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Nitrogen (N) dynamics in a post-fire landscape: A search for the missing N source

Cory C. Cleveland
The University of Montana

<u>Introduction</u> — Throughout the intermountain western U.S., both the number and extent of high-intensity wildfires are increasing (Westerling *et al.* 2006; Westerling 2016; Abatzaglou & Williams 2017). In Montana alone, wildfires consumed more than 1 million acres in 2017, and these trends are projected to continue (USDA 2017). High-intensity fire not only consumes vegetation, but also depletes much of the nutrient capital needed for recovering forests to regenerate. The majority of temperate forests are most strongly limited by nitrogen (N) availability (LeBauer & Treseder 2008), meaning that even when undisturbed, tree growth is often suppressed by insufficient quantities of N. During fire, plant biomass, litter, and soil organic matter are combusted, volatilizing N, and often leaving these ecosystems with extremely low quantities of a critical plant nutrient (Maynard *et al.* 2014).

In most ecosystems following disturbance, plants with the capacity to "fix" N – or convert biologically unusable atmospheric N into forms that plants can use to grow – quickly colonize disturbed sites. For example, in recently deglaciated sites with very low soil N capital, N-fixing plants (*e.g.,* lupine) and shrubs (*e.g.,* alder) dominate early succession. The N they add to the system via N fixation replenishes the N supply that fuels production of later generations of non-N-fixing trees (*e.g.,* spruce) (Chapin *et al.* 1994). Similarly, in tropical forest ecosystems, N-fixing trees are often the first to colonize disturbed sites, and these early colonizers fix sufficient quantities of N to sustain the N demands of subsequent generations of tree growth for decades (Batterman *et al.* 2013; Sullivan *et al.* 2013). However, many ecosystems, including many forested ecosystems of the western U.S., are largely devoid of N-fixing trees (Menge *et al.* 2016; 2017). There, several different species of putative N-fixing herbaceous plants are sometimes present, but are rarely abundant, and often show low or even negligible rates of N fixation (Turner *et al.* 2007; Burgoyne *et al.* 2009; Ganzlin *et al.* 2016). This puzzling observation informs the question I intend to address here: ***In forest ecosystems where N-fixing plant species are rare, where does the N fertility that fuels ecosystem regeneration following fire come from?*** Answering this question is key to understanding both the rate and trajectory of forest recovery in a landscape experiencing more frequent and intense wildfire.

Colleagues from the University of Wisconsin have been studying ecosystem and vegetation dynamics in lodgepole pine (*Pinus contorta*) forests since the late 1990s in Yellowstone National Park (YNP) (*e.g.,* Turner *et al.* 2007; 2009; Smithwick *et al.* 2009). Since the large fires of 1988, Dr. Monica Turner and colleagues have been measuring tree biomass and soil nutrient dynamics in a set of permanent plots located throughout YNP. In the first 15 years of recovery following the fires, they documented, among other things, large increases in herbaceous vegetation and tree stem density, both of which have contributed to large increases in aboveground biomass (Turner *et al.* 2007; 2009). As the stand has recovered, rates of plant growth (net primary production; NPP) have also increased dramatically (6 – 7.5 Mg ha^{-1} y^{-1}) (Turner *et al.* 2009). Parallel measurements of ecosystem N status (***Fig. 1***) indicate that foliar N in these stands has also accumulated rapidly (~ 50 kg N ha^{-1}), and more recent estimates indicate that the total aboveground N stock has more than doubled in the past 10 years (Dr. M. Turner, personal communication). All of these data point to a rapidly regenerating forest, fueled by significant a significant source of new N inputs. However, it remains unknown what the source of this new N is.

Cryptic sources: The missing N source? — In most ecosystems, the majority of "new" N is thought to come from biological N fixation (Cleveland *et al.* 2013). Until recently, there were thought to be two broad types of N fixers in terrestrial ecosystems: Symbiotic N fixers – representing a symbiotic relationship between plants and microorganisms in a carbon-for-nitrogen exchange (the mode of N fixation described above); and free-living N fixers, defined here as any form of biological N fixation that does not consist of a demarcated symbiotic relationship between plants and microorganisms (Reed *et al.* 2011). Free-living N fixation—also commonly called asymbiotic N fixation—is nearly ubiquitous in terrestrial ecosystems, occurring in decaying leaf litter and wood, and in soil (e.g., Roskoski 1980, DeLuca *et al.* 2002, Matzek & Vitousek 2003, Benner *et al.* 2007, Barron *et al.* 2008). However, while we have no data on free-living N fixation rates in the YNP sites, evidence from other temperate sites suggests that free-living N fixation rates are orders of magnitude lower than what would be needed to explain the rapid increase in N observed there (Cleveland *et al.* 1999; Reed *et al.* 2011). However, A growing body of evidence suggests that a novel and previously unrecognized form of N fixation may provide an important source of N to many ecosystems that could potentially explain the rapid increase in N in observed by Turner and members of her team in the forests of YNP. We refer to these as cryptic sources, and hypothesize that while overall rates of N fixation by any given cryptic source may be small, the combined N inputs from all cryptic sources, including ground lichens, canopy lichens, mosses, plant endophytes, may be sufficient to explain the increases in N following fire.

In 2018, I received support from the University of Montana University Grant Program (UGP) to collaborate with Dr. Turner to begin addressing this question. Overall, we found that indeed, cryptic sources may represent a significant source of N via fixation in these recovering ecosystems (Fig. 1). We sampled soils, decomposing plant litter, foliar endophytes, mycorrhizal symbionts, and soil crusts in even-aged lodgepole pine stands that regenerated after fires in 1988 and 2000. Rates of potential N fixation were greater in 30-yr vs. 18-yr old stands (Fig. 1). We were unable to confirm endophytic N fixation in any of our samples, and were unable to detect N fixation via TEM (although our pilot study may have been insufficient to detect this potential N source). However, we found soil crusts capable of potentially high rates of N fixation (up to 15 kg N ha^{-1} yr^{-1} by some of the foliose lichens where percent cover was high; Fig. 1). Crusts were only observed in the 30-yr old stands and visually, they seemed more abundant in more productive stands. Associative forms of N fixation carried out by cyanobacteria in partnership with lichens and mosses could be a dominant source of N in ecosystems where symbiotic N fixers are rare (Cleveland et al. 1999; Reed et al. 2011), and our preliminary data suggest that they may be an overlooked but very important N source during early postfire stand development.

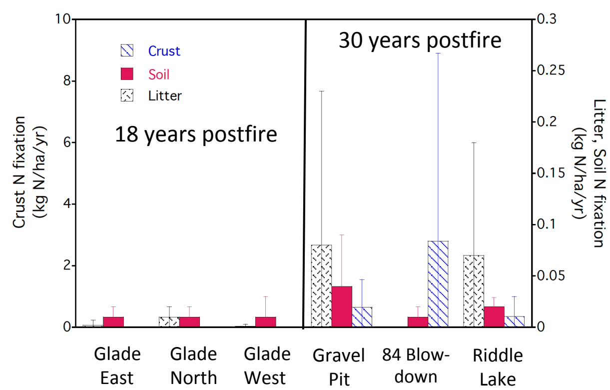

Fig. 1. Preliminary N fixation rates (mean ± SD) in aggrading postfire lodgepole pine stands for soils, litter, and lichen-dominated crusts.

In August 2019, I submitted a collaborative proposal to NSF titled, *Collaborative Research: Nitrogen recovery in posture lodgepole pine forests: cryptic sources, uncertain futures* to build on the preliminary work (NSF-DEB, $456,299 to UM, 4 years, PI). The proposed research aims to determine how N recovers in aggrading postfire lodgepole pine stands in Greater Yellowstone and how N cycling might respond to more frequent stand-replacing fire. We will address three questions: (1) What are the sources and rates of N inputs in aggrading lodgepole pine forests (<40 y postfire), and how do sources and rates vary with stand structure and time since fire? (2) What is the strength of N limitation in aggrading postfire lodgepole pine forests? (3) What are the effects of short-interval (< 30 y fire interval) stand-replacing fires on N stocks, N availability, and N sources? If funded, we look forward to testing expectations that total N fixation rates will increase with lodgepole pine biomass and N stocks, and that sources of BNF will shift from symbiotic to cryptic, free-living N fixers as tree demand increases over time and across space. If we can identify new sources of BNF, or if we can address the conundrum of how aggrading postfire conifer forests recover their lost N capital is resolved, results of this study could transform our understanding of the disturbance-recovery cycle in western forests.

References Cited

Abatzoglou, J.T., Williams, A.P. (2016). Impact of anthropogenic climate change on wildfire across western US forests. *Proc. Natl. Acad. Sci. USA*, *113*(42), 11770–11775.

Barron, A.R., Wurzburger, N., Bellenger, J.P., Wright S. J., Kraepiel, A., Hedin, L.O. (2008). Molybdenum limitation of asymbiotic nitrogen fixation in tropical forest soils. Nat. Geosci. 2:42–45.

Batterman, S.A. *et al.* (2013). Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. *Nature*, *502*.

Benner, J.W., Vitousek, P.M. (2007). Development of a diverse epiphyte community in response to phosphorus fertilization. *Ecol. Lett.* 10:628–36

Burgoyne, T.A., DeLuca, T.H. (2009). Short-term effects of forest restoration management on non-symbiotic nitrogen fixation in western Montana. *For. Ecol. Manag.* 258: 1369–1375.

Chapin, F. S., Walker, L. R., Fastie, C. L., Sharman, L. C. (1994). Mechanisms of Primary Succession Following Deglaciation at Glacier Bay, Alaska. *Ecol. Monogr.* 64: 149–175.

Cleveland, C.C. et al. (1999). Global patterns of terrestrial biological nitrogen (N_2) fixation in natural ecosystems. *Global Biogeochem. Cy.* 13: 623-645.

Cleveland, C.C., et al. (2013). Patterns of new versus recycled primary production in the terrestrial biosphere. *Proc. Natl. Acad. Sci. USA*, *110*(31), 12733–12737.

DeLuca, T.H., Zackrisson, O., Nilsson, M.-C., Sellstedt, A. (2002). Quantifying nitrogen-fixation in feather moss carpets of boreal forests. *Nature* 419:917–20.

Ganzlin, P., Gundale, M., Becknell, R. Cleveland, C. (2016). Forest restoration treatments have subtle long-term impacts on soil C and N cycling in Rocky Mountain conifer forests. *Ecol. Appl.* doi: 10.1002/15-1100.

LeBauer, D. S., Treseder, K. K. (2008). Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology*, 89, 371–379.

Matzek V., Vitousek P. 2003. Nitrogen fixation in bryophytes, lichens, and decaying wood along a soil-age gradient in Hawaiian montane rain forest. *Biotropica* 35:12–19.

Maynard, D.G., Paré, D., Thiffault, E., Lafleur, B., Hogg, K. E., Kishchuk, B. (2014). How do natural disturbances and human activities affect soils and tree nutrition and growth in the Canadian boreal forest? *Environ. Rev.*, 22, 161–178.

Menge, D.N.L., Batterman, S.A., Liao, W., Taylor, B.N., Lichstein, J.W., Ángeles-Pérez, G. (2017). Nitrogen-fixing tree abundance in higher-latitude North America is not constrained by diversity. *Ecol. Lett.*, 20, 842–851.

Menge, D.N.L., Crews, T.E. (2016). Can evolutionary constraints explain the rarity of nitrogen-fixing trees in high-latitude forests? *New Phytol.*, 211, 1195–1201.

Reed, S.C., Townsend, A.R., Cleveland, C.C. (2011). Functional Ecology of Free-Living Nitrogen Fixation: A Contemporary Perspective. *Ann. Rev. Ecol., Evol., Syst.*, 42, 489–512.

Roskoski JP. (1980). Nitrogen fixation in hardwood forests of the northeastern United States. *Plant Soil,* 54, 33–44.

Smithwick, E.A.H., Kashian, D.M., Ryan, M.G., Turner, M.G. (2009). Long-term nitrogen storage and soil nitrogen availability in post-fire lodgepole pine ecosystems. *Ecosystems*, 12, 792–806.

Sullivan, B.W., Smith, W. K., Townsend, A. R., Nasto, M. K., Reed, S. C., Chazdon, R. L., Cleveland, C. C. (2014). Spatially robust estimates of biological nitrogen (N) fixation imply substantial human alteration of the tropical N cycle. *Proc. Natl. Acad. Sci. USA*, 111, 8101–8106.

Turner, M.G., Smithwick, E.A.H., Metzger, K.L., Tinker, D.B., Romme, W.H. (2007). Inorganic nitrogen availability after severe stand-replacing fire in the Greater Yellowstone ecosystem. *Proc. Natl. Acad. Sci. USA*, 104, 4782–4789.

Turner, M.G., Smithwick, E.A.H., Tinker, D.B., Romme, W.H. (2009). Variation in foliar nitrogen and aboveground net primary production in young postfire lodgepole pine. *Can. J. For. Res.*, 39, 1024–1035.

USDA (2017). https://www.usda.gov/media/blog/2017/10/03/million-acres-scorched-montana-wildfires

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W. (2006). Warming and earlier spring increase western US forest wildfire activity. *Science*, 313, 940–943.

Westerling, A.L. (2016). Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. *Phil. Trans. R. Soc. B* 371, 20150178.