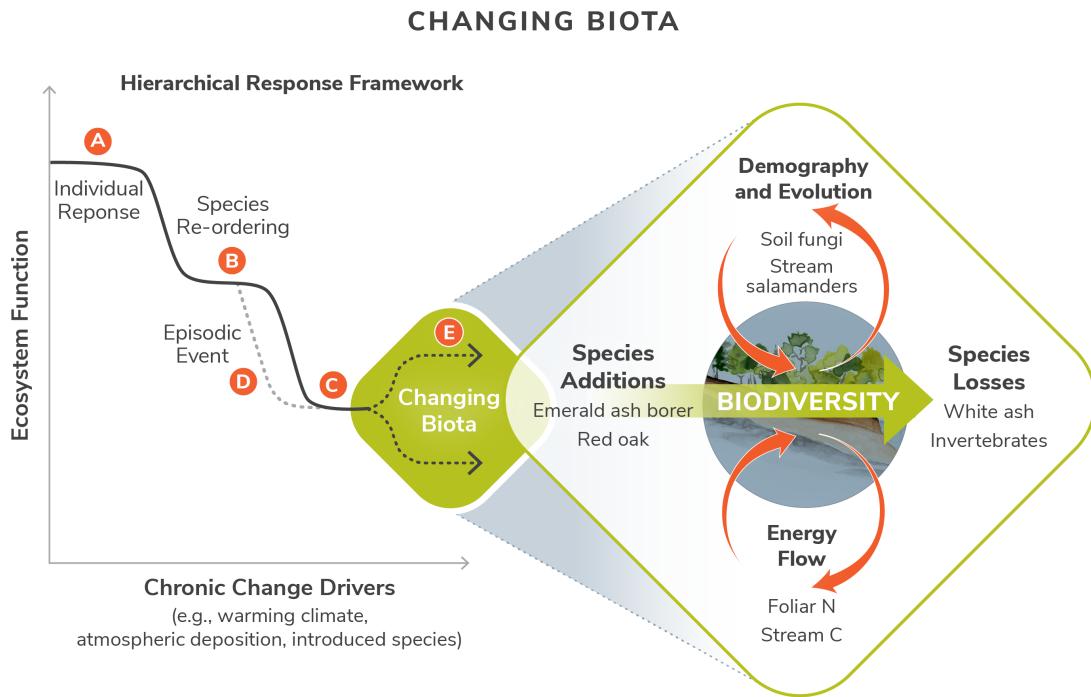


Figure 1.5: The conceptual model of the hierarchical response of ecosystem function to chronic stressors and episodic events.

Our conceptual model of the biogeophysical template on an idealized hillslope (Figure 1.6) shows five slope positions along a depth-to-bedrock gradient that results in predictable variation in soils, shallow groundwater movement, and saturation frequency. Hydro-bio-pedo interactions along these soil-slope variations structure vegetation and other biota, form linkages with temporary and perennial streams, and shape the complex functional responses of ecosystem components (Figure 1.2).

1.8 Research Approaches

The framework for the HBES is the small watershed approach which provides precise quantitative water and element input-output budgets for the forested ecosystems. In a catchment where the underlying bedrock is impermeable, water falling on the catchment leaves only by evapotranspiration (ET) or as stream discharge. By quantifying the latter, annual ET can be calculated by difference:

$$\text{Eq. 1. AET} = \text{Precipitation} - \text{stream discharge}$$

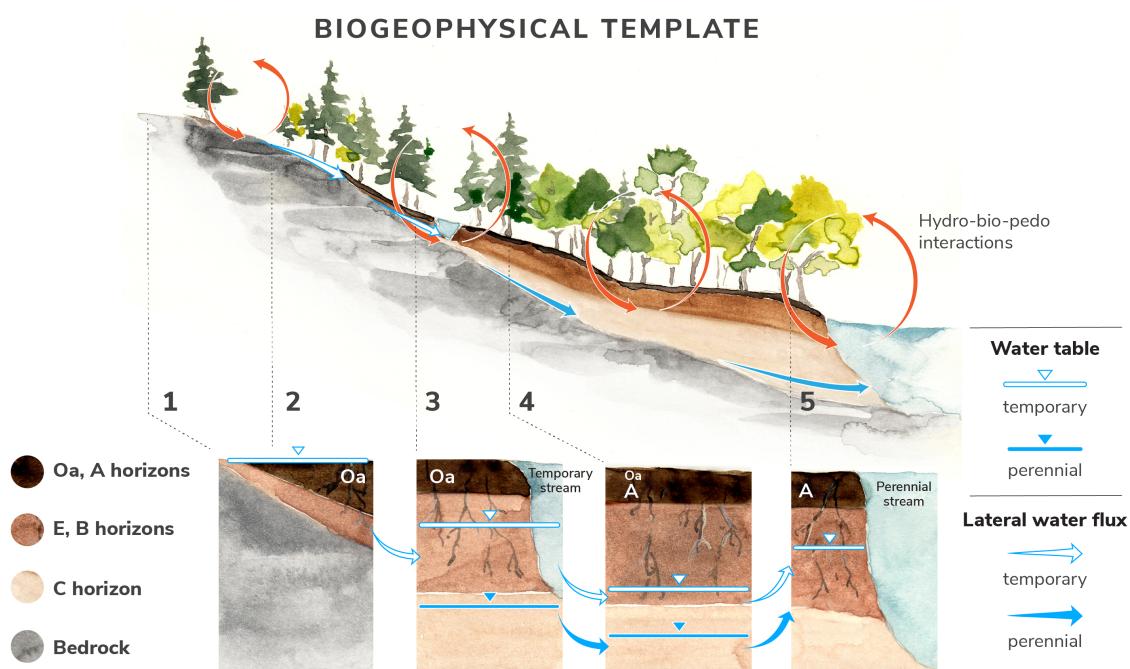


Figure 1.6: The conceptual model of the biogeophysical template on an idealized hillslope.

For chemical elements without a gas phase at Earth temperature, the small watershed also allows estimation of soil weathering (Johnson et al. 1981):

$$\text{Eq. 2. Weathering} = \text{stream output} - \text{atmospheric input} + \text{storage}$$

Here, the stream output and atmospheric input of an element are determined as the product of water flux and the element concentration in the water. The storage term refers to any change in the stock or pool of an element in the soil organic matter or vegetation biomass in the ecosystem. For example, when vegetation biomass is aggrading some of the chemicals weathered from soil minerals are accumulating in the trees rather than lost in stream discharge and the storage term is positive in Equation 2. Also, some elements enter the ecosystems as dry rather than wet deposition (e.g. dust particles), and this flux is included in the atmospheric input term.

For elements with gaseous phases (e.g., N, C), separate measurements of gas fluxes in and out of the ecosystem are needed to estimate material budgets (see below). Experimental manipulations (e.g., forest harvest, fertilization) can be applied at the small watershed scale to quantify whole ecosystem responses (Bormann et al. 1974). The internal processes determining the whole ecosystem responses are measured at the plot scale at selected locations within or nearby the small watershed. Together these measurements form the basis for much of the research in the HBES including long-term monitoring as detailed below.

1.9 Atmospheric Inputs



Figure 1.7: Atmospheric deposition collectors at Hubbard Brook.

Atmospheric deposition of elements to the ecosystem is the sum of wet and dry deposition. Measurement of wet deposition has been conducted on a weekly basis since 1963 at a network of sampling sites across the HBEF (Figure 7). All major dissolved solutes are measured and together with precipitation water volume from standard rain gauges, element fluxes in wet deposition are determined.

Dry deposition of particles and gases is more difficult to quantify than wet deposition and can constitute a substantial proportion of the input of several important elements, especially nitrogen and sulfur, that are derived partly from pollutant emissions. Some of the dry deposition can be captured on artificial samplers or as canopy throughfall, but the calculation of dry deposition flux is complex and uncertain, and we refer the reader to detailed explanations in the literature (Likens et al. 2002).

1.10 Stream Output



Figure 1.8: Photograph of a V-notch weir at Hubbard Brook

Stream discharge of water from nine small watersheds in the HBEF is measured continuously with 90° or 120° V-notch weirs located at the base of the surveyed catchments (Figure 1.8). The weirs continuously measure stage height in a stilling pond above the weir outlet. Each weir is calibrated by directly measuring the relationship between stage height and water flux. To calculate element fluxes, water samples for chemical analysis are collected weekly just above each weir. More frequent measurements to more precisely quantify storm-event fluxes have been conducted periodically using automated samplers. Flux of particulate matter is measured by removing accumulated material in the weir stilling pond periodically. The flux of fine suspended solids during large storm events also has been measured using permeable bags positioned below the weir.

1.11 Forest Vegetation

The composition, biomass and element content of the vegetation is measured periodically within the gauged watersheds and throughout the entire HBEF. The basic approach is to measure the diameter of trees across the whole watershed (e.g., WS6, WS1) or in smaller plots usually at five-year intervals. Forest biomass is estimated using allometric equations relating DBH to other tree dimensions (e.g. total biomass and biomass of tissue components like leaves, branches, etc.). These equations were developed at the site by directly measuring trees harvested during experimental manipulations (Whittaker et al. 1974, Siccama et al. 1994). The pool or stock of an element is estimated from the product of mass and element concentration in various tissues. Thus, changes in the stock of an element in the forest biomass are calculated typically at a 5-year intervals.

1.12 Soils

The mass and element stocks of soils have been estimated using the quantitative pit approach. The soil is carefully excavated manually from a 0.5 m² area through depth increments to the C horizon. Soil mass in each depth increment is weighed and sieved in the field and subsamples are taken for chemical analysis in the laboratory. Because of the large stocks and high spatial

variability of elements in soil, detection of changes through time or in response to treatments is challenging. Nevertheless, we have been able to estimate the net soil release for major elements resulting from acid deposition and forest harvest on the basis of quantitative pit sampling (Johnson et al. 1991).

1.13 Gaseous Output

The small watershed approach does not, by itself, account for outputs in gas phase, an important flux pathways for the nutrient element nitrogen. Gaseous flux of N remains a key uncertainty in the N budget at the HBEF (Yanai et al. 2013). The principal gaseous flux of N results from denitrification, a process that is notoriously variable in space and time. The flux chamber approach, in which the accumulation of gaseous N diffusing from soil is measured over short time intervals (e.g. minutes), is applied routinely to estimate flux of nitrous oxide in several plots in and around the experimental watersheds at the HBEF. Unfortunately, because of the high background in the atmosphere this approach is not effective for measuring N₂ flux. Laboratory, isotopic and modeling approaches have provided indirect estimates of N₂ flux from soils (e.g., Wexler et al. 2014).



Figure 1.9: Photograph of flux tower instrumentation at Hubbard Brook.

Fluxes of carbon dioxide and water vapor from the forest ecosystem can be estimated using aerodynamic approaches with eddy flux towers. Recently, an eddy flux tower has been installed in the lower valley at the HBEF and began collecting data in 2016 (Figure 1.9). The facility

will soon provide the first direct estimates of gross primary production, autotrophic and total ecosystem respiration, and net ecosystem productivity for the forest in the footprint of the tower.

1.14 Internal Element Fluxes

The processes regulating the biogeochemistry of the forest ecosystem include a variety of major internal element fluxes which are monitored in selected intensive plot locations in and around the experimental watersheds at the HBEF. In particular, element leaching through soils is measured using zero-tension lysimeters positioned beneath the forest floor, Bh and Bs horizons. Water fluxes at each depth, estimated with a hydrologic model, are used with measured element concentrations in soil solutions to estimate soil leaching fluxes (Cho et al. 2010).

Litterfall is measured using permanent litter traps co-located in plots with soil lysimeters. Litter is sorted by species, providing annual estimates of leaf biomass and leaf area index in these plots. Periodically, the chemistry of leaf litter is measured; combined with chemistry of live foliage from the plots, these measurements provide estimates of nutrient resorption from senescing foliage, a large internal ecosystem flux especially for N and P (Ryan and Bormann 1982). Deposition of woody litter as coarse woody debris is measured annually on cleared 2.5 m² plots co-located with litter traps. The chemistry of canopy throughfall and element fluxes in canopy leaching also have been measured in these intensive plots (Lovett et al. 1996) as well as the biomass, chemistry and turnover of fine and coarse roots, using coring and rhizotron methods, so that a comprehensive accounting of the principal internal element fluxes is available for the forest ecosystems in the experimental watersheds.

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2 Climate Change

Chapter Editor: John Campbell

Dr. Pamela Templer describes aspects of manipulations in an intensive plot and initial findings associated with Hubbard Brook's Nitrogen Oligotrophication (HBNO) study. Video filmed at HBNO Intensive Low 3 at the Hubbard Brook Experimental Forest on May 17, 2024.

2.1 Background

The Hubbard Brook Experimental Forest () was established well before the issue of climate change emerged. However, many of the long-term measurements collected at the site have become valuable climate change indicators (Table 2.1). Although these records might not provide information relative to climate change separately, combined they provide convincing evidence of climate change at the HBEF that is compatible with regional trends in the northeastern U.S. (Hayhoe et al. 2007; Melillo et al. 2014). A summary of the climatic characteristics of the HBEF most suitable for inclusion in research reports can be found in the [Introduction chapter](#) of this book.

Table 2.1: Examples of long-term climate change indicator datasets collected at the HBEF.

Meteorological	Hydrological	Soil	Biological
Air temperature	Lake ice in/out	Soil temperature	Phenology
Solar radiation	Streamflow	Soil moisture	Birds
Relative humidity	Precipitation	Soil frost	Vegetation composition
Wind speed	Stream temperature Snow depth/SWE	Stream sediment yield	Tree growth Litterfall

None of the long-term measurements at the HBEF were initiated for studying climate alone, but rather were collected to help understand other topics such as streamflow, biogeochemical dynamics, and forest growth. Some of the hydrometeorological measurements were initiated because of a need for data as input for computer models, most notably the BROOK model. BROOK was pioneering when it was first developed in the 1970's and is still in wide-use today

(Federer 2015). As a result, compared to most other similar research sites, the hydrometeorological records from the HBEF are long and comprehensive.

Although climate data at the HBEF are rich by most standards, there are some limitations that need to be considered when evaluating long-term trends. Perhaps most importantly, the methods for some of the measurements have changed over the years. For many years, the continuous measurements at the HBEF were made with analog devices, which have now all been replaced with digital sensors. In some cases, changes in instrumentation have been relatively seamless with negligible effects on the long term record, whereas in other cases the transitions have not been smooth. For example, the anemometer at the U.S. Forest Service Headquarters building malfunctioned in 2004 and was replaced with a different model with no period of overlap for correction, resulting in a step function in wind speed. Other records contain long gaps when instruments were not functioning (e.g., solar radiation, relative humidity). These types of problems cannot always be corrected reliably, hampering our ability to evaluate trends. Nevertheless, a large number of records at the HBEF have been collected consistently at the same locations using the same methods with the same or comparable instruments. In this chapter, we focus on a few of the measurements with which we have a high level of confidence and are well-suited for evaluating climate change.

The trends in this chapter were analyzed with the non-parametric Mann-Kendall test, which is commonly applied to analyses of long-term hydrometeorological data (Kendall, 1938; Helsel and Hirsch, 1992). One of the advantages of this test is that it is rank-based, making it suitable for non-normally distributed data, data containing outliers and non-linear trends such as those often encountered in long-term hydrometeorological research. The slope for each trend was calculated as the median of all possible pair-wise slopes (Sen, 1968).

2.2 Air Temperature

Air temperature has been measured at seven locations at the HBEF; one location at the U.S. Forest Service Headquarters building (HQ) and six locations in the vicinity of the gauged watersheds (Bailey et al. 2003; see also Introduction chapter, Figure 2.1). Air temperature measurements have been collected for various time periods at different locations beginning shortly after the establishment of the HBEF in 1955. The oldest records are from Station 1 (STA1) and HQ, which respectively began in 1956 and 1957.

Long-term mean annual air temperature ranges from 3.7 to 6.7 °C across the seven sites where it is measured, and generally increases with elevation slightly more than the adiabatic lapse rate (0.5 vs 0.6 °C degrees per 100 m. At STA1, mean monthly air temperature ranges from a high of 19 °C in July to a low of -8 °C in January. The highest mean daily temperature ever recorded was 37 °C on July 22, 2011 at HQ and the low was -36 °C on January 23, 1976 at STA14.

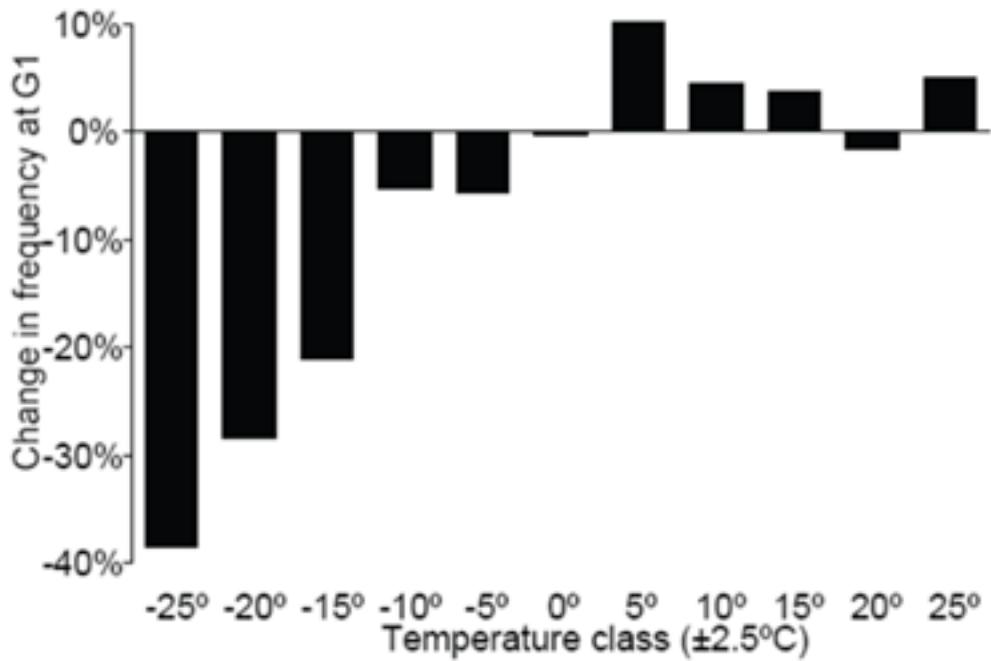


Figure 2.1: Change in the frequency of days in each air temperature class at the HBEF. Values are frequency of days in each bin between 1986 and 2005 expressed as a percentage change from its frequency between 1958 and 1977. (Hamburg et al. 2013).

Observations show an overall warming trend at the HBEF, with air temperatures increasing by about 1.4 °C over the past 60 years at STA1. Air temperature increases have been recorded across all seasons, but winter temperatures have risen the most, with average winter temperatures warming by 2.0 °C since 1956. Fall temperatures have warmed the least, amounting to 0.9 °C over this period. Daily minimum temperatures, which typically occur at night, have risen by an average of 1.7 °C, while daily maximum temperatures have risen by 1.3 °C since 1956. The number of warm days has increased slightly at the HBEF, whereas the number of extremely cold days has decreased (Figure 1). The loss of extremely cold days is one of the most striking observations in the air temperature record, and has important biological implications. For example, cold snaps during winter keep insect populations in check, and are especially important for limiting the spread of invasive species northward. Warmer winter temperatures may remove barriers to both native and non-native species, potentially resulting in declines in forest health and changes in species composition.

2.3 Precipitation

Precipitation is collected at a network of gages surrounding the area of the experimental watersheds and at the main headquarters (HQ) (for further details on instrumentation, see Bailey et al. 2003). In 2017, the network was reduced from 24 to 11 gages in an effort to reduce costs by improving the efficiency of the monitoring program (Green et al. in review). Like air temperature, the records of precipitation vary in length, with the oldest dating back to 1956 at stations 1-4.

Long-term mean annual precipitation ranges from 1326 to 1607 mm across the 24 gages where it has been measured. There is a slight increase in precipitation with elevation and there is also a slight increase from east to west (Bailey et al. 2003). In general, precipitation is frequent at the HBEF, and some form of measurable precipitation occurs in about one out of every three days. Unlike many other regions, precipitation is distributed fairly evenly throughout the year and does not follow a strong seasonal pattern. About 30% of annual precipitation falls as snow. The biggest precipitation event ever recorded began on June 28, 1973 and dropped over 17 cm of rain in 57 hours.

The annual volume of precipitation has been increasing at the HBEF, amounting to a total increase of about 300 mm since 1956 (Figure 2). Interestingly, there has been no significant increase in winter precipitation, and the increases in annual precipitation are attributed to increases that have occurred during the other three seasons. This finding differs from future climate change projections for the northeastern U.S., which predict greater increases in winter precipitation during the 21st century, and little to no change in summer precipitation (Hayhoe et al. 2007). Determining the reasons for this apparent disagreement between recent trends and model projections presents an important challenge for regional climatology.

Compared to air temperature, precipitation is more variable from year-to-year, and these increasing trends in precipitation are only significant at gages with longer records (Campbell

Figure 2.2: Trends in annual precipitation at the HBEF compared to the regional average (i.e., Bethlehem and Hanover, NH, and St. Johnsbury, VT). Data from NOAA's National Centers for Environmental Information (<https://www.ncei.noaa.gov/>). This figure is updated with current data available in the Environmental Data Initiative Repository (EDI; <https://portal.edirepository.org>) and at NOAA NCEI. Hover over graph to access interactive controls available at the top right (zoom/pan/etc).

et al. 2010). It should be noted that the rain gages that have been in operation the longest also captured a period of drought in the 1960's. This was a well-documented multi-year drought that had major impacts in the northeastern U.S. (Namias 1966). In recent decades there has been a shift toward a wet phase. Consequently, the longest precipitation records at the HBEF are bookended by a dry period at the beginning of the record and a wet period at the end of the record. The increases in precipitation that have been observed at the HBEF for this time period are slightly greater than increases in the broader region, and annual precipitation at the HBEF and broader region is greater now than ever before in recorded history.

In addition to changes in mean values, there is also evidence supporting increases in extreme precipitation events. The number of days per year with heavy precipitation, defined as days with more than 20 mm of rain, has increased significantly by about 7.4 days since 1956. This trend is consistent with observations from other locations across the northeastern U.S. showing a 70% increase in "extremely heavy storms" since the 1950s, as reported in the 2014 National Climate Assessment (Melillo et al. 2014).

Not surprisingly, increased precipitation has led to an increase in soil moisture (Groffman et al. 2012), with potential impacts on many different ecological processes. Because soil biota are so strongly influenced by available water, increases in soil moisture can enhance decomposition, mineralization, trace gas fluxes, and solute export. Additionally, the major flooding events that have occurred at the HBEF tend to happen when substantial rains fall on soils that have already been saturated from a previous storm. Therefore, these wetter conditions can increase the likelihood of major flooding events with potential economic and societal impacts. Moreover, an increase in the extent and duration of local saturation of soils could result in changes in the occurrence of anaerobic conditions and consequent microbial processes such as denitrification.

2.4 Snowpack and Soil Frost

Snowpack has been measured under the forest canopy at 21 locations for various time periods at the HBEF; however, only 5 of these sites have been monitored over the long-term and are still in operation today. The snowpack is measured weekly along a snow course that consists of 10 points spaced 2 m apart. At each point, field technicians use a Mt. Rose snow tube to measure the depth of the snow, and also to extract and weigh a core of the snowpack

to determine the snow water equivalent (SWE). Snow water equivalent is a measure of the amount of water contained in the snowpack and is more temporally stable and hydrologically meaningful than snow depth. Manual measurements of soil frost are made weekly at a single point adjacent to the snow courses. Technicians dig through the snow, use a hatchet to cut through the frozen soil, look and feel where the frost line is, and measure the total depth from the surface of the forest floor. Although both the snowpack and soil frost measurement methods are somewhat rudimentary, they are effective and have remained consistent over the entire records, providing confidence in observed trends over time.

Historically, the HBEF has had a continuous snowpack throughout the winter that on average persists from late December until mid-April, with a peak depth in March. Since air temperatures are getting warmer and the volume of precipitation in winter has not changed, it is not surprising that the snowpack has declined over the period of record. The long-term average annual maximum snow depth and corresponding snow water equivalent (SWE) ranges from 47 cm (12 cm SWE) to 101 (27 cm SWE) at HQ and STA17, respectively. At STA2, which has the longest record (beginning in 1956), maximum annual snow depth has declined by 29 cm (9 cm SWE). The length of the snow-covered period is also getting shorter. On average there are 111 days with snow cover at STA1. The number of days with snow cover has declined by about 20 days over the record (Figure 3). The changes in the snowpack have resulted in shifts in hydrology (see Hydrology chapter for more detail). The annual hydrograph at the HBEF is characterized by low streamflow during winter as precipitation accumulates in the snowpack, followed by a snowmelt peak during spring runoff. The declining snowpack has caused a flattening of the hydrograph, due to more frequent melting events during winter that recharge groundwater, and a reduction in the spring peak caused by less snowpack accumulation and melt (Campbell et al. 2011).

Figure 2.3: Long-term trends in the maximum annual snow depth, maximum annual snow water equivalent, and number of days with snow cover measured at weather station 2 at Hubbard Brook Experimental Forest. (Original figure in Campbell et al., 2007). This figure is updated with current data available in the Environmental Data Initiative Repository (EDI; <https://portal.edirepository.org>). Hover over graph to access interactive controls available at the top right (zoom/pan/etc).

Soil frost is present approximately two out of every three years at the HBEF, depending on how cold it is at the onset of winter and when the snowpack begins to develop (Campbell et al. 2010). Once the ground is frozen, it generally stays frozen beneath the snowpack throughout the entire winter. The average annual maximum soil frost depth ranges from 2 cm at STA9 to 9 cm at HQ.

The deepest soil frost ever recorded was 30 cm in 1980 at STA17. Soil frost is highly variable from year-to-year at the HBEF and no long term trends are evident. However future climate change modeling done with HBEF data indicates that although the annual maximum depth of soil frost is not expected to change much in the future, the number of freeze-thaw events will

increase and the number of days with soil frost will decline stemming from a concurrent decline in the number of snow-covered days (Campbell et al. 2010). These potential changes in soil frost regimes have important implications for forest ecosystem processes such as hydrological flowpaths during winter, biogeochemical processes in soil, and tree phenology and growth. For example, Mitchell et al. (1996) indicated that high nitrate loss from the HBEF watersheds followed severe soil frost events.

2.5 Vegetation

Climate change has the potential to affect the growth, composition and health of vegetation in many ways. The HBEF lies on the northern hardwood and spruce-fir ecotone. On the warmer, lower elevation, south-facing watersheds, northern hardwoods comprise 83 to 99% of the forest cover, whereas the colder, higher elevation north-facing watersheds have a greater proportion of spruce-fir (73 to 97%; National Land Cover Dataset, Homer et al. 2015). It has been suggested that as the climate changes, spruce-fir should recede upslope, with northern hardwoods filling in behind it (Beckage et al. 2008). However, at the HBEF there is little evidence to support this with existing data. In fact, data from the HBEF (van Doorn et al. 2011) and the larger region indicate that spruce-fir is becoming more prevalent at lower elevations (Foster and D'Amato 2015). Undoubtedly, climate is one of many factors that influences tree species composition, but it is not clear how the combination of climate change with other changes will alter future vegetation assemblages.

Extreme weather events are perhaps a more important influence on vegetation than subtle shifts in climate over time. These events are projected to increase in number and strength in the future, owing to more energy in the atmosphere. Some examples of documented extreme weather events at the HBEF with direct effects on vegetation include ice storms, hurricanes, microbursts, hail storms, droughts, floods, spring freeze events, fall snowfall events, and episodes of soil freezing. Additionally, changes in climate can open a Pandora's box of indirect effects, such as outbreaks of pests and pathogens, and fire. Because of these complexities, there is much uncertainty about how climate change may affect vegetation at the HBEF in the future.

Measurements of plant phenology provide some of the most useful information for evaluating how climate change is affecting vegetation. Tree phenology is the study of the seasonal occurrence of developmental or life cycle events, such as budbreak, flowering, or autumn leaf drop. Measurements of phenology were initiated at the HBEF in 1989 at nine plots along an elevation gradient. Each spring and autumn, field technicians visit the plots and record the phenological stage of trees.

The record at the HBEF does not indicate that significant shifts in phenology have occurred during the period of observation. However, retrospective modeling of phenology does show evidence of a longer growing season (i.e., beginning in 1957 following Richardson et al. 2006). These modeled phenology data enable comparison of shifts in phenological phases with climate change drivers (Groffman et al. 2012). For example, during spring there is a vernal transition

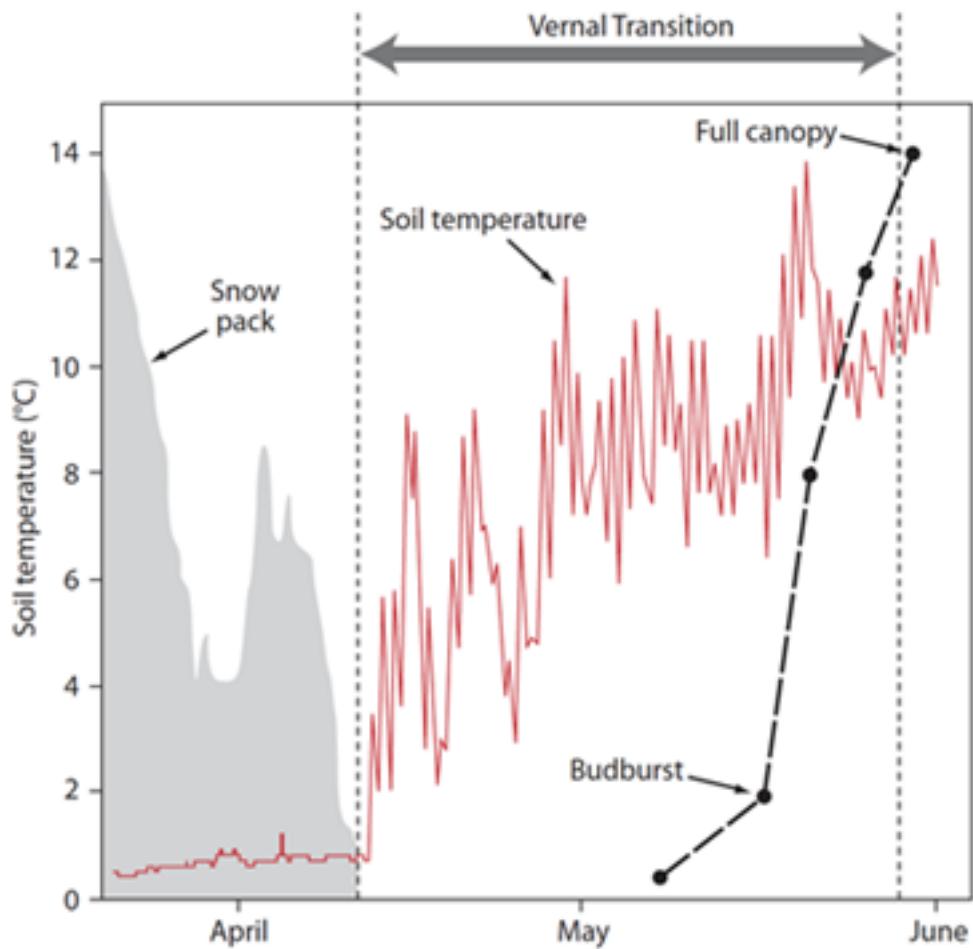


Figure 2.4: The vernal transition is defined as the period between the last day of snowpack and the day of full canopy expansion. This period is characterized by a sharp increase in soil temperature that triggers biological activity in soils. (Groffman et al., 2012).

period between the time when the snowpack completely melts and when leaf-out occurs (Figure 4). This transition period appears to be lengthening, meaning that the rate of change for leaf-out is slower than the change for snowmelt, because leaf-out is not only affected by a warmer climate, but also by photoperiod which is not changing. After snowmelt occurs, soil temperatures rapidly increase, creating a “spring trigger” that stimulates microbial mineralization, mobilizing nutrients in soil solution. Because nutrient uptake by trees is generally low before leaf-out, the greatest losses of nutrients to streams occurs during this time. As this transition period gets longer, the amount of nutrients leached to streams could increase, potentially impairing water quality and soil fertility. These observations from the HBEF illustrate the marked changes that have occurred in the physical environment in the spring and fall seasons, which may exacerbate existing seasonal asynchronies between microbial activity and plant uptake.

2.6 Climate Change Manipulation Experiments

While long-term data are valuable for identifying trends in climate and responses over time, field manipulation experiments are used to elucidate cause-and-effect relationships and improve mechanistic understanding. Ideally replicated experiments can be combined with long-term monitoring data to mechanistic models and provide a robust evaluation of climate change effects on ecosystem processes. There have been many different climate change manipulation experiments at the HBEF ranging from small laboratory experiments to larger plot-scale field studies. Here we highlight four of the more comprehensive studies that have occurred at the site (Figure 5). Soil Freezing Experiments

Soil freezing is an important below-ground perturbation, having implications for the hydrology, biology and chemistry of ecosystems. At the HBEF, soil freezing impacts have primarily been investigated using snow removal experiments beginning in the mid-1990's (Groffman et al. 1999, 2001; Figure 5a), but also more recently with natural gradients in soil freezing that occur across a range in elevation (Duran et al. 2016; Fuss et al. 2016). Snow removal experiments involve shoveling off the insulating layer of snow, thereby exposing the soil to cold winter air temperature to induce soil freezing. This research has shown that relatively mild freezing events (soil temperatures never decreasing below -4 °C) produced significant increases in soil inorganic nitrogen levels, solute leaching, root mortality and nitrous oxide flux. These responses to mild freezing were surprising in view of laboratory studies that suggested significant biogeochemical effects would only occur with a freezing event sufficiently severe (> -10 °C) to directly cause root and microbial mortality. Apparently damage to roots by mild freezing is sufficient to reduce nitrogen uptake, thereby causing increased losses of nitrate from soils (Campbell et al., 2014). Climate Change Across Seasons Experiment

Whereas many studies have evaluated the impacts of climate change on forests within a single season, few have examined the impacts of climate change across seasons and how these impacts interact. A study called Climate Change Across Seasons (CCASE) was initiated in 2012 to

determine the interactive effects of winter and growing season climate on water and nutrient uptake and carbon sequestration in northern hardwood forests (Templer et al. In Review; Figure 5b). This study involves snow removal during winter to induce soil freezing, combined with warming during summer. Summer warming was accomplished by burying heating cables and maintaining the soil at 5 °C above ambient. The investigators hypothesize that warmer soil temperatures during the growing season will increase forest productivity, as well as rates of water, carbon, and nutrient uptake by trees and saplings. However, they expect that a reduced winter snowpack and increased soil freezing will offset these changes by damaging roots. Results from this study will improve understanding of the effects of climate change on rates of carbon sequestration and nutrient retention in these forests, as well as potential effects on air and water quality.

2.7 Drought-Net Experiment

While mean annual precipitation in the Northeast is projected to increase modestly in the coming decades (especially in winter), it is expected to fall in fewer, more intense storms, with longer intervening dry periods. When combined with other changes in climate (i.e., less consistent snowpack, earlier snowmelt, and longer and hotter growing season), the altered precipitation regime may lead to a dramatic increase in growing season water stress in a region where species are not well adapted to drought. A throughfall removal experiment was initiated in 2014 to better understand the impacts of drought in mesic northern hardwood forests (Asbjornsen et al. In prep; Figure 5c). A series of troughs covering 50% of the ground surface was installed above plots to simulate a 1st percentile drought based on the long-term meteorological record. Drought and control plots are compared to determine the effect of reduced soil moisture availability on tree growth among other things. Ice Storm Experiment

Ice storms are rare and typically localized extreme weather events that are difficult to predict and have impacts that are poorly understood. An ice storm field manipulation experiment at the HBEF is being used to improve mechanistic understanding of short term ecological responses (Rustad et al. In prep; Figure 5d). During the winter of 2016, stream water was sprayed above the forest canopy when air temperatures were below freezing, effectively simulating a natural ice storm. The experimental design consists of plots with three levels of ice thickness treatment (0.25", 0.50" and 0.75" of ice accretion), as well as a control. The plots with the two more severe icing treatments experienced significant tree damage, creating canopy gaps. These plots also had large inputs of fine and coarse woody debris to the forest floor. The exposure to light and presence of brush piles in the more heavily damaged plots resulted in warming with increased spatial variability of soil temperature.

It was expected that the warmer temperatures in heavily damaged plots would result in an increase in soil respiration; however preliminary results indicate that soil respiration was actually lower in these plots possibly because of reduced root growth as noted following the natural ice storm event of 1999. It was also expected that nutrients in soil solution would increase

due to lack of uptake by damaged vegetation. However, preliminary results have shown no significant changes in soil solution losses of nutrients despite significant forest canopy damage. Further monitoring will determine whether these trends continue in the future.

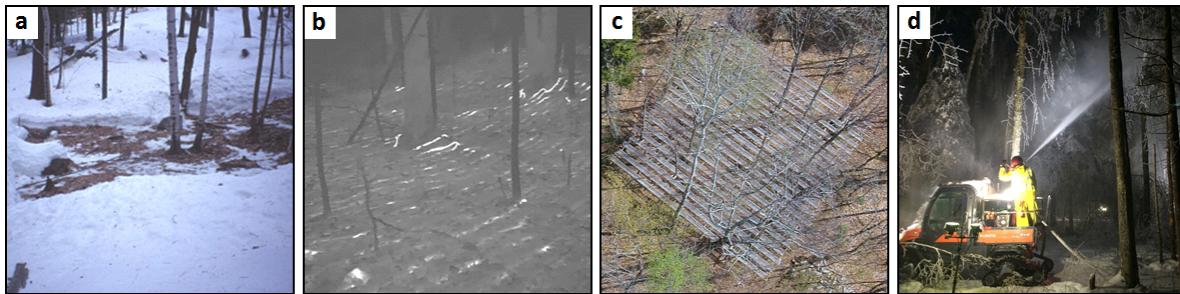


Figure 2.5: Climate change manipulation experiments at the HBEF including: (a) snow removal to induce soil freezing; (b) heating cables to warm plots as shown with a thermal image; (c) throughfall exclusion to simulate drought; and, (d) spraying water over the canopy during cold weather to create an artificial ice storm.

2.8 Questions for Further Study

- How are impacts from climate change compounded or alleviated by other local and global change drivers?
- Are there climatic thresholds that when exceeded, result in irreversible change in ecosystem structure, function and composition?
- Is climate change exacerbating ecological asynchronies?
- Will wetter soils enhance microbial processing and nutrient export including localized anaerobic processes?
- How do the impacts from aboveground disturbances, such as ice storms, differ from belowground disturbances, such as soil freezing?
- Why do model projections of regional climate change suggest increasing winter precipitation whereas records indicate increasing summer precipitation?

2.9 Access Data

- USDA Forest Service, Northern Research Station. 2021. Hubbard Brook Experimental Forest: Daily Precipitation Rain Gage Measurements, 1956 - present ver 17. Environmental Data Initiative. <https://doi.org/10.6073/pasta/453b49e8429a63b72419caf3b9ad6f98>
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See the full Hubbard Brook data catalog to find more meteorological data, and data on experimental climate manipulation projects.

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3 Hydrology

Chapter Editors: Mark Green and John Campbell

3.1 Background

The HBEF was established in 1955 for the purpose of studying the effects of forest management on streamflow and water quality, building upon pioneering work from other sites that established the efficacy of the paired small watershed approach (Bates and Henry 1928). The principle underlying the small watershed approach is that for a catchment with relatively watertight bedrock (thus minimal subsurface loss), water can leave the watershed only by stream discharge or evapotranspiration (ET). Hence, indirect measurement of annual ET (which is difficult to quantify directly) is obtained as the difference between annual precipitation and stream discharge measured using v-notch weirs (Figure 3.1).

The units in the hydrologic balance of a catchment are depth units (mm H₂O) analogous to the familiar units of rainfall events. The volume discharge of the stream at the base of the catchment is divided by the projected area of the catchment to obtain depth units. The watershed balance of the catchment and annual ET are calculated on a water-year basis at the HBEF, from June 1 to May 31. A water year is determined by the point in time when there is the least amount of change in the volume of water stored in the watershed (especially soils and groundwater). This is accomplished by comparing precipitation and streamflow for successive 12 month periods over many years and determining what period has the highest correlation. This analysis indicates when water storage is most stable, which at the HBEF occurs after spring snowmelt when trees are leafing out and water storage is at a minimum.

Hydrologists at the HBEF developed a long-term record of the water balance and annual ET for hydrologic reference watershed 3 (Figure 3.2). On average, about 40% of annual precipitation goes to ET and 60% to stream discharge. This partitioning to ET and streamflow varies considerably from year to year with a lower proportion to ET in wet years (in W3 minimum = 22% in WY 2010 and maximum = 53% in WY 1964). However, the absolute annual ET flux is relatively constant across years in the typically wet summer climate of HBEF where stomatal limitation of transpiration is less important than in drier climates. In an early experiment, WS2 was deforested, essentially eliminating transpiration (Likens et al. 1970). Of course, stream discharge dramatically increased as only about 9% of precipitation input was evaporated (Figure 3.3); because soil temperature and surface moisture were greatly elevated



Figure 3.1: Photo of V-notch weir at HB for measuring stream discharge.

Figure 3.2: Long-term water balance in four watershed at Hubbard Brook: A. WS3, B. WS6, C. WS7, D. WS8. Originally published in Campbell et al. 2011; this figure is updated with current data available in the Environmental Data Initiative Repository (EDI; <https://portal.edirepository.org>). Hover over graph to access interactive controls available at the top right (zoom/pan/etc).

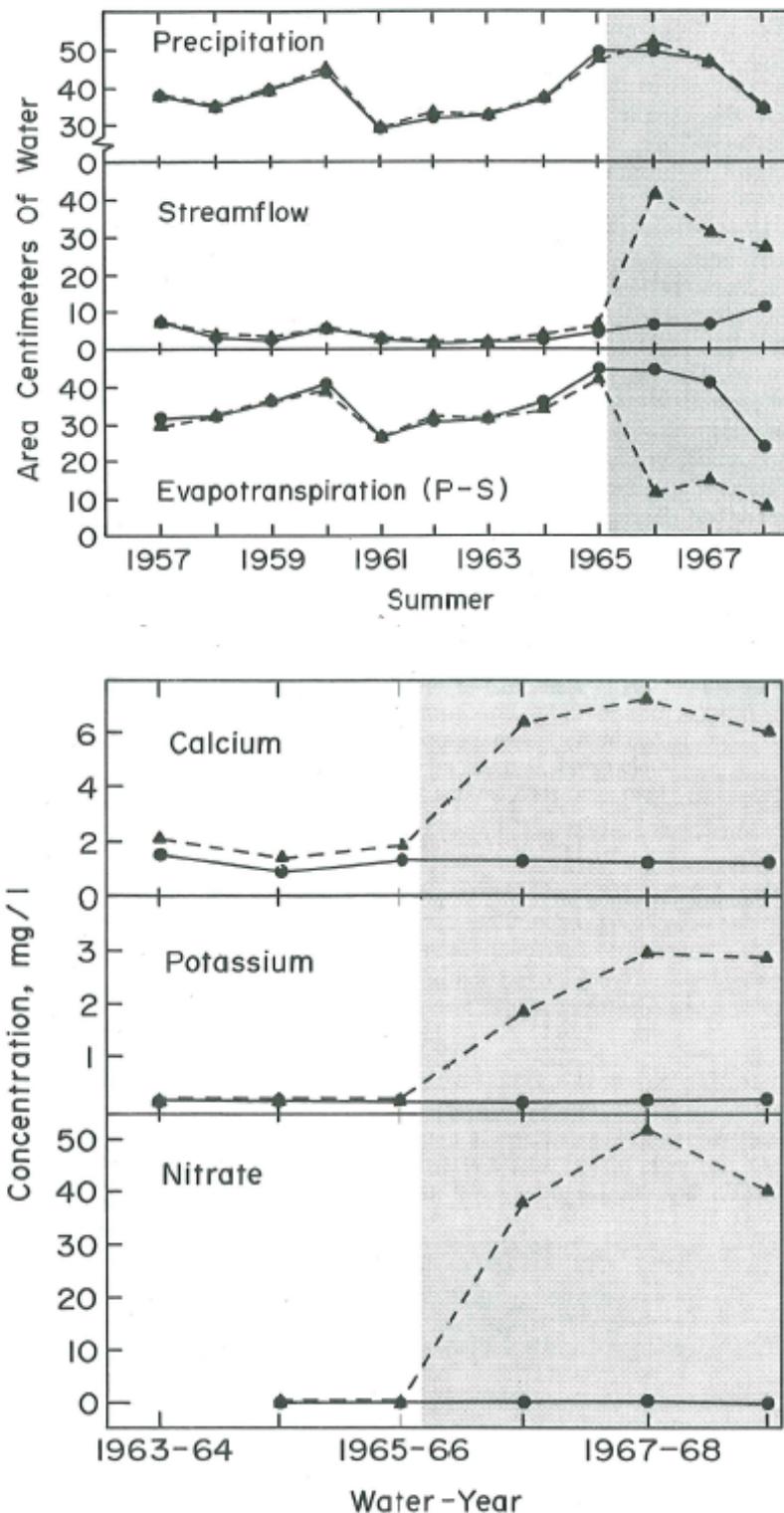


Figure 3.3: Response of streamflow, evapotranspiration and stream water nutrient concentrations to devegetation treatment (shaded) of Watershed 2. (Likens et al., 1970).

by the elimination of vegetation cover, soil and snowpack evaporation in this experiment (about 120 mm H₂O/yr) was much higher than for closed canopy forest (see below).

The long-term record at the HBEF also demonstrates the response of the forest water balance to atmospheric and climate change. Three key environmental drivers have increased gradually at the HBEF since the 1950s: air temperature, annual precipitation and atmospheric CO₂ concentration. In theory, increasing air temperature would be expected to cause higher evaporation (and ET) rates and, a longer leaf-on season of the deciduous trees, that should also contribute to higher ET. Indeed, phenological records from the HBEF indicate a lengthening leaf-on period (Keenan et al. 2014; Figure 4).

Conversely, higher atmospheric CO₂ would be expected to increase stomatal control of transpiration (Eamus 1991). Our long-term, indirect estimate of annual ET for four reference watersheds at HB (WS3, WS6, WS7 and WS8) indicate little temporal change although the pattern differed slightly between the north- (WS7 and 8) and south-facing (WS6 and 3) watersheds (Figure 3.2). Trends in ET from other small watersheds in the Northeast are also inconsistent, suggesting that local site factors override broader regional drivers of ET. The exact cause of these trends is a topic of ongoing study at the HBEF.

Most recently, water budgets in the four reference catchments indicated an approximately 30% increase in ET starting in 2010 and continuing through 2020 (Figure 3.2). We analyzed the annual water budgets, cumulative deviations of the daily P, RO and water budget residual (WBR = P – RO), potential ET (PET) and indicators of subsurface storage to gain greater insight into this shift in the water budgets (Green et al. 2021). The PET and the subsurface storage indicators suggest that this change in WBR was primarily due to increasing ET. While multiple long-term hydrological and micrometeorological data sets were used to detect and investigate this increase in ET, additional measurements of groundwater storage and soil moisture would enable better estimation of ET within the catchment water balance. Increasing the breadth of long-term measurements across small gauged catchments allows them to serve as more effective sentinels of substantial hydrologic changes like the ET increase that we observed.

3.2 Hydrologic Processes: Precipitation and Snowmelt

Early reports from the HBES indicated annual precipitation at 130 cm/yr with about 25-30% occurring as snow. Annual precipitation at the HBEF has increased by about 20% over nearly 60 yr of record, reflecting the general trend for the Northeast region (Hayhoe et al. 2008). Most of this change has been in the warm season, as winter precipitation has not changed significantly; however, because of warmer winter temperatures, snowpack depth and the number of days with snow cover have declined. As a result snowmelt-induced high spring flows have declined. Low snow years are also associated with soil freezing events because the snowpack ordinarily insulates soil from cold winter air temperatures (Campbell et al. 2010).

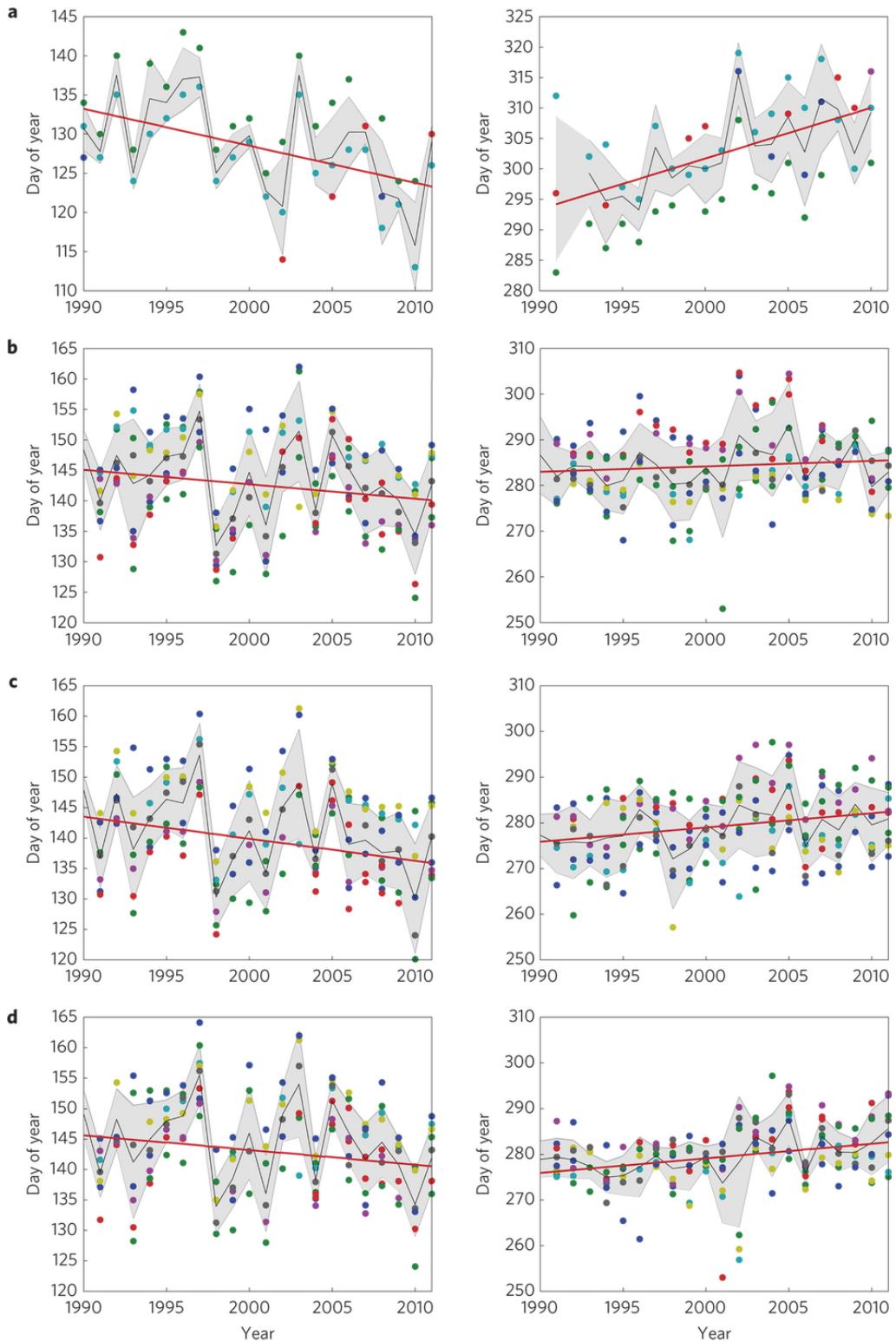


Figure 3.4: Manual ground observations of spring (left column) and autumn (right column) phenology over two decades at Harvard Forest from 1990- 2012 (Red oak (a)) and Hubbard Brook 1989 - 2012 (American beech (b); Sugar maple (c); Yellow birch (d)). (Keenan et al., 2014).

An array of gages around the HBEF illustrates meso-scale variation in precipitation. In general, annual precipitation increases slightly with elevation (40 mm/100 m) as does the proportion in the form of snow. Due to local orographic effects, a significant west-to-east gradient of decreasing annual precipitation also is observed independent of elevation. Together, elevation and longitude explain 75% of the variation in long-term average annual precipitation.

3.3 Hydrologic Processes: Canopy Interception and Evaporation

A considerable proportion of the precipitation falling on a forest is intercepted by the canopy, clings to the leaves and branches and never reaches the ground, eventually evaporating back to the atmosphere (I/E). Leonard (1961) conducted detailed studies of canopy I/E in the northern hardwood forest at HB. He estimated that 13% of gross precipitation (i.e., in the open) was lost as I/E during the leaf-on period. This value was only slightly lower (12%) during the leafless period, presumably because of high capture of snow in the canopy. Undoubtedly, canopy I/E is higher in the evergreen conifer zones. Moreover, studies in subalpine balsam fir forest near HB on Mt. Moosilauke indicated substantial augmentation of ambient precipitation by capture of cloud droplets (up to 46% of ambient rainfall; Lovett et al. 1982). Although direct measurements have not been made at HB, the magnitude of this input would be expected to be much lower as the HB environment has less wind and fog.

Evaporation from soil (Es) has not been measured at HB.

However, water isotope data at HB indicate that Es is minor relative to transpiration (Green et al. 2015). Estimates from other temperate deciduous forests suggest that Es is roughly 10% of total ET during the growing season (Moore et al. 1996).

3.4 Hydrologic Processes: Transpiration

Root water uptake and subsequent transpiration of water vapor from foliage is the principal pathway of water flux to the atmosphere. Transpiration flux depends upon environmental factors, especially air temperature, atmospheric humidity and soil moisture, as well as vegetation factors, particularly forest leaf area and leaf conductance (or resistance) to water vapor. Leaf area index (LAI) in the mature northern hardwood forest is relatively uniform spatially and temporally averaging about 6.5 (Battles et al. 2014). Recovery of leaf area following large-scale disturbance is surprisingly rapid as LAI of cutover sites reaches 90% of mature forest values within 6-10 yr. Thus, increases in water yield from cutover watersheds is transient; Hornbeck et al. (1997) observed that stream discharge on cut watersheds at HB increased for only a few years. Moreover, the role of species differences in stomatal conductance in determining forest transpiration was apparent; in particular, stream discharge from the young forest watershed on cutover WS4 was consistently about 5% higher than the reference watershed (Hornbeck et al. 1997). This was due to higher stomatal conductance (Federer 1977) of the pin cherry and

birch that dominated the young forest, as compared with maple and beech in the reference forest.

The role of soil moisture stress in regulating transpiration at HB is less important than for more xeric forests (Federer and Gee 1974), and the strong trend of increasing warm season precipitation in the region further discounts this role. However, increasing air temperature could lead to higher transpiration rates as well as more midday stomatal closure owing to greater absolute humidity deficit (Montieth 1995). At the same time, increasing atmospheric CO₂ concentration would be expected to increase water-use efficiency (WUE) of plants and some evidence of increasing WUE and decreasing ET in northeastern forests has been observed (Keenan et al. 2013). Exactly how the coincident trends of increasing CO₂, temperature and precipitation will affect forest transpiration in coming decades remains uncertain.

An unexpected result was observed regarding transpiration from the watershed-scale experimental restoration of soil Ca in WS1: stream discharge from the treated catchment decreased by about 20% for three years following the application of CaSiO₃, indicating that transpiration had increased (Green et al. 2013). The causes of this striking response are unknown although follow-up studies indicate an increase in sapflow of mature forest trees, confirming the watershed mass-balance result. Another recent intriguing result, from a stable water isotope study on W3, indicates significant sub-canopy water recycling, as transpired water vapor apparently recondenses and is re-used by the understory vegetation (Green et al. 2015).

Most recently, evidence of an unexpected increase in evapotranspiration has been suggested based on the long-term records of precipitation and runoff for the south-facing catchments at the HBEF. As explained earlier, we estimate annual AET using the annual water budget for the gauged watersheds at the HBEF, assuming minimal deep seepage or changes in soil/sediment storage. On this basis we observed a striking 30% increase in annual AET in the hydrologic reference watershed (W3) from 2010 to 2019 (Figure 1; Green et al. 2021). Although the drivers of this trend remain somewhat uncertain, analysis of water budget residuals, climatic data and evidence of possible soil storage changes indicate that subtle increases in PET and decreased canopy resistance may be driving the trend. Further study of forest physiology, soil moisture and groundwater dynamics is needed to better resolve this important issue in ecosystem hydrology.

3.5 Hydrologic Processes: Infiltration and Soil Water Redistribution

Surface soils at HB are very porous because of high organic matter content and coarse textures. Hence, infiltration capacity is very high and infiltration-excess overland flow is uncommon (Pierce 1967). Overland flow has been observed on some occasions when infiltration is impeded. Surface soil scarification and compaction by heavy equipment during logging can result in overland flow on skid roads. In winters with cold temperatures and little insulating snow cover, saturated soils can freeze, forming concrete soil frost that limits infiltration and causes overland flow during winter and early spring. Localized saturation-excess overland flow occurs

in particular landscape positions where perched water tables reach the surface during wet periods, explained below.

Rapid vertical percolation of soil water prevails under most situations in the HB watersheds. Indeed, the formation of the predominant Haplorthod soil profile is predicated on such a flow regime. (Gannon et al. 2014). However, the surface and subsurface topography and soil morphology in the HB watersheds is very complex. Bailey and co-workers (Bailey et al. 2014, Gannon et al. 2014) have demonstrated the utility of hydopedological units for characterizing this complexity at the small watershed scale: soil morphological characteristics and landscape position illustrate patterns of soil water redistribution. Observations on WS3 indicate a dynamic and spatially disconnected patchwork of water table development that depends on hillslope position, subsurface as well as surface topography and low porosity layers of dense glacial till and fragipans. These features can result in lateral subsurface flow as well as saturation-excess overland flow as detailed below. Watershed Hydrology: Stream Hydrograph, Stormflow and Contributing Area

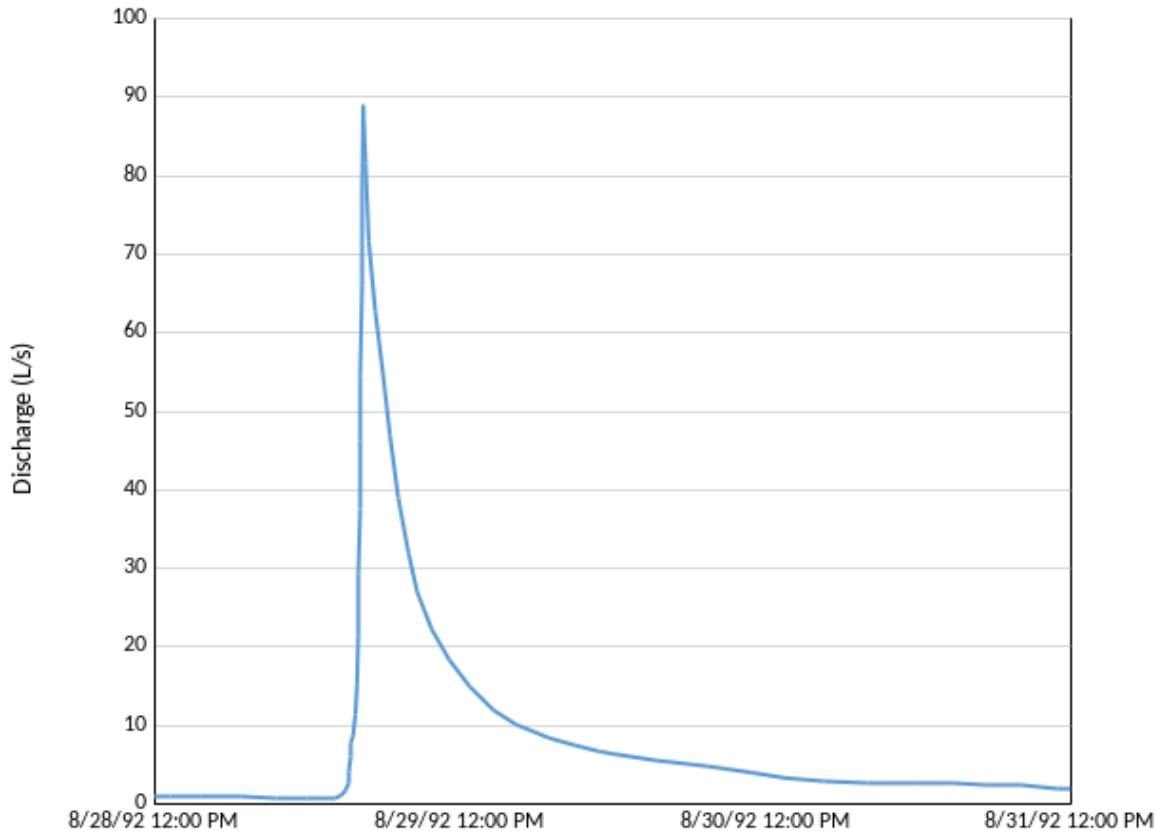


Figure 3.5: Hydrograph for watershed 6 showing stream discharge during a typical rain storm. (J. L. Campbell, unpublished data).

The flowpaths of water through soils to streams influence biogeochemical fluxes as well as temporal and spatial variation in stream discharge, all of which are key characteristics of stream habitats. An enduring challenge in watershed hydrology is understanding the processes supplying “baseflow” (i.e. streamflow following an extended interval without rain) and those generating “stormflow” and flood events.

The storm hydrograph is typically characterized by a steep rising limb following the beginning of a large rain (or snowmelt) event, a transient peak flow that can define flood effects and a prolonged receding limb following cessation of precipitation. The stream hydrograph in the HB experimental watersheds has been characterized as “flashy,” a term hydrologists use to denote a very rapid response to precipitation, a sharp peak and a quick return to baseflow (Figure 3.5). This behavior reflects the relatively short distances that water must travel in the watershed to reach the stream channel. Hooper and Shoemaker (1986) demonstrated that most stormflow discharge at HB was supplied by “old” water that resided as storage in the watershed for some time, but exactly where does this water come from?

In general, saturated areas in a catchment are capable of generating lateral flow to stream channels, and potentially supplying storm flow; such areas are denoted “active.” However, not all active areas actually contribute to the steeply-rising limb of a stormflow event. For example, if a patch of perched water table is separated by zones of low conductivity (drier soils) from other saturated zones, rapid flow from that patch will not occur. “Contributing” areas are saturated or near-saturated soils that are hydraulically connected to the stream and hence will contribute rapidly to stream discharge during rain events. The larger the contributing area in a watershed at a particular time, the greater and more rapid the streamflow response to a rain or melt event. Certainly riparian zones are most likely to be contributing areas both because of more frequent wet conditions and because of greater hydraulic connectivity to stream-channels. However, upland areas of a watershed can also be contributing areas. Gannon et al. (2014) observed differences in perched water table development among hydropedological units and different threshold responses in the storage-discharge relationships of these units, indicative of distinct subsurface flow regimes. Moreover, variably connected and disconnected active areas occur across WS3 at HB so that the contributing area for stormflow varies in complex ways with catchment storage.

The water flow dynamics of a watershed can be further abstracted to represent the age-distribution of stored water, or analogously the travel-time distribution of water reaching the stream channel. These features of catchment hydrology are important for understanding the biogeochemical behavior of the watershed-ecosystem because they integrate spatial heterogeneity and capture kinetic and equilibrium limitations on solute dynamics. Benettin et al. (2015) estimated the median travel time for water in WS3 to range from 50 to 200 days, depending upon catchment wetness (Figure 3.6). Notably, the analysis indicated a significant role of sub-soil glacial till below the tree rooting zone in supplying water (and solutes) to the stream in WS3.

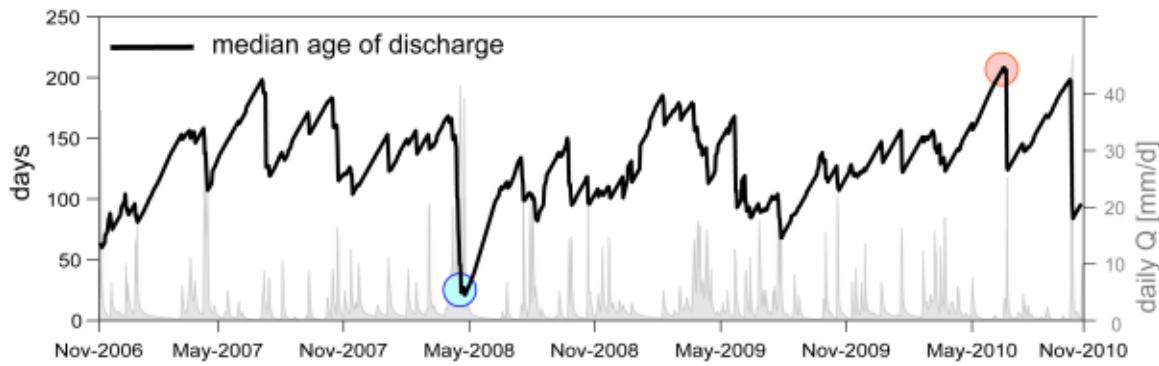


Figure 3.6: Evolution of the simulated median age of discharge during a 4 year period. Red and blue circles denote dry and wet periods; further analysis is included in Benettin et al. (2015).

3.6 Questions for Further Study

- What explains the long-term trends in AET in the gaged watersheds and will these trends continue?
- How does the pattern of hydropedology developed for WS3 apply to the broader HB Valley and the White Mountain region?
- What caused the transient increase in AET on WS1 following restoration of soil calcium and does this response have broader implications for forest hydrology in a changing environment?
- What are the sources of baseflow in first and second-order streams in upland catchments?
- Have there been systematic and significant changes in catchment-scale storage of water in the sediments of HB watersheds?

3.7 Access Data

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4 Forest Composition and Dynamics

Chapter Editor(s): John Battles

4.1 Historical Overview

Figure 1. Pollen accumulation rates for pollen types in Mirror Lake (Davis 1985).

As originally conceived by Bormann and Likens (1979), the Hubbard Brook landscape is dominated by northern hardwood forest which consists of a patchwork of stands of varying structure and composition that shifts through time, the “shifting-mosaic steady state.” The forest is dominated by three broadleaf deciduous tree species, sugar maple, yellow birch and American beech, with a mixture of several deciduous and evergreen conifer species. Above about 800 meters in the HB valley, subalpine forest of red spruce and balsam fir (and formerly mountain paper birch) is dominant, especially on thinner, less fertile soils.

The composition of the forest at Hubbard Brook has seen periods of relative stability interspersed with shifts owing to a variety of forces. These include climatic changes, natural disturbances such as pests and pathogens, and most recently human activity, especially logging in the 19th and 20th century. The Holocene forest vegetation history of the Hubbard Brook area has been reconstructed on the basis of sediment coring of Mirror Lake, located near the valley outlet (Figure 1; Davis 1985). The area was deglaciated between 13-14,000 yr BP, and the climate soon warmed to resemble the modern climate. Spruce was the first tree species to invade post-glacial tundra around Mirror Lake and pollen data suggest that it spread widely through the HB valley by 11,000 yr BP. Fir, birch and *Populus* increased about 1,000 years later and spruce abundance subsequently declined. Thereafter, pine and oak became more abundant suggestive of a warmer climate 9-8,000 yr BP. By 7,000 yr BP, abundance of fir, pine and oak declined, while maple, beech and hemlock increased. Hemlock exhibited a sudden decline at about 5,000 yr BP that has been ascribed to an insect or pathogen, (but see Foster et al. 2006), and it then gradually recovered over a 1,000 year period. With that notable exception, and a resurgence in spruce abundance beginning about 2,000 yr BP, the forest composition in the HB valley was fairly stable after 6,000 yr BP until the arrival of Europeans in the 19th century. At the time of European settlement, the composition of the northern hardwood forest in the HB valley was comparable to the modern forest, being dominated by yellow birch, sugar maple and American beech; however, based on historical records (Chittenden 1905) red spruce was more abundant and sugar maple less so in

the pre-settlement forests of the White Mountains. Spruce was selectively logged from the HB valley in the late 19th century, reducing its abundance thereafter. Much of the HB valley was subsequently heavily logged during the first two decades of the 20th century and most of the modern forest stands date from this time period. An exceptional hurricane disturbance in 1938 blew down extensive areas of the south and east facing slopes and salvage logging following this event further opened the residual forest. Notably, the 1938 hurricane caused much less damage to younger stands that arose following early 20th century logging than older lightly cut areas of the forest (Pearl et al. 1992). In summary, the modern forest in the HB valley exhibits a complex age and size structure that varies spatially as a result of these historical large-scale disturbance events. However, despite this anthropogenic disturbance history the current structure and composition of the HB forest is similar to that of a virgin remnant forest at the Bowl Research National Area located about 30 km east of HB (Figure 2, 3; Schwarz et al. 2001, Martin and Bailey 1999).

Figure 2. Size-class distribution of tree stems in old-growth (Bowl) and second-growth northern hardwood forests (Schwarz et al. 2001).

Figure 2. Size-class distribution of tree stems in old-growth (Bowl) and second-growth northern hardwood forests (Schwarz et al. 2001).

Figure 3. Basal area and density of tree species in virgin (Bowl) and secondary forests (HBEF, W6) in the mid-1990s (Schwarz et al. 2001).

Figure 3. Basal area and density of tree species in virgin (Bowl) and secondary forests (HBEF, W6) in the mid-1990s (Schwarz et al. 2001).

4.2 Modern Forest

A detailed picture of the current structure and composition of the second-growth forest at HB is provided on the basis of a valley-wide grid of 431 permanent plots. Overall, the size structure of the forest exhibits the usual “reverse-j” shaped curve typical of mature forests composed mostly of shade-tolerant species (Figure 2). Notably, sugar maple and beech are considerably more abundant and yellow birch and conifers less abundant in south-facing reference WS6 than for the entire HB valley.

Five principal forest vegetation types are distinguished within the HBEF (Figure 4) including the core northern hardwood forest; a hemlock-hardwood type, restricted to the lower valley and; a high-elevation hardwood type, marked by the increased dominance of yellow birch relative to beech, the relative scarcity of sugar maple, and the inclusion of red spruce as a common species.

Figure 4. Forest vegetation types in the Hubbard Brook Valley (Battles, unpublished data).

Figure 4. Forest vegetation types in the Hubbard Brook Valley (Battles, unpublished data).

Figure 5. Demographic factors of dominant tree species in the Hubbard Brook Valley at the turn of the 21st century (van Doorn et al., 2011).

Figure 5. Demographic factors of dominant tree species in the Hubbard Brook Valley at the turn of the 21st century (van Doorn et al., 2011).

At higher elevations, conifer dominated forests prevail with two distinct types: a spruce-fir-birch type and a fir-birch type (paper birch died out of the latter types during the early 21st century – see below). Early-successional forest stands are found on four small watersheds (WS2, 4, 5, 101) that were harvested experimentally between 1966 and 1984. On a valley-wide basis (van Doorn et al. 2011), three tree species have exhibited declining biomass in recent years (yellow birch, American beech and paper birch) while five species have been increasing (sugar maple, red spruce, balsam fir, hemlock and white ash). The decline of American beech is a consequence of an introduced disease complex (Houston 1975); similar changes are anticipated in the near future for hemlock and white ash (see below). Trends in forest structure and composition are indicated by the key population parameters of mortality, growth and reproduction. Live tree biomass of the HB forest has been nearly constant in recent years, as losses in biomass owing to tree mortality (28.5 Mg/ha) have been balanced by gains from growth of surviving trees (24.2 Mg/ha) and recruitment into the > 10 cm dbh class (2.8 Mg/ha). Losses from mortality on both a biomass and stem density basis have been greatest for yellow birch, the most abundant species in the HB valley. This trend probably reflects the age-structure of the yellow birch population that consists of veteran trees that pre-date 19th century logging and many individuals that regenerated after early 20th century logging and the 1938 hurricane. On a stem density basis balsam fir also exhibited high mortality, but these losses have been more than counterbalanced by high recruitment (Figure 5); fir also showed the highest relative growth rate of all tree species at HB. Conversely, paper birch exhibited high mortality, low recruitment and the lowest growth rate of all tree species at the HBEF. This pattern signals a species in decline, reflecting in part senescence of a cohort originating from the large-scale disturbance in the early 20th century as well as possible stresses owing to ice storm damage and severe drought in recent years. The picture for paper birch is complicated by the fact that two species (*B. papyrifera* and *B. cordifolia*) comprise the surveyed population, and future work comparing their dynamics is needed. The population of sugar maple, the second most abundant species at HB, appears to be near equilibrium on a valley-wide basis, with recruitment matching mortality on a density basis and growth exceeding mortality on a live biomass basis (Figure 6). However, as discussed below, in some areas of the HB forest, especially in and around the experimental watersheds on the south facing slope (Figure 4) sugar maple is clearly declining with high mortality and low reproduction. Moreover, at the stage of development of the HB forest, we would expect the relative abundance of sugar maple to be increasing on a valley-wide basis. Hence, sugar maple seems to be suffering from unexpected decline at HB. American beech is also declining throughout the HB valley, largely as a result of beech bark disease and losses from mortality greatly exceed growth. However, on a stem density basis, recruitment exceeds mortality, partly reflecting prolific vegetative sprouting from roots (Siccama et al. 2007). Like sugar maple, red spruce is a population near steady state in the HB valley on both a biomass and stem density basis, despite clear evidence

of its regional decline and susceptibility to damage resulting from soil base cation depletion by acid deposition (Adams et al. 1992). Finally, although red maple appears to be increasing in abundance throughout most of its range in eastern North America (Abrams 1998), this species shows no signs of expanding in the HB valley. Annual net change in aboveground biomass of 19 tree species across the entire Hubbard Brook Valley in first decade of 21st century. Error bars indicate 95% confidence intervals and numbers in parentheses are importance values.

Figure 6. Annual net change in aboveground biomass of 19 tree species across the entire Hubbard Brook Valley in first decade of 21st century. Error bars indicate 95% confidence intervals and numbers in parentheses are importance values.

Forest composition and its trends differ considerably between the south-facing experimental watersheds and the larger Hubbard Brook Valley. The relative dominance of sugar maple has been steadily declining on W6 since the 1980s (Figure 6-2). The fact that calcium remediation on W1 reversed this decline clearly implicates acid rain in this decline. Conversely, the relative dominance of American beech steadily increased until recently, reflecting in part reduced competition from sugar maple. The role of beech bark disease in mediating these patterns is complex, as explained in detail in chapter The Trouble with Beech. Note also that yellow birch is much less abundant in the experimental watersheds than the larger valley and shows no clear sign of decline, even most recently increasing on W6 perhaps responding to maple decline. Thirty years of change in the relative dominance (proportion of total basal area) for three dominant tree species on reference watershed 6 and Ca-treated W1 based on 5-year surveys of all stems on the watershed. Error bars indicate 95% confidence intervals.

Figure 6-2. Thirty years of change in the relative dominance (proportion of total basal area) for three dominant tree species on reference watershed 6 and Ca-treated W1 based on 5-year surveys of all stems on the watershed. Error bars indicate 95% confidence intervals.

4.3 Tree Reproduction Ecology

The regeneration cycle of forest trees includes seed production and dispersal; seed dormancy, germination and establishment; understory tolerance and release and; vegetative reproduction. Most of these features are quite well understood in general for the dominant tree species in the HB valley. Pulsed seed production is observed for most trees, as illustrated for two of the three dominant trees at HB, sugar maple and American beech (Figure 7). This behavior is interpreted as so-called “masting” for large-seeded species like beech, selected to satiate the mammalian seed predators that also serve as dispersal agents. The reasons for pulsed seed production of a tiny-seeded species like yellow birch is not conclusively known but could include greater efficiency of pollination. Dispersal limitation of HB tree species varies with the dispersal mechanism and typical dispersal distance of their seeds. At one extreme, the tiny, wind-dispersed seeds of birches exhibit little dispersal limitation in their spatial pattern (Schwarz et al. 2003). In contrast, dispersal distance of beech seeds that rely on small mammals is usually limited to a few tens of meters, explaining the species limited regeneration by seed after

large-scale disturbance (e.g., logging of WS2 and WS5 at HB; Hughes and Fahey 1988). The importance of “safe-sites” for germination and establishment also varies with seed size, with tiny-seeded birches being restricted to exposed mineral soil or decaying logs where moisture retention is sufficient. Even on so-called safe sites, most germinants of all species soon die, often from damage by fungal pathogens and invertebrates such as slugs and insects (Cleavitt et al. 2011). However, it only takes a small percentage of survivors to maintain a bank of seedlings in the forest understory (Marks and Gardescu 1998), poised to take advantage of any disturbance to the canopy trees that will release them from severe competition and resource limitation.

Figure 4.1: Seed production for sugar maple (ASCA) and American beech (FAGR) at Hubbard Brook Experimental Forest, NH from 1993-2016. A-B: Bars show the annual mean for all collectors and asterisks denote mast years. The long-term mean is shown by a solid line. C-D: The standardized deviation of annual seed production from the long-term means (ASD). The dotted line shows the positive reflection of the minimum standardized deviate used to denote mast years as indicated in A. These data were first published in Cleavitt and Fahey (2017). This figure is updated with current data available in the Environmental Data Initiative Repository (Fahey, T. and N. Cleavitt. 2025. Tree Seed Data at the Hubbard Brook Experimental Forest, 1993 - ongoing ver 4. Environmental Data Initiative. <https://doi.org/10.6073/pasta/19e69d787124d60ccdfede1b5b813061>). Hover over graph to access interactive controls available at the top right (zoom/pan/etc).

A particularly intriguing regeneration strategy is exhibited by pin cherry, as studied in detail at HB (Marks 1974, Thurston et al. 1992). The seeds of this extremely shade-intolerant species can remain viable in a dormant seed bank in the soil for many decades. Pin cherry only germinates when a large canopy opening has occurred creating a change in environmental conditions such as high light, soil temperature fluctuation and changes in soil nitrate. The seedlings grow very quickly in this high resource environment and soon begin flowering and fruiting, replenishing the seed bank. At HB the density of pin cherry in the seed bank apparently grew exponentially in response to the repeated disturbances in the late 19th and 20th century (Tierney and Fahey 1998).

All the deciduous trees in the HB forest are capable of vegetative reproduction by basal sprouting and some also by root sprouting (beech, aspen) and stem layering (striped maple). None of the conifers exhibit vegetative sprouting, although at higher elevations stem layering occurs in balsam fir. In theory, the role of vegetative reproduction is to allow a species to persist at a location when dispersal and genetic recombination are not possible. The competitive interaction between seedlings and sprouters varies depending upon species, site and canopy disturbance. At HB, American beech root sprouting is of particular interest: it reproduces mostly by root sprouting at higher elevations at HB, but seed reproduction is common on more favorable sites (Cleavitt et al. 2008). Root sprouting is stimulated by damage to mother trees and their root systems (Jones and Raynal 1987) and prolific sprouting (“beech hell”) is

observed across the HB valley. Some evidence suggests that this process has contributed to limited regeneration of sugar maple (Hane 2003).

4.4 Disturbance Ecology

The northern hardwood-conifer forest is dominated by shade tolerant tree species (sugar maple, beech, spruce, fir, hemlock) that rely on advanced regeneration of seedlings that persists beneath the closed forest canopy and are able to supply recruits when death of individual or small groups of overstory trees provide canopy gaps. However, intolerant (paper birch) and mid-tolerant species (yellow birch, white ash, red maple) also are abundant in the mature forest. Unlike many other North American forest regions, natural fires are uncommon in the northern hardwood region, with point return intervals exceeding approximately 3,000 years (Lorimer and White 2003). Thus, the dynamics of shifting-mosaic steady state forest (Bormann and Likens 1979) depends on other causes of tree mortality. Based on the typical lifespans of the dominant species, in a forest where canopy recruits are derived primarily from death of individual trees through senescence, the point recurrence of canopy gaps would be a few hundred years. The prevalence of pit-and-mound micro-topography is suggestive of the important role of windstorms that causes tip-ups of large trees.

Figure 8. Scene from the center of a large blowdown that occurred in June 2013 at Hubbard Brook Experimental Forest. (Photo credit: Natalie Cleavitt)

Figure 8. Scene from the center of a large blowdown that occurred in June 2013 at Hubbard Brook Experimental Forest. (Photo credit: Natalie Cleavitt)

Figure 9. Tree damage from the January 1999 ice storm.

Figure 9. Tree damage from the January 1999 ice storm.

A variety of storms in the Northeast are capable of uprooting or snapping mature trees: hurricanes; extra-tropical cyclonic storms; tornadoes; and downbursts and other straight-line winds associated with thunderstorms that accompany strong cold fronts (Peterson 2000). Lorimer and White (2003) concluded that point recurrence of large disturbances from windstorms exceeded 1,000 years for inland Northeast, considerably longer than for coastal areas visited more frequently by Atlantic hurricanes. Nevertheless, these intense windstorms can create gaps exceeding 0.1 ha and certainly provided plenty of opportunities for maintaining populations of intolerant and mid-tolerant species, as indicated by the high abundance of yellow birch even in the virgin forests at the Bowl and in Adirondack old-growth forests (Martin and Bailey 1999). At HB the legacy of the 1938 hurricane, as well as a recent downburst that created several gaps exceeding 1.0 ha in area, in and near HB (Figure 8.), are emblematic of this role. In contrast, although a severe ice storm in 1998 caused widespread canopy damage at HB (Rhoads et al. 2002; Figure 9.), it provided only minimal regeneration and recruitment opportunities because resprouting in the damaged canopy returned the forest LAI to pre-disturbance levels within three years (Weeks et al. 2009). Thus, ice storms, as well as unusual tree mortality

resulting from species-specific pests and pathogens, can be considered diffuse disturbances that do not create large, discrete canopy gaps favoring less shade tolerant species. However, anticipated mortality of hemlock due to hemlock wooly adelgid infestation (Eschtruth et al. 2013) can be expected to create many large openings because it forms some nearly pure stands in the lower HB valley (Figure 4).

4.5 Human-Accelerated Environmental Change

Since the mid-20th century, the physical and biotic environment of the NE region has been rapidly changing. In particular, atmospheric CO₂ concentration is increasing; the climate is getting warmer and wetter (see Climate Change chapter). Atmospheric deposition of sulfuric acid increased to a peak in the 1970s and has declined since (Driscoll et al. 2001); deposition of total nitrogen peaked at the turn of the century and has been declining recently (Lloret and Valiela, 2016) and several exotic pests and pathogens have or soon will invade the forest.

The effects of acid deposition, and consequent depletion of soil base cations, has clearly impacted the health of the HB forest. Experimental restoration of soil Ca on WS1 ameliorated red spruce winter injury (Hawley et al. 2006), corrected canopy decline symptoms of sugar maple, and stimulated forest aboveground productivity (Battles et al. 2014). It also favored sugar maple seedling survival and growth (Juice et al. 2006). Further striking evidence about the effects of soil calcium depletion on sugar maple is the virtual disappearance of this iconic species from the regrowing forest on W5 after the experimental whole-tree harvest in 1984. The removal of biomass significantly depleted soil base cations, most severely in the upper slope positions. In the thirty years following the harvest the relative abundance of sugar maple, originally the dominant species on the watershed, declined precipitously especially on the upper slopes (Cleavitt et al. 2018). The broader response of forest composition to current reductions in acid and N loading will be difficult to detect in the face of many other changes, and the effects of atmospheric deposition of N on forest growth and health are not conclusively known, although recent evidence suggests a possible switch from N to P limitation of tree growth (Goswami et al., unpublished data)

Native insects have occasionally caused widespread defoliation at HB, but the effects of these pests on forest composition and structure are less profound than for exotic insects. Most notable to date has been the beech bark disease which first appeared at HB in the 1970s and has caused high mortality throughout the HB valley. A complex, ongoing response is anticipated as this insect-fungus disease complex has entered the aftermath phase (Houston 1975), and prolific vegetative sprouts begin to dominate the canopy in many areas. In the immediate future, hemlock wooly adelgid and emerald ash borer are poised to invade HB in the next decade. Although neither hemlock nor white ash is among the most abundant species in the HB valley, their loss will cause some local re-sorting of forest structure and composition. Hemlock is a dominant species in the lower HB valley and its mortality is likely to facilitate

the colonization of white pine and red oak (see below). White ash is locally abundant on richer soils, and we anticipate that its mortality will favor sugar maple.

Finally, the climate at HB is becoming gradually warmer and wetter, but the consequences of these changes are highly uncertain. For example, despite increased temperatures and growing season length at HB (see Climate Change chapter), the two species that have exhibited the greatest increase in abundance in recent years are balsam fir and red spruce (van Doorn et al. 2011), trees that would be predicted to recede to higher elevations in a warming climate. Some evidence also suggests that the striking decline of paper birch at HB may be linked to drought stress, even though annual average precipitation has increased by 20% since the mid-20th century; high temperatures and periodic summer droughts appear to contravene the precipitation trend. Nevertheless, we do see some clear signs of local climate warming as two species from warmer site are colonizing the HB valley, red oak and white pine (Figure 10). Whether these species are successful at recruiting into the forest canopy will only be apparent in longer term, but the imminent decline of hemlock and white ash could be crucial to their success.

Figure 10. Seedling colonization by read oak (QURU) and white pine (PIST) into the lower valley at Hubbard Brook Exerimental forest in 2015. (J. J. Battles, unpublished data).

Figure 10. Seedling colonization by read oak (QURU) and white pine (PIST) into the lower valley at Hubbard Brook Exerimental forest in 2015. (J. J. Battles, unpublished data).

4.6 Questions for Further Study

- How will forest composition and structure respond to continuing climate change, especially increasing air temperature and summer precipitation?
- What was the role of large-scale natural disturbances (vs. single-tree replacement) in shaping the composition and structure of pre-Industrial northern hardwoods forests
- What species will replace white ash and hemlock following expected mass mortality?
- What factors facilitate the colonization of white pine and red oak in the lower valley?
- What differences characterize the demography and distribution of paper birch and mountain paper birch, and how does their recent mass mortality affect the dynamics of associated species?
- How will the continuing declines of the three dominant species – yellow birch, sugar maple, American beech – affect the future composition and structure of the HB forest?
- In the long-term how will the restoration of ecosystem calcium affect forest composition on WS1?
- Will base cation depletion resulting from whole-tree harvest of WS5 have significant effects on forest composition?

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5 Biomass Productivity

Chapter Editors: John Battles

Dr. John Battles speaks on the continuous 60-year record of forest inventory data within Watershed 6, including the lack of recovery of key tree species from acid rain. Video filmed at the Hubbard Brook Experimental Forest on May 17, 2024.

5.1 Introduction

Biomass is the living (and sometimes including recently dead) organic material synthesized by plants and other organisms. The accumulation of biomass in forests is greater than in other Earth biomes because trees must effectively lift their leaves above their neighbors in order to compete for the light resource; hence, forest biomass provides the structural material that allows the plants to grow tall. The biomass of trees in forests forms the three-dimensional structure in which all the other organisms are entrained and to which they are adapted for growth, survival and reproduction. Much of the energy and carbon stored in the forest resides in the biomass of the trees and understanding the factors regulating forest biomass and its accumulation is of fundamental importance to ecologists and foresters, alike.

Figure 1. Changes in living biomass during ecosystem development after clear-cutting based on the average of two JABOWA simulations. (Bormann and Likens, 1979).

In their classic treatise, *Pattern and Process in a Forested Ecosystem*, Bormann and Likens (1979) developed a conceptual model for spatial and temporal variation in the biomass of a northern hardwood forest, based upon observations at Hubbard Brook and other regional forests. In the temporal domain, they proposed four phases of ecosystem development following large-scale disturbances (e.g., windstorm, clearcut harvest), culminating in a steady-state phase in which total biomass fluctuates around an equilibrium value (Figure 1). Measurements at Hubbard Brook and elsewhere in the northern hardwood region have provided new insights about this conceptual model and the magnitude and timing of forest biomass accumulation.

Primary productivity is the process resulting from photosynthetic activity of the plants and determines biomass accumulation in forests. Net primary productivity (NPP) represents the difference between gross photosynthesis of plant foliage and energy losses due to respiration and mortality of plant tissues. Although NPP continues in the steady-state phase of forest development, living biomass ceases to accumulate when photosynthetic carbon gain is balanced

by losses to plant respiration and mortality. In general, the rate of biomass accumulation during the transient phases of ecosystem development depends upon forest NPP; hence, there has been great interest in understanding the factors constraining NPP and how they may be affected by forest management and environmental change.

In this chapter, we explain current understanding of forest biomass and NPP in the context of the Hubbard Brook ecosystem, including: current measurement techniques; patterns of temporal and spatial variation; the environmental and biotic factors causing this variation; and the implications for responses to global and regional environmental change.

5.2 Forest Biomass

In many biomes, direct measurement of biomass can be accomplished simply by weighing the tissue harvested from a measured area (e.g., clipping herbaceous vegetation). This is impractical in forests and indirect approaches have been developed. In general, these rely on the allometric relationships between an easily-measured dimension of the plant and its aboveground biomass. At Hubbard Brook, Whittaker et al. (1974) measured the dimensions (e.g., diameter, height, biomass, etc.) of a sample of 93 trees of different species and sites, and developed allometric equations relating the biomass of individual trees to their diameter and height. Then, by measuring the diameter and height of trees on sampling plots of known area, the forest biomass can be calculated by applying the species-specific allometric equations. A compilation of allometric equations of forest trees in USA has also been published (Jenkins et al. 2003). The statistical uncertainty of these aboveground biomass estimates can also be determined by using Monte Carlo approaches (Yanai et al. 2010)

Measuring the belowground (root) biomass of trees can be more challenging. Both direct and indirect approaches have been applied at Hubbard Brook. Whittaker et al. (1974) actually excavated the root systems of the sampled trees described above, “with the encouragement of dynamite.” This work provided a rare example in which allometric equations include the tree root system, but recovery of the smallest fine roots (<0.5 mm diameter) is incomplete, and these roots are the most functionally important. Alternatively, root biomass can be measured directly by using a quantitative soil pit approach in which all the roots are recovered from a soil pit of known ground area and volume. Fahey et al. (1988) applied this method at Hubbard Brook and found close agreement with estimates obtained using the allometric equations for the coarse roots.

Most of the tree biomass in the mature forest (e.g., 100-yr-old forest at Hubbard Brook) is contained in the woody tissues of the stem and roots (91%), the remainder being leaves (1.7%), bark (5.1%), and fine roots (2.2%). Understory vegetation comprises a very small biomass pool (<1 % of total plant biomass). The ratio of root:shoot biomass varies with site quality and forest age, as discussed later, but averages about 0.25 in mature northern hardwood forest. The biomass of heterotrophic organisms averages less than 0.6% that of plants, and is mostly (~ 96%) comprised of soil microbes (bacteria, fungi).

Figure 2. Spatial pattern of estimated aboveground biomass in the reference watershed (W6) and across the Hubbard Brook valley in 1997. The W6 map is based on a 100% survey, gridded at 25 x 25 m spatial scale. The valley-wide interpolations are based on 450 plots (0.05 ha each). Error estimates are given in the text. (Fahey et al., 2005).

Figure 2. Spatial pattern of estimated aboveground biomass in the reference watershed (W6) and across the Hubbard Brook valley in 1997. The W6 map is based on a 100% survey, gridded at 25 x 25 m spatial scale. The valley-wide interpolations are based on 450 plots (0.05 ha each). Error estimates are given in the text. (Fahey et al., 2005).

Forest biomass represents one of the largest and most sensitive carbon pools on Earth and for that reason, ecologists and policy-makers have become very interested in spatial and temporal patterns of forest biomass. Forest biomass varies markedly among forest biomes, the highest values attained in temperate and tropical rainforests, the lowest in boreal woodlands, and intermediate values in temperate deciduous forests. Within the Hubbard Brook valley a two-fold range of aboveground biomass is observed in the ca. 100-yr-old-forest, with lowest values in fir-birch-spruce forest on thin soils at higher elevations and highest values in mixed hemlock-hardwoods in the lower valley (Figure 2).

Both tree species composition and site quality influence patterns of maximum forest biomass that accumulates in the northern forest region. For example, Kelty (1989) observed that mixed hemlock-hardwood stands support significantly higher biomass than pure hardwood stands, perhaps because of canopy architecture interactions; a similar pattern is seen in the lower valley at HBEF (Figure 2). The site quality influence also appears clearly at HBEF in the considerably higher biomass in enriched soil, “cove” sites on W6 in comparison with adjacent stands on thin soils of steeper slopes (Figure 2, inset).

The northern forest is recognized as a significant sink for C, influencing the global C budget. This is in part because historical forest harvest in the region reduced forest C storage and recovery to the assumed steady-state is still in progress (Woodbury et al. 2007). How long can we expect this ecosystem service to persist? The answer to this question is complex, involving multiple environmental and biotic factors as well as management and policy decisions. The conceptual model of Bormann and Likens (1979) and its application in simulation models originally suggested a transient, maximum forest biomass attained at forest age 150-200 yr followed by slight decline to the steady-state, old-growth phase (Figure 1). Empirical data from the Hubbard Brook forest indicate that live tree biomass reached a plateau much lower than predicted and at the age of only about 80 yr, owing to a variety of factors including exotic insect pests and pathogens (e.g. beech bark disease) and species declines unrelated to such pests (e.g., sugar maple, yellow birch). By comparison, summaries for the region, based upon various sources including USDA Forest Service Forest Inventory and Analysis (Lichstein et al. 2009) suggest an intermediate pattern, with forest biomass in northern hardwoods reaching an asymptote at 125-150 years, at maximum values 30% lower than projected. Higher maximum biomass values may be reached on richer sites such as alluvial valleys (Keeton 2011). As explained below, site quality limitations partly associated with soil nutrient depletion by acid deposition, contribute to forest decline and the observed limitation of forest biomass

accumulation at Hubbard Brook and other regional forests (Battles et al. 2014). Moreover, impending invasion by additional exotic pests (hemlock woolly adelgid, emerald ash borer) and effects of changing climate may further constrain forest biomass accumulation. The implication is that the combined effects of soil nutrient depletion, invasive pests and pathogens and climate change could limit the future role of forest biomass accumulation as a continuing sink for atmospheric CO₂.

Biomass of the forest in the reference watershed, W6, has been estimated periodically since 1965 by measuring the diameter of every tree in the watershed and applying the allometric equations; these measurements provide a detailed picture of changes in biomass for this previously aggrading forest (Figure 2-2). As noted earlier, the Hubbard Brook Forest accumulated biomass from the age of about 55 years in the early 1960s until the age of about 80 years in the 1980s. Since that time live biomass on W6 has levelled off and even shown some significant decreases owing to both natural disturbances (ice storm in 1998) and tree declines. In particular, widespread decline of sugar maple has contributed to the decrease in live biomass on W6. The cause of this decline is undoubtedly associated with depletion of soil base cations by acid deposition (see Acid Rain chapter). For example, the experimental replacement on W1 of calcium, lost as a result of soil leaching in the 20th century, reinvigorated sugar maple and consequently biomass accumulation resumed in the early 21st century (Figure 2-2). Continued monitoring of these forests and perhaps another dose of calcium will be needed to further inform these trends.

Aboveground live tree biomass of the forest on reference watershed 6 and adjacent Ca-treated watershed 1. Error bars indicate 95% confidence intervals based on DBH measurements of all trees on the watersheds.

Figure 2-2. Aboveground live tree biomass of the forest on reference watershed 6 and adjacent Ca-treated watershed 1. Error bars indicate 95% confidence intervals based on DBH measurements of all trees on the watersheds.

5.3 Primary Productivity

Primary productivity (PP) is defined as the rate of energy or mass storage in organic matter of plants per unit surface area of the earth. In terrestrial ecosystems PP is conventionally divided into two components: 1) gross primary productivity (GPP) is the amount of organic material synthesized by plants per unit ground area per unit time, and 2) net primary productivity (NPP) is the amount of this organic material that remains after respiratory consumption of organic matter by the plants (Ra). All heterotrophic organisms rely on NPP for their food requirements. In forests, Clark et al. (2001) emphasized that a working definition of NPP for actual measurements must be adapted from the formal definition (above) because direct measurements of GPP and Ra are not possible and accounting for a variety of other losses of organic material from plant tissues during a measurement interval also can be challenging. In theory NPP could be quantified as:

$$\text{Eq. 1. NPP} = \text{B} + \text{M} + \text{H} + \text{L} + \text{V},$$

where B is net change in biomass and M, H, L, and V are losses of organic matter from plant tissues owing to mortality, herbivory, leaching and volatilization, respectively. The reason that we must add loss terms like mortality to B when calculating forest NPP is illustrated by the case where B=0: if live biomass doesn't change over a time interval during which losses of organic material are occurring, then the plants must have added new organic material to replace those losses. Thus, the loss terms would be equal to this new production. To estimate forest NPP at Hubbard Brook we quantify changes in live tree biomass using the allometric equations (described above) and we estimate the principal loss terms, tree mortality and mortality of ephemeral tissues (leaves and fine roots). Some of the other loss terms in Equation 1 also have been measured at Hubbard Brook. Although H, L and V usually comprise a relatively small proportion of aboveground NPP (ANPP), herbivory can be substantial during rare irruptions of defoliating insects. For example, during the peak year of a 3-yr irruption of a defoliating caterpillar (*Heterocampa guttivita*) about 44% of leaf tissue was consumed in the hardwood forest at HBEF, with local patches of 100% defoliation (Holmes and Sturges 1975). Finally, loss terms for belowground NPP (BNPP) are notoriously difficult to measure and can comprise a substantial portion of NPP that is particularly sensitive to environmental changes, climate, atmospheric CO₂ and soil fertility. Table 1. Biomass and production components of northern hardwood forest at Hubbard Brook (adapted from Fahey et al., 2005). Biomass Components g/m² (1997) Foliage 402 Branch 5436 Bark 1220 Wood 11932 Total aboveground biomass 18990 (248) Root crown 1580 Lateral woody roots 2920 Fine roots (< 1mm) 522 Total belowground biomass 5022 (638) Total plant biomass 24012

Production Components g/m²-yr (1997) Aboveground annual tissues 342 Aboveground perennial tissues 366 Total ANPP 708 (62) Fine roots 182 Coarse roots 76 Rhizosphere flux 160 Total BNPP 418 Total NPP 1126

The first estimates of ANPP of the Hubbard Brook forest were calculated in the 1960s by Whittaker et al. (1974). At that time the forest on W6 was about 50 yrs old and ANPP was estimated at 924 g/m²-yr. Since that time ANPP has declined considerably; Fahey et al. (2005) estimated ANPP of the same forest at age ca. 90 yrs to be 708 g/m²-yr (Table 1). Roughly half of this total was associated with increment of woody tissue and half with replacement of ephemeral tissue (mostly foliage). The ANPP of the northern hardwood forest at Hubbard Brook is similar to a variety of other mature Acer-dominated forests worldwide (Table 2). Table 2. Aboveground net primary productivity and forest production efficiency for selected mature Acer-dominated forests (From Fahey et al., 2005) Location Ref.d/ ANPP (g/m²-yr) FPEa/ LAI-basis FPEb/

Mass-basis Wood PEc/ HBEF, NH age = 45 yr 1 924 147 2.28 na HBEF, NH age = 85 yr 2 708 112 1.76 0.91 Indiana mesic slope 3 678 161 2.19 1.28 Indiana bottomland 3 639 141 2.06 1.04 Wisconsin 4 755 137 2.02 1.02 Wisconsin sandy outwash 5 480 161 na na Wisconsin

ground moraine 5 920 133 na na Himalayas, India 6 990 193 1.80 0.80 Upstate New York 7
772 119 2.38 1.23

Belowground production (BNPP) includes the growth of perennial woody roots, the replacement of ephemeral fine roots as well as organic matter allocated to mycorrhizal fungi and other rhizosphere fluxes (e.g. root exudation). Direct observations of fine roots at Hubbard Brook using minirhizotrons indicate that most of the smallest first-and second-order roots have lifespans of about one year while higher order (order 3-4) roots live for several years (Tierney and Fahey 2001). On the basis of these observations fine root (< 1mm) production has been estimated at 182 g/m²-yr, considerably lower than the production of aboveground ephemeral tissues (342 g/m² yr; Table 2). However, total rhizosphere C flux has been estimated to be as high as 160 g/m²-yr (Fahey et al. 2005) so that BNPP may comprise as much as 37% of total forest NPP (Table 1).

Spatial pattern of estimated aboveground net primary productivity across the Hubbard Brook valley for 1990-1995. The interpolations are based on 370 plots for which diameter growth of all trees (> 10 cm DBH) was measured. Error estimates are given in the text. (Fahey et al., 2005)

Figure 3. Spatial pattern of estimated aboveground net primary productivity across the Hubbard Brook valley for 1990-1995. The interpolations are based on 370 plots for which diameter growth of all trees (> 10 cm DBH) was measured. Error estimates are given in the text. (Fahey et al., 2005)

The spatial pattern of ANPP of the Hubbard Brook forest generally reflects that of biomass (compare Figure 2 vs. 3).

For example, 42% of the variation in woody biomass production is explained by aboveground biomass across the 370 plots represented in Figure 2 and 3. The most notable decoupling between biomass and productivity is for fir-birch-spruce dominated stands at the upper elevations, where the production:biomass ratio is notably higher than elsewhere in the HB valley. The temporal pattern of NPP following large-scale disturbance follows the usual pattern of increase to a peak value after a few decades, followed by decline at greater ages. Such an age-related decline in NPP appears to be virtually universal in all forests (Ryan et al. 1997) and has been attributed to a wide range of causes. These temporal and spatial patterns beg the basic question: what limits NPP in the Hubbard Brook forest?

Figure 4. The effect of growing season length on simulated primary productivity using the model PnET-II (Aber et al. 1995) parameterized for a northern hardwood forest at the HBEF. Leaf area duration (LAIMo) represents the product of daily estimated forest LAI and monthly time intervals for each year. (Fahey et al., 2005).

Figure 4. The effect of growing season length on simulated primary productivity using the model PnET-II (Aber et al. 1995) parameterized for a northern hardwood forest at the HBEF. Leaf area duration (LAIMo) represents the product of daily estimated forest LAI and monthly time intervals for each year. (Fahey et al., 2005).

In general, forest NPP is limited by a variety of environmental conditions (e.g., temperature) and resources. In the cold temperate climate of the Northeast the short growing season during which temperatures are suitable for plant growth (i.e., the frost-free season averages 145 d; Bailey et al. 2003) is a fundamental constraint on NPP. Temperature limitations contribute to both temporal and spatial variation in NPP at Hubbard Brook. For example, the time interval between leaf out and senescence for the broadleaf deciduous trees varies by about 30 d across years at HBEF (ca. 125-155 d; Bailey et al. 2003), and the range of this index of growing season length across elevation (480-820 m) at Hubbard Brook is about 21 days. According to the simulation model PnET about 25% of annual variation in GPP can be explained by growing season length; however, plant respiration also is greater in years with long, warm seasons, so that the effect on NPP is much lower (e.g., only 6% of annual net photosynthesis is explained by growing season length; Figure 4).

Another atmospheric condition that limits forest NPP is atmospheric CO₂ concentration as demonstrated in free-air CO₂ enrichment (FACE) studies in several forests (Norby et al. 2005). Although FACE experiments have not been conducted at HBEF, we have used the PnET model to evaluate possible effects of rising CO₂ on NPP, independent of climate change effects. One key effect of rising atmospheric CO₂ concentration on forest physiology is to allow greater stomatal control over water loss. Water-use efficiency (WUE) is defined as the ratio of plant photosynthesis per unit water loss by transpiration. Recent measurements indicate that the WUE of northeastern U.S. forests has risen steadily with atmospheric CO₂ over the past two decades (Keenan et al. 2013), probably explaining the unexpected observation that declining actual evapotranspiration from the HB watersheds has accompanied rising temperatures (see Climate Change chapter)

The water-use efficiency result emphasizes that soil resource availability serves as an important constraint on forest NPP. Although precipitation is moderately high at HBEF and evenly distributed through the year, soil moisture deficits and drought stress occur occasionally. The dominant tree species are drought avoiders that close their stomata at relatively high soil water potential, thereby reducing potential damage but restricting photosynthetic C gain (Federer 1977). Notably, regional climate warming, which in the absence of CO₂-induced increases in WUE would promote higher water loss by the trees, has been accompanied by increasing annual precipitation (see Climate Change chapter)

The role of soil fertility in limiting NPP of northern hardwood forests has received considerable study over the years. Based on a recent meta-analysis of forest fertilization studies, Vadeboncoeur (2010) concluded that NPP of most young northern hardwood forests (e.g. < 30 yr) responded to the addition of N, P, K or Ca or various combinations, with primary limitation by N being most common. Evidence for nutrient limitation of NPP in mature forests was mixed. Recent results from an ongoing N x P nutrient amendment experiment in and around HBEF suggest that P limitation may be widespread in mature northern hardwood forests.

Figure. 5. ANPP for three elevational zones of W2 (open diamond, lower third; open square, middle third; open triangle, upper third) compared with site averages for conventionally harvested sites (solid squares). (Reiners et al., 2012).

Figure. 5. ANPP for three elevational zones of W2 (open diamond, lower third; open square, middle third; open triangle, upper third) compared with site averages for conventionally harvested sites (solid squares). (Reiners et al., 2012).

The effects of natural variation in soil nutrient availability on biomass accumulation and NPP of the Hubbard Brook forest have been modified by inputs of pollutants derived from human activity: acid precipitation and nitrogen deposition. Although direct evidence that N deposition has altered NPP of the mature forest is scant, reduction of NPP owing to depletion of soil base cations by acid deposition has been shown conclusively in the Ca remediation experiment on W1 at HBEF(Battles et al. 2013). As noted earlier, the unexpected plateau in forest biomass on W6 is explained in part by this effect. Specifically, soil Ca depletion has limited biomass accumulation primarily by causing decline of the dominant species, sugar maple, which is particularly sensitive to low soil Ca availability (Long et al. 2009). Crown deterioration and reduced LAI of sugar maple, attributed to soil Ca depletion, has contributed to the relatively low ANPP and biomass accumulation on W6 (Battles et al. 2014). In addition to reduced net photosynthesis owing to LAI loss, higher costs of wound repair and plant defense accompany the impaired Ca nutrition of sugar maple in the reference forest (Huggett et al. 2007; Halman et al. 2015). As detailed by Tominaga et al. (2010), recovery of soil base cation status is expected to be delayed in the immediate future because of the high magnitude of 20th century losses and continuing acid deposition (albeit at lower levels).

An interesting case study of the development of forest biomass and NPP following large-scale disturbance in northern hardwoods is provided by the deforestation study on W2. Reiners et al. (2012) hypothesized that the extreme disturbance of the deforestation treatment on W2 (see W2 Experimental Summary) would exceed the capacity for forest ecosystem resilience. In particular, the treatment resulted in loss of 28% of the ecosystem stock of total N (as well as smaller proportions of base cations); eliminated vegetative sprouting and advance regeneration as sources of forest regeneration; and greatly reduced the abundance of fast-growing pin cherry. Surprisingly, despite an initial lag in biomass accumulation and net primary productivity, the forest on W2 followed a trajectory similar to (though on the low end) of comparable sites that had been harvested by conventional methods (Figure 5).

The slowest growth and biomass accumulation were observed in the upper elevation zone of the watershed where soils are thinner and less fertile (Johnson et al. 2000). These observations illustrate that northern hardwoods forests on moderately fertile soils exhibit strong resilience of productivity. The mechanisms contributing to this high resilience deserve further study but may include biologically-enhanced weathering of primary minerals (Blum et al. 2002), biological nitrogen fixation (Bormann et al. 1993) and enhanced mineralization of relatively stable soil organic matter.

5.4 Forest Leaf Area Index

Forest productivity is powered by the capture of solar radiant energy by plant foliage. The standard measurement of foliage abundance that carries out this function is leaf area index (LAI), defined as the

(one-sided) area of foliage in the entire plant canopy per unit ground area; essentially LAI is the number of layers of canopy foliage. In mesic forests like Hubbard Brook with a closed canopy, where LAI is little constrained by soil water availability, the maximum LAI is limited by self-shading because foliage at the bottom of the canopy receives insufficient insolation to effectively carry out the photosynthetic function. Forest LAI can be measured in a variety of ways, including LIDAR that can remotely sense objects in the canopy; however, this relatively recent tool measures plant area index, including stem/branch surfaces and requires correction factors. In the deciduous northern hardwood forest that dominates the Hubbard Brook landscape, LAI can also be measured conveniently by quantifying leaf litterfall. Litterfall records for the Hubbard Brook Forest go back over thirty years (Figure 6) and also allow estimation of LAI of each of the various tree species.

The total LAI of the northern hardwood forest adjacent to reference W6 averages a little less than 6. In the absence of disturbances LAI is pretty constant from year to year, but considerable spatial variation across the study area is observed (Figure #): the highest values of 7 to 8 are observed in coves with enriched soils and sugar maple dominance while the lowest values (3.5 to 4) coincide with thin depleted soils in the upper watershed. Comparison between the reference forest adjacent to W6 and the Ca-treated W1 (Figure #) illustrates the role of soil base status and sugar maple health in regulating forest LAI and NPP in the experimental watersheds at Hubbard Brook. These patterns reflect site quality variation that clearly constrains the NPP of the wider forest landscape.

The temporal pattern in LAI also reflects the effect of disturbances. In particular, a clear decrease in forest LAI accompanied disturbance by the 1998 ice storm: LAI was reduced in half for two years before gradually recovering to pre-disturbance levels by about 2003-4 (Figure 6). Since that time LAI has been relatively constant on a large-scale average, although localized decreases have been observed resulting from smaller disturbances (late-spring frost, microburst windstorm). Continued monitoring is needed to allow researchers to capture effects of environmental change on forest health and dynamics (Fahey et al. 2022).

Leaf area index of northern hardwood forest measured based on leaf litterfall A. adjacent to reference watershed 6 and B. calcium-treated watershed 1. Data points indicate annual estimates for six monitored forest stands adjacent to W6 and three stands in W1.

Figure 6. Leaf area index of northern hardwood forest measured based on leaf litterfall A. adjacent to reference watershed 6 and B. calcium-treated watershed 1. Data points indicate annual estimates for six monitored forest stands adjacent to W6 and three stands in W1.

5.5 Questions for Further Study.

- What are the mechanisms contributing to soil nutrient limitation of forest productivity?
- Why does forest NPP decline with stand age – so-called “age-related NPP decline”?
- How does BNPP associated with rhizosphere carbon flux vary across the forest landscape, and what environmental and biotic factors influence this flux pathway?
- How will forest NPP respond to the long-term amelioration of soil calcium depletion on WS1?
- Conversely, will the depletion of soil calcium resulting from whole-tree harvest limit forest NPP on WS5?
- How will forest NPP and biomass accumulation respond to continued changes in climate and atmospheric carbon dioxide concentration?

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