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REVIEW

THE 4C APPROACH AS A WAY TO UNDERSTAND SPECIES INTERACTIONS DETERMINING INTERCROPPING PRODUCTIVITY

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KEYWORDS

compensation, competition, complementarity, cooperation, interspecific interactions, land equivalent ratio, light, nutrients, species mixtures, water

HIGHLIGHTS

- The 4C approach considers intercropping performances as the result of joint 4C effects.
- Partial land equivalent ratios indicate which effect(s) are the major one(s).
- A major effect of complementarity is related to a better capture of abiotic resources.

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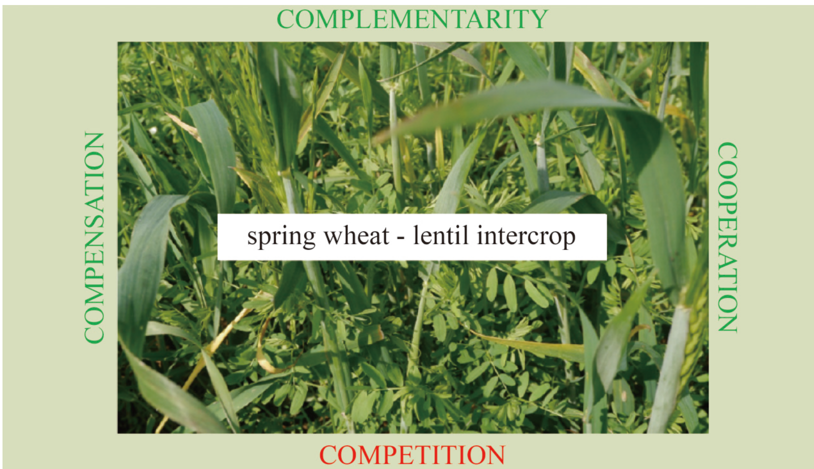
GRAPHICAL ABSTRACT



ABSTRACT

Modern agriculture needs to develop transition pathways toward agroecological, resilient and sustainable farming systems. One key pathway for such agroecological intensification is the diversification of cropping systems using intercropping and notably cereal-grain legume mixtures. Such mixtures or intercrops have the potential to increase and stabilize yields and improve cereal grain protein concentration in comparison to sole crops. Species mixtures are complex and the 4C approach is both a pedagogical and scientific way to represent the combination of four joint effects of Competition, Complementarity, Cooperation, and Compensation as processes or effects occurring simultaneously and dynamically between species over the whole cropping cycle. Competition is when plants have fairly similar requirements for abiotic resources in space and time, the result of all processes that occur when one species has a greater ability to use limiting resources (e.g., nutrients, water, space, light) than others. Complementarity is when plants grown together have different requirements for abiotic resources in space, time or form. Cooperation is when the modification of the environment by one species is beneficial to the other(s). Compensation is when the failure of one species is compensated by the other(s) because they differ in their sensitivity to abiotic stress. The 4C approach allows to assess the performance of arable intercropping versus classical sole cropping through understanding the use of abiotic resources.

1 INTRODUCTION

Diversification of agricultural cropping systems in time and space is recognized as an important strategy for ecological intensification for enhancing sustainability[1–4]. An important aim of diversification of agricultural cropping systems is to substitute agrochemicals and fossil fuels with ecosystem services based on the adaptation of ecological concepts[2,5]. Species mixtures or intercrops or intercropping allow diversification in space by growing more than one species in the same field at least for a part of the growing season. This practice may be combined with diversification in time of cash crops as crop rotation including multiservice cover crops and with the use of cultivar mixtures.

There is abundant of scientific evidence that intercrops often have higher and more stable yields than their respective sole crops[1,6–9] mostly due to a more efficient use of nutrients, light and water than in sole crops[10–13]. Intercropping and notably cereal-grain legume mixtures are therefore a recognized pathway for reducing the use of synthetic fertilizer N[13] by improving the use of soil N resource and biological N_2 fixation[14] as well as reducing the need for P fertilizer[15] through more efficient use of soil P[16].

The interactions and linked processes taking place in species mixtures are complex and occur during the entire growing period. They can be described by the 4C approach composed of Competition, Complementarity, Cooperation, and Compensation effects. Our paper describes the 4C approach as both a pedagogical and a scientific way for characterizing and assessing the performances of arable intercropping to understand the use of abiotic resources in intercropping. The relative contribution of each of the 4C effects determines the final result and can help to understand yield advantages of intercropping. A number of different indices are used to understand the performance of intercrops. Here we focus on the land equivalent ratio (LER) and the analysis of the partial LER of each species of the mixture to assess the net effect of the 4C effects on the final intercrop performance.

2 THE 4C APPROACH

Multiple mechanisms occur simultaneously in plant covers and communities. The 4C approach (Fig. 1) is a way to represent the combination of four types of effects produced by numerous ecological processes occurring simultaneously and dynamically through the growing season. It aims to describe and aid understanding of the performance of species mixtures and their variability from year to year in a given situation (i.e., variable according to pedoclimatic conditions).

The 4C approach classifies the effects of interspecific plant–plant interactions and linked underlying ecological processes as final effects into:

- **Competition** is when plants are using the same pool of abiotic resources in space and time, then competition is the result of all processes that occur when one species has a greater ability to use limiting resources (e.g., nutrients, water, space, light) than others growing in species mixture[6,17]. The definition of competition proposed by Dybzinski and Tilman in the book *The Priceton Guide to Ecology* is oriented to exploitation competition[18], defined competition as, “Most broadly, an interaction between individuals in which neither benefits. Here, we are considering exploitation competition for limiting resources in which the resource consumed or

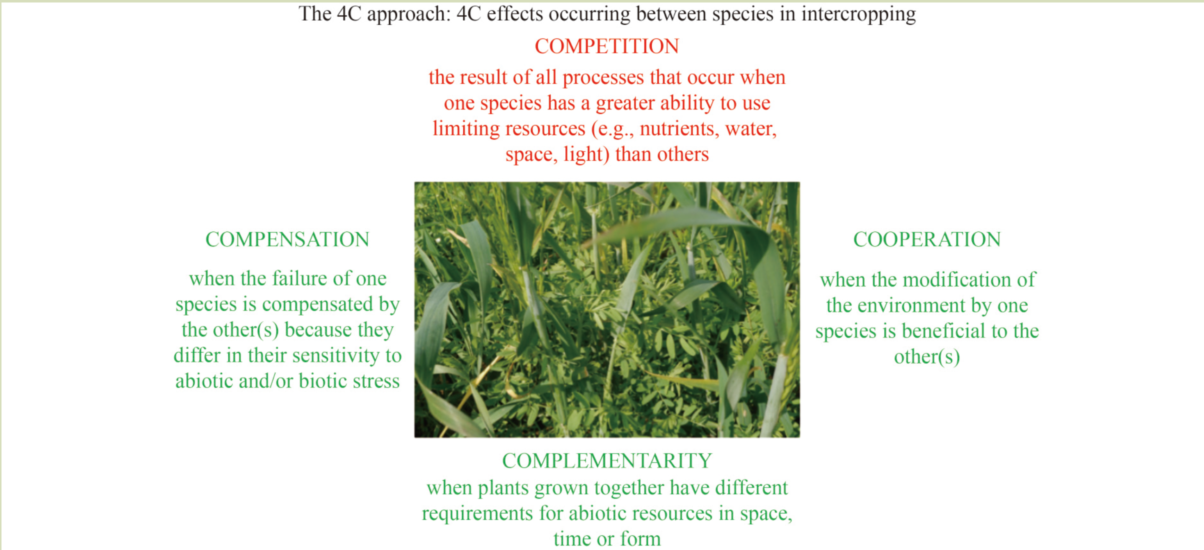


Fig. 1 The 4C approach corresponds to 4C effects of Competition, Complementarity, Cooperation, and Compensation occurring simultaneously in intercropping.

intercepted by one individual is no longer available to the second individual, thereby decreasing its fitness." As a consequence, competition still occurs if species growing in mixture have the same or similar ability to acquire resources, and thus even a species with a low ability to acquire a resource compete for light and other abiotic resources with the associated species because they are trying to get at the same resource.

● **Complementarity** is when plants grown together have different requirements for abiotic resources in space, time or form. One example is that of grain legumes using atmospheric N_2 in symbiosis with soil bacteria whereas others species such as cereals can only use nitrogen from the soil. A second example is when resources are acquired differentially in time or space[19,20] leading to reduced niche overlap between species notably when two species are able to use light in different layers of the canopy.

● **Cooperation** is when the modification of the environment by one species is beneficial to the other(s), for example, by increasing mineral N and P availability[16] or when one species is giving physical support to the other leading to increased photosynthesis or reduced lodging. Cooperation is a synonym of facilitation which is more commonly used in ecology[19] but to be more didactic we use the first one here since it allows us to use the term 4C. Another type of cooperation is the role of playing a physical stick of one specie (cereal) to avoid logging of the other intercropped species susceptible to this process in sole crop (lentil), which allows a strong reduction in mechanical harvest losses and provide economic profits, as demonstrated by for spring wheat-lentil intercrop grown in organic farming[21].

● **Compensation** is when the failure of one species is compensated by the other(s) because they differ in their sensitivity to abiotic and/or biotic stress. The equilibrium between the species is rather dynamic and one species can be strongly advantaged or disadvantaged in intercrop situations according to the abiotic and/or biotic stress. Combining species in a mixture allows growth compensation between species by capturing abiotic resources or suppressing some pests and diseases more efficiently than in sole crops.

Certainly, complementarity and competition are not exclusive. The existence of complementarity will almost certainly occur in a natural plant community or in an optimized intercrop, even if some competition occurs for a given resource or for multiple resources. Moreover, there are weak and strong competition according to the type of resources, the species characteristics associated and the pedoclimatic conditions. Ecological literature talks about, for example, niche separation, niche divergence and resource partitioning to describe these processes[19]. Then complementarity does not mean that there is no competition in the same time, it simply means that the resources captured by one species (or plant) does not prevent the capture of sufficient resources or those of another pool for the other species.

The higher and often more stable yields observed in intercropping compared to sole crops[8,19] are due to the more efficient acquisition and/or conversion of growth resources such as light, water and nutrients into biomass. Such advantages are due to the outcome of the interspecific plant–plant interactions and linked processes in the intercrop. In particular, the yield of each species of the mixture depends on the intensity and equilibrium of dynamic plant–plant interactions over the growing season and is then the result of all these interactions. Finally, interspecific interactions are very sensitive to pedoclimatic conditions, which determine the overall functioning of multispecies mixtures.

The 4C effects permit species in the intercrop or species mixture to acquire a greater range and/or quantity and/or to make improved use of the available resources. These effects can also contribute to increased suppression of some pests and diseases in intercrops compared to sole crops. Selection of species and cultivars that differ in resource acquisition in time or space is essential to maximize the benefits of intercrops. However, management factors such as plant density and their spatial arrangement are also critical.

Another way of using the 4C approach is to evaluate the final net effect of these 4C effects on the total biomass or grain yield produced in intercrops compared to their respective sole crops. This may allow the determination of the most prevalent effects, which occurred during the intercrop cycle and notably to qualify the LER and the partial LER of each species in the mixture, and then the final result.

3 LAND EQUIVALENT RATIO AND 4C APPROACH TO ASSESS THE PERFORMANCE OF INTERCROPS

The LER is defined as the relative land area required when growing sole crops to produce the yield (or to accumulate a resource) achieved in an intercrop[22]. For a cereal–grain legume intercrop, the LER is the sum of the partial LER values (defined as the intercrop yield divided by the sole crop yield) for the cereal and the legume. Even if there are some misuses of LER when authors evaluate the performance of species mixtures by failing to consider the plant density in sole crops to refer to the theoretical LER calculated in intercrop[11], it could be a relevant criteria to evaluate the performance of intercrops versus sole crops. In particular, to illustrate the pattern of competitive outcomes in intercrop experiments, Williams and McCarthy[23] suggested plotting partial LER values for the first species (e.g., legume) as a function of the partial LER of the second intercropped species (e.g., cereal). This allows the distinction of areas of interest for the two species revealing the result of interspecific interactions and similarly as the overall balance of the 4C effects (see for details Fig. 2, adapted from Bedoussac and Justes[24] and including improvements). Other indices such as competitive ratio and aggressivity are also used to show relatively competitive ability between mixed species[11,25]. These indices are relevant tools for determining the overall outcome and productivity of intercrops as the result of the combination of the 4C effects.

In Fig. 2, the diagonal line corresponding to the partial LER_{Cereal} = partial LER_{Legume} in the top left pane separates the areas in which the grain legume has a competitive advantage over the cereal for grain yield production (a) and vice versa (b). The diagonal corresponding to LER = partial LER_{Cereal} + partial LER_{Legume} = 1 in the top right pane separates the areas where sole crops are more efficient than the intercrop for grain yield production (c) and vice versa (d).

Areas in the middle panes corresponding to partial LER values below 0.5 (because each species was sown in the intercrop at half its sole crop density) for grain legume (f) and for cereal (g) indicate that species grain yield (per plant or row) is less in the species mixture than in the sole crop. Conversely, areas corresponding to values above 0.5 for grain legume (e) and for cereal (h) represent situations where species grain yield (per plant or row) is higher when intercropped.

In the lower left pane, both species are suppressed in the mixture indicating that competitive effects are stronger than complementarity and cooperation effects for both species (k) even though biotic or abiotic problems could also have affected both intercropped species (e.g., frost damage on both species at emergence, before the opportunity for interspecific relationships). This point highlights the value of intra and interspecific interactions indices comparing intercrops with sole crops sown at a similar density and not directly with sole crops sown at a normal density[11]. In area (j) the inverse is observed with both species growing better in the mixture than they did as sole crops, indicating that species complementary and cooperation effects are stronger than those of competition. This area (j) represents the optimal outcome of the 4C approach leading to an advantage from intercropping and for both species which, is targeted when growing species in mixture. In this pane, the area (i) corresponds to situations in which the grain legume suppresses the cereal while the reverse is true in area (l).

Finally, in the bottom right panel, the neutral point (n) at

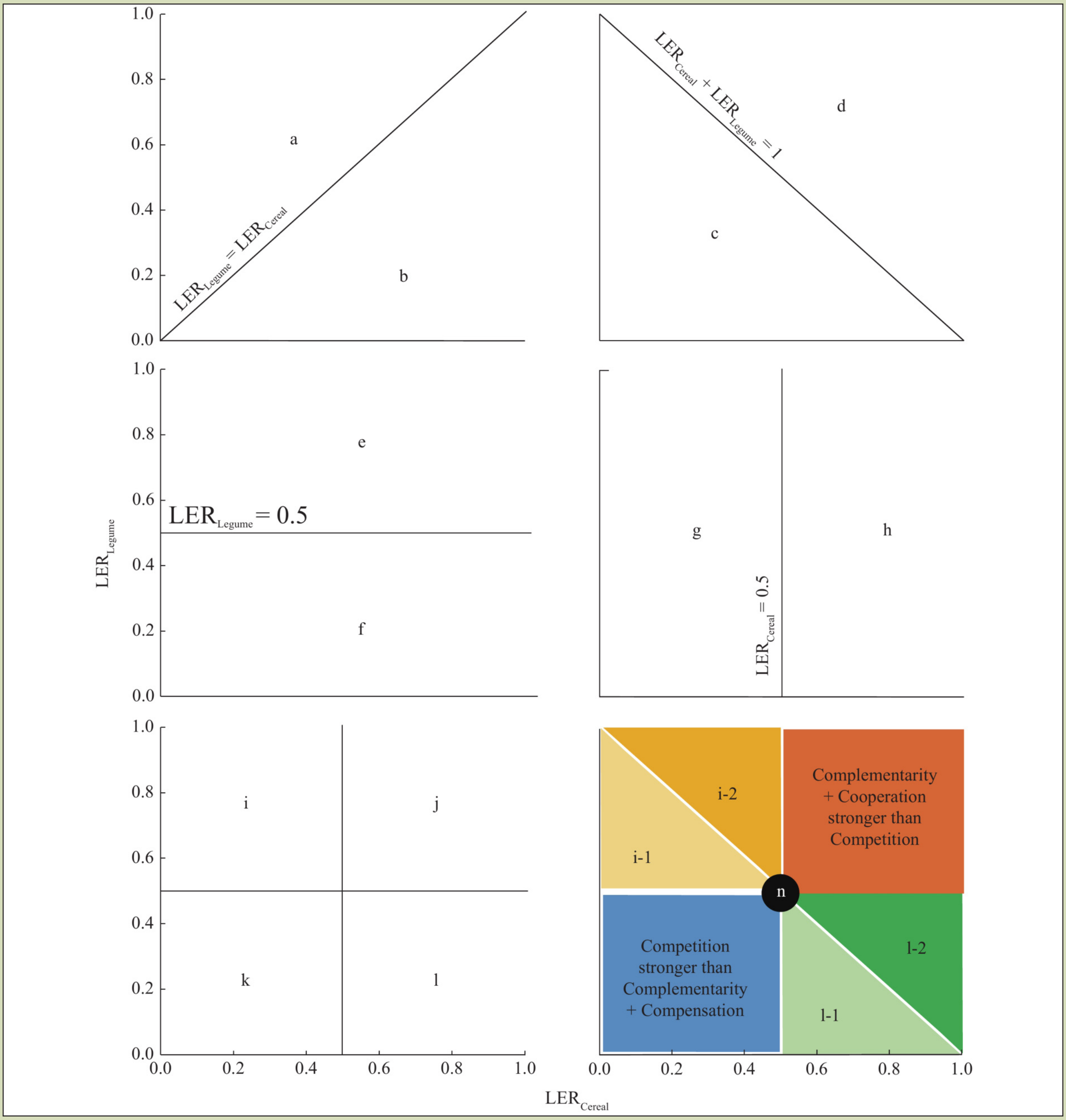


Fig. 2 Graphical representation of the partial LER (land equivalent ratio) of the two species intercropped adapted from Bedoussac and Justes[24] (with permission from Elsevier) showing all possible outcomes of an interaction experiment with two species (here a cereal and a grain legume in a substitutive design where each species was sown at half their sole crop density).

partial LER_{Cereal} = partial LER_{Legume} = 0.5 indicates situations in which for both species the grain yield per plant is similar in the mixture and in sole crops, and then competition effects equal those of complementary, compensation and cooperation. In this pane, the areas (i-1) and (l-1) are defined by intersection of areas, (c) ∩ (i) and (c) ∩ (l), respectively, and (i-2) and (l-2) are defined by intersection of areas, (d) ∩ (i) or (d) ∩ (l), respectively. All these areas correspond to competitive effects stronger than the sum of complementarity and cooperative effects for one species while the converse for the other. More precisely, the areas (i-1) and (i-2) indicate a dominance of grain legume on cereal i.e. that grain legume suppresses cereal by modifying the environment and vice versa in (l-1) and (l-2). Then the complementarity is to the advantage of one species with a stronger competition of the dominant species that benefits and compensates for the interspecific competition it exerts on the second species by increasing its production, indicating that cooperation was not efficient in the species mixture. These interactions lead to an advantage from intercropping in (i-2) and (l-2) (LER > 1 indicating more production per unit of soil in an intercrop) but to a poorly balanced mixture due to too much competition between the two species in (i-1) and (l-1); LER < 1 indicating more production per unit of soil in sole crops.

It must be noted that analysis of partial LER is very sensitive to the actual densities of each species observed in the canopy after emergence. For instance, from sowing to early stages, the interspecific relationships are not at work. But some abiotic problems (e.g., frost damage) may highly modify actual densities, and then favors the dominance of one species before the opportunity for interspecific relationships occurs. In this case, the line of reference for partial LER (for instance LER_{Legume} = 0.5 and LER_{Cereal} = 0.5) must be modified in accordance with actual densities observed in both intercrops and sole crops[24].

4 4C APPROACH AND ABIOTIC RESOURCES CAPTURE AND USE

We propose to illustrate the didactic method scientifically-based for understanding species interactions determining intercropping productivity, and not the mechanistic processes underlying dynamic plant–plant interactions. One aim was to further unravel the mechanisms of plant–plant interactions in species mixtures, due to the 4C effects between species in intercropping notably on less understood processes and effects for abiotic factors (light, water, N and P) and how the use of species mixtures can increase resilience against drought through compensation. Indeed, to improve knowledge of the 4C effects it is important to be able to determine the acquisition of the available resources and their conversion to dry matter production in species mixtures compared with the component sole crops[24,26–28]. One hypothesis is that different canopy structures and root architectures of species may lead to complementarity in acquisition and use of light, water and soil nutrient resources contributing to efficiency in light, nutrients and water use in cereal and grain legume intercrops and improved yield compared to sole crops.

4.1 4C effects and light

Light acquisition can be enhanced in intercrop systems as they have greater coverage of the soil and use radiation more efficiently across the growing season than many sole crops[29–31]. The increase in light acquisition happens because of a longer period of light acquisition in strip–relay intercrops in comparison to sole crops or to the spatial complementarity for light acquisition due to the complementarity in plant architectural development and plasticity[12,31–35]. Intercropping can also have a significant effect on light conversion efficiency. In some studies, tall C_4 plants, such as maize or sorghum, were intercropped with short C_3 species soybean and groundnut[29,36,37]. These studies show that light conversion efficiency of the C_4 plants was similar in sole crops and intercrops, whereas C_3 species had higher light conversion efficiency and lower yields in the intercrop than in the sole crop. In addition, strip intercropping of C_3 and C_4 species can also provide temporal nice differentiation, in the sense there is a limited overlapping of the intensive growing seasons. Instead, the C_3 crop is generally grown earlier than the C_4 according to temperature physiologic requirements leading to latest possible sowing date. The C_4 crop is generally more competitive, because it has a much higher radiation use efficiency and can overgrow the C_3 crop. However, because the C_4 crop is sown later than the C_3 has been already established, there is less competition for light and nutrients capture and then more temporal niche complementarity.

Despite increasing knowledge of intercrop function, it still remains crucial to improve species mixtures by finding suitable plant partners that switch from inherent light competition between plants to complementarity and/or cooperation effects to reach optimal light use. The aim of research must be twofold: (1) gain fundamental knowledge about the importance of plant–plant interactions when competing for light, and (2) find useful indicators by evaluating different combinations of grain legumes and cereals to understand which traits are of importance to ensure the success of the species mixture. The fundamental knowledge particularly concerns the effects of qualitative changes of light on plant morphogenesis. It is well established that plants respond strongly to changes in the spectral composition of light by modifying their morphogenesis[38] independently of the amount of radiation available for photosynthesis[39]. These qualitative changes in blue (400–500 nm), red (600–700 nm) and far-red (700–800 nm) radiation, described as morphogenetically active radiation[40] result from the interactions between light and plant organs and their optical properties. The capacity of plant organs to absorb, transmit and reflect light depends on the radiation wavelength. Thus, red radiation is mainly absorbed whereas far-red radiation is mostly reflected and/or transmitted. This leads, as soon as neighboring plants appear, to the decrease in red/far-red ratio long before any significant lowering in photosynthetic photon flux density occurs[41]. This feature makes this ratio an early signal for plants to anticipate competition for light.

Light quality in general, and red/far-red ratio in particular, drives several morphogenetic responses such as tillering/ramification[42] and elongation of leaves and stems[43]. This in turn can impact light absorption and photosynthetic performance[44] but available and published data of measurement of light quality in crops is scarce. In most cropping systems light conditions are mainly assessed for biomass production by using small quantum sensors measuring local photosynthetic photon flux density in the range of 400–700 nm of photosynthetically active radiation. However, a greater understanding of the dynamics of plant architecture in intercrops depends on evaluation of the ability of one species to grow with another species by measuring the intensity of photomorphogenetic responses in field conditions[45]. Therefore, data on the evolution of light quality from seedling emergence to full vegetative development are needed. According to the work of Escobar-Gutiérrez et al.[41] light quality may be estimated from photosynthetic photon flux density measurements. This could aid understanding of plant–plant interactions in intercrops according to light quality, which could be modified by one species and then perceived differently by the associated species. Finally, the light absorbed by the intercrop canopy, as measured by energy balance, is particularly useful for evaluating the performance of intercrops versus sole crops, and allows quantification of the complementarity of the species to capture light more efficiently over the whole growing season[46].

4.2 4C effects and water

Intercropping can increase the water use efficiency by 4% to 99% compared to sole crops, especially when water supply is not limited[28,47–49]. The root system can also play an important role in water acquisition in intercrops. Species mixtures have been shown to stimulate increased root length density leading to decreased water loss through evaporation[50,51]. One mechanism of complementarity in maize–pea strip intercropping is that maize plants may extract water from the pea strip during early pea growth when the peas require little water[47]. The niche complementarity of the root system in capturing water has also been demonstrated for wheat–winter pea intercrops[49]. The faster exploration of deeper soil by cereal roots compared to grain legume roots allows cereals to use more water from deeper soil layers to support plant transpiration during post-flowering stages, allowing more water in upper layers for grain legume transpiration during the grain filling phase[46]. There seems to be a need for more and systematic studies to determine the effect of intercropping systems on water use efficiency and also to find the species combinations, conditions and mechanisms underlying complementary root allocation in space and time. The development of root system models is underway and will provide useful information without the need for costly and difficult root system excavation experiments.

4.3 4C effects and nutrients

Intercropping has been shown to affect both nutrient acquisition, and conversion efficiencies of N and P and also most of the other essential nutrients[28]. Intercropping affects bioavailability of nutrients such as P, Fe, Zn and Mn, increasing their acquisition by the species[52]. Crop species differ in their capacity to mobilize or access soluble inorganic forms of these elements and intercropping can mobilize and increase acquisition for both species in the mixture as a facilitation process. This is an example of cooperation.

4.3.1 4C effects and nitrogen

Nitrogen was studied extensively since many intercropping systems include grain legumes which fix atmospheric N_2 through symbiosis with rhizobia. When the species mixture includes cereals and grain legumes both competitive and complementary processes and effects are involved. The cereal will typically obtain a greater than proportional share of mineral nitrogen (soil and fertilizer sources) due to its greater competitive ability[13,53,54]. The grain legume will compensate for the reduced availability of mineral nitrogen, by relying relatively more on symbiotic N_2 fixation (complementary use of nitrogen sources) than in a sole crop situation[54]. Therefore, intercropping can enhance N_2 fixation by grain legumes making cropping systems less dependent on fertilizers, and this can lead to an improved total nitrogen capture through niche complementarity between grain legumes and non-legumes[13,18]. However, the total N_2 fixed by the grain legume can be lower in intercrops compared to sole grain legume crops, due to competition for other abiotic resources that reduce grain legume biomass[11,54]. The amount of N_2 fixed depends on the species and varieties mixed, mineral nitrogen availability, sowing densities and other management practices[28,55]. In a faba bean-maize intercrop, Li et al.[14] found that the nodulation and N_2 fixation of faba bean were enhanced by the presence of root exudates of maize, which was considered as evidence of cooperation by two species via N_2 fixation[14].

A meta-analysis of maize–soybean intercropping literature from around the world[56] established that the nitrogen fertilizer equivalent ratio, defined as the amount of N-fertilizer in intercropping divided by the N-fertilizer amount in sole cropping to produce equal amounts of yield, was higher than the LER (1.44 and 1.32, respectively) indicating that nitrogen use efficiency was greater in intercropping. Also, the nitrogen fertilizer equivalent ratio did not change with the amount of N-fertilizer applied in case of moderate N fertilizer amounts or with soil organic matter content[56].

Both the N-fertilizer reduction and the yield advantage of the less nitrogen-intensive maize contribute to these effects. Also, the effect of partial separation of soybean and maize growing periods, corresponding to temporal niche differentiation, in a relay intercrop increase the LER and nitrogen fertilizer equivalent ratio[56]. This was also observed previously in an analysis of multiple cereal-grain legume combinations[7,57]. It has often been assumed that the nitrogen released in the soil by grain legume rhizodeposition is available for the associated non-legume. However, this nitrogen source has been shown to be of minor importance (< 10% of the N in the cereal) in the case of annual species mixtures of cereal and grain legume with no or minor temporal niche differentiation[58,59].

To assess the beneficial effect of grain legumes and to adapt the organic and mineral nitrogen fertilization strategies, it is crucial to diagnose the level of nitrogen stress of each crop in the mixture separately. A comparison of different indices[60], either based on plant traits or adapted from a dilution-curve method used in sole crops, has revealed situations in species mixtures for which these indices are operating. This particularly concerns intercropping situations where there is an unbalance between species in terms of relative proportion and height, which are governing the light attenuation within the cover profile, and then determines the leave nitrogen profile concentration. The application of such indices relevantly calculated by considering the whole cover biomass and the specific N concentrations, as proposed by Louarn et al.[61], can allow us to quantify the impact of competition and complementarity for nitrogen on the level of stress of each species, and then to estimate the nitrogen inputs required to improve the management of the species mixture.

Previous studies showed that the competition-recovery principle[61,62] partly explains the yield advantage of intercropping. For instance, in a wheat–maize intercrop, wheat as the dominant species, has a yield advantage from intercropping during the growth stages which adversely affects the growth of the associated maize, as subordinate species. After the wheat has been harvested, the maize grows much faster than sole cropped maize. However, less is known about how root morphological and physiologic changes influence the recovery growth of late-maturing species. A recent study conducted by Liu et al.[20] aimed at determining the mechanism underlying the recovery growth in terms of root distribution and nitrogen uptake in response to different nitrogen supplies. Results showed that intercropped maize has a different root length density and root distribution which enhanced its nitrogen absorption per root length unit with increasing soil nitrogen concentration, in comparison to sole crops. The root process had a direct influence on root length density of intercropped maize which was related to shoot nitrogen concentration. As a result, maize took up to 93% more nitrogen per root length unit when intercropped in comparison to the sole cropped maize. That can be viewed as an adaptation to competition resulting in increased nitrogen uptake per plant[21]. These findings indicate that the recovery growth of late-maturing species involves phenotypic plasticity of maize root architecture, and the enhanced nitrogen uptake resulted from extra soil nitrogen acquired by wheat.

4.3.2 4C effects and phosphorous

The bioavailability of phosphorus is often a limiting element for crop productivity in poor and calcareous soils. The increase in phosphorus acquisition in intercrops can be explained by higher acquisition from poorly available organic sources or inorganic sources such as oxide and hydroxide complexes[15,16]. This was investigated in greenhouse intercropping experiments by Li et al.[15] showing that faba bean can mobilize sparingly soluble phosphorus in soils through rhizosphere acidification and carboxylate exudates enhancing soil phosphorus availability to the benefit of both faba bean and maize.

Li et al.[63] found that enhanced phosphorus acquisition was due to positive complementarity effects in faba bean-maize, and to both positive complementarity and selection effects in chickpea-maize mixtures. Increased resource acquisition via complementarity and/or selection effects depended on the particular crop combination in intercropping systems[63]. Here, the complementarity effect includes the niche differentiation of the plant requirement for phosphorus, as well as interspecific cooperation.

A meta-analysis of cereal–grain legume intercropping[64] revealed that phosphorus uptake efficiency in intercropping was on average 1.24 higher than in sole cropping. On average, the intercrops took up to 3.6 $kg \cdot ha^{-1}$ P more than would have been expected on the basis of the sole crops. The efficiency with which intercropped plants converted phosphorus into biomass was lower in intercrops than in sole crops. Nevertheless, the overall phosphorus use efficiency was improved and 21% less phosphorus fertilizer was needed in intercropping to obtain the same yield as in the sole crops.

5 COMPENSATION FOR INCREASED YIELD STABILITY IN INTERCROPPING

Climate change is resulting in more erratic weather conditions causing more frequent periods of drought, waterlogging and extreme temperatures. Agricultural crops may be significantly affected by abiotic and biotic stress in interaction with climate variability and change. Cropping systems based on monoculture (continuous cultivation of the same crop on the same piece of land for several years) or based on simple crop rotations (e.g., two or three crops) are at increased risk of weed, disease and pest infestation. Therefore, these systems often rely on heavy use of agrochemicals such as herbicides, fungicides and insecticides.

Intercropping may provide insurance against complete crop failure, through compensation, when intercropped species have different sensitivity to, for example, drought or major diseases in a region[34,65]. Indeed, if abiotic or biotic stress eradicates one species more or less completely, the associated species may compensate for this loss if it is less sensitive to the particular stress. The intercrop may also be designed specifically to have components with different sensitivities to stress, so that one species may be able to use any resources unused by the species that is more severely affected by the specific stress or combination of stresses.

As an illustration, in a large field-scale experiment in southern Sweden on spring oat-pea substitutive mixtures[13,66], the 2018 growing season was extremely dry, with no precipitation between early May and harvest in August. The result was that no pea could be harvested in either sole crop or intercrop whereas oat yield was on average 4.1 $t{\cdot}ha^{-1}$ in the sole crop and 3.5 $t{\cdot}ha^{-1}$ in the intercrop even though the oat plant population in the intercrop was only 50% of the sole crop. This was probably due to the ability of oat to use available resources and thus compensate for the pea, which died due to lack of water. The relationship between specific diversity and total yield is also well-known in forage production systems based on multispecies grasslands[67]. An increase in the number of species is generally associated with an insurance effect against complete production failure in adverse conditions and a higher resource capture due to complementarity[68]. However, yield stability comes at a cost in these systems with a higher variability of mixture composition over time and a lower control on the stability of forage quality, which is highly dependent on the persistence of grain legume species over time[69].

In fields with heterogeneous soil factors it may even be possible to achieve improved use of resources and more stable yields across a field with intercropping compared to sole cropping but this question needs further evaluation. Raseduzzaman and Jensen[8] conducted a meta-analysis on the grain yield stability of intercrops over time and between sites showing that the grain yield variability over several years of grain legume–cereal intercrops was similar to cereal sole crops. However, it was much lower than of grain legume sole crops, giving evidence of a compensating and stabilizing effect of intercropping on crop yields.

6 CONCLUSIONS

The 4C approach is both a pedagogical and a scientific way of understanding the final net effect of all processes occurring simultaneously over the entire growing season and the effects explaining the intercrop performances. This approach was helpful and relevant for improved understanding of results obtained in intercropping experiments, and exemplified by the following:

- The yield gain of intercrops in a substitutive design of wheat-pea is mainly due to the complementarity (niche differentiation) and/or cooperation. It was also observed that the complementarity effect was greater in C_3/C_4 than in C_3/C_3 intercrops, in particular cereal and legume intercrops. Novel research are required to define the criteria and the conditions and what would be the best species combination that would maximize the niche complementarity for abiotic resources capture. This analysis could be done by using soil–crop model adapted crop to intercropping by simulating numerous combinations of species in various pedoclimatic conditions and analyzing the outputs, as a virtual experimentation[70].

- The quality of light (e.g., determined by the red/far red ratio), may affect crop development with intercropped wheat plants being subjected to more competition for light when intercropped with full-leafed pea cultivar in comparison to semi-leafless cultivar. This competition occurs very early in the intercrop cycle with full-leaf pea cultivar significantly reducing the red/far red ratio in comparison to semi-leafless cultivar.

Further studies are undoubtedly needed to improve the understanding of plant–plant interactions and interspecific *dialog*, as plants perceive the modification of the light quality in their close environment and react accordingly to adapt, which is crucial during the establishment of intercrop and for the plant–plant competition processes over the whole crop cycle.

● Pea–wheat intercrops increased the radiation and water use efficiency, especially in irrigated conditions and in low nutrient conditions indicating complementary and cooperation for resource acquisition. This result is now well establish for cereal–grain legume intercrops, but more analysis is needed for other types of species mixtures and levels of nutrients availability.

● Roots interactions contribute more when soil phosphorus availability is low whereas above ground interactions are of more importance when soil phosphorus availability is high explaining competition and cooperation processes underlying the plant–plant interspecific interactions. The mechanisms need to be more fully understood including the root *dialog* between species and the role of microorganisms in the rhizosphere in the root system functioning.

● Nitrogen use in grain legume–cereal intercrops showed that cereals obtain a greater than proportional share of the soil mineral nitrogen due to niche competition effects and complementary use of nitrogen sources (soil mineral nitrogen vs. atmospheric N_2). This complementarity in legume–cereal intercrops can lead to significant reduction in N-fertilizer use globally. This result is now well establish for cereal–grain legume intercrops, however further work is needed to provide more reliable estimates and forecasts of N savings and to develop fertilization plans as a decision-support systems. There is a clear need to design a framework and decision rules to adapt N fertilization to intercropping in a generic way that also allows adaptation to local conditions.

● Yield stability of grain legume–cereal intercrops over time and between sites is similar to cereal sole crops, but much greater than grain legume sole crops, giving evidence of a compensation effect in intercropping. It would be interesting to determine the conditions maximizing the yield stability and in particular which are the best species and plant traits to associate for reaching the objective. Modeling could be a relevant way to do so[70].

In conclusion, the 4C approach is relevant for analyzing and describing the functioning of intercrops while identifying the dominant processes as a net effect explaining the final performance of species mixtures in regard to the capture and the use of abiotic resources. We believe that the concept could be applied to the analysis of biotic factors for characterizing the intercrop performances in case of interactions with weeds, pests and diseases.

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Compliance with ethics guidelines

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