Cyanobacterial harmful algal blooms (cyanoHABs, or blue-green algae) are a global problem despite decades of management targeting these ancient organisms. In many cases, cyanoHABs are the main symptom of eutrophication (Figure 1), which is defined as high productivity from excessive nutrient discharges (or “loading”) into surface waters. This high productivity often appears in lakes as aquatic weeds, low oxygen, or fish kills. Climate change is an important factor in eutrophication and cyanoHABs, especially when we consider temperature, the timing and intensities of rain and drought, and how long water stays within a lake (Paerl and Huisman 2009).

The role of nutrients – mostly phosphorus (P) and nitrogen (N) – in driving cyanoHABs has received most of the attention in research, ecosystem modeling, and management. These research, modeling, and management efforts used to focus on understanding and reducing external P discharges, mostly from sewage treatment plants and industry, into cyanobacteria-impacted lakes. This P-focused approach was successful in some lakes but unsuccessful in others, mainly due to poor implementation or persistent “legacy,” or historical, P loading from lake sediments. In still other lakes, P-focused management has only temporarily reduced cyanoHABs. For example, in Lake Erie (USA), cyanoHABs returned in the mid-1990s after disappearing for over a decade (Figure 2), likely due to regulations banning P in detergents in the 1970s and the invasion of zebra mussels in the 1980s.

The return of cyanoHABs in Lake Erie came with an interesting twist, however. Unlike cyanoHABs before the P controls, today’s cyanoHABs are caused mostly by organisms that cannot fix atmospheric nitrogen gas (N₂). Many of these non-N-fixers (like Microcystis and Planktothrix) also form toxins, which have disrupted recreational and commercial uses, local and regional economies, and human and livestock health. The occurrence of cyanoHABs in lakes world-wide continues to increase, and these blooms are increasingly caused by non-N-fixing cyanobacteria.

The human health and resource usage effects of cyanoHAB toxins has added a new dimension to the global cyanoHABs problem, as evidenced by recent crises occurring in China (Lake Taihu) and the United States (Lake Erie), both of which resulted in contamination of drinking water supplies for large populations.

In China, the drinking water for ~6 million people in the city of Wuxi was contaminated with microcystin, a potent liver toxin, during a massive Microcystis bloom in May 2007 (interestingly, microcystins were originally called ‘fast-death factor’). Toledo, Ohio (population ~400,000), suffered a similar fate in August 2014, when microcystin from the annual Microcystis bloom in the western basin of Lake Erie caused the State of Ohio to shut down the city’s water supply for several days and declare a state of emergency (Figure 3).
impacts of these events were devastating (Bingham et al. 2015), and human health was put at serious risk.

Cyanohabs need a lot of N to make toxins, and high N concentrations are associated with high toxin production (Davis et al. 2015). CyanohAbs capable of fixing N can access an unlimited supply of N₂ gas in the atmosphere when N supplies are low, but at much lower growth and toxin production rates. CyanohAbs that can’t fix N₂ gas have to compete with other aquatic plants, algae, and bacteria (i.e., “primary producers”) for available N. The global problem of non-N-fixing cyanohAbs, many producing N-rich toxins, requires that we rethink the historical approach of P-focused nutrient management.

Nitrogen is important, too

The Haber-Bosch process, invented in 1909, was a landmark discovery in agriculture and fertilizer production. Atmospheric N₂ gas, which accounts for ~78 percent of the atmosphere, could now be converted in large quantities to ammonia (NH₃) for use as fertilizer. This discovery has allowed humanity to produce the vast quantities of food needed to support a growing population, but artificially produced reactive N has now led to global N surpluses, degrading drinking water quality (via nitrates) and air quality (e.g., smog), and causing cyanohAbs in lakes (Erisman et al. 2015). This glut of “new” reactive N often results in the non-N-fixing cyanohAbs producing toxins that are causing so many of the problems in lakes today.

The question for many scientists studying the fate of this “new” reactive N in aquatic systems is: Since decades of P-focused management has not prevented them from occurring, what is promoting non-N-fixing cyanohAbs, causing them to form blooms and produce toxins? A growing body of evidence shows that the amount and form of N available to primary producers plays an important role in answering this question. In water, N occurs in several different dissolved forms, both inorganic (with no carbon) and organic (containing carbon). These N forms influence primary producer communities in different ways, based largely on their abilities to convert the different N forms into biomass and compete with other organisms.

Regardless of the N form, cyanohAbs and other primary producers must convert other N forms to inorganic ammonium (NH₄+) inside the cell before they can use it for biomass or toxin production. Ammonium is the easiest N form for primary producers to acquire and
transport into the cell. By comparison, inorganic nitrate (NO$_3^-$) and nitrite (NO$_2^-$) must be chemically converted within the cell to NH$_4^+$, which requires energy and “micronutrients,” such as iron. For atmospheric N$_2$ gas fixation performed by some cyanobacteria, the energy requirement is severe and can limit bloom size and toxicity. The order of energetic preference for most primary producers follows as NH$_4^+$, urea, NO$_3^-$, SO$_4^{2-}$, and, finally, N$_2$ gas. Cyanobacteria and other primary producers use N forms as ‘currency’ for producing biomass (and toxins), with NH$_4^+$ being the easiest, most efficient way to conduct the small transactions within the cell. Using NH$_4^+$ is cheap and easy, like purchasing milk at the corner gas station on your way home. Using NO$_3^-$ is more expensive, like making a special trip to buy organic milk at the upscale grocery store. Using N$_2$ via fixation is like setting up a farm and buying the cow. All ways end with obtaining milk, but there are different levels of cost and effort to obtain the milk.

Tracking N in the lake ecosystem

In lakes monitored regularly for water quality and nutrient concentrations, N forms are often evaluated, sometimes including NH$_4^+$, and sometimes only for total N (TN) and/or oxidized N (NO$_3^-$ +NO$_2^-$). Organic and inorganic N forms are included in TN measurements, as is any N within suspended biomass (i.e., TN includes any N within the cyanobacterial cells and “critters” unlucky enough to be in the water sample). Oxidized N measurements represent a N form available for biomass and toxin production, but also represent N forms that require more energy for conversion to NH$_4^+$. Monitoring only these N forms is therefore an unreliable indicator of overall N availability to cyanobacteria and other primary producers. The organic N form, urea, is an increasing component of N fertilizers used in agriculture and is also an efficient N “currency.” However, urea is rarely measured as part of water quality monitoring programs.

In cases where NH$_4^+$ is measured in monitoring programs, the measured concentration is often minimal or undetectable, especially relative to NO$_3^-$ and NO$_2^-$. Since NH$_4^+$ is the easiest way for cyanobacteria to “purchase” N for biomass and toxins, it is not surprising that it is rarely measured at high concentrations in water samples. To complicate matters, NH$_4^+$ is difficult to measure accurately in water samples and requires careful handling during and after sample collection. Because it is so reactive and preferred by primary producers, its concentration changes rapidly in water samples unless the natural algae and plankton communities are removed. For lake managers and researchers collecting samples for monitoring programs, these rapid changes require that water samples are filtered immediately in the field using very small pore-size filters (0.2 µm) to remove all organisms from the samples. Without these procedures, water quality monitoring results do not reflect actual NH$_4^+$ concentrations in the lake. Instead, the measured concentration reflects a balance between the various processes occurring within the water sample (more on this below).

Despite the low NH$_4^+$ concentrations in water samples, however, we must not dismiss its importance in driving modern, non-N-fixing cyanobacteria, such as those caused by *Microcystis*. Here, the story of N and cyanobacteria takes another very interesting twist. When nutrients are discharged to lakes and aquatic systems, they are converted to biomass and other organic compounds. As organisms die, the N and P within their biomass is decomposed by bacteria, which consume oxygen and release much of these nutrients back into the water in dissolved form, available to be used again by cyanobacteria to sustain population size and toxicity. Organisms in the lake also feed on other organisms, and much like humans, they excrete waste products (“pee and poop”). These “wastes” include urea and NH$_4^+$, or organic material that can be broken down to NH$_4^+$, which enhances non-N-fixing cyanobacteria and toxin production (Davis et al. 2015). This process of internal NH$_4^+$ recycling supports a vicious cycle of nutrient loading, biomass production, decomposition, nutrient recycling, biomass and toxin production, and so on. The rate at which recycling processes provide NH$_4^+$ for primary producers, especially cyanobacteria, is much more important to understand and quantify than a single ‘snapshot’ NH$_4^+$ concentration measurement, which lacks context in space and time. In Missisquoi Bay, Lake Champlain (USA), NH$_4^+$ recycling provided twice as much N for primary production compared to estimated external loads from rivers (McCarthy et al. 2013). The recycling rate thus plays an important role in determining how much NH$_4^+$ is available for cyanobacteria (McCarthy et al. 2013), as well as selecting for problematic non-N-fixing cyanobacteria.

Fortunately, lakes have a natural defense mechanism, a process called “denitrification” performed by bacteria in the lake sediments. Denitrification removes oxidized N forms (NO$_3^-$ and NO$_2^-$) as N$_2$ gas, which escapes to the atmosphere and reduces the amount of N available to cyanobacteria, as well as the N available to be recycled. Unfortunately, this natural defense mechanism is less efficient as N loading rates increase, which means that the natural defenses can be overwhelmed, allowing watershed N loads to accumulate or be continually replaced by new external loads, allowing the vicious cycle of recycling to keep fueling cyanobacteria and toxin production.

Implications for lake management

What does this mean for lake management? In the short term, and on local and regional scales, it means that reducing external nutrient loads in watersheds, including both P and N, is the only way to permanently break the persistent cycles of internal “legacy” P and internal NH$_4^+$ regeneration within lakes. In agricultural watersheds, the importance of educating the agriculture industry on best management practices for fertilizer application, in terms of timing, amounts, and forms, will be crucial going forward. For example, edge-of-field buffers (Figure 4), planted with native trees, shrubs, and grasses, can reduce soil erosion and intercept nutrients before they reach lakes. In urban watersheds, storm- and wastewater management may require upgrades to effectively reduce N and P loads to receiving waters. Globally, increasing awareness of the widespread effects of surplus reactive N (reactive N is mobile in air and can travel long distances before being deposited elsewhere), and improving agricultural technology and
wastewater treatment, will provide the longest-lasting benefits to combat cyanophytes in lakes.

The scientific community has made great strides in understanding what causes cyanophytes and how and when they produce toxins, but without continued efforts to manage watershed nutrients, the vicious cycles for P and N will continue, and cyanophytes will likely get worse. We also still have much to learn about cyanophytes and eutrophication in lakes. Ongoing research, largely funded by government entities and taxpayer dollars, will allow progress to continue, with the ultimate goal of providing safe water resources to be used by all citizens in a healthy, sustainable way. As with many environmental problems, there are economic costs to preventing cyanophytes, but these costs pale in comparison to the economic impacts of responding to individual events, such as the Toledo and Taihu drinking water crises.

**References**


