

Throwing Fuel on the Fire: Synergistic Effects of Excessive Nitrogen Inputs and Global Warming on Harmful Algal Blooms

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A worldwide proliferation of harmful (toxic, food-web altering, hypoxia-generating) algal blooms (HABs) has been linked to human nutrient (phosphorus (P) and nitrogen (N)) overenrichment. In addressing this pressing environmental and human health issue, reducing P inputs has received the most attention, in part because this nutrient was first identified as driving eutrophication (1), and because P is simpler and less expensive to remove from pollution sources (e.g., wastewater, industrial effluents). Furthermore, P reductions have been prescribed to control a particularly noxious group of HABs, the N₂ fixing cyanobacteria, which can obtain N₂ from the atmosphere, thereby minimizing ecosystem-level nitrogen (N) limitation

(1). However, less than 50% of primary production demands are typically met by N₂ fixation, even when P supplies are sufficient. Furthermore, denitrification, the microbially mediated reduction of nitrate to N₂ gas, often offsets fixed N input (Table 1). The net balance of these N transformations in eutrophic waters can result in sustained ecosystem N limitation (2). Also, eutrophying freshwater, estuarine, and marine systems are increasingly plagued with non-N₂ fixing Cyanobacterial HABs (Cyanobacteria) and eukaryotic bloom-forming groups (dinoflagellates, chrysophytes, prymnesiophytes), indicating that these systems may be increasingly influenced by accelerating N loads.

Nutrient loading dynamics have changed substantially over the past several decades. While P reductions have been actively pursued, human population growth has been paralleled by accelerating N inputs, often at rates much higher than those of P. Sources of N inputs include fossil fuel combustion, agricultural fertilizers, stormwater discharge, groundwater pollution, and urban, agricultural, and industrial wastes (3). Biologically available reactive nitrogen (N_r), includes reduced (ammonium, organic N compounds) and oxidized (nitrate, nitrite) forms; inputs of all have increased dramatically. On the global scale, human activities now create approximately 2-fold more N_r than natural ecosystems, while in the U.S., anthropogenically generated N_r is about 5-fold larger than natural processes (3). A large proportion of N_r loading, generally exceeding 50%, is from diffuse, nonpoint sources (agricultural and urban runoff, atmospheric deposition, groundwater), which complicates remediation of this vast and rapidly growing supply of N pollution.

Excessive N loading has been recognized as promoting marine (estuarine and coastal) eutrophication and HAB expansion. However, the “N problem” is not isolated to these waters. Increasingly N_r plays either a primary or secondary (i.e., colimiting) role as a limiting nutrient in freshwater ecosystems. For example, oligotrophic, alpine, tropical, and subtropical, and other lakes having small watersheds relative to the lake surface/volume, and lakes experiencing various stages of eutrophication, tend to be N-limited (4). Additionally, numerous reservoirs, rivers, and fjords worldwide exhibit N limitation and N and P

TABLE 1. Ecosystem-Scale Dinitrogen Gas Flux from Several Eutrophic Lakes Indicating a Net Loss (Negative Net N₂ Flux) of Reactive Nitrogen to the Atmosphere (All Rates Reported in g N m⁻² yr⁻¹)^a

lake	nitrogen fixation	denitrification	net N ₂ flux
Lake 227 (ELA ^b), Canada	0.5	5–7	–6.5 to –4.5
Lake Mendota, Wisconsin	1.0	1.2	–0.2
Lake Okeechobee, Florida	0.8–3.5	0.3–3.0	–2.2 to 0.5
Lake Erken, Sweden	0.5	1.2	–0.7

^a Refs 1 and 2, and citations therein. ^b Experimental Lakes Area.

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69 colimitation, either simultaneously or in seasonally shifting
 70 patterns. Under these circumstances, N inputs can de-
 71 termine the spatial and temporal extent of summer
 72 nuisance blooms. Lastly, N inputs, including those from
 73 increasing levels of atmospheric deposition, impact nutri-
 74 ent stoichiometry, with cascading effects on nutrient
 75 limitation, productivity, and ecosystem nutrient cycling
 76 characteristics. Therefore, N inputs play a critical role in
 77 determining biogeochemical response, trophic state, and
 78 water quality conditions of affected freshwater ecosystems.

79 Lake Okeechobee, the largest lake in the Southeastern
 80 U.S., has experienced at least 4 decades of increased P
 81 loading coincident with high loads of N, and it periodically
 82 experiences large CyanoHAB blooms. Reactive P is highly
 83 available in this lake, and changes in N_f availability can
 84 control the magnitudes and persistence of algal blooms.
 85 In the 1980s and 1990s, blooms were predominantly caused
 86 by the N_2 -fixing CyanoHAB *Anabaena*. However, the most
 87 recent widespread bloom, which covered almost the entire
 88 lake surface in summer 2006, was caused by *Microcystis*,
 89 a non N_2 -fixing CyanoHAB that depends on dissolved
 90 inorganic N (DIN: ammonium, nitrate, nitrite) and possibly
 91 organic N for its growth. *Microcystis* is the most common
 92 toxin producer in Florida lakes, and it has the ability to
 93 store excess P from lake sediments before rising through
 94 the water column and increasing its biomass proportionally
 95 to N availability. Because Lake Okeechobee's sediments
 96 contain massive quantities of reactive P, successful control
 97 of *Microcystis* blooms will require reductions in both P
 98 and N inputs.

99 Lake Okeechobee is not an isolated case of nutrient
 100 pollution coinciding with CyanoHAB blooms. Lake Taihu,
 101 China's third largest lake is, like Okeechobee, a large, shallow
 102 subtropical lake that has, over the past 3 decades, changed
 103 from pristine, bloom-free conditions to a *Microcystis*-
 104 dominated system. Expanding blooms are attributable to
 105 accelerating N and P inputs from rapid urban and agricultural
 106 expansion in its watershed. Lake Erie, U.S.–Canada, was
 107 thought "recovered" from eutrophication in the 1970s and
 108 1980s following P (but not N) abatement programs. However,
 109 *Microcystis* blooms have proliferated since the mid-1990s
 110 even though total P inputs to the lake have remained fairly
 111 stable during this time.

112 How have CyanoHABs re-emerged, despite concerted
 113 efforts to control P? Large lakes like Okeechobee, Taihu,
 114 Kasumigaura, Japan, deeper systems like Lake Erie, and even
 115 very deep systems like Lake Tahoe, U.S. tend to be colimited
 116 by N and P (4) largely because previously loaded P and N are
 117 effectively retained and recycled. While some N is "lost" via
 118 denitrification, this process does not appear to keep up with
 119 anthropogenic N inputs. N and P colimitation appears
 120 particularly common in eutrophic systems (4), which are
 121 most highly susceptible to HAB outbreaks. Because these
 122 lakes are now so overenriched with both N and P, the efficacy
 123 of N removal through denitrification is diminished. Thus, N
 124 input reductions are an essential step in getting these lakes
 125 below the bloom threshold.

126 Global climate change (particularly warming) is a com-
 127 plicating and increasingly problematic factor that must be
 128 considered when formulating N (and P) reduction strategies
 129 aimed at arresting HABs. Many aquatic ecosystems impacted
 130 by HABs are also experiencing increasing water temperatures
 131 reflecting atmospheric warming. Warming has led to a suite
 132 of environmental changes that benefit HAB potentials. These
 133 include (1) longer seasons of elevated temperatures and ice-
 134 free conditions, (2) increased vertical stratification intensity
 135 (due to stronger surface heating), (3) salinization (increased
 136 evaporation rates and droughts), and (4) intensification of
 137 storm magnitudes and drought frequency and duration.
 138 Phytoplankton generally optimize growth as temperatures

increase, but this is particularly true for CyanoHAB species 139
 (5). Furthermore, CyanoHABs as well as other HAB taxa, most 140
 notably dinoflagellates and other bloom-forming flagellates, 141
 prefer positioning themselves in the upper water column 142
 through buoyancy regulation and motility. Under stronger 143
 thermally stratified (i.e., nonmixed) conditions, they will have 144
 a distinct advantage over nonmotile and often more desirable 145
 (from a water quality perspective) taxa such as diatoms. More 146
 extreme storms will lead to enhanced runoff and nutrient 147
 delivery. If these events are followed by severe droughts, 148
 nutrients supplied to affected waters will be retained longer 149
 because water residence times will increase. This ensures 150
 increased availability of N and P discharged from watersheds 151
 and airsheds to support blooms. 152

153 The "perfect storm" scenario would be large rainfall 153
 events (tropical cyclones, periods of thunderstorms), 154
 followed by a protracted drought during the summer–fall 155
 period when temperatures and stratification would be 156
 maximal. In addition, long-term (multiannual, decadal) 157
 increases in air and water temperatures, combined with 158
 human hydrologic alterations (e.g., increased reservoir 159
 construction due to supply/demand imbalance) would lead 160
 to increases in vertical stratification and water residence 161
 time. This complicates management strategies aimed at 162
 nutrient input control because CyanoHABs and other HABs 163
 would be favored under such a scenario. Therefore, 164
 projected climate change scenarios, especially temperature 165
 increases and their physical–chemical–biological effects, 166
 will likely promote HABs. 167

168 Management strategies must incorporate climate change 168
 in the development of predictive bloom thresholds based on 169
 the interactions of nutrient enrichment, altered thermal and 170
 hydrologic properties of aquatic ecosystems. We must re- 171
 examine our management toolbox and ensure that our Best 172
 Management Practices (BMPs) are actually the best they can 173
 be. Specifically, fertilizer applications should be at agronomic 174
 rates and timed to optimize uptake by crops, while minimiz- 175
 ing losses to downstream waters. Application schemes should 176
 take spring maximum runoff, tropical cyclone, and summer 177
 thunderstorm seasons into consideration. Municipal waste- 178
 water treatment should be expanded to reduce N (and P) 179
 concentrations in treated discharges, particularly during low 180
 precipitation periods that permit maximum treatment effi- 181
 ciency. Parallel efforts should focus on minimizing agri- 182
 cultural and urban sediment loss, as this is a significant source 183
 of both N and P. Other efforts should focus on retention and 184
 treatment of urban and rural stormwater runoff, another 185
 major source of new N inputs. Impoundment of freshwater 186
 runoff in storage ponds and reservoirs should be carefully 187
 evaluated however, as such steps will increase residence time 188
 and hence opportunities for HAB formation. Optimal use 189
 and minimal losses of N compounds, coupled to appropriate 190
 hydrologic discharge conditions should be formulated, and 191
 this may vary among watersheds and climatic regions. 192
 Controls on atmospheric emissions of all forms of biologically 193
 available N should be incorporated in regional N reduction 194
 strategies. Lastly, reductions in greenhouse gas emissions 195
 must accompany the above strategies, since they are the 196
 only "manageable" step we can take to minimize global 197
 temperature increases. These are formidable but essential 198
 challenges for balancing optimal use of watershed/airsheds 199
 with acceptable and safe use of downstream/downwind water 200
 resources. 201

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