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The impact of intercrop design on weed suppression of species mixtures: A model-based exploration

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ABSTRACT

Intercropping has frequently been reported to enhance weed suppression. A recent study combining a plant competition model and empirical data demonstrated that improved weed suppression results from a so-called selection effect, whereby the more weed suppressive crop species contributes disproportionate to the weed suppressive ability of intercrops. Here, we build on this finding and used the plant competition model to explore how species composition, mixing ratio, planting density and spatial arrangement influence the weed suppressive ability of annual intercropping systems. Analysis identified species composition as the principal design factor, since a difference in weed suppressive ability between crop species appeared the prime driver responsible for the above-average weed suppression of intercrops: the larger this difference the stronger the effect. With greatly differing levels of weed suppressive ability between crop species, even a small proportion of the stronger suppressive species greatly enhanced the intercrop's ability to suppress weeds. In such a situation, mixing ratio can thus be used to regulate the trade-off between weed suppressiveness and the risk of the less competitive crop species being overgrown. Plant density was found to be a useful modulator if crop species displayed similar levels of weed suppression. In this case, intercrops in additive design were the only option to enhance weed suppression. Proximity of component species proved a prerequisite for superior weed suppressiveness. Consequently, in strip cropping systems, the improved weed suppressive ability rapidly declined with wider strips. The acquired quantitative insights form a theoretical foundation for considering weed suppression when designing multi-functional annual intercropping systems.

1. Introduction

1.1. Weed suppression in intercrops

Intercropping is the planned cultivation of two or more crop species in a field. Intercrops have a high land use efficiency as shown by values of the land equivalent ratio (LER) that are, on average, well above one (Yu et al., 2015; Li et al., 2020). Furthermore, intercropping has multiple ecological benefits, including ecologically based suppression of pests and diseases (Boudreau, 2013; Stomph et al., 2020; Zhang et al., 2019). For weed suppression, a vote counting analysis of published studies on intercrops of two main crop species, published in 1993, indicated that weed biomass in intercrop was higher, intermediate to or lower than the weed biomasses obtained in pure stands of the two component species in 8 %, 42 % and 50 % of the cases, respectively (Liebman and Dyck, 1993). Evidently, intercrops nearly always suppress weeds better than a pure stand of the weaker suppressive component species. Almost 30 years later, a review by Gu et al. (2021) confirmed these vote-counting results. Here the weed biomass in intercrop was higher, intermediate to and lower than the weed biomasses in pure stands in 9 %, 46 % and 45 % of the cases, respectively. Furthermore, Gu et al. (2021) conducted a quantitative meta-analysis of the magnitude of the weed suppressive effect, based on over 330 data records drawn from 39 publications. It was shown that weed biomass in an intercrop was on average 58 % lower than in the pure stand of the weaker suppressing crop species and only 8 % higher than in the stronger suppressing crop species. These results confirm the above average weed suppression of intercrops, with the weed biomass in a mixed system markedly lower than the average weed biomass obtained in the pure stands of the two component species.

Mechanisms contributing to a positive relation between increased species diversity of mixed systems and improved ecosystem functioning are usually divided in two main categories: complementarity effects and selection effects (e.g. Loureau, Hector 2001; Brooker et al., 2021). Complementarity effects are associated with increased total resource

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use, resulting from processes such as niche differentiation and facilitation. The augmented weed suppressive ability of intercrops is generally believed to result from niche differentiation, whereby the two crop species together capture a greater fraction of the available resource pool, such that less is left for the weeds (e.g. Liebman and Dyck, 1993; Bilalis et al., 2010; Schöb et al., 2023). The logic of this reasoning is commonly used to explain and justify the contribution of complementarity effects to weed suppression, but a quantitative analysis has so far not been made. The study of Gu et al. (2021) is one of the first to question the important role of complementarity effects in enhanced weed suppression of annual intercrops. Contrary to expectation, if intercrops had a replacement design, they did not find a significant positive relation between the land equivalent ratio (LER; a commonly used index of complementarity) and the level of weed suppression.

Selection effects are observed when a species has particular traits that allow it to dominate a plant community and put its mark on the ecosystem functioning of a mixed species system (Brooker et al., 2023). In annual intercropping systems, species with a high early vigour are likely to dominate the intercrop and this same trait is also regularly associated with superior weed suppressive ability (e.g. Zhao et al., 2006; Andrew et al., 2015). As a result, highly competitive species add disproportionate to the weed suppressiveness of intercrops. This phenomenon was for example noticed in a study on leek-celery intercropping systems (Baumann et al., 2000). Leek is a slow growing plant with an upright stature, resulting in an open crop canopy and plenty of space for weeds to develop. Celery is a faster growing and much more leafy species, resulting in a crop with a much earlier canopy closure and better weed suppression. Accordingly, a replacement intercrop of leek and celery with alternate rows of the two species was dominated by celery, with light interception and weed suppression of the intercrop more similar to that of the celery than the leek pure stand (Baumann et al., 2001). These observations align with the selection effect.

1.2. Selection, not complementarity, at the basis of weed suppression in intercrops

Gu et al. (2022) used their earlier collected dataset to obtain further insight in the role of selection and complementarity effects in the above-average weed suppression of intercrops. As mentioned before, this dataset was made up of over 330 records retrieved from published intercropping research, with each record containing weed biomass in intercrop as well as in pure stands of the component crop species. In their analysis, the aim was to find a model that was able to accurately predict the weed biomass in intercrop based on the weed biomasses obtained in the pure stands of the component species. The aspiration was that such a model, and in particular the assumptions at the basis of this model, would provide clues on the relevance of selection and complementarity for weed suppression in intercrop. For their analysis, the well-established plant competition model of Spitters (1983) was used to describe the weed biomass evolving in pure stands of the crop species that make up the intercrop ($Y_{\mathrm{w,C1}}$ and $Y_{\mathrm{w,C2}}$; gm^{-2}) as well as the weed biomass evolving in the corresponding intercrop ($Y_{\mathrm{w,IC}}$). The principal assumption at the basis of Spitters' model is the additivity of competitive influences, whereby the influence of each species is characterized by the product of a species-specific competition coefficient and its plant density. Mathematical elaboration showed that the weed biomass in intercrop ($Y_{\mathrm{w,IC}}$) can be expressed as a function of the weed biomass in pure stands of the component species: $Y_{\mathrm{w,IC}} = f(Y_{\mathrm{w,C1}}, Y_{\mathrm{w,C2}})$. More specifically it showed that, under the assumption of additivity of competitive influences, predicted weed biomass in intercrop ($Y_{\mathrm{w,IC}}$) corresponds to the so-called weighted harmonic mean of weed biomasses in pure stands of the component crop species:

$$Y_{w,IC} = \frac{1}{\rho_1\left(\frac{1}{Y_{w,C1}}\right) + \rho_2\left(\frac{1}{Y_{w,C2}}\right)} \tag{1}$$

In this equation ρ_1 and ρ_2 are the relative densities of crop 1 and crop 2, respectively, defined as the density of a crop species in intercrop expressed as a fraction of its density in pure stand. A better appreciation of the harmonic mean can be obtained by rewriting Eq. 1 (Appendix A):

$$Y_{w,IC} = \left(\frac{\rho_1 Y_{w,C2}}{\rho_1 Y_{w,C2} + \rho_2 Y_{w,C1}}\right) Y_{w,C1} + \left(\frac{\rho_2 Y_{w,C1}}{\rho_1 Y_{w,C2} + \rho_2 Y_{w,C1}}\right) Y_{w,C2} \tag{2}$$

In this equation, by referring to the stronger weed suppressive species as crop species 1 (C1), it becomes evident that the lower weed biomass associated with the stronger weed suppressive species ($Y_{\mathrm{w,C1}}$) is weighed with an increased weight (proportional to $Y_{\mathrm{w,C2}}$), while the greater weed biomass ($Y_{\mathrm{w,C2}}$) is weighed proportional to the lower weed biomass. The expression thus clearly reflects the more than proportional contribution of the more suppressive crop species to the weed suppression of the intercrop. Obviously, the selection effect thus simply evolves as a result of the assumed additivity of competitive influences of the two component species.

Following this, Gu et al. (2022) used the over 330 records containing weed biomass in both intercrop and corresponding pure stands, to evaluate how well the harmonic mean (Eq. 1) was able to predict weed biomass in intercrop. Validation revealed a close correspondence between observed weed biomass in intercrop and the prediction following from the harmonic mean, without a systematic overestimation of actual weed biomass. This result led to the conclusion that a model based on the additive competitive effect of component species was sufficient to account for the observed weed suppression in intercropping. There was no support for a more complex model with synergistic effects, evolving from for instance niche differentiation. Consequently, the main conclusion of the study by Gu et al. (2022) was that selection is the prime mechanism responsible for the above average weed suppression of annual intercrops, whereas complementarity effects do mostly not play an important role.

1.3. Intercrop design and weed suppression

Although complementarity effects have previously been considered the main mechanism of the above average weed suppression of intercrops, the study of Gu et al. (2022) proved it is the selection effect. Here, we build on this empirical evidence and provide a theoretical assessment of how intercrop design factors like species composition, mixing ratio, planting density and spatial arrangement influence the weed suppressive function of intercrops. Spitters' plant competition model, the model at the basis of the harmonic mean, was used to characterize these influences in a quantitative manner. Such quantitative assessments are relevant, as, next to weed suppression, intercropping systems will have to deliver a good product and be able to facilitate the expression of other ecological advantages. Consequently, the ideal intercropping design will be the result of an optimization process, whereby various objectives are weighted against one another (e.g. Baumann et al., 2002). Being able to provide a substantiated prediction of how intercropping design is likely to affect the ability of intercrops to suppress weeds is highly relevant for such an optimization process.

2. Material and methods

This section starts with providing more fundamental insight in the relation between Spitters' model, the harmonic mean and the selection effect. It then explains how we used this insight to quantitatively characterize the contribution of the selection effect to the weed suppression of intercrops. This is followed by a more detailed description on how Spitters' model was used to quantify the influence of species composition, mixing ratio, planting density and spatial arrangement on the weed suppressive ability of annual intercrops.

2.1. Spitters' model, the harmonic mean and the selection effect

As mentioned in the introduction, the well-established plant competition model of Spitters (1983) was used as starting point for the analysis by Gu et al. (2022):

$$Y_{w,Ci} = \frac{N_w}{b_{w,0} + b_{w,w}N_w + b_{w,Ci}N_{Ci}} \tag{3}$$

Here $Y_{\mathrm{w,Ci}}$ is the weed biomass in a pure stand of crop species i, N_{w} is weed plant density (plants m^{-2}), b_{w0} represents the reciprocal plant weight of an isolated weed plant not experiencing competition (plants g^{-1}), $b_{\mathrm{w,w}}$ and $b_{\mathrm{w,ci}}$, are competition coefficients ($\mathrm{m}^2\mathrm{g}^{-1}$) representing the increase in reciprocal weed plant weight per unit increase in the density (plants m^{-2}) of weed plants (N_{w}) and crop species i (N_{ci}), respectively. The principal assumption at the basis of Spitters' model is that the addition of any plant to a plant population, regardless of species, increases the reciprocal of individual plant weight in an additive manner. The size of this increase is species-specific and proportional to the competitiveness of the species. Consequently, the inverse of weed biomass ($1/Y_{\mathrm{w,Ci}}$; $\mathrm{m}^2\mathrm{g}^{-1}$) increases linearly with crop plant density, whereby a steeper slope reflects a stronger competitive influence of the crop species on the weed (Fig. 1 A). Inversion of $1/Y_{\mathrm{w,Ci}}$, resulting in $Y_{\mathrm{w,Ci}}$ which expresses the amount of produced weed biomass in a more common unit (gm^{-2}), shows the additivity of competitive influences in a different perspective (Fig. 1B). Here, increasing crop plant density results in a reduction of $Y_{\mathrm{w,Ci}}$, whereby the addition of every next crop plant results in a continuously smaller marginal reduction. The relationship thus reflects that adding crop plants increases the total competitive pressure on the weed. At the same time, the increased intraspecific competition at higher crop plant densities is responsible for the gradually lesser reduction in $Y_{\mathrm{w,Ci}}$. Consequently, the influence of the addition of every next crop plant simply gets smaller. What is also obvious is that with a stronger weed suppressive crop species, $Y_{\mathrm{w,Ci}}$ drops considerably faster than with a weaker suppressive species.

Eq. 3 for weed biomass in a pure stand crop was used as a basis for studying weed biomass with two crop species in the same field. In its simplest form, the introduction of a second crop species can be realized by splitting the field in two parts, where crop 1 is grown on the first part and the second part of the field is planted with crop 2. For such an arrangement the average weed biomass ($Y_{\mathrm{w,SF}}$ with SF referring to split field) corresponds to the weighted arithmetic mean of the weed biomasses in the two pure stands (Table 1):

$$Y_{w,SF} = \frac{\rho_1}{(\rho_1+\rho_2)}Y_{w,C1} + \frac{\rho_2}{(\rho_1+\rho_2)}Y_{w,C2} = \rho_1 Y_{w,C1} + \rho_2 Y_{w,C2} \tag{4}$$

with ρ_1 and ρ_2 as the relative densities of crop 1 and crop 2, defined as the density of a crop species on a mixed field expressed as a fraction of its density in pure stand. Here these relative densities correspond to the fraction of the field planted with crop 1 and crop 2, respectively. Plotting average weed biomass as a function of the proportion of the field occupied by the stronger weed suppressor (ρ_1) results in a linear decrease from $Y_{\mathrm{w,C2}}$ in a pure stand of the weaker suppressive crop species to $Y_{\mathrm{w,C1}}$ in a pure stand of the stronger weed suppressive species (Fig. 2 A; model A).

If both crop species are mixed and planted in intercrop, weeds are simultaneously suppressed by both crop species. This combined suppression is included in an extended version of Spitters' model expressing the weed biomass in intercrop (e.g. Bastiaans and Storkey, 2017) (Table 1; model B):

$$Y_{w,IC} = \frac{N_w}{b_{w,0} + b_{w,w}N_w + b_{w,C1}\rho_1 N_{C1} + b_{w,C2}\rho_2 N_{C2}} \tag{5}$$

Mathematical elaboration of this expression showed that the inverse predicted weed biomass in a species mixture ($1/Y_{\mathrm{w,IC}}$) was linearly related to the inverse weed biomasses in the pure stands of the species contained in the mixture (Gu et al., 2022):

$$\frac{1}{Y_{w,IC}} = \rho_1\frac{1}{Y_{w,C1}} + \rho_2\frac{1}{Y_{w,C2}}$$

This is illustrated in Fig. 1 A, where $1/Y_{\mathrm{w,IC}}$ of a replacement intercrop with equal shares of the two crop species develops exactly in between the inversed weed biomasses of the two pure stands. Inversion of the terms on both sides of the equal sign yields:

$$Y_{w,IC} = \frac{1}{\rho_1\left(\frac{1}{Y_{w,C1}}\right) + \rho_2\left(\frac{1}{Y_{w,C2}}\right)} \tag{1}$$

which illustrates that, when additivity of competitive influences of both species is assumed, predicted weed biomass in intercrop ($Y_{\mathrm{w,IC}}$) corresponds to the so called weighted harmonic mean of weed biomasses in pure stands of the component crop species. The implication for weed suppression is illustrated in Fig. 1B. Here it shows that also the relation between weed biomass in intercrop ($Y_{\mathrm{w,IC}}$) and total crop plant density is found in between that of the two component species in pure stand. $Y_{\mathrm{w,IC}}$ is however much closer to the weed biomass obtained in the pure stand of the stronger weed suppressive crop species. Clearly the stronger suppressive species puts its mark on the weed suppression function of the mixture. This phenomenon is also evident in Eq. 2 and is what is referred to as the selection effect. In this case, a curved relationship

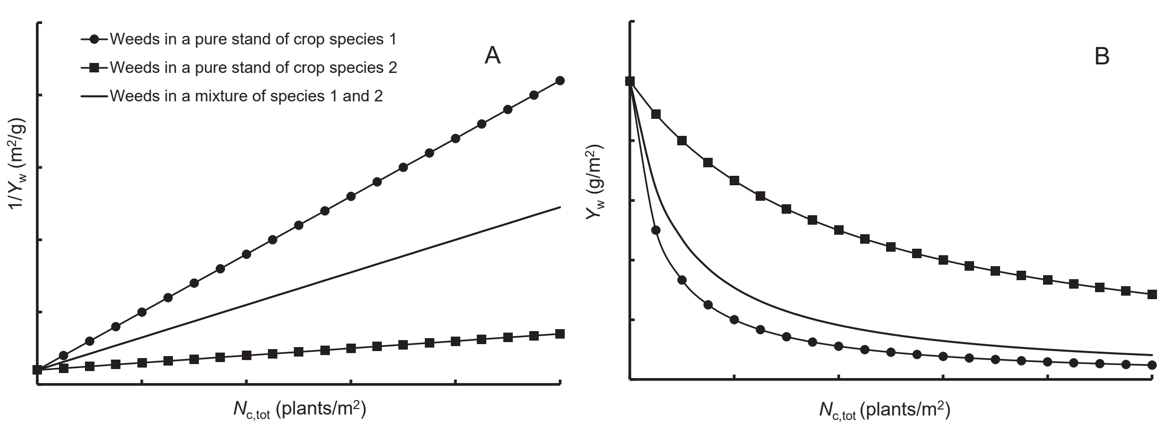

Fig. 1. Relation between reciprocal biomass ($1/Y_{\mathrm{w}}$; Fig. 1 A) and biomass (Y_{w}; Fig. 1B) of weeds in a crop stand, as a function of total crop plant density ($N_{\mathrm{c,tot}}$), following Spitters (1983). The relation is shown for a stronger (species 1) and a weaker (species 2) weed suppressive crop species and for replacement intercrops with equal contribution of the two crop species ($\rho_1 = \rho_2 = 0.5$). Note that the mixture is positioned exactly in the middle of the two pure stands when it concerns $1/Y_{\mathrm{w}}$, whereas a clear bias towards the pure stand of the more weed suppressive species is observed with Y_{w} as response variable. This bias reflects the selection effect. Mathematically, Y_{w} in intercrop corresponds to the harmonic mean (Eq. 1) of the weed biomass in pure stands of the two crop species.

Table 1
Three conceptual models for assessing weed biomass (Y_w; gm^{-2}) in a field with two crop species. Model A reflects a situation in which the two species each occupy separate parts of the field (split field; $Y_{w,SF}$). Here the weed biomass is the weighted average of weed biomass in pure stands of the two species. Model B and C reflect situations where the two crop species are combined in an intercrop ($Y_{w,IC}$). Model B is solely driven by competition between component species, resulting in a more than proportional contribution of the stronger weed suppressive species to the weed suppression of the intercrop (selection effect). Model C additionally accounts for synergy among crop species following from for instance niche differentiation (complementarity effect), which is included through an interaction term. Note that models A (arithmetic mean) and B (harmonic mean) can both be expressed as functions of the weed biomasses obtained in pure stands of the two crop species ($Y_{w,C1}$, $Y_{w,C2}$).

Model	General equation sensu Spitters (1983)	Expression based on weed biomasses in pure stands
Model A (Eq. 4) Arithmetic mean	$Y_{w,SF} = \rho_1\left(\frac{N_w}{b_{w,0}+b_{w,w}N_w+b_{w,c1}N_{c1}}\right)+\rho_2\left(\frac{N_w}{b_{w,0}+b_{w,w}N_w+b_{w,c2}N_{c2}}\right)$	$= \rho_1 Y_{w,C1} + \rho_2 Y_{w,C2}$
Model B (Eq. 1) Harmonic mean	$Y_{w,IC} = \frac{N_w}{b_{w,0}+b_{w,w}N_w+b_{w,c1}\rho_1 N_{c1}+b_{w,c2}\rho_2 N_{c2}}$	$= \frac{1}{\rho_1\left(\frac{1}{Y_{w,C1}}\right)+\rho_2\left(\frac{1}{Y_{w,C2}}\right)}$
Model C	$Y_{w,IC} = \frac{N_w}{b_{w,0}+b_{w,w}N_w+b_{w,c1}\rho_1 N_{c1}+b_{w,c2}\rho_2 N_{c2}+\boldsymbol{b_{w,ic}\rho_1 N_{c1}\rho_2 N_{c2}}}$	-

Y_w = weed biomass (gm^{-2}); $b_{w,0}$ = inverse of maximum individual weed plant dry weight (plant/g); $b_{w,w}$, $b_{w,c1}$ and $b_{w,c2}$ = competition index of weed and crop species 1 and 2 on the weed (m^2/g); $b_{w,ic}$ = index reflecting synergy between crop species ((m^2/g)/(plant/m^2)); N_w, N_{c1}, N_{c2} = plant density (plant/m^2) of weed and crop species 1 and 2 in pure stand; ρ_1 and ρ_2 = relative density, defined as density in intercrop over density in pure stand, of crop species 1 and 2, respectively. In model A these relative densities correspond to the fraction of the field occupied by crop 1 and 2, respectively.

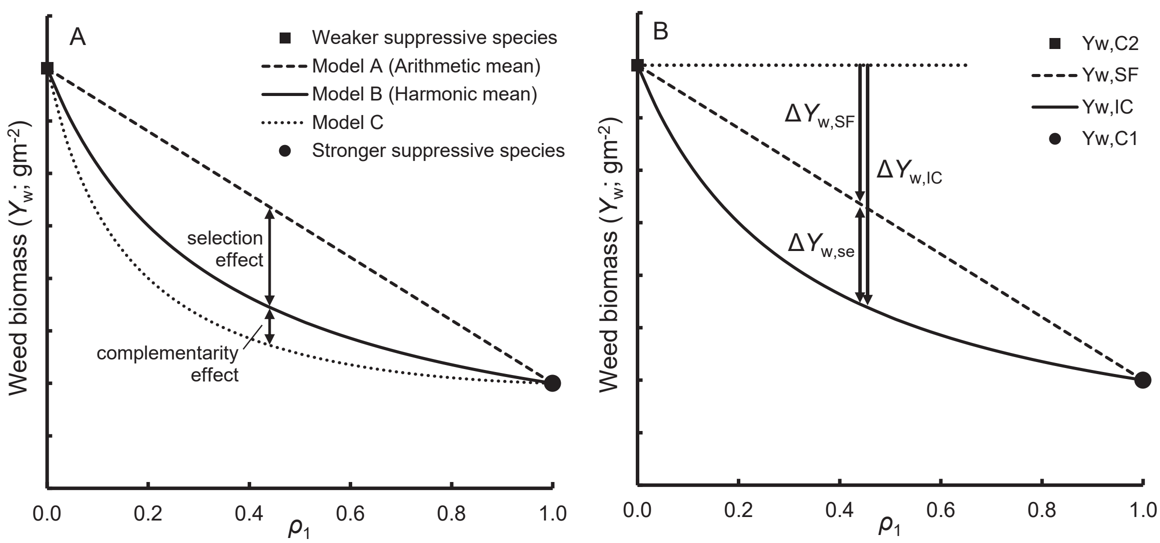

Fig. 2. 2 A. Predicted weed biomass in intercrops with a replacement design, plotted as a function of the relative density of the stronger weed-suppressive species in intercrop (ρ_1), following model A (crop species each occupy separate parts of the field; arithmetic mean), model B (accounting for the selection effect; harmonic mean) and model C (accounting for selection and complementarity) (Table 1). In this example, weed biomass in pure stand of the weaker suppressive crop species ($Y_{w,C2}$) is 4-fold larger than the weed biomass in pure stand of the stronger suppressive crop species 1 ($Y_{w,C1}$) ($a = 4$). 2B. Illustration of how $\Delta Y_{w,SF}$, $\Delta Y_{w,IC}$ and $\Delta Y_{w,se}$ are based on $Y_{w,C2}$, $Y_{w,SF}$ and $Y_{w,IC}$, which are then used to calculate the relative reductions in weed biomass: R_{SF} (Eq. 6) and R_{IC} (Eq. 7) as well as the proportion of the overall reduction in weed biomass that can be attributed to the selection effect: P_{se} (Eq. 9).

between weed biomass and the proportion of the stronger suppressive species (ρ_1) evolves (Fig. 2 A; model B). Consequently, the gain in weed suppression observed in an intercrop and following from the selection effect corresponds to the difference between the straight line and the curved relationship.

The selection effect thus simply evolves as a result of the additivity of the competitive influences of the two component species. If, on top of the selection effect, complementarity effects also play an important role in weed suppression of the intercrop, the produced amount of weed biomass would be even smaller. Such an effect can be included by extending Eq. 5 with an interaction term. This term is driven by the product of the densities of the two crop species, to express that the effect will only be operative in the presence of both species (Table 1; model C). In this way a synergistic effect, for instance resulting from niche differentiation, is represented. Accordingly, the relation between weed biomass and the proportion of the stronger suppressive species (ρ_1) shows an even further reduction in $Y_{w,IC}$ (Fig. 2 A; model C). Since synergistic effects will only occur in the presence of both species, the size of this complementarity effect cannot be derived from the performance of the two crop species in isolation. Therefore, unlike the arithmetic and the harmonic mean, model C cannot be solely expressed in terms of weed biomasses obtained in pure stands of the two crop species (Table 1). However, if complementarity would commonly contribute to the weed suppression of intercrops, the predicted weed biomass in intercrop based on the harmonic mean would have frequently resulted in an overestimation of observed weed biomass in intercrop. The absence of such a systematic overestimation of observed weed biomass in the study of Gu et al. (2022) can thus be interpreted as an important clue, illustrating that complementarity is not an important mechanism in the weed suppression of annual intercrops.

2.2. Quantifying the contribution of the selection effect to improved weed suppression in intercrops

Building on the empirically proven validity of Spitters' model (Gu et al., 2022), we made a quantitative exploration on how species composition, mixing ratio, planting density and spatial arrangement affect the weed suppressive ability of annual intercrops. In these analyses weed biomass in pure stands of two component crop species ($Y_{w,C1}$, $Y_{w,C2}$) was used as starting point. Throughout this study we referred to the stronger weed suppressive species as crop species 1 (C1). Additionally, we introduced parameter a to characterize the difference in weed suppressive ability between the two crop species:

$$a = \frac{Y_{w,C2}}{Y_{w,C1}}$$

Since $Y_{w,C2} \geq Y_{w,C1}$ it is evident that $a \geq 1$.

Based on the weed biomasses in pure stand both the arithmetic mean, representing the average weed biomass in a situation with two crops occupying a separate part of a split field ($Y_{w,SF}$; Eq. 4) and the harmonic mean, representing the average weed biomass with both species planted as component species in an intercrop ($Y_{w,IC}$; Eq. 1), were assessed. Subsequently, for both situations, the reduction in weed biomass compared to the weed biomass in the pure stand of the weaker suppressive species ($Y_{w,C2}$) was calculated ($\Delta Y_{w,SF} = Y_{w,C2}$ - $Y_{w,SF}$ and $\Delta Y_{w,IC} = Y_{w,C2}$ - $Y_{w,IC}$, respectively) (Fig. 2B). These reductions were then expressed as relative reductions (R) by dividing them by the weed biomass in pure stand of crop species 2:

$$R_{SF} = \frac{Y_{w,C2} - Y_{w,SF}}{Y_{w,C2}} = \frac{\Delta Y_{w,SF}}{Y_{w,C2}} \tag{6}$$

$$R_{IC} = \frac{Y_{w,C2} - Y_{w,IC}}{Y_{w,C2}} = \frac{\Delta Y_{w,IC}}{Y_{w,C2}} \tag{7}$$

Finally, the advantage of growing species in mixture that can be ascribed to the selection effect (*se*) was estimated as the difference in predicted weed biomass between the two species occupying separate parts of the field ($Y_{w,SF}$) and the two species mixed as intercrop ($Y_{w,IC}$) (Fig. 2B):

$$\Delta Y_{w,se} = Y_{w,SF} \quad - \quad Y_{w,IC} \tag{8}$$

This contribution of the selection effect was then related to the overall reduction in weed biomass to obtain the proportion of the reduction attributed to the selection effect:

$$P_{se} = \frac{\Delta Y_{w,se}}{\Delta Y_{w,IC}} \tag{9}$$

2.3. Relating intercrop design to weed suppressive ability

2.3.1. Species composition

To quantify the influence of species composition, we considered intercrops in replacement design with an equal share of the two component species ($\rho_1 = \rho_2 = 0.5$). The component species within these intercrops differed to a smaller or larger degree in weed suppressiveness, reflected in ratio a ranging from 1 to 10. For these intercrops we calculated R_{SF}, R_{IC} and P_{se}.

2.3.2. Mixing ratio

Similarly, for the influence of mixing ratio, we analyzed intercrops in replacement design with ratio a ranging from 1 to 10. Here we determined the relative density of the stronger weed suppressive species (ρ_1) at which the additional reduction in weed biomass following from the selection effect ($\Delta Y_{w,se}$; Eq. 8) reached its maximum size. This relative density was referred to as $\rho_{1,max}$.

2.3.3. Planting density

For the effect of planting density, we first analyzed the original dataset of Gu et al. (2021) and separated the entire dataset in replacement ($\rho_1 + \rho_2 = 1.$) and additive ($\rho_1 + \rho_2 > 1.$) intercrops. For each of the two categories we determined how the weed biomass in intercrop ($Y_{w,IC}$) related to the weed biomass in pure stands of the two component species ($Y_{w,C1}$ and $Y_{w,C2}$). Additionally, we investigated how an increase in relative density total (RDT $= \rho_1 + \rho_2$) ranging from 1 to 1.5 (representing an increase in total plant density up to 50 %), increased the relative reduction in weed biomass of intercrops (R_{IC}). For this analysis, intercrop combinations of species differing in weed suppressive ability, characterized by a-values of 1., 1.5 and 2., were used.

2.3.4. Spatial arrangement

Spatial arrangement was investigated by comparing replacement intercrops in alternate row design with strip cropping systems, where rather than single rows of each species, strips with a higher number of crop rows from crop species 1 were alternated with strips of similar width of the second crop species. The investigation focused on how weed biomass in these mixed systems gradually increased from $Y_{w,IC}$ in systems with intimate mixing of the two species to $Y_{w,SF}$ in systems with these species in two separate parts of the field.

3. Results

3.1. Species composition

Compared to a monoculture field of a weaker suppressive crop species, the replacement of this species in part of the field by a sole crop of a more weed suppressive species will lower the total amount of produced weed biomass. Taking the specific situation where the weaker suppressive crop is replaced in half of the field, resulting in an equal share of both crop species ($\rho_1 = \rho_2 = 0.5$), the relative reduction in weed biomass amounts to (Appendix B):

$$R_{SF} = \frac{\Delta Y_{w,SF}}{Y_{w,C2}} = \frac{a-1}{2a} \tag{6}$$

This equation shows that at higher values of parameter a, that is when the two crop species differ more in weed suppressive ability, R_{SF} evolves to an asymptote with a value of 0.5 (Fig. 3). This implies that in a field occupied with two crops in equal share and without mixing of these crop species, the maximum reduction in weed biomass compared to the weed biomass in a pure stand of the weaker suppressive crop species, is 50 %. Such a reduction will however only be approximated if crop species differ more than 10-fold in weed suppression.

Likewise, for an intercrop, the reduction in weed biomass relative to the weed biomass in a pure stand of the weaker suppressive species can be determined. For a replacement intercrop with an equal share of the two species ($\rho_1 = \rho_2 = 0.5$), and analogous to Eq. 6, this relative reduction (R_{IC}) can be expressed as (Appendix B):

$$R_{IC} = \frac{\Delta Y_{w,IC}}{Y_{w,C2}} = \frac{a-1}{a+1} \tag{7}$$

Obviously, it is again solely the difference in weed suppressive ability between the two crop species that determines how much the weed biomass in intercrop is reduced relative to the weed biomass in pure stand of the weaker suppressor. R_{IC} is an increasing function of parameter a: the more the species differ in weed suppressive ability, the stronger is the reduction in weed biomass (Fig. 3). Evidently, the weed suppression of the mixture is stronger than what is obtained when the two crop species are kept on separate parts of the field. Due to the selection effect, a halving of weed biomass is already achieved with an intercrop composed of species that differ no more than three-fold in weed suppressiveness (ratio $a = 3$).

The benefit, in terms of weed suppression, of growing crop species in

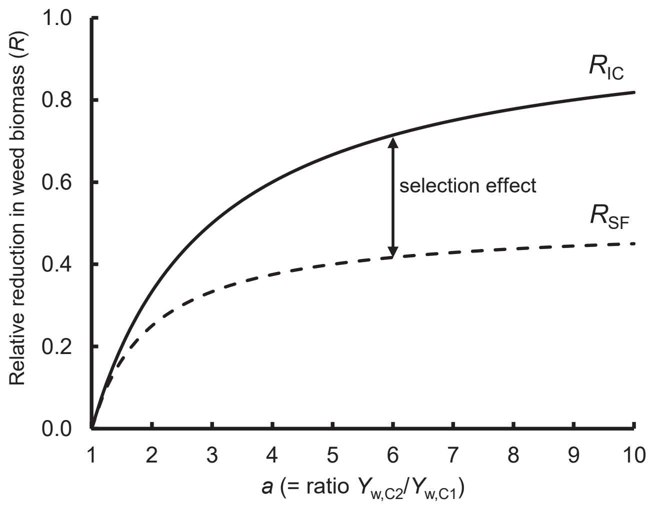

Fig. 3. Influence of the difference in weed suppressiveness between crop species, expressed as ratio a, on the relative reduction in weed biomass in an intercrop in replacement design with equal relative densities of the two crop species ($\rho_1 = \rho_2 = 0.5$) (R_{IC}; Eq. 7). Weed biomass in intercrop is estimated following model B (harmonic mean; Eq. 1) and weed biomass in pure stand of the weaker suppressive crop species is used as reference. In a similar manner weed biomass for the situation where both crop species each occupy separate halves of the field (split field) is estimated, using model A (arithmetic mean; Eq. 4). Here, the relative reduction in weed biomass is expressed as R_{SF} (Eq. 6). The better weed suppression in intercrop results from the selection effect.

mixture that can be exclusively attributed to the selection effect corresponds to the difference in predicted weed biomasses between arithmetic ($Y_{w,SF}$) and harmonic mean ($Y_{w,IC}$). For any intercrop in replacement design this difference corresponds to (Appendix C):

$$\Delta Y_{w,se} = Y_{w,SF} \quad - \quad Y_{w,IC} = \frac{\rho_1 \rho_2 (Y_{w,C2} - Y_{w,C1})^2}{\rho_2 Y_{w,C1} + \rho_1 Y_{w,C2}} \tag{8}$$

This difference in weed suppression of two species that are kept strictly separated (arithmetic mean) and the same crop species when grown as an intercrop (harmonic mean) is schematically depicted in Fig. 4. Panels A and B represent the weed biomass (coloured orange) in pure stands of a weaker (A) and a stronger (B) weed suppressive crop species, respectively. The green colour indicates the reduction in weed biomass because of the competitive suppression inflicted by the crop. Weed suppression in fields with equal shares of the two crop species is presented in the other panels. If the two crops are present on two separate parts of the field, both species keep on occupying exactly half of the diagram, and the remaining orange area is thus the average of the areas found in 4 A and 4B (Fig. 4 C). Laid out as an intercrop will facilitate the interaction between the two species, whereby selection results in a stronger contribution of the more weed suppressive crop species. Consequently, weed biomass will relate more closely to that of the pure stand of the component crop species with stronger weed suppressive ability (Eq. 2). Schematically this is represented by the stronger suppressor intruding into the area of the weaker suppressor (Fig. 4D). The level of intrusion depends on the difference in weed suppressiveness between the two crop species: the larger this difference the stronger the intrusion. The weed suppression strictly attributable to the selection effect is depicted by the rectangle in panel 4E, of which the area corresponds to the difference in weed biomass between arithmetic and harmonic mean (Eq. 8; Appendix C). An illustration of the selection effect under field conditions is presented in Fig. 5.

Relating the reduction following from selection ($\Delta Y_{w,se}$) to the overall reduction in weed biomass ($\Delta Y_{w,IC}$) provides the proportion of the reduction attributable to the selection effect. Taking once more the example of a replacement intercrop with an equal share of the two component species ($\rho_1 = \rho_2 = 0.5$) this proportion (P_{se}) can be calculated as (Appendix C):

$$P_{se} = \frac{\Delta Y_{w,se}}{\Delta Y_{w,IC}} = \frac{a-1}{2a} \tag{9}$$

This is the same function as found for R_{SF} (Eq. 6; Fig. 3). With a further increase in parameter a, reflecting the difference in weed suppressiveness between the two crop species, it is thus not only the total reduction in weed biomass that increases, but also the proportion of this reduction that is attributable to the selection effect (P_{se}) (Eq. 9). In the absence of a difference in weed suppressive ability between the two species ($a = 1$) competitive selection does not occur, whereas at higher values of a the proportion of the reduction caused by the selection effect evolves to an asymptote with a value of 0.5. Evidently, the difference in weed suppressive ability of the two component crop species is vital: it drives the selection effect and is responsible for the enhanced weed suppression of intercrops. The greater the difference in weed suppressive ability of the two pure stands, the greater is the relative gain from mixing beyond just growing the crops in two separate parts of the field. Utilization of the weed suppressive function of intercrops thus largely rests on species composition and requires mixing of species that significantly differ in weed suppressive ability.

3.2. Mixing ratio

To investigate the influence of mixing ratio on the weed suppressive ability of replacement intercrops, we derived the relative density of the stronger weed suppressive species (ρ_1) at which the additional reduction in weed biomass following from the selection effect ($\Delta Y_{w,se}$) was at its maximum. Here Eq. 8 served as a starting point. By taking the derivative of this function with respect to ρ_1, we arrived at the relative proportion at which $\Delta Y_{w,se}$ obtains its maximum, referred to as $\rho_{1,\max}$. Following this procedure it can be shown that also $\rho_{1,\max}$ depends on parameter a and equals (Appendix D):

$$\rho_{1,\max} = \frac{1}{\sqrt{a}+1} \tag{10}$$

This indicates that the influence of mixing ratio on weed biomass is predominantly determined by the difference in weed suppressive ability between component species. With a small difference in weed suppressive ability of the two component species the largest gain in $\Delta Y_{w,se}$ is obtained at a ρ_1 close to 0.5 (Fig. 6). With a larger difference in weed suppressive ability of the two component species, the largest additional reduction in weed biomass attributable to the selection effect is obtained with a gradually lower proportion of the most weed suppressive species. Evidently, if the two crop species differ markedly in weed suppressiveness, even a relatively small fraction of the stronger weed suppressive species substantially improves the weed suppressive ability of the intercrop.

3.3. Planting density

With the selection effect as main driver, a reduction in weed biomass in the intercrop below that of the pure stand of the stronger weed suppressor can only be achieved by increasing total plant density, i.e., by using an additive intercrop ($\rho_1 + \rho_2 > 1.$). This is also evident from an analysis of the results presented by Gu et al. (2021). Here, weed biomass in replacement intercrops was, on average, much lower than in pure stand of the weaker weed suppressive crop and just marginally higher than in pure stand of the stronger suppressor (Fig. 7). In additive intercrops the weed biomass was more strongly reduced and, on average, also lower than that of the weed biomass in pure stand of the stronger weed suppressing species.

Just as in pure stands, an increase in planting density in intercrops will provide better weed suppression. To investigate the influence of an increased plant density on weed suppressiveness of species mixtures, the

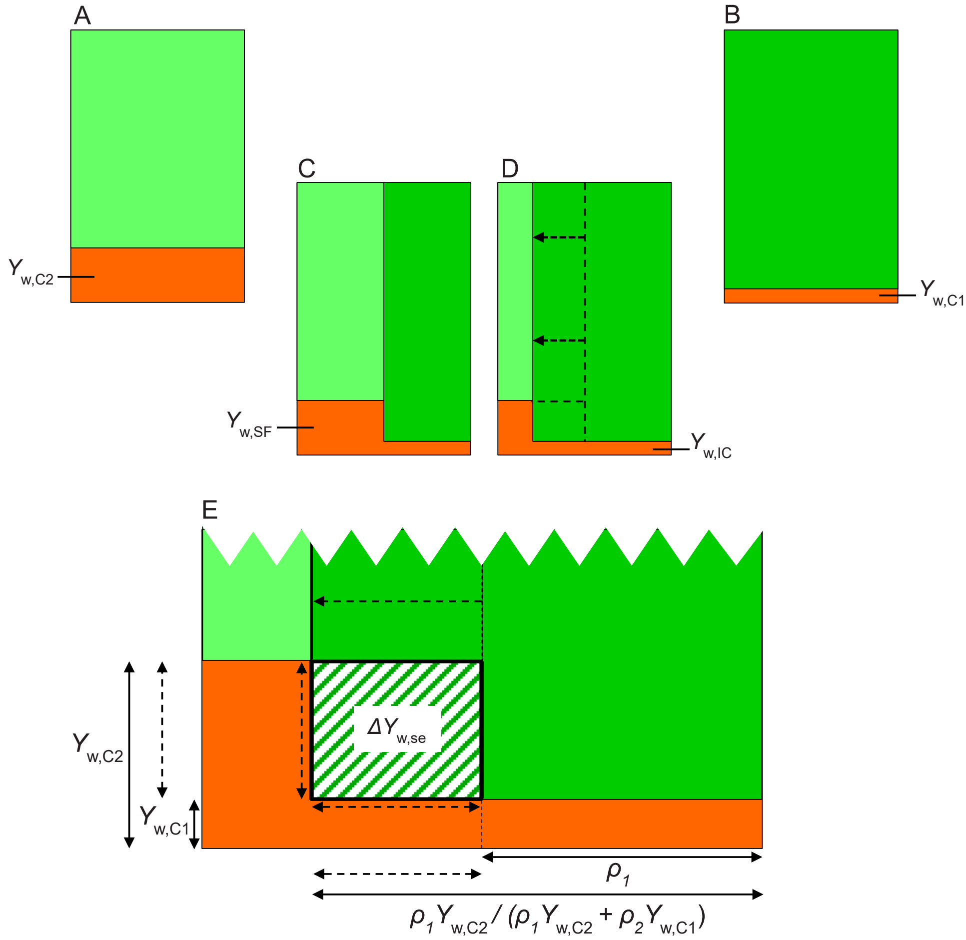

Fig. 4. Schematic representation illustrating the principle of the selection effect in the weed suppression generated by intercrops composed of two crop species. Weed biomass is coloured orange, whereas green reflects the reduction in weed biomass resulting from the presence of a crop species. The panels display the weed biomass evolving in a weaker weed suppressive crop species ($Y_{w,C2}$; 4 A), in a stronger weed suppressive species ($Y_{w,C1}$; 4B), and in fields with equal contribution of the two crop species ($\rho_1 = \rho_2 = 0.5$) either organised as a split field with the two species present on separate parts of the field ($Y_{w,SF}$; 4 C), or as intercrop ($Y_{w,IC}$; 4D). In intercrop, the selection effect is illustrated as the stronger weed suppressor intruding into the area of the weaker suppressor. This results in a lowered weed biomass (harmonic mean; Eq. 1). The lower part of 4D is magnified in panel 4E to illustrate that the level of intrusion is related to the difference in weed suppressive ability between the two crop species. The additional reduction in weed biomass following from competitive selection ($\Delta Y_{w,se}$) is depicted by the square, with an area corresponding to Eq. 8 (Appendix C).

Fig. 5. Pure stands of rye (*Secale cereale* L.) and field pea (*Pisum sativum* var. *arvense* L.) and a replacement intercrop of these two species (50 %-50 %) at 29 days after sowing, illustrating the selection effect. The soil cover of rye in intercrop (63 %) is more than half of the area it covers in pure stand (85 %). For field pea the opposite is observed, as its cover in intercrop (8 %) is less than half of its soil cover in pure stand (35 %). Rye dominates the intercrop through a partial displacement of field pea, resulting in a total soil cover (71 %) exceeding the average of the two pure stands (60 %) (unpublished results).

weed biomass in species mixture was compared to the weed biomass in a pure stand of the weaker weed suppressive species. This reduction in weed biomass was then expressed as a fraction of the weed biomass in the weaker weed suppressive species. For an additive intercrop with relative densities ρ_1 and ρ_2, this relative reduction amounts to (Appendix E):

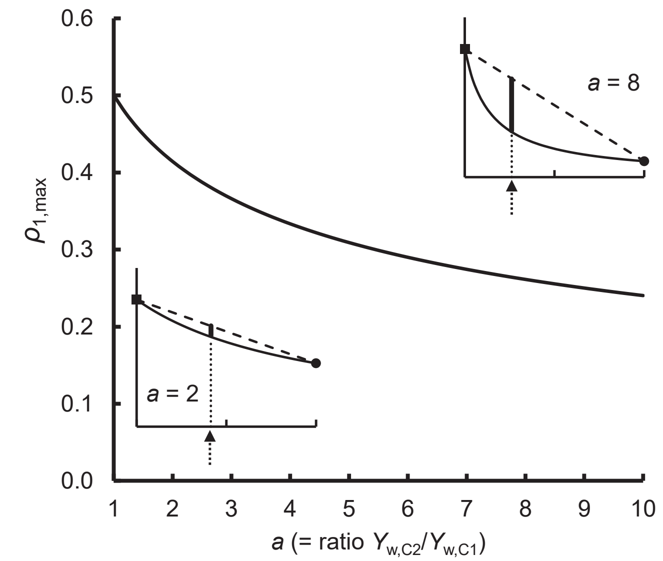

Fig. 6. Influence of the difference in weed suppressiveness between crop species, expressed as ratio a, on the relative density of the more weed suppressive crop species (ρ_1) in a replacement intercrop for which the additional reduction in weed biomass following from competitive selection ($\Delta Y_{w,se}$; Eq. 8) is at its maximum. This relative density is referred to as $\rho_{1,max}$ (Eq. 10). Insets to the figure represent Fig. 2 and show where $\rho_{1,max}$ is found if weed biomass in pure stands of the crop species differ either two-fold ($a = 2$) or eight-fold ($a = 8$) from each other.

$$R_{IC} = \frac{\Delta Y_{w,IC}}{Y_{w,C2}} = 1 - \frac{1}{a\rho_1 + \rho_2} \tag{11}$$

The current analysis thus shows that the relative reduction in weed biomass relative to that of a pure stand of the weaker suppressive crop species depends on the relative densities of the two crop species and ratio a (Eq. 11). If two component crop species differ only marginally in weed suppressive ability, an increased plant density is a potential alternative for raising the weed suppressive ability of the intercrop. For that reason, the influence of total crop plant density is presented for values of parameter a of 1., 1.5 and 2. (Fig. 8). In all instances, a replacement intercrop ($RDT = 1.$) with equal share of the two species was used as a starting point. In absence of a selection effect, when both crop species are equally weed suppressive (a=1), a 25 % increase in the density of both crop species ($RDT = 1.5$) results in a relative reduction in weed biomass of 33 % (Fig. 8B). With a-values of 1.5 and 2, when also selection adds to the overall weed suppressive ability of the intercrop, the relative reductions are larger and amount to 47 % and 56 %, respectively. If only ρ_1, the relative density of the more weed suppressive species, is increased the reductions will be somewhat larger (Fig. 8 A), whereas the opposite is observed if only ρ_2, the relative density of the weaker suppressive weed species, is increased (Fig. 8 C). At high enough relative density totals the weed suppressive ability of the intercrop equals or surpasses that of the pure stand of the stronger suppressive crop species. Such situations are more readily achieved if intercrops do contain a larger contribution of the stronger weed suppressive species.

3.4. Strip cropping

Conditions for meeting the validity of Spitters' model, and thus the validity of the harmonic mean as a derivative of this model, encompass mixing of individuals of the crop species at a sufficiently fine spatial grain. Such proximity can be realized by mixing the component species in the row or by an alternate row design of the species with narrow row spacing. In strip cropping systems a less intimate mixing is used, to create better opportunities for individual management and harvesting of the component species. Here strips of the two species, composed of several rows of one crop species, are alternated. With strips of multiple rows of one crop species, competitive selection will only occur at the border of two neighbouring strips. Consequently, any advantage of crop mixtures regarding an increased weed suppression will rapidly diminish with increased strip width.

Under the assumption that the weed suppression in between two neighbouring rows is predominantly determined by the plants that make up these rows, the overall weed biomass in a strip cropping system, with each strip composed of r rows, can be assessed as:

$$Y_{w,STRIP} = \frac{(r-1)Y_{w,C1} + (r-1)Y_{w,C2} + 2Y_{w,IC}}{2r} \tag{12}$$

Relative to the additional weed suppression due to the selection effect in a fully mixed intercrop ($\Delta Y_{w,se} = Y_{w,SF} - Y_{w,IC}$), the additional weed suppression in a strip cropping system then amounts to the following proportion (Appendix F):

$$P_{STRIP} = \frac{Y_{w,SF} - Y_{w,STRIP}}{Y_{w,SF} - Y_{w,IC}} = \frac{Y_{w,SF} - Y_{w,STRIP}}{\Delta Y_{w,se}} = \frac{1}{r} \tag{13}$$

Evidently, the advantage of strip cropping systems in terms of an improved weed suppression rapidly decreases as a function of the number of rows (r) within a strip (Fig. 9). Eq. 13 implies that with every doubling of strip width, only half of the additional weed suppression following from the selection effect remains e.g., with strips of two rows just 50 % of the advantage obtained in an intercrop with alternate row design remains and this benefit drops further to 25 % and 12.5 % with a strip width of 4 and 8 rows, respectively. Clearly, the size of the above average weed suppression of intercrops is strongly related to the level of intimate mixing of crop species in the intercrop. Partial segregation of species as is used in strip cropping systems, is thus at the cost of the weed suppressive ability of the mixed system.

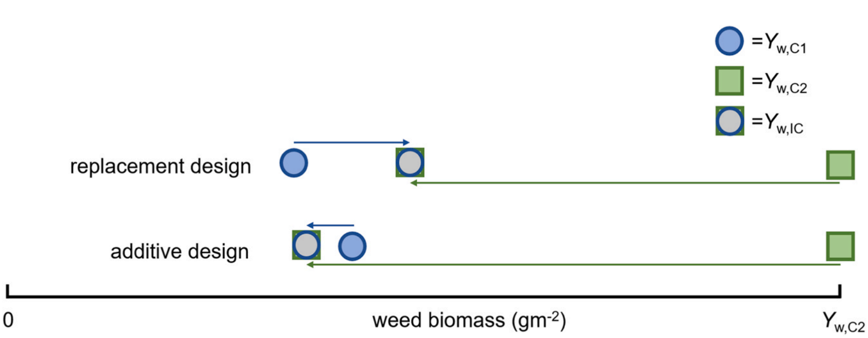

Fig. 7. Weed biomass in intercrops with replacement and additive design ($Y_{w,IC}$) expressed relative to the weed biomass obtained in pure stands of the component species ($Y_{w,C1}$; $Y_{w,C2}$). Average values are based on the records reported by Gu et al. (2021).

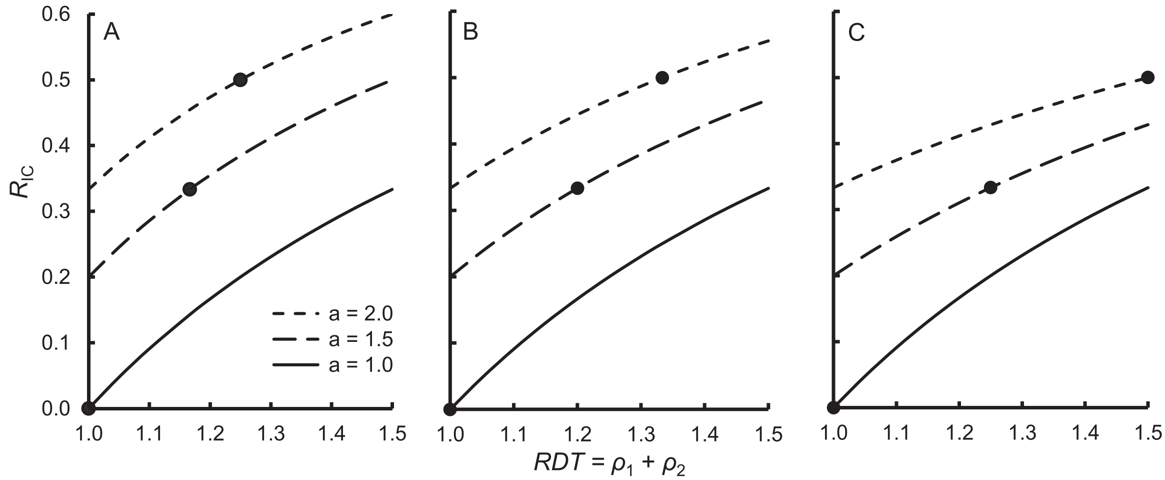

Fig. 8. Influence of relative density total ($RDT = \rho_1 + \rho_2$) on the relative reduction in weed biomass (R_{IC}; Eq. 11), whereby the weed biomass in a pure stand of the weaker suppressive crop species ($Y_{w,C2}$) is used as reference. The relation is depicted for a-values of 1., 1.5 and 2. In all situations a replacement intercrop with $\rho_1 = \rho_2 = 0.5$ is used as starting point. Relative density total is then increased by solely increasing ρ_1, while $\rho_2 = 0.5$ (7 A), by increasing ρ_1 and ρ_2 to a similar extent (7B) and by solely increasing ρ_2, while $\rho_1 = 0.5$ (7 C). The bold dot (•) is used to indicate the relative density total of the additive intercrop for which the weed suppressiveness of the intercrop matches that of the pure stand of the stronger weed suppressor. Beyond this point the intercrop is more weed suppressive than pure stands of either crop species.

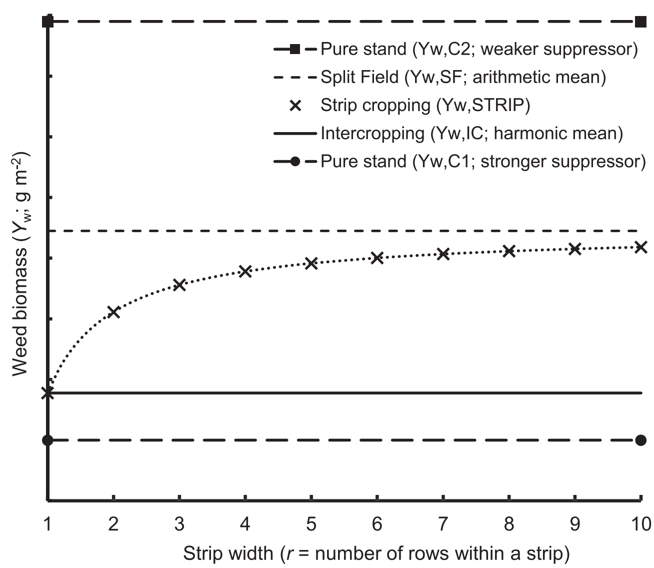

Fig. 9. Weed biomass in a strip cropping system composed of two crop species ($Y_{w,STRIP}$) as a function of strip width (r = number of crop rows within a strip). Weed biomass of the two pure stands ($Y_{w,C1}$, $Y_{w,C2}$) and the weed biomasses in fields with equal contribution of the two crop species ($\rho_1 = \rho_2 = 0.5$) either organised as a split field with the two species present on separate parts of the field ($Y_{w,SF}$; arithmetic mean: Eq. 4), or as intercrop ($Y_{w,IC}$; harmonic mean: Eq. 1) are presented as horizontal lines. Following from an increase in number of rows within a strip, $Y_{w,STRIP}$ gradually increases from $Y_{w,IC}$ in an alternate row design ($r = 1.$) to approximate $Y_{w,SF}$ in a system with wider strips (Eq. 12).

4. Discussion

4.1. Design and weed suppressiveness of annual intercrops

Displacement of a less competitive species by a more competitive species is the prime mechanism for explaining why intercrops are more weed suppressive than the average of the two pure stands (Gu et al., 2022; Fig. 4). Additivity of competitive influences of the two component species generates the selection effect and is the reason why the harmonic mean provides an accurate estimate of the weed biomass obtained in intercrop. Here we used the plant competition model at the basis of the harmonic mean to provide a theoretical assessment on how species composition, mixing ratio, planting density and spatial arrangement are expected to influence the size of the selection effect and thereby the weed suppressive function of annual intercropping systems.

4.1.1. Species composition

The study revealed that, related to weed suppression, species composition is the most important design factor. The difference in weed suppressiveness between component species drives the selection effect and, through that, the above average weed suppression of intercrops. Competitive selection results in a greater influence of the stronger weed suppressive species, and a diminished influence of the weaker weed suppressor. The net result is a better weed suppression than expected based on the average weed biomass of the two pure stands. Competitive selection, and the additional weed suppression following from it, typically only occurs with component species differing in weed suppressiveness: in absence of a difference in weed suppressive ability ($a = 1$) no advantage evolves. With component species differing in weed suppressive ability ($a > 1$), a continuously increasing function between the difference in weed suppressiveness of the species (expressed as ratio a) and the advantage in weed suppressiveness of an intercrop composed of these species was found (Fig. 3).

4.1.2. Mixing ratio

With a too large difference in weed suppressive ability of component species, there is the danger of the weaker weed suppressive species being overgrown. In the leek-celery intercropping study of Baumann et al. (2000), celery not only suppressed weeds adequately, but also put a too strong competitive pressure on leek. For leek this resulted in a too small individual plant size, which endangered the marketability of this crop. The current study showed that, in situations with a large difference in weed suppressiveness between component crop species, reducing the fraction of the more weed suppressive species in intercrop is commendable. With an increasing difference in weed suppressive ability between crop species, the maximum additional reduction in weed biomass following from the selection effect is obtained with a gradually smaller fraction of the more weed suppressive species (Fig. 6). Consequently, for crop species combinations with a substantial difference in weed suppressive ability, lowering the fraction of the more weed suppressive species will reduce the ability of the intercrop to suppress weeds only slightly. Adjusting the mixing ratio of the intercrop seems an intelligent means of protecting the weaker suppressor while maintaining adequate weed suppression.

4.1.3. Plant density

For crop species that do not differ much in weed suppressiveness, the use of additive intercrops is an alternative option for raising the suppressiveness of a species mixture. Small increases in relative density total already provide marked reductions in weed biomass (Fig. 8). Additive intercrops might also result in weed suppressiveness of the intercrop exceeding that of the pure stand of the stronger suppressive crop species. Increasing plant density as a measure to increase the weed suppressive ability of a canopy is however not a measure exclusive to intercrops, as many studies with species in pure stand have demonstrated a positive association between crop plant density and weed suppressiveness (e.g. Zhao et al., 2007; Wu et al., 2021). Care should be taken that the increased competitive pressure following from an increased total plant density does not negatively influence quality or quantity of the harvestable product. A cautious use of raising the overall plant population is particularly relevant if the market requires a minimum individual plant size, or if competition has a negative influence on the harvest index of a crop (e.g. De Wit et al., 1979).

4.2. Strip cropping systems

Selection effects resulting in improved weed suppression only come to expression if the component species of the intercrop are intimately mixed. In an agricultural setting, proximity between heterospecifics is realized if species are mixed within the row or sown in alternate rows with narrow row spacing. Such intense mixing of individuals of different plant species easily creates practical problems, which are mostly related to crop management and harvesting operations. To maintain the advantages of intercropping and minimize practical and agronomic problems, strip cropping has been proposed (e.g. Juventia et al., 2022). Strips serve as the fundamental unit of strip cropping systems and are composed of multiple rows of one crop species, varying in width from just 3 m up to 27 m. Major advantage of strips is that available mechanisation can still be used, facilitating an easier transition from conventional agriculture with pure stands towards strip cropping systems.

Despite the less intimate mixing of crop species in strip cropping systems, several ecosystem services persist. This particularly holds for regulating services regarding pests and diseases. Pest and disease control through intercropping is partly due to the disruptive influence of the second species, which reduces the likelihood of insects and fungal spores reaching the next host plant (e.g. Finch and Collier, 2000; Finckh et al., 2000). Presence of another crop species still serves as an obstacle in strip cropping systems, though mainly through a disruption of the movement from one strip to another (e.g. Ditzler et al., 2021). Disturbed movement does not occur in weeds, as plants are bound to a fixed position. It is the interaction that follows from the proximity of individuals of the two crop species that causes the enhanced weed suppression. In strip cropping systems such an effect is thus limited to the borders of two neighbouring strips. With increased strip width these borders make up a gradually smaller part of the field and therefore the enhanced weed suppression following from the selection effect rapidly declines with increased strip width (Fig. 9). Consequently, strip cropping systems with strips composed of many rows do not have much to offer in terms of an enhanced weed suppression. Still, strip cropping might contribute to weed management by other means. Following research on weed seed predation, it is not unlikely that the heterogeneity in vegetation types and crop residues in fields with strip cropping practices, might provide improved shelter for weed seed predators (e.g. Gallandt et al., 2005; Fox et al., 2013). Such potential influences of strip cropping systems on weed seed predation deserve further investigation.

4.3. Empirical data, model analysis and exploration

The meta-analysis of Gu et al. (2021) reinforced by a subsequent model analysis (Gu et al., 2022) provided the foundation for the current investigation into the relationship between intercrop design factors and weed suppressive ability of crop species mixtures. In their second study, the model of Spitters (1983) was used to connect weed biomass in intercrop with the weed biomass obtained in pure stands of the component species. The close correspondence between empirical data and model predictions served as the justification for the use of Spitters' model in the current study, where the aim was to explore how intercrop design factors are likely to influence the weed suppressivieness of intercrops. The current explorations provide best bets based on currently available knowledge and present clear insights in the implications of previous findings. However, it is evident that their validity remains to be tested under field conditions as model explorations contain a level of uncertainty and might overlook elements that are highly relevant under specific conditions. This particularly holds if it concerns extrapolations. In this study the strip cropping system can be considered an extrapolation, as, compared to most systems contained in the empirical data set, the system is characterized by a relatively low level of mixing between individuals of the two crop species.

4.4. Considerations around the selection effect

Complementarity effects, and in particular niche differentiation, have frequently been held responsible for the enhanced weed suppression of annual intercrops (e.g. Liebman and Dyck, 1993; Schöb et al., 2023). Niche differentiation refers to a situation where the component species occupy partly different niches, resulting in an increased total resource use. Consequently, the resource pool available to weeds is smaller, resulting in a reduced weed biomass production and a lowered weed-induced crop yield loss. Contrary to the logic of this reasoning, the study of Gu et al. (2022) showed that generally the weed biomass in intercrops corresponds to what might be expected based on the joint competitive pressure of the two crop species that make up the intercrop. This additivity of competitive influences generates a selection effect, through which the more weed suppressive species provides a more than proportional contribution to the weed suppression of the intercrop. No empirical evidence for weed suppression beyond the selection effect was found, suggesting that niche differentiation generally does not cause a further reduction in weed biomass in annual intercrops.

An important reason for the absence of a strong contribution of complementarity effects to improved weed suppression of annual intercrops might be the dynamics characteristic of arable production fields. With crops being present for relatively short periods of time (3–6 months), a rapid succession of crops and crop-free periods is commonly observed. Regular clearing of deliberately sown, or spontaneous, vegetation through a variety of activities, like soil tillage, seedbed preparation, weeding and harvesting, creates a high level of disturbance. Not surprisingly therefore, most arable weed species are pioneer or ruderal species (Grime, 1979). These species have several traits that secure their survival and success in agro-ecosystems (e.g. Baker 1974). One such trait is the ability to rapidly colonize disturbed areas. In agreement with this, various elements of an integrated weed management strategy are directed towards a fast colonization of the production field by crop plants. Weed suppressive cultivars, transplanting, increased crop plant densities and a more uniform planting pattern (e.g. Andrew et al., 2015; Zhao et al., 2007; Olsen et al., 2005) are all aimed at a fast soil cover and an enhanced shading capacity of the crop canopy, to prevent weeds from taking a dominant position. In annual cropping systems, the contest between crop and weeds is thus decided during the early stages of crop development. This view is supported by the strong sensitivity of the initial slope of Cousens' hyperbolic yield loss-weed plant density relation to differences in emergence time between crop and weeds (Cousens et al., 1987): a rapidly closing crop canopy is crucial for regulating the competitive relations between crop and weeds in favour of the crop. The same notion is reflected in the concept of the minimum weed free period (Nieto et al., 1968), following from which crops are kept weed-free during the first part of the growing season to minimize crop yield losses. The implication is that, even if resource complementarity between crop species occurs during later development stages of the crop, this is of relatively minor importance for the level of weed-induced crop yield loss and the weed biomass produced. This aligns with the observation by Gu et al. (2021), who reported the absence of a significant positive relation between LER of replacement intercrops and the weed suppressive ability of these intercrops.

With competitive selection as the main driver of the above average weed suppression of intercrops, the performance of the mixed system can be derived or predicted based on the performance of crop species in pure stand. This adds relevant insight to the discussion whether selection for suitable companions in intercrops should be conducted in mixtures or can be confined to selection in pure stands (e.g. Annicchiarico et al., 2019). As far as weed suppression is concerned, the findings imply that species or variety selection for use in an intercropping system can be limited to choosing the proper components based on established weed suppressive ability of individual species in pure stand.

The disproportional acquisition of resources by the more weed-suppressive species at the basis of the selection effect might not only result in improved weed suppression but might also be at the cost of the productivity of the second component crop. This contrasts a situation where complementarity would be the main driving mechanism, as in that situation the increased overall resource acquisition might prevent or compensate for a lower yield of the second component species. With selection as the responsible mechanism, trade-offs between weed suppressive and yielding ability are thus likely to occur and this underscores the importance of quantitative knowledge on how intercrop design affects weed suppressive ability. Such insight is an essential element for optimization of intercropping systems.

5. Conclusion

The relations derived in this study provide a theoretical assessment of how species composition, mixing ratio, total planting density and spatial arrangement influence the weed suppressive ability of annual intercropping systems. The study revealed the dominant position of species composition, with the difference in weed suppressive ability between crop species as the principal driver responsible for the above average weed suppressiveness of intercrops. Mixing ratio was identified as a useful modulating factor for avoiding overdominance of the more weed suppressive species, without a too high trade-off in terms of weed suppressive ability. The analysis further confirmed a positive influence of planting density on weed suppression, indicating that, in absence of a clear difference in weed suppressive ability between component species, an additive design offers the ability to raise the weed suppressiveness of intercrops. Finally, the spatial arrangement should guarantee an adequate level of proximity and mixing of individuals of the two species at a sufficiently fine spatial grain to allow for a positive contribution of the selection effect to weed suppressiveness. Combined with quantitative information on the relation between intercrop design and other ecosystem services, the relations derived above form a sound basis for the design of multifunctional intercrops.

CRediT authorship contribution statement

van der Werf Wopke: Writing – review & editing, Methodology, Conceptualization. **Bastiaans Lammert:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of Competing Interest

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors. The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Appendix A. Relating weed biomass in intercrop to the weed biomasses in pure stand crops

Weed biomass in an intercrop of two crop species can be predicted as the harmonic mean of the weed biomasses obtained in the pure stands of the component species (Gu et al., 2022):

$$Y_{w,IC} = \frac{1}{\rho_1\left(\frac{1}{Y_{w,C1}}\right) + \rho_2\left(\frac{1}{Y_{w,C2}}\right)} \tag{A1}$$

Equalizing the denominators in the two terms in the denominator of this expression results in:

$$Y_{w,IC} = \frac{1}{\left(\frac{\rho_1 Y_{w,C2}}{Y_{w,C1} \cdot Y_{w,C2}}\right) + \left(\frac{\rho_2 Y_{w,C1}}{Y_{w,C1} \cdot Y_{w,C2}}\right)} = \frac{Y_{w,C1} \cdot Y_{w,C2}}{\rho_1 Y_{w,C2} + \rho_2 Y_{w,C1}}$$

In a replacement intercrop, where $\rho_1 + \rho_2 = 1$, this corresponds to:

$$Y_{w,IC} = \rho_1 \frac{Y_{w,C1} \cdot Y_{w,C2}}{\rho_1 Y_{w,C2} + \rho_2 Y_{w,C1}} + \rho_2 \frac{Y_{w,C1} \cdot Y_{w,C2}}{\rho_1 Y_{w,C2} + \rho_2 Y_{w,C1}}$$

which can be rewritten as:

$$Y_{w,IC} = \frac{\rho_1 Y_{w,C2}}{\rho_1 Y_{w,C2} + \rho_2 Y_{w,C1}} Y_{w,C1} + \frac{\rho_2 Y_{w,C1}}{\rho_1 Y_{w,C2} + \rho_2 Y_{w,C1}} Y_{w,C2} \tag{A2}$$

Corresponding to a weighted average of the weed biomasses in pure stands of the two crop species.

Appendix B. Weed biomass reduction in intercrop in presence and absence of the selection effect

If two crop species are each assigned to a separate half of a field (split field), the weed biomass of the entire field can be estimated as:

$$Y_{w,SF} = 0.5Y_{w,C1} + 0.5Y_{w,C2}$$

Compared to the weed biomass in a pure stand of the weakest suppressing species, and with species 2 as the weaker weed suppressive species, the reduction in weed biomass amounts to:

$$\Delta Y_{w,SF} = Y_{w,C2} - Y_{w,SF} = Y_{w,C2} - 0.5\left(Y_{w,C1} + Y_{wC2}\right) = 0.5\left(Y_{w,C2} - Y_{w,C1}\right)$$

Putting this reduction on a relative scale, using $Y_{\mathrm{w,C2}}$ as reference, results in:

$$R_{SF} = \frac{\Delta Y_{w,SF}}{Y_{w,C2}} = \frac{0.5(Y_{w,C2} - Y_{w,C1})}{Y_{w,C2}}$$

Using ratio $a = Y_{\mathrm{w,C2}}/Y_{\mathrm{w,C1}}$ then results in:

$$R_{SF} = \frac{a-1}{2a} \tag{B6}$$

In a similar manner, in a replacement intercrop with an equal share of the two component crops ($\rho_1 = \rho_2 = 0.5$), and following Eq. 2, the weed biomass in intercrop amounts to:

$$Y_{w,IC} = \frac{2Y_{w,C1}.Y_{w,C2}}{Y_{w,C1} + Y_{w,C2}}$$

Here the reduction in weed biomass compared to the weaker suppressive species can be formulated as:

$$\Delta Y_{w,IC} = Y_{w,C2} - Y_{w,IC} = Y_{w,C2} - \frac{2Y_{w,C1}.Y_{w,C2}}{Y_{w,C1} + Y_{w,C2}}$$

Expressing this reduction on a relative scale, using $Y_{\mathrm{w,C2}}$ as reference, results in:

$$R_{IC} = \frac{\Delta Y_{w,IC}}{Y_{w,C2}} = \frac{Y_{w,C2} - \frac{2Y_{w,C1}.Y_{w,C2}}{Y_{w,C1}+Y_{w,C2}}}{Y_{w,C2}} = 1 - \frac{2Y_{w,C1}}{Y_{w,C1} + Y_{w,C2}} = \frac{Y_{w,C2} - Y_{w,C1}}{Y_{w,C1} + Y_{w,C2}}$$

Substitution with ratio $a = Y_{\mathrm{w,C2}}/Y_{\mathrm{w,C1}}$ then yields:

$$R_{IC} = \frac{a-1}{a+1} \tag{B7}$$

Appendix C. Contribution of the selection effect to the weed suppression of intercrops

Following from Appendix B, the additional reduction in weed biomass following from competitive selection corresponds to the difference between the arithmetic and the harmonic mean:

$$\Delta Y_{w,se} = Y_{w,SF} - Y_{w,IC} \tag{C8}$$

For any intercrop in replacement design ($\rho_1 + \rho_2 = 1$) this can be formulated as:

$$\Delta Y_{w,se} = \left\{\rho_1 Y_{w,C1} + \rho_2 Y_{w,C2}\right\} - \left\{\left(\frac{\rho_1 Y_{w,C2}}{\rho_1 Y_{w,C2} + \rho_2 Y_{w,C1}}\right)Y_{w,C1} + \left(\frac{\rho_2 Y_{w,C1}}{\rho_1 Y_{w,C2} + \rho_2 Y_{w,C1}}\right)Y_{w,C2}\right\}$$

Since $\rho_1 + \rho_2 = 1$ this can be rewritten as:

$$\Delta Y_{w,se} = \left\{\rho_1 Y_{w,C1} + \rho_2 Y_{w,C2}\right\} - \left\{\frac{Y_{w,C1}.Y_{w,C2}}{\rho_1 Y_{w,C2} + \rho_2 Y_{w,C1}}\right\}$$

Putting both elements on the same denominator results in:

$$\Delta Y_{w,se} = \left\{\frac{{\rho_1}^2 Y_{w,C1} Y_{w,C2} + \rho_1\rho_2 {Y_{w,C1}}^2 + \rho_1\rho_2 {Y_{w,C2}}^2 + {\rho_2}^2 Y_{w,C1} Y_{w,C2}}{\rho_1 Y_{w,C2} + \rho_2 Y_{w,C1}}\right\} - \left\{\frac{Y_{w,C1}.Y_{w,C2}}{\rho_1 Y_{w,C2} + \rho_2 Y_{w,C1}}\right\}$$

Which after rearrangement corresponds to:

$$\Delta Y_{w,se} = \left\{\frac{\rho_1\rho_2 {Y_{w,C1}}^2 + ({\rho_1}^2 + {\rho_2}^2 - 1) Y_{w,C1} Y_{w,C2} + \rho_1\rho_2 {Y_{w,C2}}^2}{\rho_1 Y_{w,C2} + \rho_2 Y_{w,C1}}\right\}$$

Using ($\rho_1 + \rho_2 = 1$) to rewrite the squared versions of ρ_1 and ρ_2 results in:

$$\Delta Y_{w,se} = \left\{\frac{\rho_1\rho_2 {Y_{w,C1}}^2 + \{\rho_1(1-\rho_2) + \rho_2(1-\rho_1) - 1\} Y_{w,C1} Y_{w,C2} + \rho_1\rho_2 {Y_{w,C2}}^2}{\rho_1 Y_{w,C2} + \rho_2 Y_{w,C1}}\right\}$$

Which after rearrangement gives:

$$\Delta Y_{w,se} = \left\{\frac{\rho_1\rho_2 {Y_{w,C1}}^2 - 2\rho_1\rho_2 Y_{w,C1} Y_{w,C2} + \rho_1\rho_2 {Y_{w,C2}}^2}{\rho_1 Y_{w,C2} + \rho_2 Y_{w,C1}}\right\}$$

Resulting in a general expression for the difference in predicted weed biomass according to the arithmetic and the harmonic mean model, which corresponds to the additional reduction in weed biomass in intercrop following from competitive selection:

$$\Delta Y_{w,se} = Y_{w,SF} - Y_{w,IC} = \frac{\rho_1 \rho_2 (Y_{w,C2} - Y_{w,C1})^2}{\rho_2 Y_{w,C1} + \rho_1 Y_{w,C2}} \tag{C8}$$

For the specific situation of a replacement intercrop with an equal share of the two component crops ($\rho_1 = \rho_2 = 0.5$)

$$\Delta Y_{w,se} = \frac{0.5(Y_{w,C2} - Y_{w,C1})^2}{Y_{w,C1} + Y_{w,C2}}$$

Expressing this weed biomass reduction, attributable to the selection effect, as a proportion of the total difference in weed biomass between the weaker suppressive crop species and the mixture, results in:

$$P_{se} = \frac{\Delta Y_{w,se}}{\Delta Y_{w,IC}} = \frac{\frac{0.5(Y_{w,C2} - Y_{w,C1})^2}{Y_{w,C1} + Y_{w,C2}}}{Y_{w,C2} - \frac{2Y_{w,C1} \cdot Y_{w,C2}}{Y_{w,C1} + Y_{w,C2}}} = \frac{0.5(Y_{w,C2} - Y_{w,C1})^2}{Y_{w,C2}(Y_{w,C1} + Y_{w,C2}) - 2Y_{w,C1}Y_{w,C2}} = \frac{0.5(Y_{w,C2} - Y_{w,C1})}{Y_{w,C2}}$$

Introduction of ratio a, whereby $a = Y_{w,C2}/Y_{w,C1}$, demonstrates that the proportion of the reduction in weed biomass following from competitive selection amounts to:

$$P_{se} = \frac{\Delta Y_{w,se}}{\Delta Y_{w,IC}} = \frac{a-1}{2a} \tag{C9}$$

NOTE: In the schematic representation of the harmonic mean model (Fig. 4E) the surface area of the square resembles the additional reduction in weed biomass following from competitive selection. This surface area can be calculated as:

$$\Delta Y_{w,se} = length \times width = \left\{ \left(\frac{\rho_1 Y_{w,C2}}{\rho_2 Y_{w,C1} + \rho_1 Y_{w,C2}} \right) - \rho_1 \right\} \times (Y_{w,C2} - Y_{w,C1})$$

$$\Delta Y_{w,se} = \left(\frac{\rho_1 Y_{w,C2} - \rho_1(\rho_2 Y_{w,C1} + (1-\rho_2)Y_{w,C2})}{\rho_2 Y_{w,C1} + \rho_1 Y_{w,C2}} \right) \times (Y_{w,C2} - Y_{w,C1}) = \frac{\rho_1 \rho_2 (Y_{w,C2} - Y_{w,C1})^2}{\rho_2 Y_{w,C1} + \rho_1 Y_{w,C2}}$$

Which corresponds to Eq. 8.

Appendix D. Relating the relative density of the more weed suppressive species to the selection effect

Taking the derivative of the general equation for expressing the additional reduction in weed biomass due to competitive selection (Eq. 8) with respect to ρ_1 and resolving where the derivative equals zero reveals the proportion of species 1 for which the maximum additional reduction in weed biomass is obtained. For this, the equation is first rewritten to only include the relative density and weed biomass of species 1, using $\rho_1 + \rho_2 = 1$ and ratio $a = Y_{w,C2}/Y_{w,C1}$

$$\Delta Y_{w,se} = \frac{\rho_1 \rho_2 (Y_{w,c2} - Y_{w,c1})^2}{\rho_2 Y_{w,c1} + \rho_1 Y_{w,c2}} = \frac{\rho_1 (1-\rho_1)(aY_{w,c1} - Y_{w,c1})^2}{(1-\rho_1)Y_{w,c1} + \rho_1 a Y_{w,c1}} = \frac{(a-1)^2 Y_{w,c1}(-\rho_1{}^2 + \rho_1)}{1 + (a-1)\rho_1}$$

$$\frac{d\Delta Y_{w,se}}{d\rho_1} = (a-1)^2 Y_{w,c1} \left\{ \frac{(1+(a-1)\rho_1)(-2\rho_1+1) - (-\rho_1{}^2 + \rho_1)(a-1)}{(1+(a-1)\rho_1)^2} \right\}$$

$$\frac{d\Delta Y_{w,se}}{d\rho_1} = (a-1)^2 Y_{w,c1} \left\{ \frac{-(a-1)\rho_1{}^2 - 2\rho_1 + 1}{(1+(a-1)\rho_1)^2} \right\}$$

$$\frac{d\Delta Y_{w,se}}{d\rho_1} = 0 \text{ if } -(a-1)\rho_1{}^2 - 2\rho_1 + 1 = 0$$

Since $0 \le \rho_1 \le 1$, the only valid solution, and the relative density for which the reduction in weed biomass attributable to the selection effect is at its maximum, is:

$$\rho_{1,\max} = \frac{2 - \sqrt{4 + 4(a-1)}}{-2(a-1)} = \frac{\sqrt{a} - 1}{(a-1)} = \frac{1}{\sqrt{a} + 1} \tag{D10}$$

Appendix E. Relating the reduction in weed biomass to the relative density total of the intercrop

Using ratio a, the general equation for weed biomass in intercrop can be expressed as a function of the weed biomass in the weaker weed suppressive crop species:

$$Y_{w,IC} = \frac{1}{\rho_1 \left(\frac{1}{Y_{w,C1}} \right) + \rho_2 \left(\frac{1}{Y_{w,C2}} \right)} = \frac{1}{\rho_1 \left(\frac{a}{Y_{w,C2}} \right) + \rho_2 \left(\frac{1}{Y_{w,C2}} \right)} = \frac{1}{(a\rho_1 + \rho_2)\left(\frac{1}{Y_{w,C2}} \right)} = \frac{1}{(a\rho_1 + \rho_2)} Y_{w,C2}$$

Compared to the weed biomass obtained in the weaker weed suppressive species the reduction in weed biomass in intercrop amounts to:

$$\Delta Y_{w,IC} = Y_{w,C2} - \frac{1}{(a\rho_1 + \rho_2)} Y_{w,C2} = \left(1 - \frac{1}{(a\rho_1 + \rho_2)}\right) Y_{w,C2}$$

Putting this reduction on a relative scale, using the weed biomass of the weaker suppressive crop species ($Y_{w,C2}$) as reference, results in a general expression of Eq. 7 that is also valid for additive intercrops:

$$R_{IC} = \frac{\Delta Y_{w,IC}}{Y_{w,C2}} = 1 - \frac{1}{a\rho_1 + \rho_2} \tag{D11}$$

Appendix F. Weed biomass reduction in strip cropping systems as affected by strip width

In a strip cropping system of two species, with strips composed of *r* rows, a unit entails 2*r* rows and 2*r* inter-rows. Of these inter-rows, (*r*-1) are bordered by two rows of species 1, (*r*-1) are bordered by two rows of species 2 and two inter-rows are bordered by one row of species 1 and one row of species 2. Under the assumption that the weed suppression in between neighbouring rows is predominantly determined by the plants that make up these rows, the average weed biomass in such a strip cropping system can be estimated as:

$$Y_{w,STRIP} = \frac{(r-1)Y_{w,C1} + (r-1)Y_{w,C2} + 2Y_{w,IC}}{2r} \tag{E12}$$

Relative to a mixed intercrop, the proportion of the additional weed suppression following from competitive selection that remains in a strip cropping system amounts to:

$$P_{STRIP} = \frac{Y_{w,SF} - Y_{w,STRIP}}{Y_{w,SF} - Y_{w,IC}} = \frac{Y_{w,SF} - \left(\frac{r-1}{2r}\right)\left(Y_{w,C1} + Y_{w,C2}\right) - \left(\frac{2}{2r}\right)Y_{w,IC}}{Y_{w,SF} - Y_{w,IC}}$$

Which can be further transformed into:

$$P_{STRIP} = \frac{Y_{w,SF} - \left(\frac{r-1}{r}\right)Y_{w,SF} - \left(\frac{1}{r}\right)Y_{w,IC}}{Y_{w,SF} - Y_{w,IC}} = \frac{\frac{1}{r}\left(Y_{w,SF} - Y_{w,IC}\right)}{Y_{w,SF} - Y_{w,IC}} = \frac{1}{r} \tag{E13}$$

Data availability

No data was used for the research described in the article.

References

Andrew I.K.S., Storkey J. & Sparkes D.L. (2015). A review of the potential for competitive cereal cultivars as a tool in integrated weed management. *Weed Research* 55, 239-248.
Annicchiarico, P., Collins, R.P., de Ron, A.M., Firmat, C., Litrico, I., Hauggaard-Nielsen, H., 2019. Do we need specific breeding for legume-based mixtures? Adv. Agron. 157, 141–215.
Baker H.G. (1974) The evolution of weeds. *Annual Rev. Ecol Syst.* 5: 1-24.
Bastiaans, L., Storkey, J., 2017. Descriptive and mechanistic models of crop-weed competition. In: Hatcher, P.E., Froud-Williams, R.J. (Eds.), Weed Research: Expanding Horizons. Jon Wiley & Sons Ltd, pp. 33–60.
Baumann, D., Kropff, M.J., Bastiaans, L., 2000. Intercropping leeks to suppress weeds. Weed Res. 40, 359–374.
Baumann, D.T., Bastiaans, L., Kropff, M.J., 2001. Competition and crop performance in a leek-celery intercropping system. Crop Sci. 41, 764–774.
Baumann, D.T., Bastiaans, L., Kropff, M.J., 2002. Intercropping system optimisation for yield, quality and weed suppression combining mechanistic and descriptive models. Agron. J. 94, 734–742.
Bilalis, D., Papastylianou, P., Konstantas, A., et al., 2010. Weed-suppressive effects of maize–legume intercropping in organic farming. Int. J. Pest Manag. 56, 173–181.
Boudreau, M.A., 2013. Diseases in intercropping systems. Annu. Rev. Phytopathol. 51, 499–519.
Brooker, R.W., George, T.S., Homulle, Z., Karley, A.J., Newton, A.C., Pakeman, R.J., SchöB, C., 2021. Facilitation and biodiversity-ecosystem function relationships in crop production systems and their role in sustainable farming. J. Ecol. 109, 2054–2067.
Brooker, R.W., Hawes, C., Ianetta, P.P.M., Karley, A.J., Renard, D., 2023. Plant diversity and ecological intensification in crop production systems. J. Plant Ecol. 16. https://doi.org/10.1093/jpe/rtad015.
Cousens, R., Brian, P., O'Donovan, J.T., Ashley O'Sullivan, P., 1987. The use of biologically realistic equations to describe the effect of weed density and relative time of emergence on crop yield. Weed Sci. 35, 720–725.
De Wit, C.T., van Laar, H.H., van Keulen, H., 1979. Physical potential of crop production. In: Sneep, J., Hendriksen, A.J.T. (Eds.), Plant Breeding Perspectives. Pudoc, Wageningen, pp. 47–82.
Ditzler, L., van Apeldoorn, D.F., Schulte, R.P.O., Tittonell, P., Rossing, W.A.H., 2021. Redefining the field to mobilize three-dimensional diversity and ecosystem services on the arable farm. Eur. J. Agron. 122.
Finch, S., Collier, R.H., 2000. Host-plant selection by insects – a theory based on 'appropriate/inappropriate landings' by pest insects of cruciferous plants. Èntomol. Exp. Et. Appl. 96, 91–102.
Finckh, M., Gacek, E., Goyeau, H., et al., 2000. Cereal variety and species mixtures in practice, with emphasis on disease resistance. Agronomie 20, 813–837.
Fox, A.F., Reberg-Horton, S.C., Orr, D.B., Moorman, C.E., Frank, S.D., 2013. Crop and field border effects on weed seed predation in the souteastern U.S. coastal plain. Agric., Ecosyst. Environ. 177, 58–62.
Gallandt, E.G., Molloy, T., Lynch, R.P., Drummond, F.A., 2005. Effect of cover-cropping systems on invertebrate seed predation. Weed Sci. 53, 69–76.
Grime, J.P., 1979. Plant Strategies and Vegetation Processes. Wiley, New York.
Gu, C., Bastiaans, L., Anten, N.P.R., et al., 2021. Annual intercropping suppresses weeds: a meta-analysis. Agric., Ecosyst. Environ. 322, 107658.
Gu, C., van der Werf, W., Bastiaans, L., 2022. A predictive model for weed biomass in annual intercropping. Field Crops Res. 277, 108388.
Juventia, S.D., Norén, Selin, van Apeldoorn, D.F., et al., 2022. Spatio-temporal design of strip cropping systems. Agric. Syst. 201–103455.
Li, C.J., Hoffland, E., Kuyper Th, W., et al., 2020. Syndromes of production impact yield gains in intercropping. Nat. Plants 6, 653–660.
Liebman, M., Dyck, E., 1993. Crop rotation and intercropping strategies for weed management. Ecol. Appl. 3, 92–122.
Loureau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412, 72–76.
Nieto, J.N., Brondo, M.A., Gonzalez, J.T., 1968. Critical periods of the crop growth cycle for competition from weeds. *PANS* (C.) 14, 159–166.
Olsen, J., kristensen, L., Weiner, J., Griepentrog, H.W., 2005. Increased density and spatial uniformity increase weed suppression by spring wheat. Weed Res. 45, 316–321.
Schöb, C., Engbersen, N., López-Angulo, J., Schmutz, A., Stefan, L., 2023. Crop diversity experiment: towards a mechanistic understanding of the benefits of species diversity in annual crop systems. J. Plant Ecol. 16. https://doi.org/10.1093/jpe/rtad016.
Spitters, C.J.T., 1983. An alternative approach to the analysis of mixed cropping experiments. 1. Estimation of competition effects. Neth. J. Agric. Sci. 31, 1–11.
Stomph, T.J., Dordas, C., Baranger, A., et al., 2020. Designing intercrops for high yield, yield stability and efficient use of resources: are there principles. Adv. Agron. 160, 1–50.
Wu, Y., Xi, N., Weiner, J., Zhang, D.Y., 2021. Differences in weed suppression between two modern and two old wheat cultivars at different sowing densities. Agronomy 11, 253.
Yu, Y., Stomph, T.J., Makowski, D., et al., 2015. Temporal niche differentiation increases the land equivalent ratio of annual intercrops: a meta-analysis. Field Crops Res. 184, 133–144.
Zhang, C.C., Dong, Y., Tang, L., et al., 2019. Intercropping cereals with faba bean reduces plant disease incidence regardless of fertilizer input; a meta-analysis. Eur. J. Plant Pathol. 154, 931–942.
Zhao D.L., Atlin G.N., Bastiaans L. & Spiertz J.H.J. (2006) Developing selection protocols for weed competitiveness in aerobic rice. *Field Crops Research* 97: 272–285.
Zhao, D.L., Bastiaans, L., Atlin, G.N., Spiertz, J.H.J., 2007. Interaction of genotype x management on vegetative growth and weed suppression of aerobic rice. Field Crops Res. 100, 327–340.