Cover Crop Mixture Diversity and Function

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Abstract

The diversity-productivity hypothesis proposes that increasing plant diversity increases average biomass productivity. The goal of this study was to review this hypothesis in the context of cover crop mixtures. The lower yielding legumes lowered the average productivity of the low functional richness category as compared to the high functional richness category where the higher yielding grasses and brassicas compensated for the low production of the legumes. In terms of practical cover crop management, there was no evidence of any mixture out-yielding the highest yielding monoculture at each site. While the diversity productivity hypothesis was supported—this paper suggests a rather simple, mathematical mechanism by which increasing diversity can increase average productivity.

Keyword- Cover crop; crop mixture; monoculture; soil nutrient; weed suppression

Introduction

Cover crops have long been used for a wide variety of functions including adding organic matter, suppressing weeds, decreasing nutrient leaching, and stimulating soil biota. Recently, however, there has been increased interest in the use highly diverse mixtures of cover crops. While it's been asserted that mixing cover crops does everything from increasing biomass productivity, to increasing weed suppression, to enhancing nutrient retention, to fostering soil health through stimulating increased soil biota, to buffering against environmental variability, there is actually little empirical evidence to support these claims. It has been proposed that the many functions of cover crops are only improved with the use of more cover crop species, but these claims are based less on empirical evidence and based more on an intuition about diversity that prevails in both the fields of agriculture and ecology. The overarching objective of this project was to determine the effects of increasing cover crop mixture diversity on cover crop function. Cover crops are used for various functions and the goal of this project was to see if increasing cover crop diversity could be used as a tool to positively manage these functions.

Cover crop mixture diversity and productivity

The diversity-productivity hypothesis proposes that greater diversity should lead, on average, to greater total biomass productivity (Tilman, 2001). The most common argument is that a single species leaves resources unexploited that another species might be able to come in and exploit—i.e., that more diverse systems are more productive due to increased niche complementarity or resource use efficiency. While many authors have observed a positive correlation between manipulated diversity and average productivity, the interpretation of these results as evidence of niche complementarity is contested (rev. deLaplante and Picasso, 2011). Despite the controversy surrounding the diversity-productivity hypothesis, the idea that increased diversity equates increased average productivity has been entrenched in many fields as fact—particularly in agriculture. It's not uncommon, for example, to read in the agricultural sciences that mixed cropping is associated with increased productivity (Seran and Brintha, 2010). In one telling line, Ćupina et al. (2011) states that intercropping is "a practical application of ecological principles based on biodiversity." Thus, it's clear that at least by some agricultural scientists, the diversity-productivity hypothesis is taken as proven principle instead of as an unproven hypothesis. It should be noted that other workers in the field are much more cautious with their language. Rather than saying that intercropping increases productivity, they say that carefully designed mixtures have the potential to increase productivity—a subtle, but important difference (Malezieux et al., 2009). Putting aside empirical evidence in favor of or against the hypothesis for a moment, why might we expect diversity to be positively related to productivity? The reasons given in both the ecological and agricultural sciences are the same—though slightly different language is favored. In the field of ecology, it's not uncommon to hear reference to "niche differentiation", "partitioning", and "complementarity" (Lawton et al., 1998). In the field of agriculture, it's more common to hear reference to "resource use efficiency" (Seran and Brintha, 2010). The logic, however, is the same—that each species has different resource needs and different resource acquisition abilities. A monoculture therefore leaves some resources unexploited that another species might be able to exploit—e.g., through its differential root or canopy architecture. Thus, plant mixtures should have the potential to out produce plant monocultures because mixtures should be able to more fully exploit available resources (Vandermeer et al., 2002). That is, mixing plants should be able to raise the ceiling on biomass productivity reached by plant monocultures. This, however, is a different conclusion than increasing diversity increases average productivity. Interestingly, the logic commonly used to argue in favor of the diversity productivity hypothesis, when taken to its logical conclusion, supports a different hypothesis. Increasing average productivity is not the same as increasing the ceiling on productivity. According to the logic of niche complementarity, increasing diversity shouldn't necessarily increase average productivity. Rather it should increase the ceiling on productivity. This disconnect between the theoretical underpinnings of the diversity productivity hypothesis and the theoretical conclusions of the diversity-productivity hypothesis indicates two things. First, it indicates that we should be testing the theory of niche complementarity by testing whether increasing mixture diversity raises the ceiling on productivity rather than average productivity. Second, it indicates that niche complementarity is not a sensible explanation for the diversity-productivity hypothesis as stated, or the necessary conclusion to be drawn from diversity-productivity observations. The original objective of this study was to test the diversity-productivity hypothesis in the context of cover crop mixtures. The result has been to technically support the diversity-productivity hypothesis—i.e., to show an increase in average productivity with increased diversity—but to also demonstrate some flaws with the traditional interpretation of this as evidence of niche complementarity. The primary and most unrelenting criticism of diversity-productivity research has been that the experimental designs of these studies are such that more productive species are more likely to be present in the higher levels of diversity. This effect has been variously called the "sampling effect", the "selection effect", the "sampling bias", and the "selection bias" with the results of a study with such an effect being called "experimental artifact" (Wardle, 1999). In this paper it will be demonstrated that even without sampling bias, positive diversity-productivity relationships can still persist, and even so, niche complementarity need not be invoked as the driving mechanism. Rather, a simple mathematical explanation exists to explain the observation—specifically, the average productivity of lower levels of diversity is drawn down by low yielding species while the average productivity of higher levels of diversity is not drawn down to the same degree because high yielding species make up for low yielding species in mixture. Before delving into the study, however, I want to briefly address the topic of facilitation. Facilitation effects between species are also cited as a possible mechanism for positive diversity-productivity relationships. However, I think listing this as an additional mechanism to niche complementarity confuses the issue. Facilitative effects are a mechanism by which a particular species might enhance the growth of another. This is more of a pair-wise interaction rather than the effect of diversity itself. Certainly the likelihood of this pair-wise interaction increases with increasing diversity. It's my opinion that we cannot point to positive pair-wise interactions in our justification of the diversity-productivity hypothesis without also acknowledging the potential for negative pair-wise interactions. Furthermore, while the likelihood of including particular pair-wise interactions increases with increasing diversity, the relative effect of that pair-wise interaction is decreased or diluted with increasing diversity. As yet another source of potential confusion, facilitation is sometimes regarded as a kind of complementarity (e.g., Cardinale et al., 2007). Here, however, sharp distinction can be drawn for complementarity, which can be regarded as the result of individual species having differing requirements, and facilitation, which can be regarded as the ability of one species or individual to modify the environment favorably for another (Callaway and Pugnaire, 2007).

Cover crop mixture diversity and weed suppression

The diversity-invasibility hypothesis proposes that species rich ecosystems are more resistant to invasion than species poor ecosystems. This hypothesis is predicated on the premise that a single species fails to fully occupy all the available niche space in an environment and that by "saturating" or "packing" all the available niche space in an environment with different resident species, we can thus pre-empt its use by invaders. Elton (1958), who is often asserted to be the first to articulate the diversity-invasibility hypothesis—which has also been variously called the biotic resistance hypothesis, the diversity-resistance hypothesis, and the ecological-resistance hypothesis—put it this way: "[invaders] will find themselves entering a highly complex community of different populations, they will search for breeding sites and find them occupied, for food that other species are already eating, for cover that other animals are sheltering in meeting ecological. Despite the empirical evidence in favor of this hypothesis being sparse (Levine and D'Antonio, 1999; Richardson and Pyšek, 2006) and of questionable validity (Huston, 1997) the hypothesis has nevertheless been entrenched in agriculture as conventional wisdom. Despite the lack of empirical evidence in favor of this contention in agriculture as well as ecology (Moody and Shetty,
1981), it is assumed by many scientists that crop mixtures are better able to capture a greater share of 36 available resources than single species and thereby better able to suppress weeds (Buhler, 2003). The competition-relatedness hypothesis, which has also been called the theory of limiting similarity, is traceable to Charles Darwin in the Origin of Species. In Darwin's words: "as the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with

each other, than between the species of distinct genera." Darwin's examples are of different birds, mammals, and insects displacing one another. However, in its modern applications, scientists have applied this hypothesis to the management of plant invasions. That is, it has been supposed that plant species are better able to "repel" invaders similar to them because they occupy the same kind of niche. The ability of cover crops to suppress weeds has been well established (Teasdale et al., 2007), but how does cover crop mixture diversity and similarity to target weed species affect this suppressive ability? The objectives of this study were to test both the diversity-invasibility hypothesis and the competition-relatedness hypothesis in the context of cover crop mixtures and weed suppression. Specifically, our research questions were does increasing cover crop mixture diversity enhance weed suppression, and are grass cover crops better at suppressing grass weeds than broadleaf cover crops and vice versa?

Cover crop mixture diversity and soil nutrient retention

It's well documented that cover crops can be used to decrease soil nutrient leaching losses—particularly of those nutrients that are relatively mobile in the soil. However, it's not clear to what extent cover crop mixture diversity affects the ability of a cover crop to retain soil nutrients. Different plant species certainly have different root and shoot architectures that develop at different rates over different time frames. However, does this spatial and temporal diversity in root and shoot development translate into improved soil nutrient retention? It has been hypothesized that increasing plant mixture diversity should decrease nutrient leaching losses and increase nutrient retention—the diversity-nutrient retention hypothesis—but empirical evidence is limited (Tilman et al., 2001). The objective of this study was to test this hypothesis in the context of cover crop mixtures and soil nutrient retention. Specifically, this study evaluated the effect of cover crop mixture species richness on soil extractable nitrate, phosphorus, potassium, sulfate, and chloride concentrations and distributions. Of all soil nutrients, soil nitrate has received the most attention with regards to cover crops. The ability of cover crops to decrease nitrate leaching has been well documented (Strock et al., 2004). Like nitrate, sulfate and chloride are also highly mobile in the soil (Bray, 1954). Predictably then, their loss from the soil is also diminished by the presence of standing vegetation (Erikson and Thorup-Kristensen). Phosphorus and potassium are relatively immobile as compared to nitrate, sulfate, and chloride, and consequently little work has been conducted on the effect of vegetation on their retention in the soil. However, while these nutrients are relatively immobile, they are not completely immobile. Soil potassium leaching losses under cropland conditions have been documented to range from 0 to 245 kg ha-1 yr-1 with cropped soils tending to have less potassium leaching losses than uncropped soils (Quémener, 1986). Soil phosphorus leaching losses are typically less than soil potassium leaching losses and have been documented to range from 0.03 to 1.85 kg ha-1 yr-1 with minimal effect of cropping observed on soil phosphorus losses (Djodjic et al., 2004) While the effect of vegetation on soil nutrient retention has been relatively well studied, it's not clear to what extent plant mixture diversity affects soil nutrient retention. In a meta-analysis, Balvanera et al. (2006) estimated there to be a positive effect of plant diversity on soil nutrient supply. Unfortunately, the authors' link to the data they used for their meta-analysis is defunct, so it is difficult to see the literature they used to draw this conclusion. In my own survey of the literature, however, I find the evidence to be much less conclusive.

Cover crop mixture diversity and soil microbial biomass and community structure

Vegetated soils typically have greater soil microbial biomass than un-vegetated soils as well as altered soil microbial community structures as compared to bare soils (Lehman et al., 2014). It's not clear though, whether or not plant mixture diversity predictably affects soil microbial biomass or community structure. Some authors have observed a positive correlation between plant mixture diversity and soil microbial biomass metrics (De Deyn et al., 2011) while others have observed more idiosyncratic effects of mixing plants on soil microbial biomass (Wortman et al., 2013). The literature on the effect of plant mixture diversity on soil microbial community structure is even less clear with some authors observing that increasing plant mixture diversity does alter soil microbial community structure (Carney and Matson, 2004) and others not observing an effect (Wortman et al., 2013). While the hypotheses that increasing plant mixture diversity should increase soil microbial biomass and alter soil microbial community structure have been tested in many places, these hypotheses are rarely formally named. Following the lead of Chapman and Newman (2010), however, I will refer to these hypotheses as the diversity increased abundance and diversity-altered microbial community hypotheses. 90 The goal of this study was to test these two hypotheses in the context of cover crop mixtures—asking the questions of whether increasing cover crop mixture species or functional richness increases soil microbial biomass and predictably alters soil microbial community structure.

Conclusion

Increasing cover crop mixture diversity does increase average productivity. Crop diversity is often correlated to metrics of weed suppression, soil nutrient retention, soil microbial biomass, soil microbial community structure, and stability, but also that these correlations can largely be explained by variations in productivity. If our concern is increasing weed suppression, nutrient retention, soil microbial biomass, or stability of biomass productivity, then we should focus our attention on increasing cover crop biomass rather than cover crop mixture diversity. It's difficult to imagine a scenario in which we can ever control for all the covarying and confounding factors in diversity research. By its very nature, when we compare diverse plant assemblages to monocultures we allow many different variables to vary at once. Nevertheless, it's not until we at the least control for biomass productivity that we can start to guess at the true magnitude of diversity effects on function.

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