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Review

Going where no grains have gone before: From early to mid-succession

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ABSTRACT

Annual-based arable agroecosystems experience among the greatest frequency, extent and magnitude of disturbance regimes of all terrestrial ecosystems. In order to control non-crop vegetation, farmers implement tillage practices and/or utilize herbicides. These practices effectively shift the farmed ecosystems to early stages of secondary succession where they remain as long as annual crops are grown. Humanity's long-standing dependence on a disturbance-based food and fiber producing ecosystem has resulted in degraded soil structure, unsustainable levels of soil erosion, losses of soil organic matter, low nutrient and water retention, severe weed challenges, and a less-diverse or functional soil microbiome. While no-till cropping systems have reduced some hazards like soil erosion, they remain compromised with respect to ecosystem functions like water and nutrient uptake, and carbon sequestration compared to many later successional ecosystems. Recent advances in the development of perennial grain crop species invite consideration of the ecological implications of farming grains further down the successional gradient than ever before possible. In this review, we specifically explore how the nitrogen (N) economy of a mid-successional agroecosystem might differ from early-successional annual grain ecosystems as well as native mid-successional grassland ecosystems. We present a conceptual model that compares changes in soil organic matter, net ecosystem productivity, N availability, and N retention through ecosystem succession. Research from the agronomic and ecological literatures suggest that mid-successional grain agriculture should feature several ecological functions that could greatly improve synchrony between soil N supply and crop demands; these include larger active soil organic matter pools, a more trophically complex and stable soil microbiome that facilitates higher turnover rates of available N, greater N retention due to greater assimilation and seasonal translocation by deeply rooted perennial species as well as greater microbial immobilization. Compared to native mid-successional grasslands that cycle the majority of N required to maintain productivity within the ecosystem, a mid-successional agriculture would require greater external N inputs to balance N exports in food. Synthetic N fertilizer could make up this deficit, but in the interest of maximizing ecological intensification in order to minimize inputs and associated environmental consequences, we explore making up the N deficit with biological N_2 fixation. The dominant approach to addressing problems in agriculture is to target specific shortcomings such as nutrient retention or weed invasion. Moving agriculture down the successional gradient promises to change the nature of the ecosystem itself, shifting attention from symptom to cause, such that ecological intensification and provision of a broader suite of ecosystem services happen not in spite of, but as a consequence of agriculture.

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Contents

1. Introduction

In contrast to native ecosystems, agricultural ecosystems tend to include far fewer species of plants and animals. Agroecologists have recognized this distinction for some time, and the topic of how much and what type of planned agrobiodiversity would improve the functionality and ecological intensification of agriculture continues to receive a great deal of attention (Bommarco et al., 2013; Lin, 2011; Swift et al., 2004). A second broad distinction between native and agroecosystems—one that has received far less attention from agroecologists—is that of succession. Following disturbance, native ecosystems regain functionality through successional changes that strengthen a range of internal, regulating feedbacks. In contrast, due to recurring tillage events or herbicide applications, annual crop ecosystems remain arrested in a disturbed, less regulated state of early secondary succession (Smith, 2014). As a result, degrading processes of soil erosion (Montgomery, 2007), nutrient and water leaching (MEA, 2005; Vitousek and Reiners, 1975), soil organic matter decline (Davidson and Ackerman, 1993), and extensive weed establishment (Liebman and Mohler, 2001) compromise the agroecosystems themselves as well as ecosystems situated down wind, hill or stream. Under these conditions, the opportunities for achieving production goals through ecological intensification are limited (Tittonell and Giller, 2013).

In attempts to rein in the consequences of chronic perturbation, agronomists and ecologists have developed cropping systems that attempt to maximize continuous plant cover on the landscape through cover crops or integration of perennial buffer strips or forage crops (Blesh and Drinkwater, 2013; Liebman et al., 2013). These systems have demonstrated improvements in nutrient retention, carbon (C) accumulation and weed suppression through reduction of soil disturbance and vegetation replacement, and there is good reason to incentivize their adoption. However, these efforts fall short of addressing the root of agriculture's successional stagnation. Critical to the development of numerous ecosystem functions in native ecosystem succession—indeed critical to succession itself—is the transition from community dominance by annual to perennial plant species (Connell and Slatyer, 1977). The prospect of establishing a parallel successional trajectory in agriculture could be transformative (Fig. 1). To this end, breeding programs in multiple countries are now developing hybrid plant populations or new domestications of perennial grain crops, with promising early results for perennial wheat (*Triticum* spp. × *Thinopyrum* spp.), rice (*Oryza sativa* × *O. longistaminata*), sorghum (*Sorghum bicolor* × *S. halepense*), pigeon pea (*Cajanus cajan*) and oilseeds (Batello et al., 2013; Kantar et al., 2016).

A perennial crop agriculture that exists in a later stage of succession is predicted to change – in some cases dramatically – with respect to multiple agroecosystem processes and attributes including soil and nutrient retention, C sequestration, water infiltration and uptake efficiencies, weed suppression, phosphorus (P) and N availability and soil structure (Glover et al., 2007; Robertson et al., 2011). All of these merit consideration, but here we focus on how the N economy of a mid-successional agroecosystem might change across successional seres, highlighting differences between perennial and annual agroecosystems, as well as unique positive and negative attributes of a mid-successional ecosystem that have yet to be considered in an agricultural context. Although we focus primarily on N, we also examine ecosystem attributes and feedbacks that govern the N economy such as changes in soil C balance, microbiome, and dominant forms of soil P.

1.1. Why nitrogen?

The importance of N in sustaining food production, and the serious challenges faced by farmers to manage N resources efficiently make it a salient topic in the context of disturbance and succession. Nitrogen is the nutrient that most commonly limits the productivity of agroecosystems and, either alone or with P, native terrestrial ecosystems (Robertson and Vitousek, 2009; Vitousek and Howarth, 1991). Yet on average, only 30–50% of N applied is recovered in a fertilized grain crop, and beyond that, $<7\%$ of the applied N is recovered in up to six subsequent crops (Gardner and Drinkwater, 2009; Ladha et al., 2005). Low N fertilizer uptake efficiencies, caused by the application of high concentrations of the most soluble N forms to fields at times when annual crop roots are either underdeveloped or not present at all, result in substantial N losses to the environment (Robertson et al., 2011). Nitrate-N and to a lesser extent dissolved organic N is lost to surface or groundwater via hydrologic pathways, causing local contamination of