Cover Crop Mixtures, Biodiversity, and Agriculture

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Farmers are using cover crop mixtures, hoping the power of biodiversity will transform their soils, improve yields, and regenerate their agroecosystems. Is this hope warranted? This article examines the ecological basis for mixtures, the results of cover crop mixture research, and the mechanisms that might cause mixtures to outperform monocultures. Earn 1 CEU in Crop Management by reading the article and taking the quiz at https://bit.ly/3lHmAhU. View all CEUs online at https://web.sciencesocieties.org/Learning-Center/Courses.

Iowa farmers look over a cover crop mixture. NRCS/SWCS photo by Lynn Betts.

Farmers are using cover crop mixtures, hoping the power of biodiversity will transform their soils, improve yields, and regenerate their agroecosystems. Is this hope warranted? Can biodiversity produce these benefits? While the benefits of cover crops are well documented, the benefits of using multi-species cover crop mixtures are less clear. Here I examine the ecological basis for mixtures, the results of cover crop mixture research, and the mechanisms that might cause mixtures to outperform monocultures.

Species Mixtures in Ecological Research

Ecological principles suggest that increased biodiversity of species in mixtures will increase productivity or improve other ecosystem services compared with monocultures. This is called the biodiversity–productivity or biodiversity–ecosystem relationship. The idea is that there will be increasing complimentary effects rather than competition between the species in increasingly diverse mixtures (Vanelslander et al., 2009), which will cause increased biomass production or other improvements in function when compared with their monoculture counterparts.

Several large, long-term experiments have studied the biodiversity–productivity relationship, including the often-cited Cedar Creek plots in Minnesota (Tilman, 2014) and the Jena experiment (http://the-jena-experiment.de/) (Buchmann et al., 2018) in Germany. Since the early 1990s, hundreds of similar shorter-term experiments have been carried out around the world. Recently, studies using meta-analysis have summarized the large amount of data generated from these experiments over the years (Cardinale et al., 2011). What this ecological research on plant diversity has found is that higher species diversity *is linked* to higher ecosystem function.

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The common message transferred to agriculture is that we should expect increased *crop* diversity to improve agroecosystem function. These ecological research results spurred research into cover crop mixtures, continuing in the path of previous intercropping research, except that with cover crops, we can more easily mix more species as harvest is not an issue. However, before looking at the results, we must understand the differences between ecological and agricultural research in terms of how the results should be evaluated.

Overyielding vs. Transgressive Overyielding

Ecological research is done to mimic nature. Ecologists select and plant random mixtures of species from a pool of native species along with their respective monocultures. They then look for a general pattern of higher-diversity plant mixtures performing better in general than lower-diversity mixtures and monocultures. Performance is most often measured by biomass production, a proxy for ecosystem function. Figure 1 shows how the results are often displayed.

The biomass production ranges widely at the monoculture level and less so as diversity increases. Ecology studies take the average of this range of production levels at each level of plant species diversity; for one-species monocultures, two-species mixtures, three-species mixtures, and so on, producing the orange line. Research generally shows that this average biomass production increases with increasing plant species diversity.

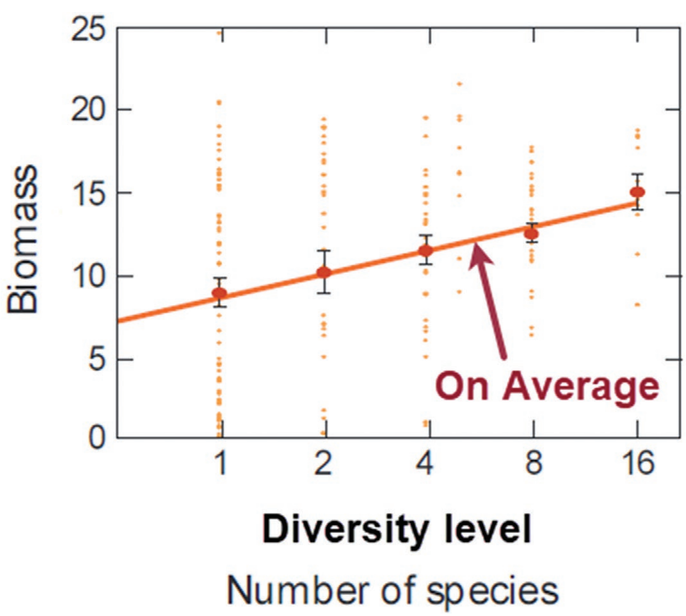

Figure 1. Biomass production by level of species diversity. The line is the average of production at each level of diversity. Modified from Tillman et al., 2014.

This is called overyielding and can be evaluated by a variety of metrics (Schmid et al., 2008).

This is fine if you are looking at random mixtures for an unmanaged nature. However, in mimicking nature, ecological research differs from how agricultural research is conducted and how we interpret the results (Schulze et al., 2018). In agriculture, we use *management*— intelligent choices based on experience and research. We know some species are top producers and so must be in a mixture. Others are not, and so we exclude them unless they bring some other benefit to the mix. Because of this management, the standard relevant for agriculture is not the average increase with increasing plant species diversity but rather the comparison of the best monocultures and the best mixtures as shown in Figure 2.

This is called transgressive overyielding. In robust research, each small dot is the average of multiple plots. This allows a statistical comparison of each species' monoculture with each mixture at each level of diversity. Now, using this standard, we can see what cover crop research has found.

Results of Cover Crop Mixture Research

As mentioned, there has been a significant amount of cover crop mixture research in the past 20 years. In 2020, Angela Florence

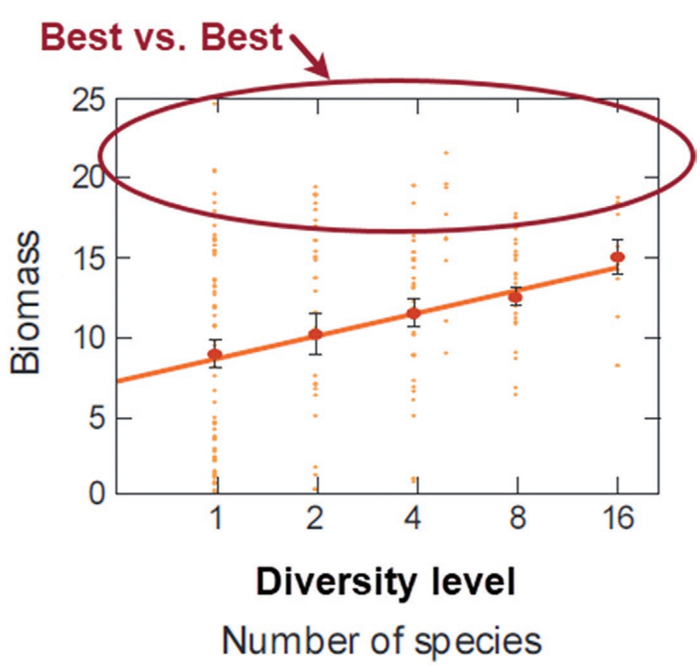

Figure 2. Biomass production by level of species diversity. The circle shows where evaluation for transgressive overyielding takes place; the comparison is between the best monocultures and the best mixtures. Modified from Tillman et al., 2014.

and I published a systematic review of this cover crop mixtures research (Florence and McGuire, 2020). Our search of the literature discovered 27 studies from 10 counties. These gave us 243 full comparisons of the best mixture with the best monoculture for these measurements:

- Cover crop biomass
- Weed suppression
- Nitrogen retention
- Water conservation
- Soil biology promotion
- Following crop yield
- Biomass stability over time

A diverse cover crop mixture. Do ecological principles regarding biodiversity apply to annual crops in agriculture?

Although the results differed for each measurement, the best mixture did not outperform the best monoculture consistently in any of them (see Figure 3).

Overall, we found mixtures were better in 2% of the comparisons, monocultures in 10%, and for the remaining 88% of comparisons, the best mixture performed comparably to the best monoculture. For those cases where there was a statistical difference between the best mixture and best monoculture, the monoculture produced more biomass in 17 comparisons, the mixture in only two.

Thus, contrary to expectations based on ecological research results, the cumulative evidence currently shows that cover crop mixtures do not give a clear advantage over monocultures. This also matches the results of much earlier reviews of intercropping (Trenbath, 1974) and even of ecological research using the standard of transgressive overyielding (Cardinale et al., 2011). If there are meaningful advantages of mixtures over monocultures in agriculture, they are rare or difficult to attain. Why is this?

Agriculture Is Not Nature

Besides the management factor, which demands a performance standard relevant for agriculture, there are other differences between agricultural and ecological research. Ecology studies use native species to imitate nature; agricultural studies use crops bred to produce food. Breeding has removed many of the characteristics of native plants from our crops such as anti-herbivore defenses (thorns, poisonous compounds, etc.), long ripening periods, and responses to crowding. Because the plants used in each type of research differ, we cannot assume they will produce the same results (Chacón-Labella et al., 2019).

Furthermore, the native plants that ecologists use are perennials while agronomists often use annual crops, especially for cover crops. Using perennials allows ecologists to follow the performance

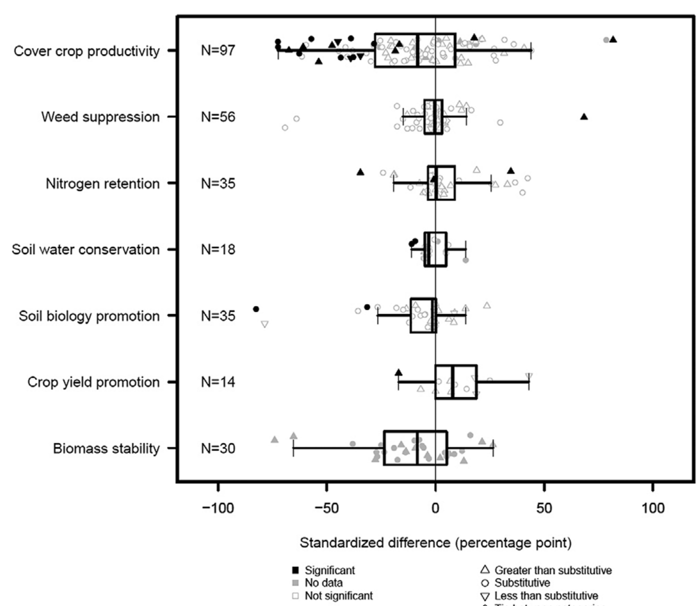

Figure 3. Standardized difference between cover crop mixture and monoculture performance (*N* = 285) separated by metric category. Positive values show where mixtures were superior to monocultures. Negative values indicate where monocultures were superior to mixtures. From Florence and McGuire (2020).

TABLE 1. Differences between ecological and agricultural research.

Factor	Ecology (Nature)	Agriculture
Human influence	Unmanaged, unguided	Managed to produce food
Performance standard for mixtures	Average biomass yields at each diversity level	Best mixtures vs. best monocultures
Plants used in research	Native perennials High anti-herbivore defenses High % of *inedible* biomass	Domesticated annual crops Lower anti-herbivore defenses High % of edible food
Biodiversity	High biodiversity in space	High biodiversity in time (crop rotations of annual crops)
Soil nutrient status	Low to moderate	High to moderate
Export of food/biomass	Low	High

of the mixtures for years, sometimes decades. Doing this, they have found that biodiversity effects take time to kick in, three to five years in several studies (Cardinale et al., 2007; Reich et al., 2012). This is much longer than short-term annual crops and especially cover crops. Other differences are shown in Table 1.

Ecology and Agriculture Have Different Goals

These differing research methods and interpretations of results stem from the different aims of biodiversity research and those of agriculture. This is especially evident in the need for an actual mechanism behind biodiversity benefits.

The term "biodiversity" was first used as a tool to move conservation science into policy actions as a response to the biodiversity crisis (Devictor & Meinard, 2020; Maier, 2012). For this purpose, ecology wants to know whether higher-diversity (random) mixtures (of native perennials) promote better function and stability of ecosystems (on average, in the medium to long term). To justify conservation of biodiversity, all ecology needs to show is that higher biodiversity is *linked to* higher function; identification of the actual mechanisms is not needed. Instead, ecology studies most often point to the "complementary effect," which is statistically determined and only hints at the actual mechanisms. Or they name potential mechanisms in general terms: better resource use, complementarity, facilitation, etc. (Fridley, 2001; Vanelslander et al., 2009). However, the true causes are more often assumed than identified.

Nevertheless, many who read about the results of biodiversity research will often misconstrue the results as showing biodiversity itself as the cause. This is an easy mistake to make given all the ecological papers that use causal language to describe the link. And so, we have researchers claiming the diversity drives this or that function (Chen et al., 2021; Grange et al., 2021), who are mostly content with showing the link between plant diversity and biomass production. And we have farmers planting 20-, 30-, or 50-species cover crop mixtures. Both often lack a solid idea of what mechanism is going to produce benefits other than "higher biodiversity." And if one believes that biodiversity is the cause, then why look further? Thus, the different purpose of ecology has distracted agriculture's attention from the fact that behind every benefit of "biodiversity" is an actual mechanism, a cause explained by physics, chemistry, and biology.

Crop diversity may result in, be linked with, or be related to these benefits, but diversity itself is not the cause and is not a mechanism. This is a clear case of correlation, not causation. Plant diversity is a feature of species mixtures, not a driver of function. The actual cause—the specific physical and chemical interactions between species in the mixtures—is rarely determined, despite a multitude of crop and plant diversity studies (Cardinale et al., 2011; Barry et al., 2019; Barry et al., 2020; Letourneau et al., 2011; Turnbull, 2014; Wuest et al., 2021). While satisfying ecology's main goals, these results are less than helpful in agriculture: without knowing the actual mechanism, mixtures are just a guess, and benefits are uncertain. Agriculture wants to know *which* mixtures would provide greater productivity, resource-use efficiency, or other benefits above those found in monocultures. Even more important, it wants to know the mechanisms behind such effects.

> "Diversity is the outcome of ecological processes and not an ecological process in itself… Alas, diversity is not good or bad, it simply is."
>
> **—Shade (2017)**

Agriculture Needs Mechanisms to Manage

A monoculture mustard cover crop planted after wheat harvest.

In agriculture, we don't want to guess which mixtures will perform best. We don't need more observed links between crop diversity and function. We need to know the real cause of benefits coming from the better-performing mixtures. We can manage a cause but not reliably a correlation. To achieve this, we must shift our focus from biodiversity itself to determining the specific interactions between specific species in specific environments. There are good examples of papers that look for, and sometimes find, the actual mechanisms, including benefits of legume + non-legumes mixtures that are not related to nitrogen (Hu et al., 2021). Hard work? Yes, but necessary to improve reliability of all forms of crop diversity.

Given all the intercropping and plant diversity research done over the years, we have found two primary mechanisms. First, there is the long-known nitrogen effect (mostly) of mixing legumes with non-legumes on low-nitrogen soils (Ofori & Stern, 1987). The other, more recently identified (van Ruijven et al., 2020), is not because of anything happening in mixtures but rather a disadvantage of monocultures. In monocultures of perennials, or continuous cropping of annuals, soilborne disease builds up and eventually leads to reduced yields. Mixtures avoid this fate by dispersing host plants of specific soilborne pathogens.

Mixtures may provide benefits through two other strategies that are not mechanisms of interactions between plant species but arise from the individual adaptations of specific species. The first is multifunctionality or providing more services than a monoculture. Some monocultures can provide many, but not all functions. A mixture can provide functions of all the species it contains but at a cost: the level of a species' services is often related to the biomass it produced (Finney et al., 2016; Wendling et al., 2019). The service will therefore be reduced in a mixture in proportion to the reduced biomass of that species. Finney and Kaye (2016) found that multifunctionality of cover crop mixtures was only weakly related to the number of species in a mixture. Their study "does not support the hypothesis that increasing the number of species in a mix will lead to predictable increases in multifunctionality at levels that are agronomically or ecologically relevant."

Finally, bet hedging is a risk management strategy of using mixtures that can be beneficial in highly variable climates or growing windows. This is similar to the selection effect in ecology (Cardinale, 2007). Here again, there are trade-offs. The mechanism at play is the differing adaptations of species to varying weather, primarily temperature and precipitation. Planting multiple species increases the odds that at least one crop will find favorable growth conditions. However, the strategy presupposes a loss in the cost of the seed of those included crops that do not find favorable conditions.

Implications for Ag Professionals

So then, current science tells us that cover crop mixtures are no better than monocultures. However, plant diversity has a place in agriculture. Crop mixtures with legumes have long been used to take advantage of their nitrogen-fixing ability. Some intercrops make sense because of their pest control benefits, even with lower yields. And diversity in time through crop rotation is a time-honored practice. Beyond these examples, we must test

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Be sure to check out the author's blog at https://extension.wsu.edu/grant/andrew-mcguires-homepage for more on this topic and many others of potential interest.

biodiversity in agriculture by the standards and requirements of agriculture, not those of ecology.

Some practical points from all this:

- Management changes the relationships found by ecologists in unmanaged ecosystems. Therefore, the results of ecological biodiversity experiments do not always transfer well to agriculture. And recommendations to increase diversity for a specific benefit with no guidance on the specifics of the diversity needed should be viewed with skepticism.
- Transgressive overyielding is the standard more relevant to agriculture for comparing mixtures to monocultures.
- Because biodiversity is not the cause, focus on managing plausible causes of the benefits in mixtures.

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1. The ecological principle suggesting that increased biodiversity will increase productivity (or other ecosystem services) compared with monocultures is called

a. the biodiversity–productivity relationship.

b. the Cedar Creek Effect.

c. the ecosystem services model.

d. the biodiversity–ecological relationship.

2. Which of the following is the most common metric for measuring cover crop performance?

a. Number of species.

b. Biomass production.

c. Diversity level.

d. Transgressive overyielding.

3. When Florence and McGuire compared the best cover crop mixtures to the best monocultures, they found that monocultures ________ compared with mixtures in ________% of comparisons.

a. outperformed, 2

b. underperformed, 10

c. outperformed, 88

d. underperformed, 2

4. Several ecological studies discovered that biodiversity effects in mixtures of perennial plants take ________ years to kick in.

a. 1–2.

b. 2–3.

c. 3–5.

d. 5–7.

5. According to Table 1, which of the following is NOT a factor in ecological research?

a. Plants contain a high percentage of edible biomass.

b. Biodiversity is high in space, not time.

c. Research plants are native perennials.

d. Humans do not manage plants.

6. Biodiversity was initially an ecological term applied in policy, related to understanding whether higher diversity of mixtures of native perennials promote better long-term function and stability of ecosystems.

a. True.

b. False.

7. Though crop biodiversity may be related to other ecosystem benefits, biodiversity is not itself the mechanism causing these benefits.

a. True.

b. False.

8. Through multifunctionality, a mixture of cover crops can provide multiple functions at levels related to their biomass production.

a. True.

b. False.

9. Growing perennials or annuals in continuous monoculture can lead to

a. increased ecosystem services.

b. buildup of soilborne diseases.

c. increased biomass production.

d. All of the above.

10. Which one of the following is an a well-documented mechanism through which cover crops impact productivity?

a. Higher-diversity plant mixtures outperforming monocultures.

b. Increased biodiversity increasing weed suppression.

c. Biodiversity promoting increased soil biology.

d. The nitrogen effect of mixing legumes with non-legumes on low-nitrogen soils.