Agriculture, Ecosystems and Environment 241 (2017) 88–99

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Specific interactions leading to transgressive overyielding in cover crop mixtures

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ARTICLE INFO

Article history:
Received 2 September 2016
Received in revised form 28 February 2017
Accepted 4 March 2017
Available online xxx

Keywords:
Intraspecific and interspecific competition
Response surface design
Resource partitioning
Facilitation
Relative dominance
Land equivalency ratio (LER)

ABSTRACT

Growing mixtures of species instead of sole crops is expected to increase the ecosystem services provided by cover crops. This study aimed at understanding the interactions between species and investigating how they affect the performance of the mixture. Four species were combined in six bispecific mixtures in a field experiment. The performance of each species when grown in a mixture was compared to its performance as a sole crop at different sowing densities, to characterise the influence of intra- and interspecific competition for each species. Intra- and interspecific competition coefficients were quantified using a response surface design and the hyperbolic yield-density equation. Interactions between the four species ranged from facilitation to competition. Most of the mixtures exhibited transgressive overyielding. Without nitrogen (N) fertilisation, high complementarity between species allowed to achieve the highest biomass. With N fertilisation, high dominance of one mixture component should be avoided to achieve good performance. A revised approach in the use of the land equivalent ratio for the evaluation of cover crop mixtures is also proposed in this study. It allows to better identify transgressive overyielding in mixtures and to better characterise the effect of one species on the other within the mixture.

1. Introduction

Currently, there is growing interest in improving integration of cover crops in cropland. Cover crops are grown between two cash crops and can provide a wide range of ecosystem services such as weed control (Brust et al., 2014), soil protection against erosion (De Baets et al., 2011) or increase of soil organic matter (Ding et al., 2006). They are also able to recycle large amounts of nutrients and may thus prevent their losses (Thorup-Kristensen et al., 2003). Some species can mobilise poorly available nutrient forms (Hunter et al., 2014; Nuruzzaman et al., 2005) and legume species can symbiotically fix nitrogen (N) (Büchi et al., 2015). Cover crop cultivation also contributes to increasing diversity in cropland, which is paramount for the sustainability of agroecosystems (Altieri, 1999).

Growing mixtures of cover crop species instead of sole crops may improve the services offered, but also allow providing several services at the same time. Currently, most studies showing benefits of mixed cropping systems with cover crops involve associations of legume and non-legume species. It has been reported that these mixtures can simultaneously reduce nitrate leaching and fix N from the atmosphere (e.g. Tosti et al., 2014; Tribouillois et al., 2015). Tosti et al. (2014) showed that the carbon to nitrogen (C/N) ratio of the mixture barley-vetch should allow faster mineralisation than that of barley as a sole crop. Other services, such as a higher weed suppression by the mixture compared to legume alone (Akemo et al., 2000), have been reported. Contrary to mixtures of legume and non-legume species, associations of two non-legume species are rare (e.g. Finney et al., 2016). These mixtures may however be of interest for diversifying the ecosystem services, such as weed control and nutrient recycling, especially when N is not limiting.

Most of the services provided by cover crops are intimately related to the biomass productivity of the crops (Finney et al., 2016). Maximising biomass production is thus an interesting way to optimise the services provided by a cover crop. This could be

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http://dx.doi.org/10.1016/j.agee.2017.03.003
0167-8809/

achieved for mixtures exhibiting 'overyielding' or, even better, 'transgressive overyielding' (Sainju et al., 2006; Schmid et al., 2008; Wang et al., 2012). Overyielding occurs in a mixture 'when its biomass production is greater than that of the average monoculture of the species contained in the mixture' (Schmid et al., 2008). Transgressive overyielding appears 'when the productivity in mixture is larger than the maximal productivity of the constituent species' (Gravel et al., 2012). Transgressive overyielding should thus be the main goal when associating cover crop species.

However, to improve biomass production of mixtures, a better understanding of how species interact is essential. Studies on species interactions in cover crop mixtures are limited but intercropping systems, where two or more crops are growing simultaneously in the same field, can be used as references (Vandermeer, 1989; Bedoussac et al., 2015; Brooker et al., 2015; Yu et al., 2015). Several types of interactions can be observed, ranging from negative effects due to competition to positive effects through facilitation. Facilitation, i.e. positive influence of the associated species, is of crucial importance as it leads to a better performance of the focal species in mixture than in sole crop (Brooker et al., 2016). For example, Maltais-Landry (2015) found that cereals in mixtures with legumes produce a greater biomass, and achieve a higher phosphorus (P) uptake and N concentration, than as sole crops. Facilitation can result from several mechanisms such as an increased resource availability (Zhang and Li, 2003; Li et al., 2014), or a decrease in disease and pest attacks (Hauggaard-Nielsen et al., 2008).

By contrast, some species may have a negative influence on the other species, resulting in a decreased performance in mixture compared to the sole crop. Negative influence may arise from competition for a limiting resource, such as nutrients, water or light, or from modification of the growing conditions (interference), for example allelopathic effects (Vandermeer, 1989).

In some cases, species may not influence each other. This situation can be observed when species use complementary resources and thus do not compete for the same resources. This leads to a more efficient resource capture of the mixture compared to sole crops. Complementarity in the use of N sources has been largely evidenced for associations of legume and non-legume species (e.g. Hauggaard-Nielsen et al., 2001a; Bedoussac and Justes, 2010; Cong et al., 2015; Li et al., 2016). In these associations, legume species increase their reliance on atmospheric N as the non-legume species are more competitive for soil N. Hauggaard-Nielsen et al. (2001b) showed that complementarity can also occur along the soil profile, between species exhibiting complementary rooting depths, such as pea and barley, leading to a better soil exploration.

Interactions between species are complex and influenced by many factors like nutrient availability, mixture density and the relative proportion of species (Connolly et al., 1990). In the case of mixtures combining legume and non-legume species, it has been shown that N fertilisation favours mainly the non-legume species at the expense of the legume, while at low N availability, the contrary was observed (Möller et al., 2008). Changes in species proportion and sowing density can also modify species relative competitive strength (Hauggaard-Nielsen et al., 2006).

In order to get the highest benefits from mixtures, it is thus essential to understand the influence of the following factors on mixture performance: relative proportion of species, sowing densities and fertilisation levels. It is also important to characterise and quantify intra- and interspecific interactions. To investigate species interactions in bispecific mixtures, Inouye (2001) suggested using a response surface design in which the density of each species is varied independently. This design allows distinguishing the effects of intra- and interspecific competition, through the coefficients of the yield-density equation (Wright, 1981). The benefit of mixtures over sole crops (e.g. transgressive overyielding) and species influence on the performance of the associated species can also be assessed with this design. The strength of the response surface design is to allow a global assessment of mixture performance, while more simple designs, such as replacement series coupled to commonly used indices such as land equivalency ratio (LER), only quantify the performance of each single mixture separately.

In this study, in order to understand interactions in bispecific mixtures, a response surface design involving four contrasting species, commonly used as cover crops under European conditions, was set up. The chosen species were: Indian mustard (*Brassica juncea*), field pea (*Pisum sativum*), black oat (*Avena strigosa*) and phacelia (*Phacelia tanacetifolia*). Mustard is expected to be a highly competitive species due to its allelopathic potential, while pea could have a positive influence on the associated species as it is able to biologically fix N. Oat and phacelia should have more neutral effects.

The main objectives of this study were (i) to evaluate the potential advantage of bispecific mixtures over sole crops, (ii) to determine the influence of each species on the performance of the associated species and (iii) to investigate how the interactions between species influence the performance of the mixture. All these factors were studied with and without N fertilisation to assess the importance of nutrient availability in driving species interactions and mixture performance.

2. Materials and methods

2.1. Site description and experimental design

The study was conducted in 2014 at Agroscope Changins (46°23′44.6″N, 6°14′24.6″E, 426 m asl), Switzerland, on a Cambisol (FAO classification system) with 244 g/kg of clay and 294 g/kg of sand in the top 20-cm soil layer. The average total annual precipitation is 999 mm and the mean temperature 10.2 °C (30-year averages, 1981–2010). Mineral N after cover crop emergence was 27 kg/ha for the 0–30 cm layer, 34 kg/ha for 30–60 cm and 24 kg/ha for 60–90 cm. Two field experiments were carried out with four species commonly used as cover crops under Swiss conditions: Indian mustard (*B. juncea* cv Vitasso), field pea (*P. sativum* cv Arkta), black oat (*A. strigosa* cv Pratex) and phacelia (*P. tanacetifolia* cv Balo).

In the main experiment, each species was grown in bispecific mixtures in combination with each of the other species, resulting in six different mixtures. For each mixture, twenty variants were studied: five different 'relative proportions' of the two species (0:1, 1:3, 1:1, 3:1 and 1:0) and four 'mixture sowing densities' (50%, 75%, 100% and 125%) (Fig. S1, Supporting Information). The sowing density of each species was thus the product of species relative proportion and mixture sowing density. The experiment was conducted with two nitrogen (N) fertilisation levels: 0 kg/ha and 30 kg/ha, applied as ammonium nitrate 12 days after sowing. The design of this experiment corresponded to a response surface design (Inouye, 2001) and included 176 plots (no replicates).

The main experiment was complemented by another experiment, set up on the same date and in the same field. In this experiment, each species was sown as a sole crop at six different sowing densities: 10%, 20%, 35%, 50%, 75% and 100% of their standard sowing density (see below). The experimental design followed a randomised block design with four replicates. 30 kg/ha of N were applied to the whole experimental field 12 days after sowing. This complementary experiment was used to assess the influence of sowing density on the biomass production of sole crops and thus allowed to characterise intraspecific competition. It