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SCIENTIFIC PERSPECTIVES

Defining and improving the rotational and intercropping value of a crop using a plant–soil feedbacks approach

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Abstract

Crop rotations and intercropping are an ever-present sustainable practice across a diverse array of agroecosystems. These management practices can suppress weeds, reduce cycles of disease, build soil organic matter, and increase above- and belowground biodiversity, all of which improve the yield of a companion or subsequent crop. Here, we propose the terms 'rotational' and 'intercropping value' as a way to measure the overall effect of these benefits. Additionally, we articulate how to quantify different ecosystem services provided by rotational and intercrops including weed and disease suppression, enhancing microbial communities, and nitrogen fixation using a framework that accounts for how these services support other crops in agroecosystems. By providing a method of identifying and quantifying these rotational and intercropping traits, it may facilitate the breeding of better crops for rotations, for cover cropping, and for intercropping.

1 | INTRODUCTION

Temporal and spatial alternation of crop species is a common practice of most annual and short-duration agricultural systems. Rotations and intercropping of crops can break cycles of disease and pests, improve soil fertility, suppress weeds, and improve food and nutritional security (Reviewed in Fageria, Baligar, & Bailey, 2005; Sharma et al., 2018; Wick, Berti, Lawley, & Liebig, 2017). Although rotations and intercrops are widely used in agriculture, the effect of a crop as a rotational or intercrop partner is not typically estimated or systematically studied (Ingerslew & Kaplan, 2018), let alone considered as a breeding target. In a recent meta-analysis of 154 studies, it was discovered there were no consistent science-based criteria to justify the use of one crop rotation over another (Dias, Dukes, & Antunes, 2015). Here we coin the terms 'rotational value' and 'intercropping value' and offer an equation to measure the utility of crops in spatial and temporal mixtures to provide a consistent, science-based criteria to quantify crop rotations, cover crops, and intercrops. By precisely measuring and quantifying the value of crops as rotational and intercropping partners, we can provide scientists, farmers, and policy makers with estimates of value that can encourage more sustainable practices that may provide greater long-term agricultural and ecological benefits.

Abbreviations: IV, intercropping value; PSF, plant–soil feedback; RV, rotational value.

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1.1 | Plant–soil feedbacks: A framework to quantify rotational and intercropping value

A method to quantify rotational and intercropping value is to use the framework of plant–soil feedbacks (PSFs, e.g., Bever, 1994; Callaway, Thelen, Rodriguez, & Holben, 2004; Ehrenfeld, Ravit, & Elgersma, 2005; Kulmatiski, Beard, Stevens, & Cobbold, 2008; van der Putten, Bradford, Pernilla Brinkman, Voorde, & Veen, 2016; van Nuland et al., 2016), a powerful approach for interpreting the effects of one species of plant on other species indirectly through their impact on soil biota or soil chemistry (Reviewed in Mariotte et al., 2018). Although the majority of PSF research has primarily focused on natural systems, the temporal and spatial crop diversification within agricultural systems provide an excellent model to use the PSF framework to increase agriculture production (Barel, Kuyper, de Boer, Douma, & De Deyn, 2018; Cheng & Cheng, 2015; Huang et al., 2013; Mariotte et al., 2018; Wang et al., 2017). Thus, we can improve agricultural production by measuring the direction and strength of PSF for different crops or management practices and implementing the practices with the highest PSF values (Barel et al., 2018; Huang et al., 2013; Ingerslew & Kaplan, 2018; Mariotte et al., 2018). The concept of PSF has underutilized potential in agroecosystems; therefore, we adapted this concept and coined the terms rotational value (RV) and intercropping value (IV) and defined the terms as to how well a crop relatively benefits the yield or growth of another crop. We believe the terms rotational and intercropping value directly conveys a nonspecialist meaning of the PSF concept that can be easily understood by the entire agricultural community. Additionally, we provide an equation to measure RV and IV adapted from the PSF literature (Bever, 1994, Ingerslew & Kaplan, 2018, Wang et al., 2017):

$$\text{RV or IV} = \ln(Y_\varepsilon / Y_c)$$

Where Y_ε is the yield or growth of the subsequent crop on rotated soil or grown with an intercrop; Y_c is the yield or growth of the subsequent crop on control soil (nonrotated soil or grown with no intercrop); RV or IV equal to zero indicates no effect on yield or growth vs. control soil; RV or IV greater than zero indicates increased yield or growth vs. control soil; and RV or IV less than zero indicates decreased yield or growth vs. control soil.

In the framework of PSFs, a rotational or intercropping value variety trial requires, at a minimum, a measurement of the impact of the variety and a control on soil biota and chemistry. Improvements in soil chemistry or alteration of soil biota can indicate improved conditions for subsequent or paired crops. Equally important, they may indicate trends for longer-term benefits, such as soil organic matter, nitrogen, and other micronutrients, or presence of beneficial or antagonistic microbes, which can be challenging to understand in other frameworks. However, these experiments are best expanded to measure the performance of the subsequent or paired crops and characterization of shifts in microbiomes.

The benefit of measuring RV and IV is that it provides a straightforward framework to consistently quantify the effect of a cover crop or intercrop on the yield or growth of another crop in any setting. Notably, these values can be negative, such as with rotational partners like lupin (*Lupinus albus* L.) and pea (*Pisum sativum* L.) that are susceptible to the same diseases and can amplify them when both are in rotations (Gaulin, Jacquet, Bottin, & Dumas, 2007). Additionally, by calculating a numerical value that normalizes results by comparing them with nonprimed soil (nonrotated soil or no intercrops present); it provides scientists, breeders, and farmers with a simple quantifiable measurement to compare agricultural practices and crops using classical statistics. Furthermore, since RV and IV calculates the directionality and magnitude of the effect of the management practice on growth and yield of another crop, it allows for the simple identification and implementation of practices that most effectively increase yields in agroecosystems. The simple interpretation of the value also facilitates extension outreach efforts by providing them with another tool in their toolbox to help them explain to growers which practices to implement to increase yields. For instance, extension personnel can help a grower identify the most effective cover crop to increase corn (*Zea mays* L.) yields by providing a list of RVs for all appropriate cover crops for their agroecosystem. This approach allows the value of the ecological benefit of a cover or intercrop (i.e., ecosystem service) to be framed as an economic value. Lastly, when comparing RVs and IVs among crops or management practices, we strongly suggest that environmental factors (climatic conditions, etc.) soil chemistry, soil biotic factors, and soil history (previous planted crops, management practices, pest presence, etc.) should be used as a covariate to control for differences between field sites to alleviate potential drawbacks and increase the applicability of results. For instance, research has shown that the legacy of land-use history can influence plant physiology; consequently, the results obtained in cover crop and intercrop studies may in part be due to a legacy effect (Li et al., 2019). Therefore, RV and IV are context dependent on the type of agroecosystem in which they were measured and being implemented in. To gain the most out of RV and IV, we should account for environmental factors, soil chemistry, and soil history.

Although the use of the PSF framework to quantify the RV or IV is straightforward and can be easily conducted in a field or greenhouse setting, this approach may overlook a broader range of long-term agroecological benefits. For example, relatively short-term rotational experiments of a couple of seasons may overlook longer-term benefits, such as increased soil contribution, microbial activity, or a broader set of ecosystem services, that are more likely to be apparent over longer rotational cycles or geographic scales (Capó-Bauçà, Marqués, Llopis-Vidal, Bota, & Baraza, 2019; Gabriel, Hontoria, & Quemada, 2016; Schmidt, Gravuer, Bossange, Mitchell, & Scow, 2018). However, long-term experiments are harder to replicate on a wide scale and often exceed the timeframe within which researchers need to complete research. As shorter-term measurements, RV and IV can allow longer-term trends to be included in breeding efforts.

Furthermore, this approach does not estimate or identify the underlying mechanisms that contribute to the RV or IV. Understanding the underlying mechanisms that influence RV and IV provides scientists with predictive insight into why certain crops and management practices are beneficial while also allowing the identification of target traits. For instance, if the RV of legumes is primarily derived by its ability to host symbiotic nitrogen-fixing rhizobia, the PSF framework would not be able to identify these traits as the primary mechanism contributing to its RV. These mechanisms would only be identified by measuring nitrogen fixation among all treatment groups during the experiment. Similarly, the rotational value of a daikon-type tillage radish (*Raphanus sativus* L. var. *sativus*) is primarily derived by its ability to act as a biodrill. The daikon-type tillage radish has the capacity to penetrate a compacted soil, as well as mop-up excess nutrients left in a field by a previous crop (e.g., Chen & Weil, 2010; Gruver, Weil, White, & Lawley, 2014). These mechanisms would only be identified by measuring soil compaction, as well as other traits such as root architecture and radish breakdown rate (Gruver et al., 2014). Thus, to gain a more comprehensive understanding of the effects of management practices in agroecosystems and to identify potential breeding targets, we believe that rotational and intercropping studies need to measure ecosystem services in addition to calculating the RV and IV of crops and management practices. The literature on ecosystem services and their valuation is too vast and complex to review here (readers are directed to de Groot, Wilson, & R.M, 2002; Guerry et al., 2015; Power, 2010; Swinton, Lupi, Robertson, & Hamilton, 2007; Zhang, Ricketts, Kremen, Carney, & Swinton, 2007 for a small sample of the growing literature) but our framework can easily handle any ecosystem service.

1.2 | Ecosystem services could be bred for to improve rotational and intercropping values

Crop rotations and intercropping are an aspect of many contemporary and historical agricultural systems that provide several short- and long-term benefits (Reviewed in Fageria et al., 2005; Sharma et al., 2018; Wick et al., 2017) and sometimes trade-offs or negative consequences (e.g., Finchk et al., 2017). Rotations and intercrops, in general, provide many ecosystem services such as suppressing weeds, hindering disease cycles and pest outbreaks, sequestering carbon to build soil organic matter, supporting pollinator and natural enemy populations, and helping mobilize other limiting nutrients such as phosphorus (Altieri, Letourneau, & Risch, 1984; Krupinsky, Bailey, McMullen, Gossen, & Kelly Turkington, 2002; Snapp et al., 2005; Teasdale, Abdul-Baki, Mills, & Thorpe, 2004; Wick et al., 2017). Conversely, some rotations may amplify diseases or pest problems, adversely impacting other crops in a system. These diverse rotational and intercropping ecosystem services can be quantified in numerous ways (see above) and, thus, can be treated as rotational and intercropping traits that can be selected and bred for to enhance RV and IV (Figure 1). For instance, if we continue with the previous example of legumes, we could increase the rotational value of legumes by breeding legumes for enhanced nitrogen fixation whether through increased nodulation or a broader range of host specificity with rhizobia. Alternatively, in the case of cereals, we can potentially increase their rotational value by increasing their ability as weed suppressors or nutrient scavengers by breeding for enhanced ground cover, allelopathy, or nutrient acquisition (e.g., Worthington & Reberg-Horton, 2013). Therefore, improving the ecosystem services that a cover crop or intercrop provides should hypothetically increase their RV or IV. However, breeding for the enhancement of an ecosystem service can be challenging because determining the most appropriate measurement for each service can be difficult. Most ecosystem services are not as simply quantified as other agronomical traits such as plant height, yield, and tolerance to biotic or abiotic stress (e.g., de Groot et al., 2002; Zhang et al., 2007). We explore this dilemma in the upcoming paragraphs for key rotational and intercropping traits and identify different methods of quantifying ecosystem services that may be useful for the enhancement of RVs and IVs (e.g., Schipanski et al., 2014).

A commonly used rotational and intercropping trait of crops is the suppression of weeds. Within crops, legumes may perform more poorly than cereals and may permit greater weed biomass (Baraibar, Hunter, Schipanski, Hamilton, & Mortensen, 2018; Hodgdon, Warren, Smith, & Sideman, 2016). Thus, mixtures of different crops may

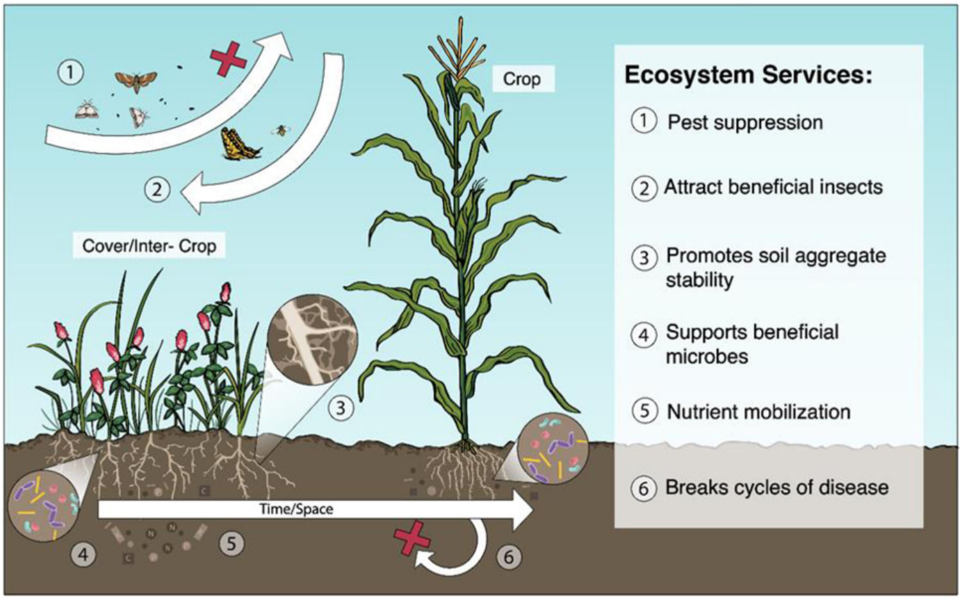

FIGURE 1 Temporal (e.g., crop rotation) or spatial (e.g., intercropping) crop biodiversity can benefit cash crops in numerous ways such as (1) suppressing pests, (2) attracting beneficial insects, (3) promoting soil aggregate stability, (4) supporting beneficial microbes, (5) mobilizing nutrients, and (6) breaking cycles of diseases. These benefits can contribute to the rotational or intercrop value of a crop, or how well a crop benefits the yield or growth of a cash crop. By identifying which benefits facilitate the yield or growth of a cash crop, we can select for the enhancement of those traits, thus increasing the rotational or intercrop value of the crop and making them a better rotational or intercropping partner

be most effective at weed prevention (Baraibar et al., 2018; Florence, Higley, Drijber, Francis, & Lindquist, 2019). Crop mixtures that are sown as polycultures, or undersowing a primary crop with a shorter-stature secondary crop, provide a greater competitive impact on weeds, thereby raising yields (Chauhan et al., 2012). Weed suppression can be measured in weed-control savings, weed abundance, or weed biomass. The risk, as with other rotational and intercropping traits, is that weed pressure is notoriously variable, so estimates are context dependent. In addition to the quantifying weed suppression, identifying the mechanisms of how the crop is suppressing weeds (shading, allopathy, or nutrient acquisition) is imperative for the breeding process as it will narrow the range of traits that breeders or farmers will need to select for to increase RVs or IVs (Florence et al., 2019; Worthington & Reberg-Horton, 2013). Furthermore, the use of highly diverse multispecies mixtures to reduce weeds may lead to a refinement of traits that are compatible with mixtures. Both RV and IV can help us quantify the weed suppressive value of a cover or intercrop as its value to another crop and balance that with impacts that the weed suppressive traits may have on the crop's own yield.

Another important aboveground rotational and intercropping trait is the increase of aboveground biodiversity and the suppression of pests (Smith & McSorely, 2000). Rotational and intercrops have been shown to increase the presence of pollinators and natural predators of pests, an ecosystem service hypothesized to reduce yield gaps in agroecosystems (Bommarco, Kleijn, & Potts, 2012; Hummel, Walgenbach, Hoyt, & Kennedy, 2002; Rusch, Bommarco, Jonsson, Smith, & Ekbom, 2013). For instance, cover crops and intercrops were seen to increase the presence of pest predators in cotton (*Gossypium hirsutum* L.) (Tillman et al., 2004) and broccoli (*Brassica oleracea* L. var. *italica* Plenck) (Ponti, Altieri, & Gutierrez, 2007). Additionally, ground cover in almond [*Prunus dulcis* (Mill.) D. A. Webb] orchards was correlated with increased pollinator presence, specifically increasing native bee presence (Saunders, Luck, & Mayfield, 2013). Because of the direct correlation this trait has on yield, aboveground biodiversity is a crucial contributor to a crop's RV and IV and should be measured. This trait can be measured by numerous methods such as the abundance and presence of pests and pollinators and herbivory damage (Buckland, Magurran, Green, & Fewster, 2005). However, similar to weed suppression, identifying the mechanisms as to why certain crops increase aboveground biodiversity or deter pests is imperative to the breeding process. For instance, some crops may give off volatile compounds, while others provide resources to attract pollinators (e.g., Baldwin, 2010) or natural enemies like ants (e.g., Jones, Koptur &

von Wettberg, 2017). Identifying which plant mechanisms helps provide the ecosystem service will supply breeders and farmers with a narrowed selectable trait list to increase RVs and IVs. Both RV and IV allow us to integrate these values into our breeding, where we measure their value as value to other crops in the system.

A key contributor to RV and IV is the contribution plants make to the soil. Plants contribute to the soil in two primary ways: through exudates, mixtures of organic compounds from their roots that can constitute a staggering 20–40% of the entire metabolism of a plant; and as decaying roots and aboveground parts that remain in the soil or are incorporated into the soil after the plant senesces (e.g., Kuzyakov & Domanski, 2000). Root exudates likely are involved in several key functions (Friesen et al., 2011, van Dam & Bouwmeester, 2016): (a) providing carbohydrates to beneficial symbiotic soil partners like rhizobia and mycorrhizal fungi, (b) recruiting other growth-promoting or defensive microbes to the root surface, (c) helping plants obtain limiting nutrients such as phosphorus and iron that adhere strongly to soil particles and can be released when roots secrete weak organic acids to dissolve them, (d) buffering the effects of potentially toxic aluminum and heavy metals in the soil, and (e) inhibiting pathogens and herbivores such as bacteria, fungi, nematodes, and soil insects. Although these functions are well known, measuring exudate variation across soil conditions, between species and genotypes, or as interactions between genotype and environment is quite challenging because soil microbes will metabolize root exudates upon their release from roots (e.g., Jacoby & Kopriva, 2018; Oburger & Jones, 2018; Pétriacq et al., 2017; van Dam & Bouwmeester, 2016).

Despite the limitations of quantifying root exudation, one can quantify the effects of rotations and intercrops on microbial soil communities. Understanding the effect of crops on microbial diversity and functional activity is critical since these services have been positively associated with soil health and crop productivity (McDaniel, Tiemann, & Grandy, 2014; Tiemann, Grandy, Atkinson, Marin-Spiotta, & Mcdaniel, 2015). For instance, it has been shown that cover crops increased microbial diversity and activity in agroecosystems, which led to increased yields in potato (*Solanum tuberosum* L.) (Larkin, Griffin, & Honeycutt, 2010), grapevine (*Vitis vinifera* L.) (Ingels, Scow, Whisson, & Drenovsky, 2005), cucumber (*Cucumis sativus* L.) (Tian, Zhang, Liu, & Gao, 2011) and cotton (Mbuthia et al., 2015; Nouri, Lee, Yin, Tyler, & Saxton, 2019). Additionally, in the past two decades, methods for measuring soil microbial communities have changed radically, opening up new possibilities for research on plant–microbe interactions. These new methods to quantify soil microbial communities fall into three community characterization categories: size, composition, and activity (Reviewed in Harris, 2003). There are benefits and limitations to each measurement and characterization approach, and deciding which approach to use is dependent on how microbial communities increase RVs and IVs. For example, if the RV or IV is increased with an increase in soil microbial populations, then characterizing the microbial community by its size through microbial biomass measurements is sufficient. However, if a specific microbial community composition increases the RV or IV, then a more precise and advanced shotgun metagenomics approach will be necessary. Nevertheless, all characterization approaches are quantifiable and, therefore, should be measures we can integrate into breeding programs. These approaches allow us to make microbial mediation of RV something tractable.

Furthermore, one can calculate the ability of a crop to break cycles of disease attack by the decreased cost of pesticides or by infection rates (Larkin et al., 2010). With next-generation sequencing, one can measure pathogen presence and population size before and after a rotation as well as compare different rotations and their impact on pathogen presence. This capacity allows us to a much more precise measure of this benefit as well as potential trade offs. Furthermore, a rotational or intercrop may help recruit antagonists of pathogens, such as *Trichoderma* and *Pseudomonas*, which induces plant immune responses (Bakker, Pieterse, & van Loon, 2007; Han, 2019; Korolev, David, & Elad, 2008; Shoresh, Yedidia, & Chet, 2007; Vitti et al., 2016). For instance, Wang et al. (2017) found positive legacy effects of intercrops believed to be due to shifts in soil communities, which reduced the negative effects of soil pathogen buildup. However, identifying these mechanisms of disease suppression requires experimental designs that can take several seasons to implement. Moreover, these trait measurements estimated from experiments, particularly at a single site, are highly context dependent and may depend on the presence of natural predators or other local factors impacting the presence of pathogens. Understanding this context dependence can allow one to manipulate natural predators, encouraging their populations or making them available in particular rotations (e.g., Jones et al., 2017). Altogether, this makes breeding for disease suppression by natural enemies a complex task.

Lastly, for legumes, an important rotational and intercropping trait is nitrogen fixation. However, legume-hosted biological nitrogen fixation does vary substantially depending on the species, the genotype, the availability of efficient symbiotic rhizobia in a particular field setting, and the effectiveness of the symbiosis in that field setting (Busby et al., 2017; Hardarson et al., 1993; Vyn, Faber, Janovicek, & Beauchamp, 2000). Nitrogen fixation tends to be lower in field settings than in laboratory settings because of factors such as poor adaptation to the host, poor adaptation of the rhizobia to the soil, abiotic stress that limits the effectiveness of the symbiosis, or other factors (see Busby et al., 2017; Thrall, Broadhurst, Hoque, & Bagnall, 2009). However, breeding for enhanced nitrogen fixation overlooks the timing of nitrogen availability. Depending on management conditions, only some nitrogen from a subsequent cover or rotational crop is likely to be available to the next crop (Burity, Ta, Faris, & Coulman, 1989; Vyn et al., 2000). As a result, this will most likely affect true RVs and IVs in a field setting.

1.3 | Rotational and intercropping value: Next-generation breeding targets

All of these conceptions of RVs and IVs that increase the value of rotational and intercrops expand the range of breeding targets that can be used in developing more effective crop rotations and intercrops. We propose that RV and IV can fit into a range of breeding frameworks, from ideotype breeding (Donald, 1968) to genomic selection frameworks using indices of multiple traits (e.g., Sölkner, Grausgruber, Okeyo, Ruckenbaur, & Wurzinger, 2008). For those seeking an ideotype of a good rotational partner, it can focus attention on the necessary traits for the ecosystem services provides. For selection with indices of traits (e.g., Falconer & Mackay, 1996), it facilitates optimization of a range of traits that include ecosystem services as well as the yield or market value of the crop itself. For instance, if a legume is the breeding target, the association with rhizobia has long been known to be a beneficial trait, but RV and IV can help us focus on nitrogen provided to paired crops under realistic conditions. For rotational traits of tillage crops, such as daikon radish, it may be its effect on soil compaction and timing of nutrient uptake and release. For cereals used as covers, it may be growth rate, allelopathy, or cold hardiness. Across all crops used for rotational benefits or intercropping, breeders will ideally have a range of traits that can be measured effectively such as increasing soil organic matter (with favorable C/N ratios), providing weed suppression, lowering infection rates of diseases, and mobilizing nutrients. These are all traits for which genetic variation in crops almost certainly exists and could be useful breeding targets to increase agricultural sustainability and productivity.

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AUTHORS CONTRIBUTIONS

E.M. and E.J.B.v.W conceived the idea; A.K. created the figure; all authors wrote the manuscript.

CONFLICT OF INTERESTS

All authors declare that there are no conflict of interests.

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SUPPORTING INFORMATION

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