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Non-chemical weed management: Which crop functions and traits to improve through breeding?

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ABSTRACT

The agro-ecological transition aims at reducing the anthropogenic impacts of crop production on the environment, for instance by decreasing drastically the applications of pesticides, among which herbicides are the most prevalent. In this review, we focus on management of arable weeds in agro-ecological systems, considering a perspective of steady reduction of synthetic herbicides by fostering the breeding of varieties adapted to non-chemical weed management. Diverse strategies of non-chemical weed management are discussed, taking into account agronomic levers and identifying breeding targets. Weed suppression by enhancing crop competition from cash or cover crops, grown in pure stands or as intercrops, is a key strategy that could be considered together with dense canopies and optimal nitrogen management, also in addition to growing varieties that are tolerant to weed competition and/or characterized by low nitrogen requirements. Then, escaping weed competition could be achieved by shifting sowing dates and/or diversifying crop rotations, particularly by targeting varieties of different maturity groups, more productive spring-sown crops and integrating more frequently minor crops in the rotation. Weeds can be also suppressed by mechanical control that requires varieties tolerant to mechanical weeding. Allelopathy is a less applied strategy that deserves further studies *e.g.* the screening of allochemical composition among varieties of cash and cover crops. For each crop-related agronomic lever contributing to integrated weed management, we identify the functional crop traits to target, *i.e.* the set of morpho-physiological traits associated with an effective weed management, to be screened within the commercial variety panels or to be integrated in a genetic improvement scheme. For all the functional traits and according to the crop species, the potential availability of genetic resources, as well as the ability of varieties to meet the required genetic variability have been explored while, where relevant, the development of appropriate phenotyping methods and trait assessment procedures have been considered. Finally, we propose a set of non-chemical weed management strategies, functional effect traits and agronomic practices associated, as well as their synergies and antagonisms with the other cropping practices for cash and cover crops. We conclude that, to better combine a set of agronomic levers with crop varieties or reinforcing the efficacy of these levers, there is a need to complete classical agronomy and weed science approaches by plant genetics and breeding when designing and evaluating non-chemical weed management strategies.

1. Introduction

Currently, farmers are experiencing real difficulties to control weeds due to the increasing number of cases of herbicide resistance, the withdrawal of active ingredients not compensated by new authorizations, the costs of mechanical weeding and the hazards due to climate

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change (Délye et al., 2007, 2016; Birthisel et al., 2021; Storkey et al., 2021; Chauvel et al., 2022). Based on the literature, we assume that the efficient combination of genetic and agronomic levers would make it possible to take advantage of biological regulations within agro-ecosystems to, at least partially, overcome these difficulties (Petit et al., 2015; Lamichhane et al., 2016; Weisberger et al., 2019). Moreover, this would allow contributing to the conservation of water quality and biodiversity in response to the aspirations of a safer environment by the society and farmers (van der Werf, 1996; Lechenet et al., 2017).

For at least three decades, several agronomic levers have been suggested in a context of integrated weed management (IWM) towards the reduction of the dependency on herbicides applied on croplands (Clements et al., 1994; Debaeke, 1997; Liebman and Gallandt, 1997; Melander et al., 2005; Nazarko et al., 2005; Blackshaw et al., 2006; O'Donovan et al., 2006; Pannaci et al., 2017; Birthisel et al., 2021), notably to control arable weeds in organic farming, which is strictly dependent on non-chemical levers (Bond and Grundy, 2001). Now, moving towards agroecological systems, additional levers have been suggested and evaluated for weed control (e.g. crop diversification; Gaba et al., 2014; Weisberger et al., 2019; Riemens et al., 2022). Beyond the steady reduction of herbicides applied, a new aim has also emerged, a pesticide-free agriculture (Jacquet et al., 2022), requiring to substitute systematically the chemical options by a panel of agronomic and genetic levers. The implications of integrated weed management for plant breeding have not been extensively reported so far and crop competitiveness has not been considered as a priority goal for breeders (Pester et al., 1999), except in organic farming (Wolfe et al., 2008; Rolland et al., 2017). In this context, the released varieties are characterized by a reduced competitiveness against weeds as compared to ancient varieties (Lever et al., 2022a; Federico et al., 2023).

The present review aims to determine the crop functions that should be emphasized for efficient non-chemical weed management and the related traits that should be promoted by breeding. One main avenue is to increase crop diversification in time and space, including the use of major and minor cash and cover crops, either grown as sole crops, intercrops or relay crops, as well as their optimal sequencing in a rotation and the choice of the best varieties. To sustain the competitiveness against weeds, other production-oriented levers such as sowing date, crop density and amounts of nitrogen fertilisation must be optimized to increase the efficiency of weed control. Therefore beyond the traits related to crop competitiveness, this integrated weed management approach aims to highlight a new set of traits for breeding and variety choice.

For each crop-related agronomic lever contributing to integrated weed management, we identified the functional crop traits to target, *i.e.* the different traits associated with an effective weed management to be screened within the panels of commercial varieties or to be integrated in a breeding improvement scheme. In the present review, we used the term functional trait in a broad sense, *i.e.* by considering a trait as any morphological, physiological or phenological characteristic measurable at the individual level (Violle et al., 2007), but also including other characteristics not measurable at the individual level. In this respect, consideration have been given to the rules to assemble the various agronomic levers. For all the functional traits, the potential availability of genetic resources and sufficient genetic variability have been explored, and the development of appropriate phenotyping methods has been considered. To summarize, we propose to discuss a set of non-chemical weed management strategies, functional traits and associated agronomic practices, as well as their synergies and antagonisms with other weed management strategies for cash and cover crops.

These non-chemical levers fell into three categories:

- The first category is based on the competitive ability of the crop species, and their associated management, grown as sole crops or intercrops, cash crops or cover crops (§ 2-6);
- The second category is based on several escaping strategies based on the diversification or changes of sowing dates and crop sequences in rotation which offer more opportunities to control weeds and reduce the exposure of the crop to severe flushes of weed emergence (§ 7-8);
- The third category is based on various weeding techniques such as mechanical destruction of emerging weeds or weed suppression using biocontrol techniques notably allochemicals released by main crops or cover crops, also known as service crops, as living stands or residues (§ 9–10).

2. Crop competitiveness against weeds based on canopy cover capacity

Crop competitiveness against weeds includes two components, *i.e.* the ability of high weed suppression and a high tolerance to weed competition (Lemerle et al., 2001; Zerner et al., 2016). Weed suppression corresponds to a reduction in weed biomass and/or weed seed production by the crop, thus considering consequences on the replenishment of the soil seed bank and seed dispersal (Coleman et al., 2001; Mason et al., 2008; Worthington and Reberg-Horton, 2013; Zerner et al., 2016). Crop tolerance means lower yield loss in the presence of a same weed flora (Lemerle et al., 2006; Zerner et al., 2016). Covering the soil rapidly after sowing and maintaining the canopy cover throughout the season is a strategy for maximising radiation capture, limiting soil water evaporation and controlling weed development. Canopy cover capacity is a function to be improved genetically in a perspective of integrated weed management (Andrew et al., 2015), which is already partially exploited, in particular in organic farming (Wolfe et al., 2008; Fontaine et al., 2009; Rolland et al., 2017; Lever et al., 2022a). So far, most of the studies have been conducted on straw cereals (Lemerle et al., 2001; Mason and Spaner, 2006). However, opportunities exist also for oilseed rape (Sim et al., 2007a; Lemerle et al., 2014; Mwendwa et al., 2020a), soybean (Hammer et al., 2018) and grain legumes (*e.g.* lentils, chickpeas, field peas) which severely suffer from competition with weeds during early growth (Tepe et al., 2005; Paolini et al., 2006; Harker et al., 2008; Jacob et al., 2016).

In a context of input reduction and climate change, crop competitiveness should necessarily also include competition for soil nutrients and water, which means to consider root system architecture and functioning. However, this section focuses on the special case of canopy cover capacity, related to the architecture of the canopy and its growth over time.

2.1. Associated traits

The canopy cover capacity and the related shading ability depend on the speed of soil cover by leaf area, a criterion combining the architecture of the aboveground parts with their growth rates (Wolfe et al., 2008; Fontaine et al., 2009). The literature mentions a set of traits, usually referred to as early vigour, canopy closure or light interception (Christensen, 1995; Huel and Hucl, 1996; Benaragama et al., 2014; Worthington et al., 2015a; Mwendwa et al., 2020b; Kucek et al., 2021; Aharon et al., 2021; Hendriks et al., 2022). As canopy cover capacity is an integrative criterion, it includes simpler functional traits such as leaf area, leaf habit, plant height, growth habit, growth rate and tillering capacity for cereals (Didon, 2002; Mason et al., 2007a, 2008; Szewczyk, 2013; Hendriks et al., 2022; Lever et al., 2022a). The germination and emergence of weeds may also be affected by crop shading if weed seeds fall and germinate on the soil surface as in no-till systems (Batlla and Benech-Arnold, 2014). In addition, if the crop root system develops fast enough and uses most of the available water, weed seeds will lack water to germinate and emerge successfully. The relative responses of crop and weed plants to shading (quantitative and qualitative changes in radiation) is also a key factor in crop ability to compete with weeds (Holt, 1995; Ballaré and Casal, 2000; Colbach et al., 2019; Kucek et al., 2021). The relative time of emergence of weeds and crops will modulate the efficacy of canopy cover for controlling weed survival and growth (Fahad et al., 2015).

2.2. Associated agronomic practices

The date and method of sowing, crop density and row width are associated with agronomic practices to be adapted locally to each crop and type of variety to reinforce the influence of the canopy cover capacity and the competitiveness of the variety, whether the latter should cover the row only (in case of hoeing of inter-rows) or also the interrow (Rasmussen et al., 2004; Hansen et al., 2007; Mason et al., 2007b; Sim et al., 2007b; van der Meulen and Chauhan, 2017; De Vita et al., 2017; Lazzaro et al., 2017; Hammer et al., 2018). As an example, higher crop density and/or reduced row width will enhance the competitive ability of a variety. In early or late spring sowings, starter fertilisation and/or supplementary irrigation may be sometimes necessary to foster crop establishment and soil cover under less favourable conditions (Mohammadi and Amiri, 2011). With climate change, due to the increasing occurrence of drought, these practices could be also relevant for early-sown autumn crops such as oilseed rape in order to promote plant establishment and early vigour.

2.3. Evaluation methods

The canopy cover capacity can be estimated directly by visual assessments using a predefined well-chosen grading scale for the functional trait measured, or indirectly by proxies derived from dynamic measurements of reflectance with on-board (UAV, satellite) or handheld sensors as the Normalized Difference Vegetation Index (NDVI) (Xie and Yang, 2020). These proxies can estimate the soil cover rate or directly the leaf area index (LAI) at the canopy scale, especially in the absence of early biotic and abiotic stresses (*e.g.* frost damage, early senescence due to leaf disease). They also give access to the potential canopy growth dynamics (Huel and Hucl, 1996; Worthington et al., 2015a; Zerner et al., 2016; Aharon et al., 2020; Milan et al., 2020). The Light Detection and Ranging (LiDAR) technology is a powerful tool for direct 3D measurement of plant structure giving access to canopy height (Omasa et al., 2007). These methods can be easily applied to common plot-based experimental designs used for comparing the performances of a set of varieties under multi-environment trials. Traits should be measured in standard conditions (e.g. crop density, nutrients and water availability, either in field or controlled experiments) in order to be used as parameters in process-based models.

3. Crop tolerance to reduced nitrogen supply

Reducing the application of mineral nitrogen fertilizers in crops is required to decrease their negative environmental impacts (Sutton et al., 2011). Several positive effects could also be expected in straw cereals, such as (1) maximising nitrogen use efficiency (Jeuffroy et al., 2013), (2) reducing the development of some foliar diseases (*e.g.* brown rust, septoria, Simon et al., 2003), and (3) limiting the risk of physiological lodging (Wu et al., 2019). In addition, temporary crop nitrogen deficiencies do not systematically lead to crop yield losses, especially in case of early deficiencies (Ravier et al., 2017). Therefore, reducing the use of mineral nitrogen fertilizer under certain circumstances can be both environmentally and economically profitable in cereals (Loyce et al., 2012).

For a moderate nitrophilic crops species such as wheat, adjusting nitrogen fertilisation to crop nitrogen requirements or below may theoretically lead to beneficial effects to manage weeds, especially by reducing the growth of nitrophilic weeds that are generally the most problematic ones (Moreau et al., 2014). However, in some field experiments, weed pressure was not lowered when the use of mineral nitrogen fertilizers was reduced. Perthame (2020) indicated that, in most cases, weed pressure even increased, suggesting complex interactions among different factors (crop traits, cropping practices, composition of the weed flora, initial amount of soil nitrogen) and making it difficult to identify general rules. To go further, simulation studies based on a mechanistic model are in progress (Moreau et al., 2021).

3.1. Associated traits

Knowledge is available on which crop traits provide a competitive advantage over arable weeds. In standard situations with soil nitrogen availability, crop plants with a high growth potential, a low root to total biomass ratio, a high efficiency of each root unit to take up nitrogen, and a low nitrogen demand (per unit of leaf biomass) could have a competitive advantage (Moreau et al., 2014; Perthame et al., 2020). In situations of low soil-nitrogen availability, root traits could become more crucial. For instance, a large proportion of fine roots could become useful as fine roots pre-empt the larger part of soil resources (Freschet and Roumet, 2017). Also, roots with a large diameter could provide an advantage as they can penetrate through soil layers and elongate faster (Eissenstat, 1992; Pagès, 1995), thereby providing access to the deepest soil resources, such as leached nitrate (Chen et al., 2013).

3.2. Associated agronomic practices

Different agronomic practices related to nitrogen fertilisation can be implemented to drive crop-weed competition (Perthame, 2020). Modifying the amount of nitrogen fertilizer was discussed above. Alternatively, modifying the timing of nitrogen application could affect crop-weed competition but, depending on the studies, either weeds or crops may benefit from such modifications (Perthame, 2020). Nitrogen can also be applied locally on the sowing row (rather than broadcasted) in order to make it more directly available to crop plants than to weed plants emerging in the inter-row (Rasmussen et al., 1996). This method proved its effectiveness in promoting crop growth and maintaining crop yield for wide row crops, such as maize or sunflower (Perthame, 2020). To adapt nitrogen fertilisation to each particular production situation (*i.e.* cropping system, weed flora, soil and climate), models and decision support tools that simulate the crop nutritional status and crop-weed interactions can be used (Moreau et al., 2021).

3.3. Evaluation methods

Currently, measurements of the crop traits described above remain complex and time-consuming in field conditions. Other non-destructive methods could be tested based on sensors for determining the plant nutrition status or the change in leaf area resulting from the application of N fertilization (based on canopy reflectance, leaf transmittance, or chlorophyll and polyphenol fluorescence) (Munoz-Huerta et al., 2013; Xie and Yang, 2020). Field experimental designs with monitored soil and plant nitrogen status and sown weeds or natural infestations could be implemented. Differences between varieties in root traits can be more easily analysed in controlled conditions, using high-throughput phenotyping of root structures (Jeudy et al., 2016).

4. Intercropping of annual crops to suppress weeds

The practice of intercropping by combining two annual crops has shown multiple potential benefits (Martin-Guay et al., 2018; Zhang et al., 2019; Yan et al., 2024), including weed suppression. In a recent meta-analysis, Gu et al. (2021) emphasized that weed biomass was lower in the intercrop than in both crops tested in pure stands in 45% of the cases studied. In addition, weed suppression by intercrops was on average comparable to that of pure stand of the more competitive species in the mixture. These results hide differences due to the composition of intercrop, from maize/soybean to straw cereal/grain legume intercrops, both in terms of experimental designs and geographical areas. The better weed suppressive ability of intercrops seems to mainly originate from the stronger weed suppressive crop component, while the weaker competitive component may also be affected by competition of the most competitive crop, requiring finding a relevant balance between the two crop components (Gu et al., 2021). Weed suppression is related to the increased capture of light resources by the intercrop compared with sole crops (Stomph et al., 2020). The measurement of weed suppressive ability currently considers only the reduction of weed biomass due to the composition of intercrop compared to pure stands, without taking into account the functional traits of the crops. However, some studies suggest relationships between traits chosen and the performance of the intercrop (Demie et al., 2022).

4.1. Associated traits

In a recent paper, Kiær et al. (2022) defined three categories of traits as breeding targets for cereal/legume intercropping, including complementary traits related to species synergy during the growth period, such as mixing ability. We propose to include the competitiveness of the mixture in this category, knowing that the competitive ability is based probably on a set of traits common to the mixing ability. Breeding for intercrops therefore requires to define the targeted level of interactions between crop species in comparison to the targeted level of weed suppression, for example by increasing the competitive ability of the expected less competitive component of the intercrop (see *e.g.* Annicchiarico et al., 2021). This search for a trade-off between the weed suppression ability and the yield of the least competitive crop components also explains the choice of crop species for intercropping, *e.g.* for lentil-based (Kiær et al., 2022) or soybean-based (Cherière et al., 2020).

4.2. Associated agronomic practices

Several agronomic practices influence weed suppression in intercrops, including the composition of the intercrop, the plant density (which is higher in additive sowing designs), and the type of row intercropping (with species mixed within the rows being more suppressive than two species sown in alternate rows; Gu et al., 2021). Other agronomic practices do not influence weed suppression in intercrops compared to pure stands, such as nitrogen supply rate or relay cropping vs simultaneous intercropping (Gu et al., 2021).

4.3. Evaluation methods

Current issues focus on the definition of breeding schemes adapted to intercropping (Kiær et al., 2022), including the development of efficient experimental designs (Haug et al., 2021; Moutier et al., 2022).

Until now, the assessment of mixing ability is generally focused on the yield of the two components in sole crops and in intercrops. Even if herbicides are not applied in intercrops, the resulting weed biomass is not routinely measured to appreciate the efficacy of various cultivar mixtures in suppressing weed growth.

5. Weed suppression using temporary cover crops

Weed growth can be also limited or suppressed by competition with temporary or permanent cover crops, which are not harvested, either sown before (during fallow period) or simultaneously with the harvested crop (Hartwig and Ammon, 2002; Hiltbrunner et al., 2007a, 2007b; Verret et al., 2017a, 2017b; Vincent-Caboud et al., 2019; Bhaskar et al., 2021). In both cases, the term multi-service crop (Justes and Richard, 2017) is now used as these cover crops provide several ecosystem services and benefits for farmers, including weed suppression (Gerhards and Schappert, 2019).

Several recent reviews and meta-analyses confirmed that sowing autumn-to-spring cover crops is an efficient method for suppressing weeds and volunteer crops in temperate areas, thus constituting a main component of integrated weed management programs in annual and perennial cropping systems (Osipitan et al., 2018, 2019; Gerhards and Schappert, 2019; Kumar et al., 2020; Fernando and Shrestha, 2023). Weed-suppressive cover crop stands can limit seed rain from summer- and winter-annual weed species, reducing weed population growth and ultimately weed pressure in future cash crop stands.

In temperate areas, cover cropping is possible between the harvest of winter- or early-spring sown crops and the sowing of spring-sown crops. A vegetation period of at least 6 weeks with favourable growing conditions is required but the vegetation duration could range from 3 to 8 months depending on the termination date (nature of the cover crop, sowing date of subsequent crop, soil type, winter harshness). Cover crops are generally mechanically (e.g. disking, mowing, rolling, undercutting) or chemically destroyed in autumn or early spring, and sometimes frost-killed in some regions (Gerhards and Schappert, 2019). Cover crops can be sown no-till immediately after harvesting the cash crop or 1–2 weeks later after shallow stubble tillage. Rapid emergence and canopy closure of cover crops is crucial for successful suppression of weeds and volunteer crops. The most common winter-killed cover crops are *Sinapis alba*, *Phacelia tanacetifolia*, *Raphanus sativus* and several clover species and grasses. Cover crops more adapted to dry and warm weather conditions include *Avena strigosa*, common buckwheat, *Guizotia abyssinica*, *Vicia sativa*, linseed, sunflower and *Camelina sativa*. Frost-tolerant cover crops also exist such as winter rye and ryegrass species (Gerhards and Schappert, 2019).

The effects of cover crops on weed suppression and the underlying mechanisms are not fully understood. However, in the recent literature, cover crops have been reported to suppress weed populations using various mechanisms of plant interactions (Kruidhof et al., 2008; Lemessa and Wakjira, 2015; Kunz et al., 2016; Osipitan et al., 2018; Gerhards and Schappert, 2019; Kumar et al., 2020; Fernando and Shrestha, 2023; Camargo Silva and Bagavathiannan, 2023; McKenzie-Gopsill and Farooque, 2023). First, a direct weed suppression is caused by competition for light, water, nutrients, and space by the cover crop. Second, an indirect reduction of weed density is due to the promotion of granivorous predators. Third, the effect of cover crop residues can act as a physical barrier for germination and emergence (*e.g.* reduction of light transmittance) and change the seedbed microclimate (soil temperature and moisture) with opposite effects on weed seed germination. Fourth, weed development may be affected by the release of allelochemicals from living and decomposing cover crop tissues.

Overall, cover crops would be able to suppress 70%–95% of weeds and volunteer crops in the autumn-to-spring period between two main crops with an additional suppressive effect of cover crop residues on weed emergence during early development of the following cash crop (Gerhards and Schappert, 2019). The degree of weed suppression by a cover crop depends on the residue persistence, the soil surface coverage, the accumulated biomass and the management practices applied for both cover crop and main crop (Osipitan et al., 2019).

However, these effects have mainly been assessed in the short term, i.e. during the cover crop growth cycle (Petit et al., 2018). Quantification of the effects over the longer term (i.e. in subsequent crops and at the level of crop rotation) remains rare: few studies seek to determine how this reduction in weed biomass during the fallow period translates into seed production and how the weed seed bank was really impacted in the following years (Hodgdon et al., 2016; Nichols et al., 2020; Adeux et al., 2021; Rouge et al., 2023). However, these studies generally concluded to an insufficient weed control effect in subsequent crops. Even under no-tillage conditions and low herbicide use (tillage and herbicides being major weed management levers that can mask the regulating effects of cover crops as such), the effect of cover crops remains weak.

5.1. Associated traits for the cover crops

The ability of cover crops to suppress weeds depends on their competitiveness, which is related to rapid shoot and root growth (plant vigour), nitrogen acquisition, and canopy closure. This also requires a rapid seedling emergence and good establishment of cover crops soon after harvest of the previous cash crop, sometimes under dry and warm conditions.

Among cover crops, grasses and cereals are generally considered more weed suppressive than broadleaf plant species (Baraibar et al., 2018). Osipitan et al. (2019) in their meta-analysis showed that there were differences in level of weed suppression at termination among 26 cover crop species. Cereal rye, oat, triticale, wheat, ryegrass and sorghum were the most weed suppressive even with moderate seeding rates; among broadleaves, clovers and vetches were the most suppressive, buckwheat, radish, pea and mustard being the less suppressive according to the literature. Weed suppressive species emerge relatively fast, cover the soil quickly and produce high amounts of shoot and root dry matter. For instance, where cereal rye (*Secale cereale* L.) provided weed suppression from 75 to 85%, cover cropping with pea only resulted in 0–56 % of suppression (Akemo et al., 2000). Among overwintering cover crops, cereal rye is often appreciated due for its fibrous root system, tolerance to low-fertility soils, high N capture, and soil coverage which makes it extremely weed suppressive as a result of both competitive and non-competitive mechanisms (Kumar et al., 2020; Camargo Silva and Bagavathiannan, 2023). Therefore, to be effective, low biomass-producing legumes and other broadleaf cover crops may need to be sown in mixtures with productive grass species to improve weed suppression.

Based on leaf traits, Tribouillois et al. (2015) identified Brassicacae as highly competitive among 36 cover crops species. All Brassicaceae (except *Camelina sativa*) and *Helianthus annuus* were identified as highly competitive due to their ability to rapidly grow, acquire nitrogen after sowing and occupy the space. Crop growth rate (CGR) and crop nitrogen acquisition rate (CNR) can be used as two indicators of the ability of cover crops to grow and uptake nitrogen. Leaf functional traits as specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen content (LNC) and leaf area (LA) were used to evaluate in a simpler way CGR and CNR.

A greater coverage of the soil surface by the residues has also a subsequent negative impact on weed seed germination and seedling emergence due to a physical barrier depending on the nature of the mulch (Teasdale and Mohler, 2000); this lengthens the duration of weed suppression due to competition.

Most of the studies compared the suppressive abilities of a range of cover crops but with a difficulty to separate the interactions due to competition and allelopathy (Kunz et al., 2016). Allelopathy that also suppresses weeds after termination of cover crops in the winter and early spring could vary among cover crop species and varieties. The amount of residues and their ability to release sufficient allochemical compounds until the next cash crop could differentiate cover crops in their weed suppressive ability.

It would be beneficial to quantify the competitive, physical and biochemical weed control effects of cover crops separately and determine the traits associated to each of these functions. This would help breeders and growers selecting and choosing cover crop species and combining mixtures with multiple weed suppressive abilities and increase the range of ecosystem services that cover crops may provide (Baraibar et al., 2018). Competitive species are important for early weed growth suppression while allelopathic species can reduce weed emergence via biochemicals released from living plants and their residues after cover crop termination. The efficacy of cover crop mixtures could be improved by identifying competitive and allelopathic species and combining them appropriately.

5.2. Associated agronomic practices

In their meta-analysis, Osipitan et al. (2019) showed that several management decisions could influence the suppressive performance of cover crops, including the choice of species and their assemblages, the sowing date, the seeding rate, the termination date, the delay in main crop sowing after termination of cover crop, and the tillage system. However, very few papers compared the performances of varieties of cover crops for crop biomass and termination effectiveness (Wells et al., 2016).

There is not a clear consensus if sowing multispecies cover crop is more successful in producing biomass and residue to suppress weeds than a single species or mixtures of two cover crops. However, based on several experiments, Smith et al. (2020) concluded that farmers are more likely to achieve better results sowing the most weed-suppressive cover crop as a monoculture than a mixture. However, mixtures better compensate temporal and spatial variation in sub-optimal growing conditions and fluctuating climatic conditions and thus tend to outperform single species by ensuring that at least some species grow every year at every site (Kumar et al., 2020). Respecting optimal sowing date is crucial for adequate plant establishment and maximum cover crop biomass. Generally, the earlier sowing date resulted in greater weed suppression, but this depends on the species characteristics and weather conditions. For instance, spring- or autumn-seeded cover crops tend to perform better than a late summer-sown cover crop in dry environments because of the available moisture at time of seeding (Kumar et al., 2020). However, in most environments, autumn-sown cover crops provided greater weed suppression than spring-sown cover crops (Osipitan et al., 2019). As was expected, increasing seeding rate of the cover crop species generally increase the biomass production and soil surface cover. A delay in termination date generally results in subsequent greater weed suppression, irrespective of the management of the cover crop residue (either incorporated or left at the soil surface).

If biomass of cover crop residue is often reported to be correlated to weed suppression, little research is available regarding the composition of cover crop residue (*i.e.*, carbon, nitrogen, lignin, cellulose, and hemicellulose) and its additional effect on weed suppression. Cover crop residue can act as a mulch that will suppress weeds, but as the residue degrades, weed suppression diminishes. However, if the cover crop biomass has high C:N ratio (e.g grasses), it will keep the soil covered longer due to reduced decomposition rate as compared to residue with low C:N ratio (e.g. legumes) and consequently it will increase the duration of weed suppression (Pittman et al., 2020). Grass-legume mixtures could be a good compromise between two services offered by cover crops: N release and weed suppression (Muzangwa et al., 2015).

5.3. Evaluation methods

Classical field experiments comparing the cover crop biomass and effectiveness of termination method could be set up for comparing both species and intraspecific diversity using high throughput phenotyping methods developed for cash crops. To separate the competitive from the allelopathic effects of cover crops, experiments in laboratories, greenhouses, and growth chambers could be useful, although this appears very difficult to implement currently (Mahé et al., 2022). The response of emergence rates of cover crop species and varieties to seedbed temperature and water content could also be tested under controlled conditions and completed by modeling. For instance, the SIMPLE model predicts the emergence duration and rate of crops by considering species and seed characteristics in interaction with seedbed conditions (Constantin et al., 2015).

6. Weed suppression using living mulch acting as companion crops

The term “companion crops” is used when non-harvested species are sown alongside the cash crop either before or at sowing to reinforce weed control, increase beneficial predatory insects and improve soil health (Verret et al., 2017b a-b). When sown simultaneously with the cash crop, cover crops could be considered as intercrops (Malézieux et al., 2009) as seen above. For instance, intercropping frost-sensitive legume crops with winter oilseed rape is now currently used in France in order to reduce weed competition, insect damage, and improve nitrogen use efficiency (Cadoux et al., 2015). Relay cropping consists in sowing one crop into standing second crop prior to its harvest whereby, often, the first crop is cash crop and the second crop is sown either for grain, biomass or cover cropping (Lamichhane et al., 2023). This practice has been shown in several studies to be very effective at helping to manage weeds by suppressing weed emergence (Gesch et al., 2023).

When the harvested crop is undersown directly in an established companion cover crop, this cover is called "living mulch". The different species have to coexist within a plot while maintaining the services provided by each of them, *i.e.* grain production for the harvested crop and weed control, reduction of soil water evaporation and sometimes nitrogen fixation for the cover crop. In such a system, there is a need to find a trade-off between maximising the suppression of weed growth and minimising the reduction of cash crop growth (Cougnon et al., 2022). For instance, undersowing wheat with living mulches decreased crop yield in comparison with wheat cropped alone but this was depending on the biomass of the cover crop (Carof et al., 2007a). In addition, living mulch can act as a weed if the cover crop starts to reproduce and the seeds fall on the soil becoming a new problem to control. This risk is important to consider when choosing a cover crop: its reproduction cycle should be taken into account regarding the following crops.

There is little research on the effects of living mulch on weed and crop emergence. The effect of soil structure on emergence, through a physical barrier effect and an effect on soil hydrothermal conditions, and the effect of mulch on soil properties have been reported as beneficial for the crop (Schlautman et al., 2021). Ryan et al. (2021) showed that mulch has no depressive effect on winter wheat emergence.

It is therefore essential to understand the interactions between harvested crops and cover crops in order to define which combinations of species and varieties will match. Introducing non-selective herbicides for suppressing poor covers and make easier the establishment of new crops or cover crops is a drawback that has to be balanced with the expected reduction of selective herbicides used for controlling weeds during crop season.

As the combinations to explore are numerous, simulation models are essential and should be developed in order to define the relevant associations and then identify the genetic progress to be made as was developed on grassland communities (Faverjon et al., 2019; Louarn et al., 2020).

6.1. Associated traits for both the cover and harvested crops

The choice of cover species and varieties has an effect on weeds (White and Scott, 1991; Petit et al., 2018) but also on cash crop via competition in particular for light, water and nutrients (Bergkvist, 2003; Carof et al., 2007b; Cougnon et al., 2022). The establishment of the cover crop should be fast enough to control weeds but then the growth should be reduced during critical development phases of the harvested crop, *i.e.* corresponding to a short prostrate type. Or, once installed, the cover crop should grow preferentially after the harvested crop has become dominant such as winter dormant cover types with winter crops (Carof et al., 2007a). This can be achieved by screening different morphologies and/or growth dynamics (phenology) between canopy and harvested crop.

Another possibility is to establish the cover crop first, possibly under a previous harvested crop such as sunflower, and then sow a second harvested crop within this cover. For example, a cover of alfalfa could be established in spring and cut in autumn to sow a winter wheat. In that case, the harvested crop should be chosen for having a good establishing potential despite the cover, *i.e.* ability to emerge under a mulch, for example with a large amount of seed reserves allowing a fast autonomous growing. The ability to emerge successfully in such a system is a trait to evaluate among crops and varieties. In addition, traits may be selected in cash or cover crops to facilitate mechanical weed control (residue shredding, harrowing, etc.).

It has been observed in organic farming that the most stable harvested crop varieties for yield are often those that have lower nitrogen requirements, knowing that this criterion is often linked to a better efficiency in converting absorbed nitrogen into yield; therefore, this avenue should also be explored. Furthermore, as it is impossible to always ensure optimal growth of both species, the ability to compensate for a low yield component is a trait to be sought and valued for the harvested crop. For example, in cereals, the decrease in a stand of ears can be compensated by ear fertility, i.e. by the number of grains/m^2 or by the unit kernel weight.

Traditionally, sown forage species or grassland species including new species to be tested, are a good start for building perennial covers (Hiltbrunner and Liedgens, 2008). However, breeding has created productive varieties that may be too competitive with the harvested crop, such as for alfalfa, whose growth has to be slowed down when combined with cereals (Ilnicki and Enache, 1992; Baresel et al., 2018; Radicetti et al., 2018). It might be interesting to screen the genetic resources of these species again with the objective of characterizing ecosystem services such as weed control and nitrogen supply (Cougnon et al., 2022).

The species constituting the perennial cover can also present distinct growth dynamics over time. For example, it is possible to combine a species that establishes very quickly to control weeds but has a short lifespan, with a slower-establishing but more persistent species that will take over *e.g.* fenugreek (*Trigonella foenum graecum*) in combination with alfalfa or clover.

Once the types of both cover and harvested crops have been chosen, it is possible to go further in the selection of co-adapted varieties by breeding directly in mixtures (Sampoux et al., 2020).

Various studies conclude that, in order to maintain several species within an ecosystem, intraspecific genetic diversity could be a determining factor by allowing fine local adaptation of each species (Meilhac et al., 2019). However, little is currently known about the optimal ranges of variability and the key traits.

6.2. Associated agronomic practices

Another way than the choice of varieties to drive the relationship between the harvested and the cover crops is to play with agronomic practices. It would be beneficial to stimulate cash crop growth and resource acquisition in the early phase by increasing its sowing density, reducing row width and choosing varieties with high cover capacity. This also requires genetic resistance to fungal diseases and lodging, both factors favoured by the dense canopy. In the case of a non-N_2-fixing harvested crop such as cereals with a legume cover crop, in the event of early nitrogen deficiency, it would be wise to apply nitrogen earlier in order to favour the growth of the harvested crop and reduce the growth of the permanent cover legume.

The competition of the living mulch with the harvested crop could be reduced mechanically before sowing the harvested crop and during the growing season with specific equipment (Thorsted et al., 2006) or grazing (Jones and Clements, 1993), or chemically with herbicides which could be not environmental-friendly (Bergkvist, 2003; Shili-Touzi et al., 2010).

In conclusion, for harvested crops under perennial cover, the choice of varieties to be sown must be considered jointly for all the species in the agro-ecosystem in a given soil and climate context, with given production objectives and a chosen management. This type of agriculture, with limited inputs, renews basic breeding objectives and opens the way for the use of new species.

7. Shifted crop sowing dates for escaping weed emergence

Depending on the crop species, two opposite strategies (early- vs late sowing) can be considered to reduce weed pressure.

Delayed sowing is relevant for autumn-sown crops, especially cereals. Indeed, the most harmful weeds emerge during the optimal sowing period of the crop (Fried et al., 2008; Perronne et al., 2015; Gaba et al., 2017). A later sowing date leaves more time to weeds to germinate during the summer fallow, leaving fewer weed seeds in the soil to emerge after sowing (Lutman et al., 2013). This technique is even more efficient by using false seedbed, i.e. triggering additional weed seed germination via repeated shallow stubble tillage in the autumn-to-spring season (Rasmussen, 2004). The first stubble tillage stimulates weed seed germination while subsequent stubble tillage controls the emerged weed seedlings and induces new seeds to germinate. In addition, delaying sowing would reduce the competitive advantage of weeds and the relative growth rate would be in favour of the cereal at least for some autumn-emerging weeds such as blackgrass (Andrew and Storkey, 2017). Delayed sowing requires choosing crop varieties to avoid a reduction in yield resulting from suboptimal soil and climatic conditions and a shorter vegetative phase (Shah et al., 2020). Furthermore, due to climate change, it could be necessary to postpone sowing, *e.g.* for winter wheat requiring vernalization, in order to avoid excessive crop development leading to a higher susceptibility to pathogens and frost damages (Minoli et al., 2022). However, the varietal recommandations already take into account both the pedoclimatic conditions and the preceding crop in order to define optimal sowing and harvest time. In particular cases, spring varieties could even be sown in autumn, but later than winter varieties.

Earlier sowing appears as a better strategy for late summer-sown crops such as for oilseed rape, to compete with weeds as fast as possible by targeting a quick canopy closure (Dejoux et al., 2003; Sim et al., 2007b). However, this means that crops and varieties sown can germinate and emerge in relatively dry seedbeds.

A significant advance in sowing dates for spring crops has been observed due to climate change, either by sowing early late-maturing varieties to aim a longer crop cycle and higher yields, or by sowing early varieties at conventional or later dates to avoid end-of-cycle abiotic stresses. In the future, maintaining high stable production for crops such as maize and sunflower can only be achieved by sowing significantly earlier (Minoli et al., 2022). For instance, Wang et al. (2013) indicate that early sowing in spring can increase the yield of lentils, and can be used as an indirect method of weed control in some organic farming systems. However, sowing early in spring under too cold conditions could lengthen the time necessary for a complete canopy closure and/or result in incomplete soil cover promoting predation. Depending on the differential base temperatures of the crop and the weeds (Gardarin et al., 2016; Brown et al., 2022), some weed species with low temperature requirements could be more competitive under such conditions.

7.1. Associated traits

Cereal varieties adapted to late sowing require a set of traits, especially a crop cycle escaping the main biotic and abiotic stresses. The ability to germinate and emerge in harsher conditions (drought, hydromorphy, cold, more compacted soil) is necessary in this context, as well as a better cold tolerance to avoid the risk of frost damage on seedlings with only little hardening (Castel et al., 2017). This will be crucial with climate change where more frost damage is expected because of less hardening during winter.

In straw cereals, the ability to produce leaves more quickly (shorter phyllochron or phyllotherm) may also be relevant to partly escape leaf diseases. Moreover, part of the reduction in potential yield could be offset by an adapted morphogenesis (tillering ability, fertility of the ears, size and weight of the grains), in particular due to a better nitrogen use efficiency (Yin et al., 2019). Cold tolerance and early vigour appear also important for spring varieties sown in autumn or in early spring.

However, in some conditions, the earlier sowing of spring crops could increase the weed pressure, justifying to increase also the canopy cover capacity of these varieties and more generally their ability to grow under sub-optimal temperatures (e.g. soybean - Petcu et al., 2023), as well as traits favouring mechanical weeding, sowing under mulch or for relay cropping.

7.2. Associated agronomic practices

Delayed sowing can be combined with previous false seedbed operations in conditions promoting weed emergence. In this case, the conditions of the last pre-sowing tillage should be relevant because, in moist conditions, this may trigger a new flush of weed emergence (Botto et al., 2000; Juroszek et al., 2002, 2017). The increase of sowing density due to later sowing associated with a superior risk of seed and seedling losses needs to be modulated according to the region and the type of soil to ensure a non-limiting tillering for cereals.

7.3. Evaluation methods

Laboratory experiments on seed germination and pre-emergence growth to determine hydrothermal requirements and sensitivity to soil compaction are required (Gardarin et al., 2016; Nosratti et al., 2023). Field experiments comparing contrasted sowing dates and detailed observations on phenology, canopy development, yield components for a range of crop genotypes grown under weedy and weed-free conditions could be set up and completed by crop modelling.

8. Increased proportion of spring crops in rotations as a diversification strategy

A greater proportion of spring crops in the commonly grown cereal-based rotations allows alternating more frequently between winter and spring crops. This lever is highly effective for managing weed populations by avoiding the development of a specialised weed flora difficult to control in simplified crop sequences (Anderson, 2005, 2015; Adeux et al., 2019; San Martin et al., 2019; Weisberger et al., 2019). Beyond the general effect of preventing the increase of this flora in the soil seedbank each year, alternating sowing periods can greatly reduce the soil seedbank of short-lived seeds of certain weed species (*e.g. Bromus* spp., Blackshaw, 1994). Moreover, alternating spring and autumn sowing periods enables the germination of weed species unable to produce seeds during the crop cycle, such as late-emerging spring weeds in winter cereals or autumn-emerging weeds in spring crops (Chauvel et al., 2001; Gaba et al., 2017). This strategy is expected to be more conducive on weed population changes than delaying or anticipating sowing dates within the same species. To achieve this objective, the performance of spring crops should be improved on a range of criteria whereas their introduction should be combined with other agronomic practices. The range of profitable spring crops should be also extended by significant breeding efforts, especially on minor crops (Peltonen-Sainio et al., 2016).

First, diversifying rotations with new crops, beyond new sowing periods, brings many advantages, among which a better management of weeds, animal pests and diseases. Currently, depending on the production situations, crop sequences are more or less diversified, and the expected gain will be greater for the currently most simplified crop sequences (Adeux et al., 2019, 2022; Weisberger et al., 2019). A set of major or minor crops, eventually in mixtures, can be considered, depending on the production situation (e.g. field pea, sunflower, soybean, buckwheat, flax, camelina), each presenting advantages and disadvantages now and in the future. For weed management, the advantages are based not only on the change in sowing periods, but also on the differences in weeding methods (simplified use of mechanical weeding in crops with wide inter-rows, complementary between active ingredients applied, higher competitiveness of some crop species) (Liebman and Dyck, 1993; Anderson, 2005, 2015).

Second, yields need to be improved and nitrogen fertilisation reduced for several winter crops to diversify the crop sequences, for instance by including a legume-based cover crop sown in autumn to precede the spring cash crop. Successful improvements have been implemented in spring barley in Western Europe, with gains in yield and protein content associated with a reduction of inputs (Cabeza-Orcel, 2020). However, these modifications have been largely neglected for spring wheat by breeders and farmers, as this crop almost completely disappeared in favour of winter wheat varieties in France. Increasing the proportion of spring wheat would provide the same benefits as barley, but their adoption can only be done in case of genetic improvement.

8.1. Associated traits

Introducing more spring crops in the rotation in a context of increasing water shortage and air temperature will require more drought-tolerant species and genotypes in case of normal sowing date, under rainfed or limited irrigation conditions. As crop adaptation to climate change means avoiding or escaping water and heat stresses by earlier sowings, early vigour and cold tolerance at early developmental stages will be targeted traits for breeding to rapidly cover the soil (Debaeke et al., 2021). The cold tolerance must be improved by reducing the sensitivity to low temperatures, particularly during the floral transition and increasing the ability to produce biomass at suboptimal temperatures (Allinne et al., 2009; Yi et al., 2021). The flowering date must be chosen to be appropriate to the duration of the crop cycle while the harvest index should be improved to increase yield potential without focusing solely on earliness group. Varieties must provide yield gain by increasing fertility of ears and grain weight for spring cereals. Such breeding goals would also make it possible to provide varieties that are probably less water-consuming by escaping the most evaporative periods.

8.2. Associated agronomic practices

The choice of spring crops can be combined with early sowing under mulch or under cover crop, either in permanent cover or in case of relay cropping. Sowing of spring crops can be tied up to a potentially simplified use of mechanical weeding in row crops as well as the use of available herbicides when necessary. In conditions where irrigation is fully available, several spring crops (e.g. soybean, sunflower, sorghum, maize, buckwheat, camelina) could be sown as double crops after early-harvested winter crops (e.g barley, pea, rapeseed) increasing rotation diversity (Pitchers et al., 2023). This will require very early maturing crops in order to complete the cycle and allow autumn harvest in a reasonable time window (Debaeke et al., 2021).

8.3. Evaluation methods

Most of the phenotyping methods have been developed on cereals, mainly wheat and maize, with some applications on oilseed rape, sunflower and pea (Jeudy et al., 2016; Tardieu et al., 2017; Gosseau et al., 2019). Increasing cultivated diversity will require generic tools and protocols for getting information and analysing the traits for a wider range of crop species. This will concern in priority drought, cold and heat tolerance. Field and controlled high-throughput platforms will be completed by ecophysiological modelling and multi-environment trials for evaluating a wide range of genotypes and environments in relation with genotypic data (Araus and Cairns, 2014; Ghanem et al., 2015; Xie and Yang, 2020). For example, the suitability of soybean in Europe and the optimal maturity groups to grow as a function of irrigation availability was explored using ensemble crop modeling and future climatic scenarios (Nendel et al., 2023).

9. Selectivity of mechanical weed control

Mechanical weeding is one of the most important alternatives to chemical weed control, particularly in wide row crops (some annual spring crops, fruit species and vine, Chicouene, 2007; Peruzzi et al., 2017; Fogliatto et al., 2019). However, mechanical weeding requires specific equipment depending on the crop, the production situation and the targeted weed flora, and its efficacy is often reduced by inappropriate soil and weather conditions. In order to ensure the widest management window in each production situation and maximize the selectivity, varieties must have traits suitable for mechanical weeding techniques, especially hoeing, harrowing and rotary hoeing, including intra- and inter-row weeding depending on the developmental stages of the crops and the weeds (Fogelberg and Dock Gustavsson, 1998; Rasmussen et al., 2004; Osman et al., 2016). Beyond genetic improvement, the implementation of new practices must also be done, such as sowing with wider inter-rows to facilitate hoeing or/and relay cropping to increase competition with weeds (Kolb et al., 2010; Melander et al., 2018; McCollough and Melander, 2022; Gesch et al., 2023).

9.1. Associated traits

A set of traits should be studied and improved to ensure a better selectivity of mechanical weeding operations. To improve weed control efficiency and accuracy over a wider application window, considering a same inter-row distance, an erect growth habit would be more relevant, although appearing potentially antagonistic to a higher canopy cover capacity at early stages of the crop cycle. However, barley varieties with a high seedling density after a pre-emergence harrowing and tall at post-emergence harrowing benefit most from mechanical weeding (Hansen et al., 2007). Currently, it is possible for farmers to choose straw cereal varieties that are either more covering or more upright and characterized by different earliness (Lever et al., 2022b), in order to minimize the negative impact of mechanical weeding operations. As an example, concerning harrowing, taller higher-yielding barley genotypes with a high leaf area index (LAI) tend to be less tolerant to post-emergence weed harrowing than shorter and lower-yielding genotypes with a low LAI. However, although being most damaged, these taller high-yielding genotypes remained the highest yielding after weed harrowing (Rasmussen et al., 2004). In case of use of tine harrow or rotary hoe for weeding, varieties could be less sensitive to weeding by improving their root anchorage as well as their earliness and vigour. If the crop is sown deeper, the growth speed and length of the coleoptile or hypocotyl as well as their tolerance to soil compaction must be increased to reduce pre-emergent seedling loss, these traits being correlated to seed reserves and embryo size (Rebetzke et al., 2007; Fayaud et al., 2014; Gardarin et al., 2016). Wider inter-rows, especially in straw cereals, could result in a lower yield, depending on mechanical weeding method and weed pressure (Melander et al., 2003, 2018; Rasmussen, 2004; Kolb et al., 2010; Gerhards et al., 2020; McCollough and Melander, 2022). However, the crop proportion that has been covered by soil due to weed harrowing could also decrease yield in some conditions (Rasmussen et al., 2010; Rueda-Ayala et al., 2011), depending on the straw cereal species (Rasmussen et al., 2009).

9.2. Associated agronomic practices

Several agronomic practices need to be considered to ensure a better selectivity of the mechanical weeding operation in straw cereals. These levers include the timing, the direction and the orientation of the weeding operation, the interrow width, the number of passes and the speed during the operation, as well as the nitrogen rate, fertilizer placement and the moisture conditions during the operation (Rasmussen et al., 1996; Kurstjens et al., 2000; Melander et al., 2003; Rasmussen, 2004; Rasmussen et al., 2008; Rasmussen et al., 2010; Fogliatto et al., 2019; Melander et al., 2018). However, these levers have generally not been studied on a range of genotypes. Moreover, only a few studies focused on potential trade-offs between the competitiveness of genotypes, their tolerance to weeding and their impacts on weed development (Rasmussen et al., 2004; Hansen et al., 2007), limiting recommendations on the relevant ideotype (Lever et al., 2022a).

9.3. Evaluation methods

Several methodologies have been developed to assess the tolerance and selectivity to mechanical weeding, including visual assessments using a predefined grading scale and digital image analysis with an automated procedure, information being obtained prior and just after weeding operation (Hansen et al., 2007). Moreover, mechanical weeding techniques have made significant progress using camera-guided for hoeing in order to reduce the injuries on crop plants (Gerhards et al., 2020).

10. Use of allelopathic crops

The use of crop plants able to produce allelochemicals capable of significantly inhibiting the germination and/or growth of certain weeds is frequently proposed as an additional lever for weed management (Singh et al., 2003; Khamare et al., 2022; Hickman et al., 2023). This capacity has been extensively studied under controlled conditions, but rarely in field conditions (Mahé et al., 2022). Indeed, field trials face a main problem, *i.e.* dissociating allelopathy from other mechanisms. Considering allelopathy by living crops, the main challenge is to discriminate allelopathy from competition, as these two mechanisms occur concomitantly in field conditions (Worthington and Reberg-Horton, 2013; Kunz et al., 2016; Reiss et al., 2018a, 2018b). A systematic review of the literature identified that, in most published field trial studies, the role of crop competition is disregarded or not exhaustively studied (Mahé et al., 2022). Actually, only few articles provide convincing evidence of allelopathy in the field and, even for these studies, a key role of competition could not be totally excluded. Therefore, in spite of strong expectations regarding this mechanism, to which extent allelopathy by living crops can provide a lever to regulate weeds remains an open question.

When considering allelopathy by crop residues (used as dead mulch or incorporated into the soil), the difficulty is to dissociate the effects of allelopathy from those of nitrogen immobilization generated by crop residue decomposition. Indeed, immobilization can alter soil nitrogen dynamics, affecting plant nutrition in the following crop and generating potential confounding effects (Doré et al., 2004). Some studies nonetheless provided some field-based evidence of allelopathy by residues on weeds (Petersen et al., 2001). In this situation, care should be taken to avoid adverse allelopathic effects of residues on the growth of the following cash crop or/and cover crop (Mennan et al., 2020). In this context, even though many papers identified allelopathy as a key mechanism to target towards sustainable weed management (*e.g.* Singh et al., 2003; Scavo and Mauromicale, 2021), it is necessary to remain cautious given the difficulties to quantify the effects in the field.

Another aspect is that the allelopathic capacity of a variety must not adversely affect plants of the same variety or/and companion plants. Such a trade-off was observed in straw cereals, with a negative correlation between allelopathic potential and crop yield (Bertholdsson, 2010). Conversely, other studies found no correlation between allelopathic capacities observed under controlled conditions and competitive ability and grain yield loss in winter wheat in fields (Worthington et al., 2015b). Improving the allelopathic capacity via plant breeding seems to be possible in rice (Kong et al., 2011) but getting information about the key metabolites released and how they are transformed in the rhizosphere seem crucial before investments from breeders (Hussain et al., 2022). Other ways of using allelochemicals could be to introduce or reintroduce crops (known for their allelopathic capacities under controlled conditions) into rotations as cover crops (living or dead mulches) or to incorporate crop residues into the soil (Jabran et al., 2015; Scavo and Mauromicale, 2021).

10.1. Associated traits

Crop traits associated to allelopathy mainly refer to the nature and the intensity of emission of allelochemicals (Reiss et al., 2018a, 2018b; Mwendwa et al., 2021). Allelochemicals have been considerably documented for different crop species (Hickman et al., 2023), i.e. either used as cash crops (rice, sorghum, sunflower, wheat, barley) or cover crops (rye, different Brassicaceae). However, the performance of allelopathic crops on weeds can be very variable. Indeed, the emission of allelochemicals is highly dependent on environmental conditions, while the sensitivity of weeds to these allelochemicals also depends on the species and the phenological stage. The extension of the root system should also be important to explain the influence of allelochemicals on weed control.

10.2. Associated agronomic practices

The choice of the crop species and variety has been so far the most studied factor (Scavo and Mauromicale, 2021). Other cropping techniques may also be involved, such as seeding rate and date (influencing the intensity and timing of allelochemical emission) and fertilisation (allelochemical production can vary with the nutritional status of the crop). For allelopathy by crop residues, authors recommend that the residues of crops with a high allelopathic activity be incorporated into the soil after their destruction (Mennan et al., 2020).

10.3. Evaluation methods

Several methodological devices have been developed under controlled conditions (*e.g.* Wu et al., 2000; Jensen et al., 2008), but so far very few studies rigorously evaluated the effects of allelopathy by living plants of different crop varieties on weeds under field conditions. Indeed, quantifying the effects of allelopathy in the field requires combining several types of experiments on the same varieties (*i.e.* field measurements on weeds and crop varieties, and assessment of allelopathic potential in laboratory), with the measurements of many traits at different stages (to characterise both competition and allelopathy) and relevant statistical methods to cross data (*e.g.* multiple regression) (Mahé et al., 2022). Applying such approaches in crop breeding programs would be particularly tricky, as well as time- and cost-consuming, to improve the allelopathic capability (Hussain et al., 2022), although early results suggest potential for cereal breeding (Reiss et al., 2018a). Even though allelopathic capacity differs among genotypes, substantial research is still needed to develop methods suitable for screening lines in field conditions and breeding procedures to improve genotypes (Worthington and Reberg-Horton, 2013; Scavo and Mauromicale, 2021; Hussain et al., 2022; Mahé et al., 2022; Rebong et al., 2023).

11. Exploration of genetic diversity for non-chemical weed management

The assessment of genetic diversity and heritability of targeted traits is a preliminary step in a breeding program. We identified several priority avenues for the contribution of plant breeding to integrated weed management and more generally to non-chemical weed control (Fig. 1). Before being included in a breeding program, new traits need to be examined on variety trials to identify the most interesting phenotypes. For instance, varieties with rapid canopy closure could be detected more easily in the near future with on-board sensors or drones, which are becoming affordable equipments for breeding companies, technical institutes or examination offices.

11.1. Developing competitive varieties for cash and cover crops

In general, choosing competitive genotypes is a low-cost lever for integrated weed management to reduce the dependence of cropping systems on herbicides. The genetic diversity of the canopy cover capacity is wide among genotypes as well as between straw cereal species (Huel and Hucl, 1996; Coleman et al., 2001; Fontaine et al., 2009;

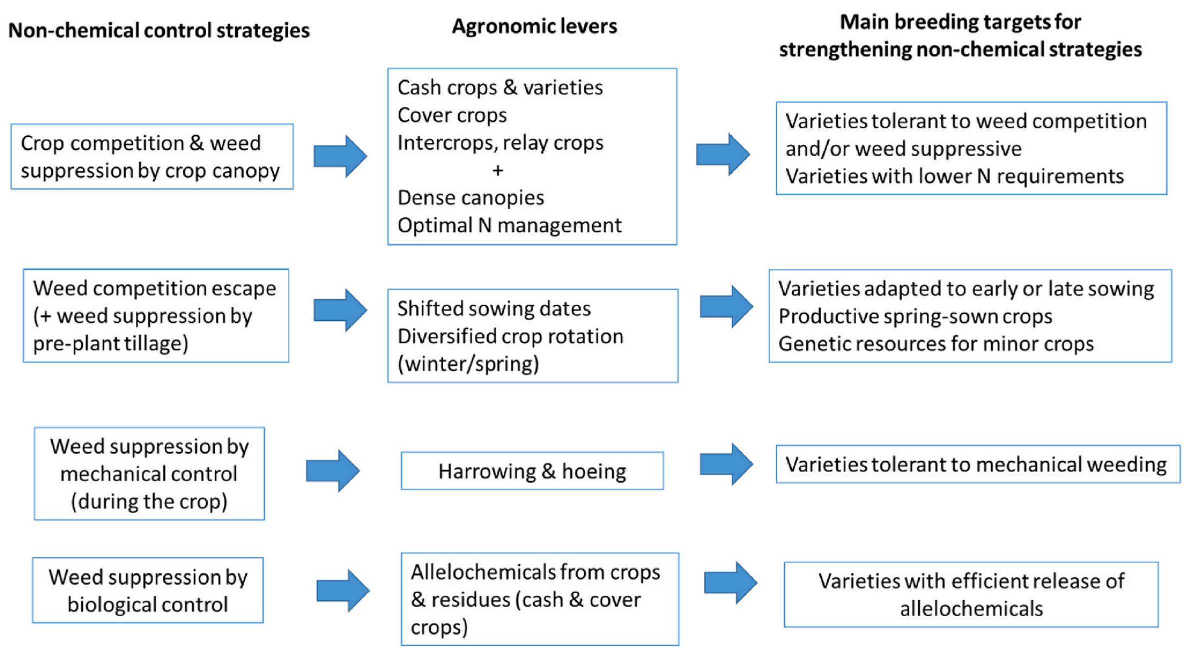

Fig. 1. Non-chemical weed control strategies, agronomic levers and main breeding targets.

Worthington et al., 2015a), but is still underused (Pester et al., 1999; Benaragama et al., 2014; Rolland et al., 2017; Aharon et al., 2021; Hendriks et al., 2022; Lever et al., 2022a). Research and development projects have identified bread wheat varieties with contrasting canopy cover capacity at various stages of development (Fontaine et al., 2008; Massot et al., 2018). However, no variety was characterized by a high canopy cover capacity until flowering so far. Furthermore, traits affecting canopy cover capacity (early vigour, earliness at various stages, height, leaf growth, leaf area and tillering capacity) are partially independent or positively correlated. Only a few studies evaluated correlations among traits until now (*e.g.* Murphy et al., 2008; Fontaine et al., 2009; Hendriks et al., 2022), opening the way to the selection of new combinations of traits. Indeed, it is possible that two varieties have a similar ability to compete with weeds due to different combinations of traits (*e.g.* for winter wheat high tillering ability, small leaves and semi-erect growth habit vs low tillering ability, large leaves and high spreading or creeping growth), as has also been shown in simulation studies (Colbach et al., 2022). Canopy cover capacity being an integrative trait, it seems more relevant to investigate the genetic determinism of each specific component. However, apart from wheat, very few studies reported such results on other crops although there is probably intraspecific variability to exploit. In oilseed rape, Sim et al. (2007a) in UK and Lemerle et al. (2014) in Australia reported some evidence of differential competitive tolerance between genotypes. Moreover, developing soybean varieties with rapid canopy closure is now an objective for organic farming in Switzerland (Klaiss et al., 2020).

11.2. Developing crop varieties tolerant to mechanical weeding

Developing varieties more tolerant to mechanical weeding represents a potential avenue of research (Osman et al., 2016). Indeed, even if few studies have been conducted until now on a low number of genotypes, there is genetic variability on tolerance to mechanical weeding within straw cereal species (Rasmussen et al., 2004; Hansen et al., 2007), as well as among different species (Rasmussen et al., 2009).

11.3. Developing crop varieties tolerant to N deficiency or with lower N requirement

Developing varieties of cereals tolerant to N deficiency could be a way to disadvantage nitrophilic competitive weeds. Genetic diversity is high in wheat regarding traits allowing lower nitrogen requirements, increased N use efficiency and tolerance to temporary nitrogen deficiencies (Cormier et al., 2016). A large number of QTLs related to the nitrogen status of the plant have been identified in cereals such as wheat (Laperche et al., 2007) and rice (Sandhu et al., 2021). This strategy, as a part of integrated weed management, is obviously restricted to cereals and probably oilseed rape, which receive the highest rates of N fertilisation.

11.4. Breeding spring-sown crops adapted to early sowing

The decision to include more spring-sown crops to diversify the crop rotation in the central and northern parts of France and Europe especially depends on the availability of adapted varieties which means early-maturing groups (e.g. sunflower and soybean) as was done for maize in the past decades. Growing summer crops at higher latitudes and sowing earlier with climate change will require cold tolerant varieties expressing a good early vigour for a rapid canopy closure. In recent years, considerable progress has been made in elucidating the mechanisms of maize in response to cold tolerance and large differences in the morphological and physiological changes (seed germination, root phenotypes, shoot photosynthesis) caused by cold stress have been explored among maize varieties highlighting tolerant genotypes (Zhou et al., 2022). Jähne et al. (2019) identified a cold tolerance-specific QTL in soybean that is important for increased chilling stress tolerance, especially when flowering occurs.

11.5. Better exploiting the allelopathic properties of crops

The genetic diversity of the allelopathic capacity is high among genotypes in controlled conditions, being however highly dependent on assessment methods and conditions (Wu et al., 2000, 2003; Bertholdsson, 2005, 2010; Jensen et al., 2008; Chung et al., 2020; Debaeke et al., 2021). Allelopathic capacity of crop genotypes has been demonstrated as a quantitative trait for wheat and rice in controlled conditions (Wu et al., 2003; Jensen et al., 2008; Vieites-Álvarez et al., 2023). Several works identifying QTLs linked to the allelopathic capacity have highlighted relevant chromosome regions for both wheat (Wu et al., 2003) and rice in these controlled conditions (Jensen et al., 2008; Chung et al., 2020). However, in straw cereals, a negative correlation between the allelopathic capacity and the yield of the variety was found as part of a breeding program (Bertholdsson, 2010). Rye germplasm also exhibits large variability in allelopathic activity, which could be used to breed rye with enhanced weed suppression for cover cropping (Rebong et al., 2023). Moreover, no work has been done on data obtained under field conditions due to the difficulties associated with the evaluation of allelopathy in the field (Mahé et al., 2022).

12. Conclusion

Reducing the reliance of agriculture on synthetic herbicides represents a major challenge to take up in order to successfully achieve the agro-ecological transition. Sustainable and integrated weed management requires the development of combinations of solutions using different levers with cumulative partial effects, usually depending on the production situations (Bond and Grundy, 2001; Hatcher and Melander, 2003; Moss, 2019; Birthisel et al., 2021). Genetic improvement leading to breeding of new genotypes constitutes one of the key lever, both for improving competitiveness against weeds and for enabling the implementation or increasing the efficiency of key agronomic practices (Rasmussen et al., 2004; Osman et al., 2016; Lever et al., 2022a; Weiner, 2023). Accelerating research on weed competitive crops should lead to more economical, effective and feasible integrated weed management programs for all crops.

The relevant functional traits are numerous and characterized by effects that can be additive, synergistic but also antagonistic, furthermore depending on environmental conditions and agronomic practices. Mobilizing genetic resources in absence of sufficient variability in the elite varieties could be necessary, as well as developing and selecting new crops to be introduced in rotations, intercrops and cover crops.

The diversity of traits potentially useful for weed management raises the question of the prioritization of their genetic improvement and their inclusion into future breeding schemes. In view of the huge task represented by testing all the relevant functions and the underlying trait combinations for a set of species and production situations, it is clear that modelling and predictive approaches remain to be developed and applied to help breeders identifying the most influential crop traits and the promising ideotypes (Bastiaans et al., 1997; Jeuffroy et al., 2014; Martre et al., 2015; Tao et al., 2017; Colbach et al., 2021, 2022). In addition, there are trade-offs between traits during the breeding process that are important to evaluate through the study of their genetic determinants. This work will be made achievable by the steady improvement of the phenotyping methods for measuring traits and proxies with regard to technological advances in machinery, remote sensing and data science (Tardieu et al., 2017). Current variety assessment (designs and protocols) also needs to be updated to better take account of the diversity of production situations, species and varieties.

Furthermore, targeted traits for improving weed control, although important, can only be considered among a set of other traits under selection. Considering together a set of complex traits within a breeding scheme can be a particularly difficult task. Many breeding programs already use traits and QTLs related to vigour and phenology (*e.g.* Hendriks et al., 2022). Focusing specifically on traits for increasing weed control through a pre-breeding program is a time-consuming and complex activity to set up which needs to identify the most relevant traits to target. Highlighting the main traits to target and the relevant evaluation methods requires previous research. Moreover, some species which can be used as cover or companion crops have been neglected by breeders, especially due to their lower profitability. Relaunching breeding programs by increasing the interest in these species should make them more attractive to farmers. For decades, breeding activity was focusing mainly on the genotypes of a crop species, the phenotypic assessments of these multiple genotypes taking place in the same environment, mostly without taking into account other management levers (mechanical weeding, companion crops). Faced with the double challenge of the agro-ecological transition and climate change, breeders would benefit from designing with agronomists and weed scientists more relevant plant ideotypes (Rebong et al., 2023; Weiner, 2023).

The objective of weed control must not make us forget the relationship between the cost of the investment and the impact on crop production, with the maintenance of yield and quality that can be valued by the crop markets. A thorough analysis of the benefits and costs of enhancing crop competitiveness is probably needed. The key scientific cooperation between geneticists and agronomists must also encompass other research disciplines and co-innovation with the agricultural sectors, thus conditioning the expression of the expected agro-ecological functions due to the varieties used. Given the diversity of cropping systems and production situations that must be preserved and developed as an insurance of resilience in the face of climatic and economic hazards, the best combinations of levers mentioned in this review cannot be stated *a priori* for a given year over the entire country. It will have to be assessed on a case-by-case basis by each farmer in his/her own production system according to the economic and climatic context of the year, his/her technical possibilities (working time, equipment and weed control solutions available). It is therefore important to present a wide range of technical combinations that can be tested, sometimes antagonistic, so that farmers can choose those that should work for them each year. Competitive crops should certainly be more available in the future as part of a reliable and profitable integrated weed management package for farmers.

CRediT authorship contribution statement

Philippe Debaeke: Writing – review & editing, Writing – original draft, Supervision, Investigation, Conceptualization. **Rémi Perronne:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Conceptualization. **Nathalie Colbach:** Writing – review & editing, Writing – original draft. **Delphine Moreau:** Writing – review & editing, Writing – original draft. **Philippe Barre:** Writing – review & editing. **Fabien Lecouviour:** Writing – review & editing. **Mylène Durand-Tardif:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare to have no financial interests/personal relationships which may be considered as potential competing interests.

Data availability

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

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