The response of weed and crop species to shading: Which parameters explain weed impacts on crop production?

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Nathalie Colbach[1*], Antoine Gardarin[2], Delphine Moreau[1]

[1] Agroécologie, AgroSup Dijon, INRA, Univ. Bourgogne, Univ. Bourgogne Franche-Comté, F-21000 Dijon

[2] UMR Agronomie, INRA, AgroParisTech, Université Paris-Saclay, 78850 Thiverval-Grignon, France

* Address for correspondence
Nathalie Colbach
INRA
UMR1347 Agroécologie
BP 86510
17 rue Sully
21065 Dijon Cedex
France
Nathalie.Colbach@inra.fr

Highlights

- Virtual experiments were run for diverse regions, cropping systems and weed floras
- Plant-morphology and shade-response parameters were related to crop production
- The same parameter values promote crop and weed species in mixed canopies
- Successful species reduce leaf thickness and are taller and wider per unit biomass
- There is a trade-off between yield promotion and weed suppression traits

Abstract

Crops compete with weeds for light, and choosing competitive crop species contributes to managing weeds. The objective was to identify which crop and weed parameters related to competition for light drive weed harmfulness for crop production. In a previous experiment, we measured parameters to characterize species potential plant morphology in unshaded conditions and species response to shading for a range of 60 crop and annual weed species. Here, we integrated the measured parameter values into an existing simulation model that uses an individual-based 3D representation of crop-weed canopies to predict weed dynamics and crop production from pedoclimate and cropping system information. The model, i.e. FLORSYS, was used to run virtual experiments in seven French and Spanish regions, with 272 cropping systems varying in terms of crop rotations, herbicide use and tillage intensity etc. A series

of statistical methods (RLQ, fourth corner analysis, Principal Component Analysis, Pearson correlation coefficients, analysis of variance) were used to identify the key weed and crop parameters that drive crop yield loss and other weed harmfulness indicators. The weed species that caused the highest yield loss had a large leaf area at emergence. When young, they presented a large specific leaf area and a uniform leaf area distribution along plant height. They were also taller per unit plant biomass and their populations were more homogeneous in terms of plant width. At later stages, harmful weed species presented a smaller interception area to herbicides, with thicker leaves located lower on the plant. When shaded, harmful weed species shifted their leaves upwards and decreased their plant width per unit biomass. Weed-suppressive crop species had a large specific leaf area, wider plants per unit biomass, and a uniform leaf area distribution along plant height. When shaded, they increased their plant height and width per unit biomass. There was a trade-off between parameters driving potential crop production and those minimizing weed-inflicted yield losses.

Keywords. Weed damage; trait; photosynthetically active radiation PAR; yield loss; yield gap; ideotype

1 Introduction

When herbicide use is reduced due to environmental and health issues, crops are more often confronted to competition with weeds. In temperate climates with high-input crop management, the main resource for which crops and weed compete is light. As a consequence, choosing light-competitive crop species and varieties is a major lever for non-chemical weed management (Drews et al., 2009; Paynter and Hills, 2009; Mhlanga et al., 2016). Once emerged, species competitiveness for light depends on how much light a species intercepts and how little it leaves to competing species. In terms of growth, this translates into three questions: how fast a species occupies empty space, how much space it occupies, and how it avoids shading or reacts to shade.

Field trials can investigate the effects of cultural techniques that drive canopy structure (e.g. crop species, cultivar, sowing density and interrow width) on weed biomass and/or crop production (Kristensen et al., 2006; Olsen et al., 2006; Drews et al., 2009; Paynter and Hills, 2009). These experiments though often focus on one or a few crop and/or weed species in a single location, disregarding long-term effects, thus lacking in genericity. Consequently, mechanistic models have been developed to describe processes in detail (e.g. light interception, absorption and transformation) at the scale of crop canopies or single plants within these canopies (Renton and Chauhan, 2017). The earliest of the crop-weed competition models considered bispecific homogeneous crop-weed canopies based on detailed ecophysiological functions driving crop-weed competition for light and other resources (Spitters and Aerts, 1983; Wilkerson et al., 1990; Kropff and Spitters, 1992). These were later updated to 3D individual-based bispecific competition models (Brainard and Bellinder, 2004). Conversely, the earliest multiannual weed dynamics model simplified competition processes to include weed seed bank

processes and impacts of cultural techniques (Cousens et al., 1986; Ballaré et al., 1987; Debaeke, 1988). The combination of the two approaches led to individual-based three-dimensional models combining simplified 3D plant representation with multiannual species dynamics and detailed effects of cultural techniques. Such models are the best compromise to represent heterogeneous crop-weed canopies and test contrasting cropping systems with different weed floras and pedoclimatic conditions (Colbach et al., 2014a).

The process-based FLORSYS model follows this principle. It simulates multi-specific and multi-cohort weed dynamics and their impact on crop production as a function of cropping systems and pedoclimate, at a daily scale over several years or decades (Gardarin et al., 2012; Munier-Jolain et al., 2013; Colbach et al., 2014b; Munier-Jolain et al., 2014). The 3D multispecies crop-weed canopy consists of individual plants whose leaf area is distributed inside cylinders, predicting light availability in each 3D pixel ("voxel") (Munier-Jolain et al., 2013; Munier-Jolain et al., 2014). In addition to light availability, plant dimensions and leaf area are driven by species parameters determining early growth, potential plant morphology and shading response (Colbach et al., 2014b; Colbach et al., in revision). Shading response is a key process in plant-plant interaction, particularly in multispecies heterogeneous canopies where morphological plasticity allows weeds to avoid shade cast by crops (Cavero et al., 2000). The latter model as well as earlier crop-weed competition models (Kropff et al., 1992) have already been used to identify pertinent weed state variables (e.g. weed biomass) linked to crop yield loss, similarly to what was already attempted in field trials (Regnier and Stoller, 1989; Pike et al., 1990; Cavero et al., 1999).

Previous models worked with state variables describing crops, weeds and canopies, which vary with plant stage as well as cultural and pedoclimatic conditions. Conversely, in the present study, we worked with generic universally valid parameters that describe plant properties intrinsic to a species, focusing on those crucial for plant-plant interaction, i.e. those related to plant morphology and shade response. This switch from site-dependent to intrinsic species properties is essential to draw generic conclusions valid in a large range of situations. The objective of the study was to use the FLORSYS model to run a multi-site, multi-annual and multi-species simulation (i.e. a virtual field network) in order to investigate (1) which annual weed species and weed parameters drive crop yield loss due to crop-weed competition for light and other weed impacts on crop production, (2) which crop species parameters reduce this competition-driven yield loss, and (3) at which plant stages the parameter values are crucial for the outcome. The final aim was to identify crop ideotypes (i.e. theoretical ideal crop plants that combine all the characteristics required to reach one or several goals in a production situation, Martre et al., 2015) for arable cropping systems in order to promote weed suppression by crop competition.

2 Material and methods

2.1 The "virtual-field" model FLORSYS

2.1.1 Weed and crop life cycle

FLORSYS is a virtual field on which cropping systems can be experimented with a large range of virtual measurements of crop, weed and environmental state variables. The structure of FLORSYS is presented in detail in previous papers (Gardarin et al., 2012; Munier-Jolain et al., 2013; Colbach et al., 2014b; Munier-Jolain et al., 2014; Mézière et al., 2015).

The input variables of FLORSYS consist of (1) a description of the simulated field (daily weather, latitude and soil characteristics); (2) all the crops and management operations in the field, with dates, tools and options; and (3) the initial weed seed bank, which is either measured on soil samples or estimated from regional flora assessments (Colbach et al., 2016). These input variables influence the annual life cycle of annual weeds and crops, with a daily time-step. Pre-emergence stages (surviving, dormant and germinating seeds, emerging seedlings) are driven by soil structure, temperature and water potential. Post-emergence processes (e.g. photosynthesis, respiration, growth, shade response) are driven by light availability and air temperature. At plant maturity, weed seeds are added to the soil seed bank; crop seeds are harvested to determine crop yield. Crop-weed competition was considered for light only in the present FLORSYS version. The model is currently parameterized for 25 frequent and contrasting annual weed species, 11 cash crop species (sold for profit) and 15 cover and forage crop species (grown for services and not for sale), including several varieties of wheat, field bean and pea (section **A.2** of the supplementary material online).

2.1.2 The parameters driving morphology and shading response

Early post-emergence growth, potential plant morphology and response to shading by neighbours are key processes that drive crop-weed competition and that determine how fast plants occupy space once they emerge, how much space they occupy and how they try to capture light when surrounded by neighbour plants. In FLORSYS (which considers water and nutrient conditions to be non-limiting), these processes are driven by temperature and light. Species strategies are described by 145 parameters measured either in field trials (Munier-Jolain et al., 2014) or in garden plot experiments (Colbach et al., in revision). Early post-emergence plant growth in the absence of shading is driven by two parameters per species, i.e. leaf area at emergence and plant relative growth rate, which determine how fast a species occupies the field after emergence (Table 1, and section B online). Potential plant morphology in unshaded conditions depends on eight parameters per species and stage for 11 plant stages. These parameters determine plant dimensions, its leaf area and leaf area distribution along plant height. A further five parameters per species and stage drive species response to shading, determining whether shaded plants invest more into plant height versus width or into leaf versus stem biomass, and whether they shift their leaves upwards or downwards.

2.1.3 Effect of cultural techniques

Life-cycle processes depend on the dates, options and tools of management techniques (tillage, sowing, herbicides, mechanical weeding, mowing, harvesting), in interaction with weather and soil conditions on the day the operations are carried out (section A.3 online). For instance, weed plant survival probabilities are calculated deterministically depending on management operations, biophysical environment as well as weed morphology and stage; the actual survival of each plant is determined stochastically by comparing this probability to a random probability.

2.1.4 Indicators of weed impact on crop production

FLORSYS simulates crop yield as well as a set of indicators assessing weed impacts on crop production (Mézière et al., 2015) (see section **A.4** online). Here, we investigated (1) crop grain yield loss which is the difference in yield in weed-including vs weed-free simulations relative to yield in weed-free simulations, (2) harvest pollution by weed seeds and debris resulting from weed biomass and seeds harvested with the crop grain, and (3) field infestation by weed biomass during crop growth. In addition, (4) annual weed seed production in crops was examined, as a proxy for the risk of future weed infestations. Finally, (5) potential crop yield was analysed, predicted by the weed-free simulations. To make yields of different crop species comparable, yield in MJ/ha (instead of t/ha) was preferred, multiplying the grain yield in t/ha by its energy content (see details in Lechenet et al., 2014).

2.1.5 Domain of validity

FLORSYS was previously evaluated with independent field data on weed short and long-term dynamics at French national scale, over a large range of existing arable cropping systems. It showed that crop yields, daily weed species densities and, particularly, densities averaged over the years were generally well predicted and ranked as long as a corrective function was added to keep weeds from flowering during winter at more southern latitudes (Colbach et al., 2016). A further critical analysis of yield loss was carried out in a previous simulation study covering the same regions as and cropping systems that were used here (Colbach and Cordeau, 2018). They concluded that the model's prediction quality was adequate for the model's purpose, i.e. to predict orders of magnitude and to rank situations in terms of cropping systems and crop species. Higher crop yield losses than those reported in previous field studies mostly resulted from the simulation plan. This does not adapt practices to simulated weed floras and interannual weather variability (as farmers or trial managers would do), in order to discriminate the effect of crop species and management practices on weeds from the effect of weeds on the choice of crops and practices (Colbach and Cordeau, 2018).

2.2 The simulated field network

A virtual field network was simulated combining (1) a large number of contrasting cropping systems from several regions, (2) different weather series, and (3) presence or absence of weeds. Several sources were used to gather data on contrasting cropping systems from six French regions (Burgundy, Paris region, Aquitaine, Poitou-Charentes, Lorraine, Picardie) and one Spanish region (Catalonia). These systems were all already used in previous simulation studies (find the detailed list of sources and references in Colbach and Cordeau, 2018) and were reused here, focusing on different factors and impacts, to tackle our new research questions. In total, 272 arable cropping systems were simulated with FLORSYS (section **C** online). They included both conventional and organic systems, with a tillage intensity varying from no-till to annual mouldboard ploughing. Rotations were mainly based on cereals (wheat, barley, maize) and oilseed rape, with occasional legume crops (lucerne, faba bean etc), non-legume broadleaved crops (sunflower, flax etc) and temporary grassland, with proportions and crop species depending on regions.

Two series of simulations were run. The first simulated the cropping systems starting with a typical regional weed seed bank consisting of the 25 annual weed species currently included in FLORSYS (section **A.2** online). The second series ran without an initial weed seed bank. Comparing series 1 and 2 gave the weed impact on crop production and led to calculating a crop yield loss due to weeds.

In each series, each cropping system was simulated over 27 years (running from summer to summer), repeating the basic rotational pattern (e.g. oilseed rape/wheat/barley) over time. For each region, a typical soil (texture etc.) was based on soil analyses from locations inside the simulated regions (section **C.2** online). Daily weather variables were recorded by INRA weather stations in the different regions (INRA Climatik platform) and by the experimental station La Tallada in Catalonia. Each system was repeated 10 times with 10 different weather series consisting of 28 randomly chosen weather (calendar) years from its region of origin, using the same 10 series for each system of a given region.

2.3 Statistics

First, we analysed which weed parameters drive crop yield loss and other indicators of weed harmfulness for crop production. RLQ analyses were used to identify significant relationships between weed-impact indicators and weed species parameters, using the library ade4 (Chessel et al., 2004) of R (R Core Team, 2016). The RLQ analysis was initially developed to analyse correlations between cultural techniques (R matrix) and species traits (Q matrix) via weed species densities (L matrix). Here, we used annual indicator values of yield loss, harvest pollution and field infestation from the 27 simulated years and 10 weather repetitions for the R matrix. The Q matrix consisted of the 145 parameters of Table 1 for the 25 weed species in FLORSYS. These parameters discriminate species for their ability to compete for light. The L matrix comprised the plant density of each weed species for each of the 27 years and the 10 repetitions, using the maximums of the daily weed species densities between crop sowing and harvest.

Only parameter-indicator relationships significant at p=0.05 after a 4th corner analysis were considered, using the fourthcorner() function of R. This analysis tests whether species are distributed independently of their effect on indicators and of their traits, retaining for each indicator × trait combination the highest p values of models permuting either indicators or traits. To check whether weed species could be aggregated into functional groups in terms of impact on crop production related to plant morphology and shading response, species were grouped based on a Ward ascendant hierarchy classification using the hclust() function of R according to the Euclidian distances separating coordinates of species in the RLQ multidimensional space.

Then, we analysed which crop parameters reduce weed-caused crop yield loss and other weed harmfulness indicators. A Principal Component Analysis (PCA) was carried out on annual yield potential (i.e. yield from weed-free simulations), crop yield loss (relative yield difference in weed-free vs. weed-infested simulations) and annual weed seed production as a proxy for the risk of future weed harmfulness. Among the 145 parameters of Table 1, those most correlated to the PCA axes were projected onto the PCA correlation circle. Analyses were carried out with the FactoMineR package of R.

Finally, to evaluate the relative contribution of crop species and cropping systems on weed harmfulness, crop yield loss and weed seed production were both analysed with linear models as a function of crop species, cropping system, region, weather repetition, time since simulation onset as well as interactions between factors, using PROC GLM of SAS. Cropping systems and weather repetitions were nested within regions. Mean crop yield loss and weed seed production were compared per crop, with a least-significant difference test.

3 Results

3.1 Weed harmfulness

3.1.1 Which weed species drive weed harmfulness

At the annual scale, the three actual immediate weed harmfulness indicators, i.e. crop grain yield loss, harvest pollution and field infestation, were correlated (Pearson correlation coefficients ranging from 0.65 to 0.73, $p<0.0001$, section D.1 online). Conversely, there was no correlation at all between actual immediate and potential future harmfulness, i.e. weed seed production (Pearson correlations ranging from 0.04 to 0.06, $p<0.0001$). When focusing on actual immediate weed harmfulness, it appeared that weed species were the most discriminated by harvest pollution (longest arrow on Figure 1.A) and the least by yield loss (shortest arrow) though all three harmfulness indicators were orientated into the same direction, along the left-hand side of axis 1. This axis explained almost all of the variance of the indicator values (97.7%, section D.2.2 online), a large part of the trait-value variance (61.6%) and nearly the entire cross-variance between the traits and the indicators (98.0% of axis 1 in Figure 1).

Weed species could be clustered into several groups, depending on their contribution to weed harmfulness averaged over all cropping systems, crops, years and weather repetitions (Figure 1.B). The

most harmful ones were *Galium aparine* (GALAP) and *Avena fatua* (AVEFA). The second most harmful group, especially in terms of yield loss and harvest pollution, consisted of six species including *Alopecurus myosuroides* (ALOMY), *Chenopodium album* (CHEAL), *Echinochloa crus-galli* (ECHCG), *Geranium dissectum* (GERDI), *Panicum milleaceum* (PANMI), and *Stellaria media* (STEME). Three other clusters included the species that were the least harmful in terms of harvest pollution (*Senecio vulgaris*, SENVU; *Sonchus asper*, SONAS; *Veronica persica,* VERPE), crop yield loss (*Abutilon theophrasti*, ABUTH; *Ambrosia artemisiifolia*, AMBEL; *Poa annua*, POAAN) and field infestation (*Mercuralis annua,* MERAN, *Fallopia convolvulus,* POLCO, *Polygonum persicaria,* POLPE), respectively. The remaining seven species located at the centre of the graph presented an intermediate harmfulness.

3.1.2 Which weed parameters drive weed harmfulness?

The parameters determining the potential morphology and shading response of the most harmful weed species are shown in Figure 1.C. The most harmful weed species irrespective of crops, cropping systems, years and weather repetitions had a high initial leaf area at emergence (LA0 at the left-hand side of Figure 1.C); in unshaded conditions, they presented a high specific leaf area at early stages (SLA0 and SLA1), and they were taller per unit plant biomass from the end of vegetative stage onwards (HM7, HM8, HM9, HM10). In the most harmless weed species, plant width increased with plant biomass (b_WM9, b_WM10 on the right-hand side of Figure 1.C). Harmless species also had a larger interception area per unit leaf biomass at later stages, with a high specific leaf area from flowering onwards (SLA8, SLA9, SLA10), with leaves mostly located at the top of the plant (RLH6, RLH7). When shaded, harmful species shifted their leaves upwards in mature plants (mu_RLH10 at the left) whereas species that increased their plant width per unit biomass (mu_WM8, mu_WM9, mu_WM10 on the right) were harmless.

There were few differences between the weed parameters driving the three types of investigated weed harmfulness. Generally, harvest pollution was the most driven by parameters increasing plant height (HM7, HM8, HM9, HM10 at the left top quadrant) and placing leaves above the combine cutting, i.e. shifting leaves upwards in shaded mature plants (mu_RLH10). Yield loss was the most driven by parameters that ensured a large light interception and shading area very early via a large leaf area both in absolute value and per unit of leaf biomass (LA0, SLA0, SLA1 on the left-hand side of the first axis). Finally, weeds with a larger interception area per unit leaf biomass, with a high specific leaf area (SLA8, SLA9, SLA10 in the upper right quadrant) and increased plant width per unit biomass when shaded (mu_WM8, mu_WM9, mu_WM10) contributed the least to field infestation.

Conversely, only one parameter relevant for weed seed production could be identified. This proxy for future weed harmfulness was the highest in species that increased their plant width per unit biomass when shaded, particularly at early stages (mu_WM2, Pearson correlation coefficient identified by fourth-corner analysis = 0.24, section D.2.1 online).

Though many indicator-trait correlations were identified by the RLQ analyses, the correlation coefficients were generally low (below 0.30, section D.2.1 online). This, together with the relative low variance of the trait values accounted for by the two RLQ axes (a total of 58.5%, compared to 99.9% for indicator values, section D.2.2 online), shows that trait combinations rather than single trait values drive weed species impact.

3.2 Which crop parameters reduce weed harmfulness?

Crops differed more in terms of potential yield than weed suppression. The Principal Component Analysis (PCA) showed that the situations (cropping system x year x weather repetition) that maximised potential yield were generally not those that minimized weed harmfulness as the two categories were perpendicular on the PCA variable graph (Figure 2.A). But, this also means that there were situations that reconciled both high yield potential and low yield loss due to weeds. Moreover, the two harmfulness indicators, i.e. yield loss and weed seed production, were also perpendicular when switching PCA axes (Figure 2.C), indicating that the situations with a low yield loss did not necessarily present a low weed seed production.

Crop species and varieties were roughly ranked along the second axis of the PCA (Figure 2.B) which was driven almost entirely by potential yield (Figure 2.A). Averaged over all cropping systems, years and weather repetitions, wheat (TRZAX) was potentially the most productive crop (toward the top of the second PCA axis), followed by sunflower (HELAN) and maize (ZEAMX). The species with the lowest potential yield (toward the bottom of the second axis) were flax (LIUUT), winter barley (HORVX and soybean (GLXMA). The difference between species was greater than the difference among cultivars of a given species. The middle group consisted of field bean (VICFX), sorghum (SORVU), pea (PIBSX) and oilseed rape (BRSNN).

The crop species differed much less in terms of weed suppression, here illustrated by weed-related crop yield loss and annual weed seed production (as a proxy for future weed-borne crop yield loss). Indeed, species were roughly at the centre of the first PCA axis which was driven by the two weed-harmfulness indicators (Figure 2.A and B). Plotting the third vs the first PCA axis made it a bit easier to see crop differences, as the third axis allowed to separate the two harmfulness indicators (Figure 2.C). This graph showed that crops differed a little bit more in terms of yield loss than weed seed production as the crops were distributed along the y=-x line (i.e. the direction of the yield loss arrow) with little variability along the y=x line (i.e. the direction of the weed seed production arrow) (Figure 2.D). Averaged over all cropping systems, years and weather repetitions, maize (ZEAMX) and oilseed rape (BRSNN) were the crops with the lowest crop yield loss (left upper quadrant). Conversely, flax (LIUUT), spring pea (PIBSX) and barley (HORVX) presented the highest yield loss (lower right quadrant).

3.2.1 Crop species is not the main driver of yield loss

The analysis of variance confirmed that crop species was not the main driver of crop yield loss in this simulation study (Table 2.A). Yield loss mostly depended on cropping system (partial R^2 = 0.49=0.27+0.05+0.17 out of total R^2 of 0.68), albeit in interaction with weather (partial R^2 = 0.17) and crop species (partial R^2 = 0.05). Crop species explained three times less variability than cropping system (partial R^2 = 0.16 = 0.10+0.05+0.01), and part of this depended on cropping system (partial R^2 = 0.05). Using a method that accounted for the main driver of weed harmfulness (i.e. cropping systems) allowed to better discriminate crops in terms of yield loss and, particularly, weed seed production (Table 2.B). The general ranking was the same as the one observed in the PCA of Figure 2.D. Among the species with enough situations, the crops with the highest yield loss due to weeds were legumes, i.e. pea and soybean. Conversely, early-sown broadleaved crops (oilseed rape) and summer crops (maize and sunflower) presented the lowest yield loss. Autumn-sown cereals (wheat, triticale) were intermediate, except for the Caphorn wheat cultivar, which presented a very high yield loss.

The crop ranking for weed seed production as a proxy for the risk of future yield loss was very different (Table 2.B). The crops with the lowest weed seed production were early-sown crops, i.e. wheat and oilseed rape, those with the highest weed seed production were late-sown crops, i.e. sunflower and soybean. Interestingly, the crops and varieties with the highest yield loss presented very low (wheat cv Caphorn) or moderate weed seed production (pea).

3.2.2 Which crop parameters drive potential yield and weed harmfulness?

The projection of the crop parameters driving potential plant morphology and shading response onto the PCA axes allowed to identify the key parameters driving yield potential (along the first PCA axis, Figure 2.A), crop yield loss (along the y=-x line, Figure 2.C) and, to a lesser degree, weed seed production (along the y=x line in Figure 2.C). In the absence of shading, the crops with the highest potential yield invested in leaf biomass to the detriment of stem biomass, particularly at earlier stages (LBR0-LBR4 at the top of second PCA axis, Figure 2.A), with an uneven leaf distribution along plant height (b_RLH8-b_RLH10 at the top of second axis). High-potential crop species were more homogeneous in terms of plant height which depended less on plant biomass, particularly at late stages (b_HM8-b_HM10 at the bottom of second axis). When shaded, the high-potential crops were able to etiolate, producing taller plants per unit biomass, particularly during the vegetative stage (mu_HM5-mu_HM8), but they kept a uniform leaf area distribution along plant height, particularly at early stages (mu_RLH0-mu_RLH5 at the bottom of second axis).

The optimal crop morphology and shading response for limiting yield loss was different. When unshaded, crops with the lowest yield loss were those with thinner leaves, maximising their leaf area per unit leaf biomass, particularly at early stages (SLA0-SLA4 in the left upper quadrant of Figure 2.C), with wider plants per unit biomass during vegetative stages (WM4-WM7), particularly for plants with a lower biomass (b_WM6-b_WM7 in the right lower quadrant), and a uniform leaf area distribution

along plant height (b_RLH5-b_RLH7). When shaded, the crops with the lowest yield loss were able to occupy even more space, by increasing their plant width per unit biomass at early stages (mu_WM2-mu_WM4 in the left upper quadrant) and, even more importantly, their plant height per unit biomass, both at early (mu_HM3-mu_HM4 in the left upper quadrant) and late stages (mu_HM8-mu_HM9 in the left upper quadrant). It was impossible to identify individual key crop parameters related to weed seed production (Figure 2.C).

3.3 Crop ideotypes and weed "harmtypes"

The most relevant crop parameters could be combined into crop ideotypes, i.e. the optimal combination of parameter values to maximise yield in weed-free (i.e. potential yield) or weed-infestation situations (i.e. actual yield) (Figure 3). Except for the shade response resulting in increased height per unit biomass (mu_HM), the parameters that maximise one or the other type of yield were not the same or even contrary (leaf area distribution b_RLH). In both situations, though, the relevant parameters aimed at two effects, i.e. occupying the field space before any other plant and reacting to shade once neighbour plants start to compete for space and light.

Early space occupation was also the main success of the generalist weed species that were harmful in all crops, cropping systems and regions (Figure 4). Even more interesting, several parameters that made species successful in multispecies canopies were the same for both crops and weeds (SLA, b_WM, b_RLH). However, later in the weed life-cycle (at the time when foliar herbicides were sprayed in the simulations), inconspicuous weeds with a lower leaf area per unit leaf biomass (smaller SLA) and plant width per unit biomass (smaller mu_WM), were more harmful. Harvest pollution was very much related to weed morphology at harvest itself, which explains why weed species contributed more to this pollution when their leaf area was concentrated at the top of the plant. Conversely, no generalized parameter profile could be identified for weed seed production, which is a proxy for weed harmfulness for future crops, indicating that this function depends much more on cropping system and regional conditions.

4 Discussion

4.1 A novel approach to determine crop ideotypes and weed "harmtypes"

The present simulation-based approach allowed us to determine crop ideotypes maximising yield potential and minimizing weed-caused crop yield loss as well as weed "harmtypes" most harmful for crop production in large range of contrasting cropping systems and regions. The study also demonstrated that the crop parameters driving the yield potential were not those driving yield-loss reduction and that none of the investigated crop species answered to all requirements of the crop ideotypes. Both for crop ideotypes and weed "harmtypes", it was all about early field occupation and later shade response though

the exact features depended on the goal (i.e. yield potential vs weed suppression, current or future harmfulness). Weed "harmtypes" also included characteristics that would allow the plants to avoid late-season herbicides.

The novelty of our approach consisted in combining detailed measurements on plant morphology and shading response carried out on individual plants in controlled conditions (Colbach et al., in revision) with a simulation study to test the different species and cultivars in a multi-annual and multi-site virtual farm field network. Tardy et al. (2015; 2017) similarly used detailed individual-plant measurements but combined them with expert knowledge to define the characteristics of the ideotypes for weed-suppressive cover crop species in banana cropping systems. They then identified the best species within the panel of experimented cover crop species as the one with characteristics the closest to those of the ideotype.

Most authors usually worked with canopy or weed state variables such as early ground cover or canopy closure, plant height, leaf area index, weed density or leaf area, either in fields (Regnier and Stoller, 1989; Pike et al., 1990; Cavero et al., 1999; Paynter and Hills, 2009; Reiss et al., 2018) or in simulations (Kropff et al., 1992). These variables are specific to cropping systems and pedoclimate, which makes it more difficult to draw generic conclusions, particularly as these studies worked with a single crop species and a very limited number of species (three or less). Conversely, we worked here with parameters that described species-intrinsic performances and were closer to processes driving competition for light, which allowed us to identify pertinent parameters and to go further in understanding crop-weed competition. For instance, most studies report that taller cultivars are more weed-suppressive than shorter cultivars (section 4.2). Here, we demonstrated that crop plant width per unit plant biomass is the key morphological trait in unshaded conditions and that plant height per unit plant biomass is an efficient response strategy when shaded (i.e. in the presence of weeds). The drawback is that these parameters are difficult to measure and not among those that are routinely measured by plant breeders (Zhao et al., 2006).

Experimental studies also have trouble to measure the attainable yield as it is notoriously difficult to achieve a continuously totally weed-free situation in fields, particularly when monitoring many fields at a time (Colbach et al., submitted). As in our study, yield-gap analyses thus often estimate the attainable yield from simulations (Grassini et al., 2015). In contrast to these studies, we used simulations to both estimate attainable yield and actual yield. This ensured that any difference between these two yields was due to the limiting factors that we aimed to investigate, i.e. weeds, and not due to errors in field observations used for simulation inputs on one hand, actual yield on the other hand.

4.2 Simulation results consistent with field observations

Our results are conditional on the prediction quality of FLORSYS which was shown to be adequate in a previous study (section 2.1.5). This evaluation concluded that FLORSYS correctly predicted and ranked weed species densities but could not assess the harmfulness of individual weed species for crop production. Coverage by the literature on this topic is scant. Some establish harmfulness thresholds for

425 different weed species in a single crop (e.g. see review by Caussanel, (1989) or link weed densities
426 observed in field communities to yield loss in different crop types (Milberg and Hallgren, 2004).
427 Extension services establish harmfulness scores based on expert opinion, usually also for a given crop
428 (CETIOM, 2008) or aggregate qualitative knowledge (http://www.infloweb.fr). Among the weed
429 species present both in literature and here, *A. fatua* and *G. aparine* were among the most harmful species,
430 *A. myosuroides* and *S. media* among the second most harmful species, *F. convulvus*, *V. persica* and *V.*
431 *hederifolia* among the least harmful ones (Caussanel, 1989; Wilson and Wright, 1990). Other authors
432 though found different results. For instance, *G. aparine* was deemed rather harmless in Sweden (Milberg
433 and Hallgren, 2004) but that was on spring cereals whereas we established a crop-independent
434 harmfulness ranking. Indeed, the impact of a given weed species also depends on the identity of the
435 infested crops (Fried et al., 2017), the weed floras and, of course, on which resource crops and weeds
436 compete for (Zimdahl, 2004). The above-cited field studies did not discriminate between competition
437 causes whereas we exclusively focused on competition for light and our simulations ensured that there
438 were no other abiotic or biotic stresses. Moreover, our weed species ranking was established over many
439 contrasting cropping systems, crops, weed floras and pedoclimates. Conversely, yield-loss field studies
440 either investigate one weed species in one crop species in bi-specific trials (Caussanel, 1989), which is
441 an unrealistic situation disregarding weed-weed interference, or the impact of multispecific weed floras
442 without discriminating individual species (Keller et al., 2014), which is consistent with farming
443 situations but does not allow to draw conclusions on individual species.
444 Though many simulation and field studies analysed canopy and weed state variables related to yield loss
445 (see Introduction), few studies investigate correlations between weed species parameters and weed
446 harmfulness for crop production as we did here. The few exceptions confirmed our findings on which
447 weed parameters drive harmfulness, such as the importance of early space occupation (Spitters and
448 Aerts, 1983), plant height surpassing crop canopy (Spitters and Aerts, 1983; Fried et al., 2017), a high
449 stem elongation rate, particularly in shaded conditions (Weinig, 2000) (consistent with our higher plant
450 height per unit biomass, particularly at later stages when shading is more likely), or a large specific leaf
451 area (SLA) at early stages and a small one at later stages (Storkey, 2004; Storkey, 2005) (which is
452 identical to our results). The harmfulness of a small SLA late in the weed life-cycle seems surprising at
453 first, but such plants are less likely to be affected by foliar herbicides, which may be applied later in the
454 cropping season and enter via weed leaves.
455 Reports on crop parameters relevant for yield potential and weed suppressiveness are more common but
456 they usually compare different cultivars rather than species, as we did here. Again, our results are mostly
457 consistent with previous experimental studies. The most frequent reported feature of weed-suppressive
458 species and cultivars is plant height (Ford and Pleasant, 1994; Christensen, 1995; Lemerle et al., 1996;
459 Mennan and Zandstra, 2005; Østergård et al., 2008; Drews et al., 2009; Fried et al., 2017; Jha et al.,
460 2017) which is consistent with our height efficiency. A large leaf area, leaf area index or light
461 interception area also increase weed suppression (Ford and Pleasant, 1994; Christensen, 1995; Lindquist

and Mortensen, 1998; Drews et al., 2009) which is consistent with our large specific leaf area and wider plants per unit plant biomass. Some parameters reported in literature required a more detailed plant description than we used here, such as leaf inclination (Drews et al., 2009). Conversely, other features used in literature are not actual parameters but the result of several processes such as rapidly shading canopies or high ground cover (Holt, 1995; Drews et al., 2009). Both are though consistent with our results demonstrating the need of an early space occupation by crops.

4.3 Can weed-suppressive crop ideotypes contribute to weed management

Choosing crop species and cultivars that tolerate or suppress weeds is expected to be a major lever for integrated crop protection (see introduction). The present study identified the features that make species and cultivars "generalist winners", i.e. that produce a high yield in weed-free situations or that are weed-suppressive, regardless of the cropping system and pedoclimate. But, even if some of the crop species studied here were better than others, none of them combined all the parameter values minimizing weed impacts on crop production, far less those reconciling low weed impact with high potential production. This frequently reported antagonisms (Sardana et al., 2017) may correspond to the theoretical trade-off between community performance and competitiveness (Denison et al., 2003): crop plants with traits that maximize their competition towards weeds compete among themselves in the absence of weeds, reducing their overall performance in resource capture and biomass production. However, Denison et al (2003) concluded that "there is no reason to expect the structure of natural ecosystems […] to be a reliable blueprint for agricultural ecosystems". The antagonism between yield potential and weed suppression is thus not inevitable as shown by recent varietal improvement (section **Error! Reference source not found.**).

Even when focusing on the sole weed suppression aspect, there was a trade-off between crop species that minimize weed-caused crop yield loss and those that limit weed seed production, i.e. the risk of future yield loss. For instance, pea presented a high weed-caused crop yield loss but a low weed seed production, which partially explains, in addition to the use of different herbicides and the absence of mineral nitrogen fertilization, why pea is a very interesting diversification crop in winter rotations resulting in an impressive reduction of weed infestation (Chauvel et al., 2001). This again demonstrates the necessity to combine crop/cultivar choice with all other cropping-system components.

The present study focused on parameters driving crop-weed competition for light, albeit in a large range of crops and cropping systems. But, as the lower-input crop management and weed management strategies required by new farming policies must be robust to hazards resulting from climate change, it will be necessary to similarly consider crop and weed parameters related to competition for nitrogen and water or those to frost damage. Indeed, other parameter-based studies have shown the importance of, e.g., photosynthesis response to temperature or photosynthetic pathway (Spitters and Aerts, 1983). The same applies to parameters that drive crop and weed phenology and, for weeds, seed persistence. This

is essential when aiming to tailor advice to particular crops and cropping systems as the most successful weeds were shown to be those mimicking crops in terms of emergence and maturity dates (Fried et al., 2008; Fried et al., 2009).

Down-scaling the present approach to investigate intra-species variability in crop robustness to weeds is a promising avenue. The goal is not only to assist the choice of the best varieties to sow, but also to identify key selection criteria to focus on, in order to create new high-yielding crop varieties that are robust to weed impacts (Martre et al., 2015; Rotter et al., 2015). Recent studies suggested that, at least in rice, high yield potential and improved weed-suppressive ability are compatible (Mahajan *et al.*, 2014; Mahajan *et al.*, 2015).

5 Conclusion

The present study identified generic rules on which species parameters make annual weeds harmful for crop production and crops tolerant to crop-weed competition for light, across a large range of arable cropping systems and pedoclimates. Crop and weed species that were successful in mixed canopies were shown to be similar in terms of potential plant morphology and shading response. These rules can be used as pointers for selecting crops in agroecological cropping systems aiming to regulate weeds by biological interactions. The study also demonstrated a trade-off between crop traits that promoted potential yield and those that made crops tolerate or suppress weeds. Further research is thus needed to resolve this trade-off and identify combinations of crop species traits that reconcile high potential yield and low yield loss.

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8 Tables

Table 1. Species parameters for characterizing initial growth, potential plant morphology and response to shading (based on Colbach et al., in revision). For each species, there are 11 values for each potential-morphology and shading-response parameter, corresponding to 11 BBCH[$] stages ranging from emergence (0) to death (10). Ranges of variation correspond to the 25 weed species and 33 crop species investigated by Colbach et al.

Parameter name	Relative advance of growth stage at the time of parameter measurement	Unit	Median [min,max][§]
A. Initial growth (without neighbour shading or self-shading)			
RGR	Relative growth rate	$cm^2 \cdot cm^{-2} \cdot °Cday^{-1}$	0.0172 [0.0055, 0.0461]
LA0	Leaf area at emergence	cm^2	0.179 [0.01, 3.10]
B. Potential morphology (morphology variables in unshaded conditions)			
SLA	Specific Leaf Area (total leaf area vs total leaf biomass[&]) - *Leaf area efficiency*	$cm^2 \cdot g^{-1}$	153 [10, 1204]
LBR	Leaf biomass ratio (leaf biomass vs total above-ground biomass) – *Leafiness*	none	0.75 [0, 1]
HM	Specific (allometric) plant height – *Height efficiency* (height vs. total above-ground biomass ratio)	$cm \cdot g^{-1}$	20 [1.2, 838]
b_HM	Shape parameter b for specific plant height – *Height efficiency of heavy vs light plant*	none	0.27 [0.0005, 0.99]
WM	Specific (allometric) plant width – *Width efficiency* (width vs. total above-ground biomass ratio)	$cm \cdot g^{-1}$	22 [0.82, 3464]
b_WM	Shape parameter b for specific plant width – *Width efficiency of heavy vs light plant*	none	0.37 [0.02, 1.70]
RLH	Median relative leaf height (relative plant height below which 50% of leaf area are located)	$cm\ cm^{-1}$	0.48 [0.20, 0.81]
b_RLH	Shape parameter for leaf distribution along plant height – *Unevenness of leaf distribution*	none	2.7 [0.24, 58]
C. Response to shading (variation in morphology variables with shading intensity)			
mu_SLA	Response of specific leaf area to shading	none	0.48 [-0.56, 1.72]
mu_LBR	Response of leaf biomass ratio to shading	none	-0.01 [-0.66, 1.02]
mu_HM	Response of specific height to shading	none	0.43 [-0.53, 2.27]
mu_WM	Response of specific width to shading	none	0.27 [-1.53, 1.87]
mu_RLH	Response of median relative leaf height to shading	none	0.01 [-1.00, 1.39]

[$] The BBCH-scale is a generic scale applying to both mono and dicotyledonous weed species to identify their growth stages (Hess et al., 1997)

[§] Median, minimum and maximum values over all crop and weed species. For B and C, these are over all stages

[&] All biomass-based units refer to dry plant or leaf biomass

Table 2. Which factors influence crop yield loss the most?

A. Analysis of variance of yield loss as a function of simulation factors with PROC GLM of SAS. Cropping systems and weather repetitions were nested within regions. All factors were significant at p=0.0001

Factors	Partial R^2	
	Crop grain yield loss	Weed seed production
Years since simulation onset (log10-transformed)	0.03	0.00
Crop species	0.10	0.01
Region	0.04	0.01
Cropping system (within region)	0.27	0.27
Weather repetition (within region)	0.01	0.00
Crop species x cropping system (within region)	0.05	0.09
Crop species x weather repetition (within region)	0.01	0.00
Cropping system x weather repetition (within region)	0.17	0.05
TOTAL	0.68	0.44

B. Comparison of means. Variation in yield loss relative to mean loss. Numbers followed by the same letter are not significantly different at p=0.05. Crops between brackets are based on a too small number of situations and reflect the effect of cropping system and region rather than the crop species

Crop species		N	Variation in			
			Crop grain yield loss (%)[§]		Weed seed production (seeds/m²)	
Maize	ZEAMX	17342	-31.4	a	5682	d
Oilseed rape	BRSNN	10452	-26.8	b	-26853	b
(Field bean)	(VICFX cv Gladice)	210	-15.8	c	-26365	abc
Sunflower	HELAN	3127	-1.7	d	43898	f
Spring barley	HORVX	1421	-0.6	de	-1540	d
Wheat	TRZAX cv Cézanne	18187	0.4	e	-12321	c
Triticale	TTLSS	655	0.5	e	8209	de
Wheat	TRZAX cv Orvantis	3939	0.9	e	-33635	a
Soybean	GLXMA	689	4.3	f	61057	g
Pea	PIBSX cv Enduro	446	7.7	fgh	-2250	cd
(Sorghum)	(SORVU)	241	7.8	fgh	32872	f
(Flax)	(LIUUT)	258	8.2	fgh	-21315	bc
Barley	HORVX	6901	8.6	g	17	d
Wheat	TRZAX cv Caphorn	3028	11	h	-40991	a
Spring pea	PIBSX	4340	26.9	i	13537	e

[§] Yield loss is 100 (yield in weed-free – yield in weed-infested simulation)/(yield in weed-free simulation)

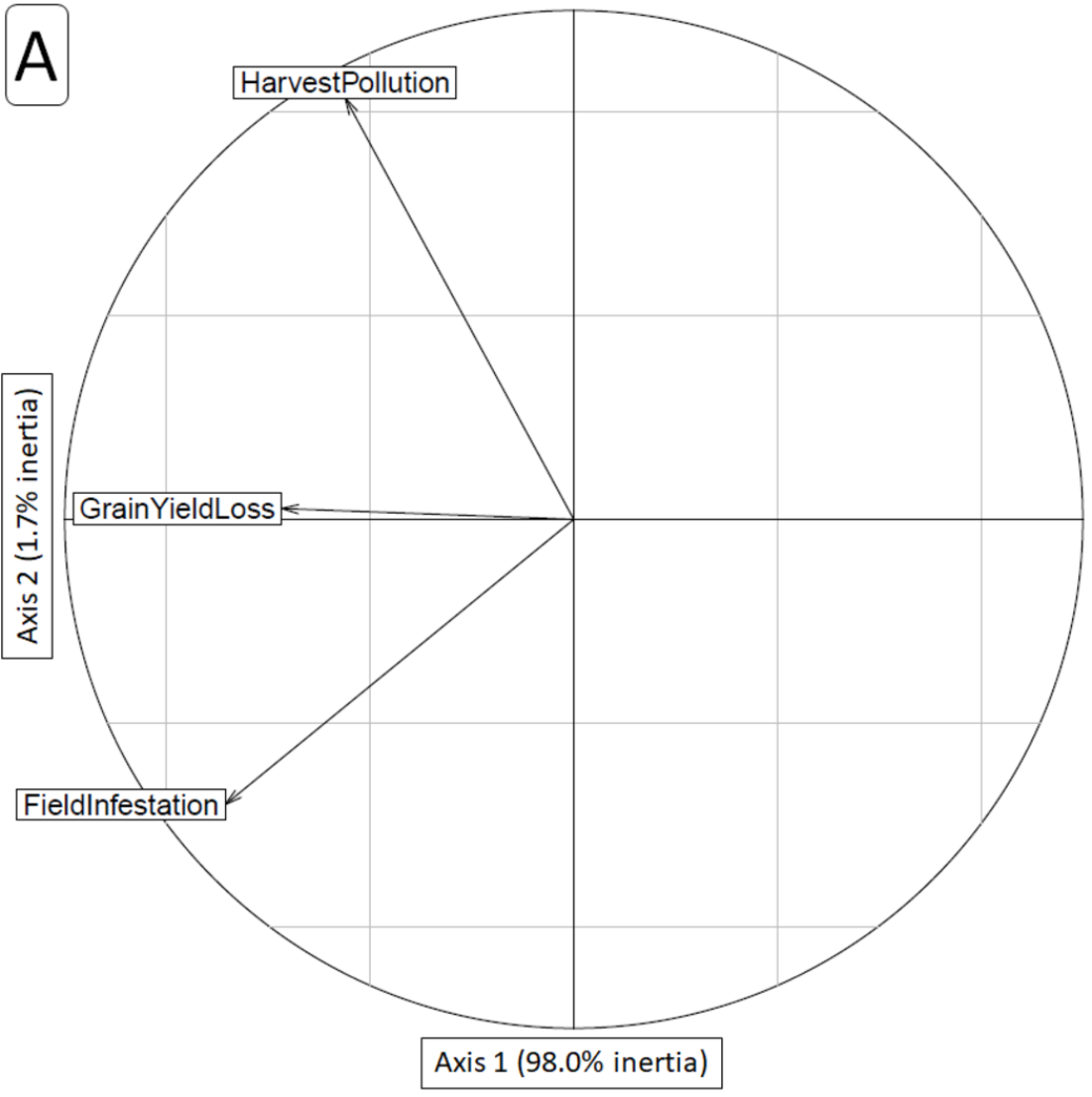
9 Figure captions

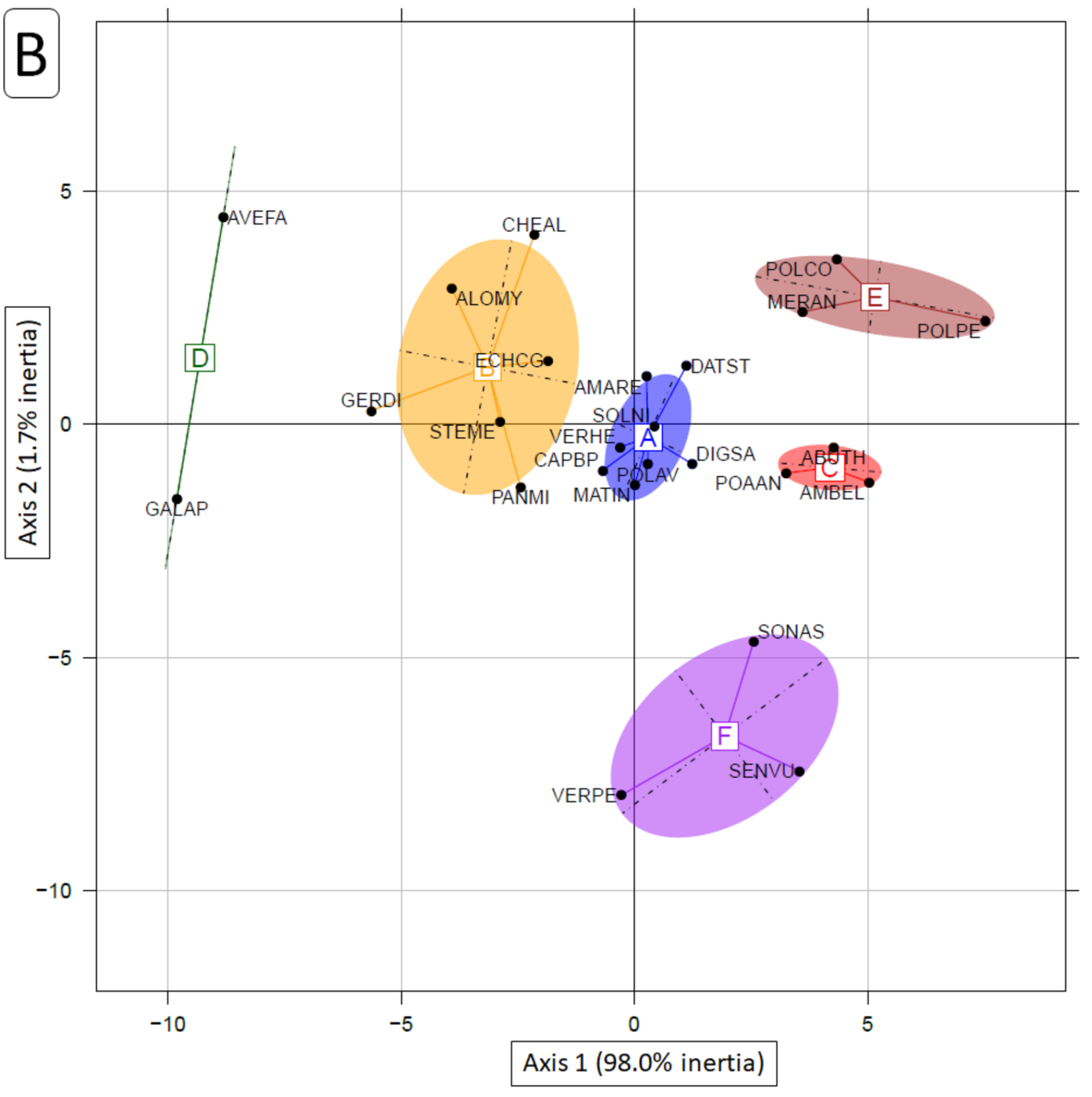
Figure 1. The weed species (shown with EPPO codes) and species traits that explain weed harmfulness for crop production, irrespective of crops and cropping systems. Synthetic representation of the RLQ results with weed-impact indicators and weed plant density in simulated fields as matrix R and L, respectively, and parameters driving morphology and shading as matrix Q. A. Weed-impact indicators with correlation circle, B. Weed species, clustered into groups, following a Ward ascendant hierarchy classification, C. species parameters, with those positively or negatively correlated to weed harmfulness for crop production in respectively red and green; parameters in gray are not significantly correlated to weed harmfulness based on fourth-corner analysis (LA0 is hidden behind SLa0, mu_RLH6 and 7 behind mu_RLH10). For the meaning of species parameters, see Table 1. (Nathalie Colbach © 2018)

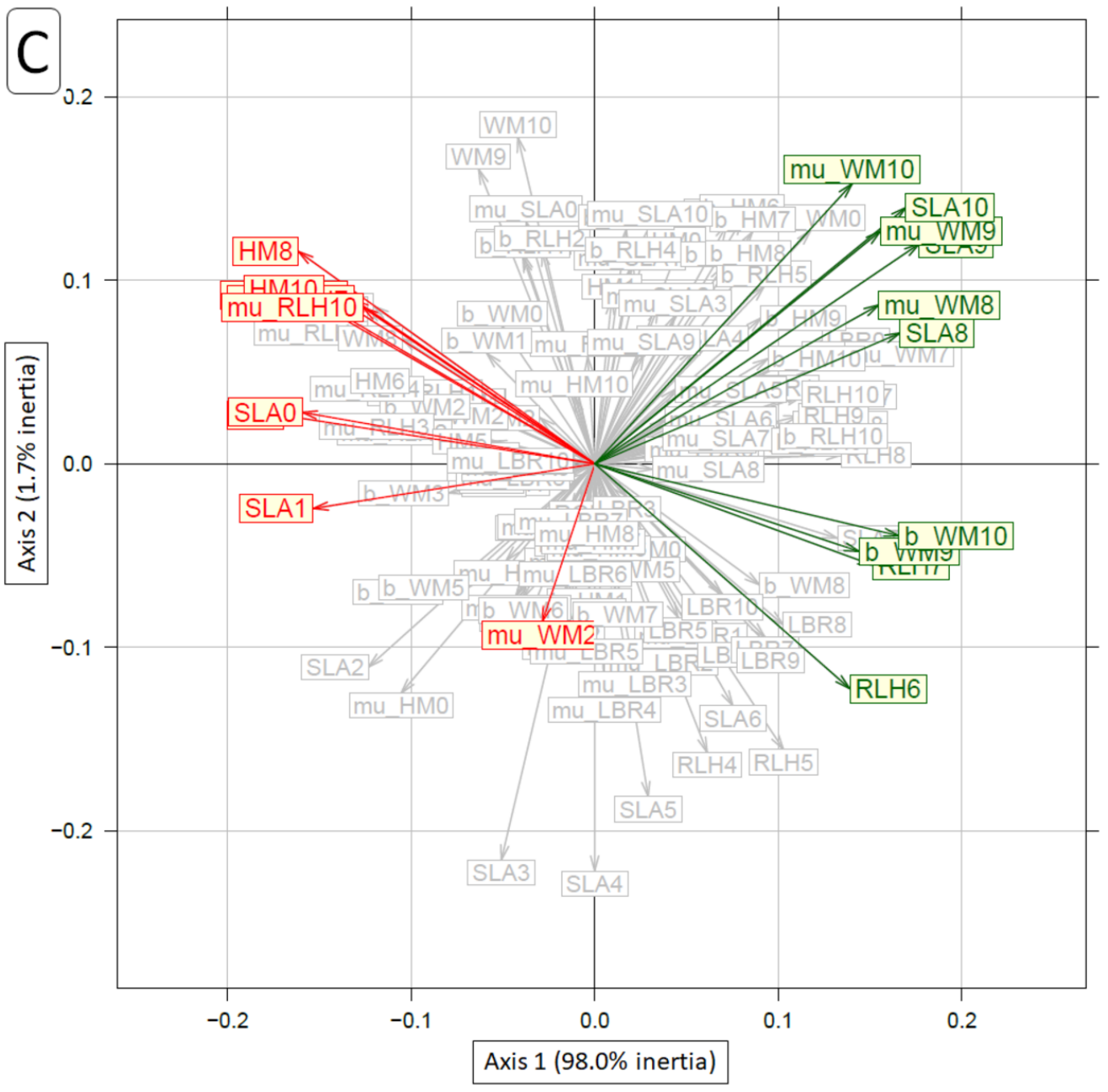
Figure 2. Annual crop performance in terms of weed-caused crop yield loss (100 t/t), weed seed production (seeds/m²) and potential yield (MJ/ha), and the correlation with crop parameters driving potential plant morphology and shading response. Principal Component Analysis (PCA) on annual performance indicators. A and C: arrows show performance variables, with a projection of the most correlated crop parameters. B and D: dots show annual performance of 272 cropping systems x 27 years x 10 weather repetitions as symbols and crop species (EPPO codes) at the center of 95% ellipses. For the meaning of the crop parameters, see Table 1. (Nathalie Colbach © 2018)

Figure 3. Schematic representation of crop ideotypes in terms of potential plant morphology and shade response for maximising potential yield and limiting weed-caused yield loss across a large range of contrasting cropping systems and pedoclimates. Based on crop parameters shown to increase potential yield in weed-free simulations (A) and decrease yield loss (B) by Principal Component Analysis of Figure 2. Parameters describing plant morphology in unshaded conditions drive space occupation before other plants (top); parameters describing shade response drive the reaction to neighbour plants (bottom) in monospecies (A) and multispecies canopies (B). For the names of the crop parameters, see Table 1. (Nathalie Colbach © 2018)

Figure 4. Schematic representation of weed "harmtypes" in terms of potential plant morphology and shade response that drive immediate harmfulness for the current crop irrespective of cropping system and pedoclimate. Based on weed parameters shown to increase yield loss, field infestation, harvest pollution (A), only yield loss and field infestation (B), only harvest pollution (C) by RLQ analysis of Figure 1. Parameters describing plant morphology in unshaded conditions drive space occupation before other plants (top); parameters describing shade response drive the reaction to neighbour plants in multispecies canopies (bottom). For the names of the crop parameters, see Table 1. (Nathalie Colbach © 2018)


A
HarvestPollution
GrainYieldLoss
FieldInfestation
Axis 2 (1.7% inertia)
Axis 1 (98.0% inertia)


B
AVEFA
CHEAL
ALOMY
POLCO
MERAN
E
POLPE
D
ECHCG
B
DATST
AMARE
GERDI
SOLNI
STEME
VERHE
A
DIGSA
CAPBP
ABUTH
C
POLAV
POAAN
MATIN
AMBEL
PANMI
GALAP
SONAS
F
SENVU
VERPE
5
0
−5
−10
−10
−5
0
5
Axis 2 (1.7% inertia)
Axis 1 (98.0% inertia)


C
Axis 2 (1.7% inertia)
Axis 1 (98.0% inertia)
0.2
0.1
0.0
−0.1
−0.2
−0.2
−0.1
0.0
0.1
0.2
mu_WM10
SLA10
mu_WM9
mu_WM8
SLA8
b_WM10
RLH6
HM8
mu_RLH10
SLA0
SLA1
mu_WM2
WM10
WM9
mu_SLA0
mu_SLA10
b_RLH4
b_WM0
mu_SLA3
mu_SLA9
b_WM1
mu_HM10
mu_SLA7
mu_SLA8
b_WM3
mu_HM8
mu_LBR6
b_WM5
b_WM6
b_WM7
b_WM8
LBR10
LBR8
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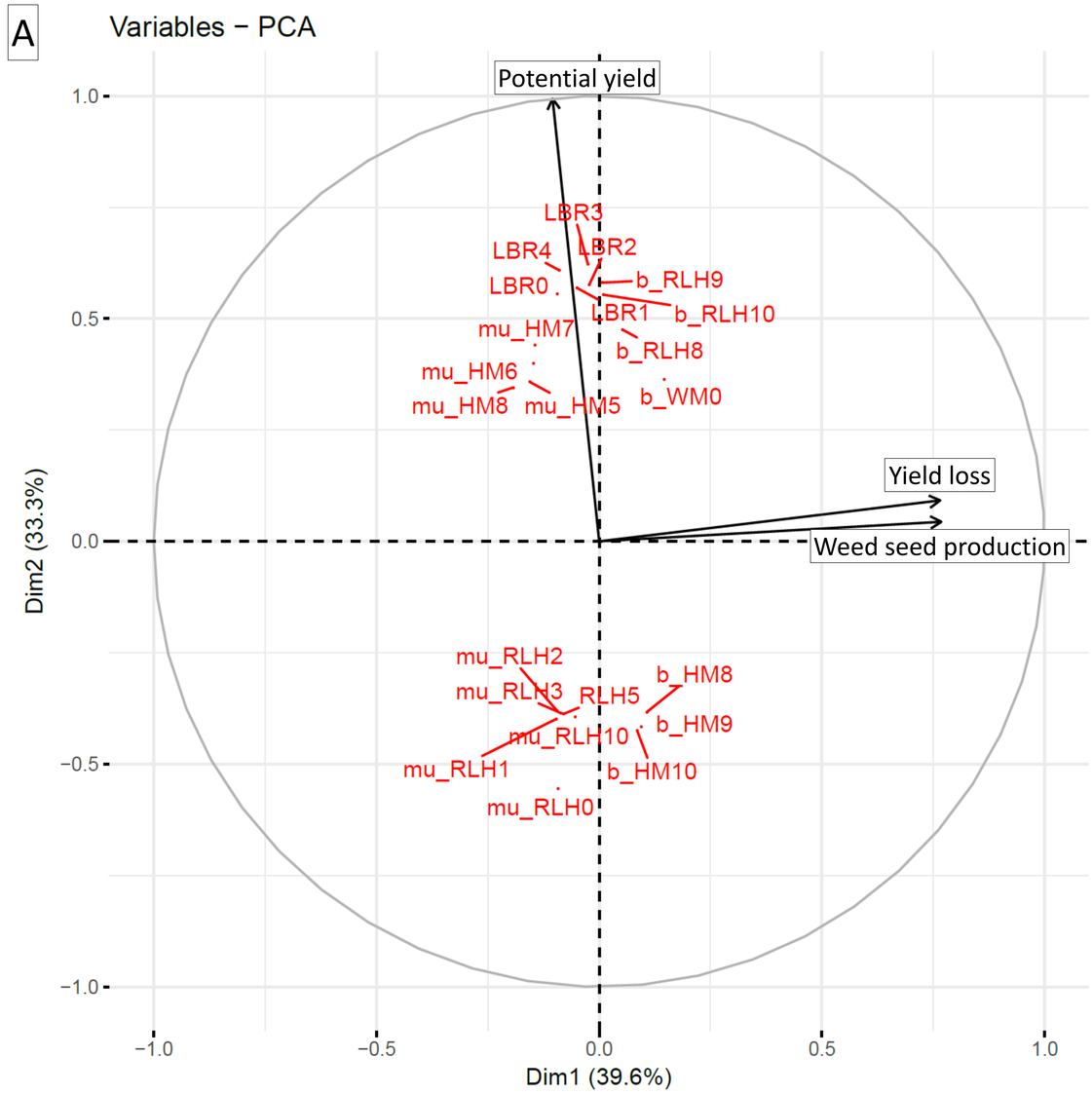
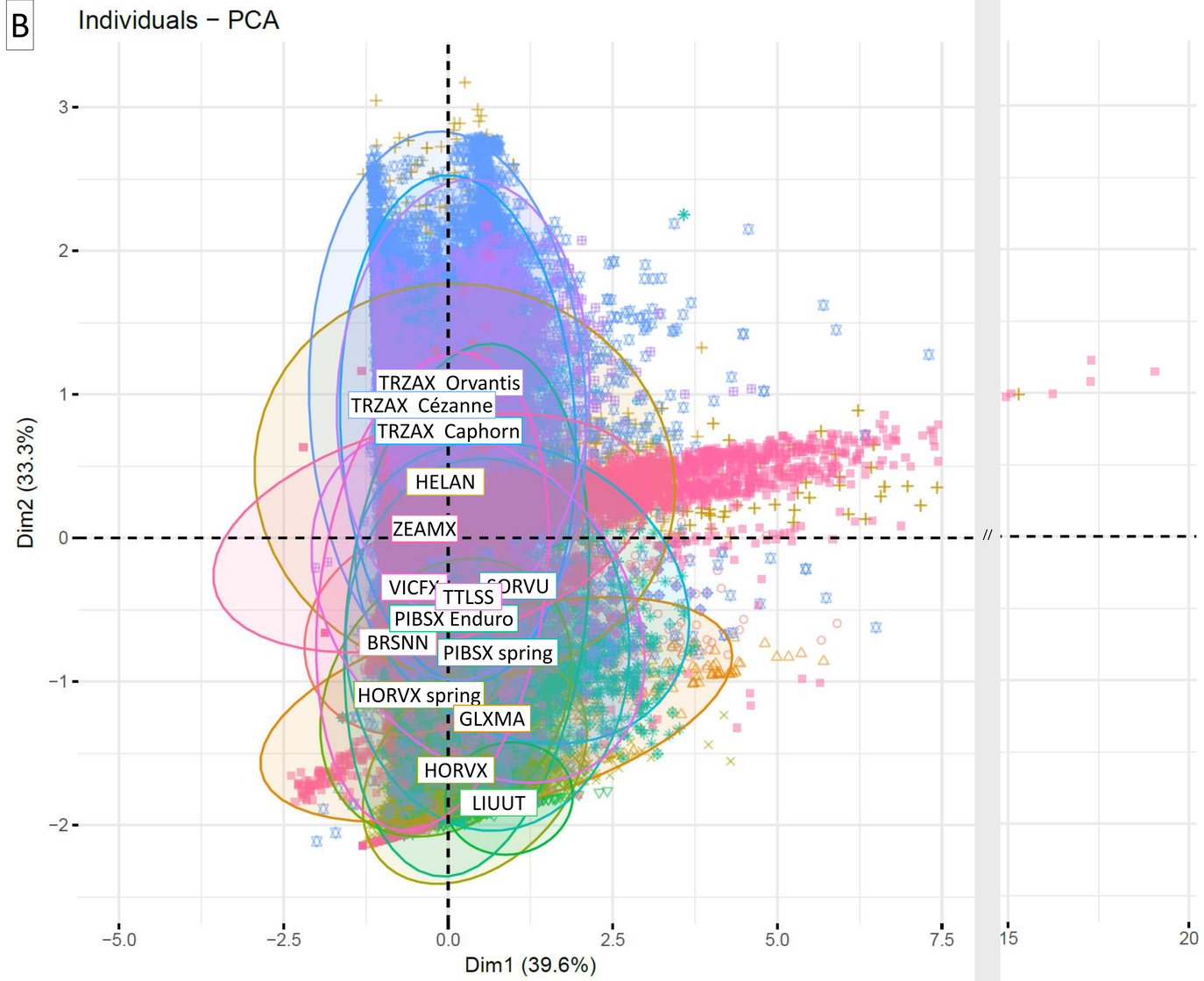
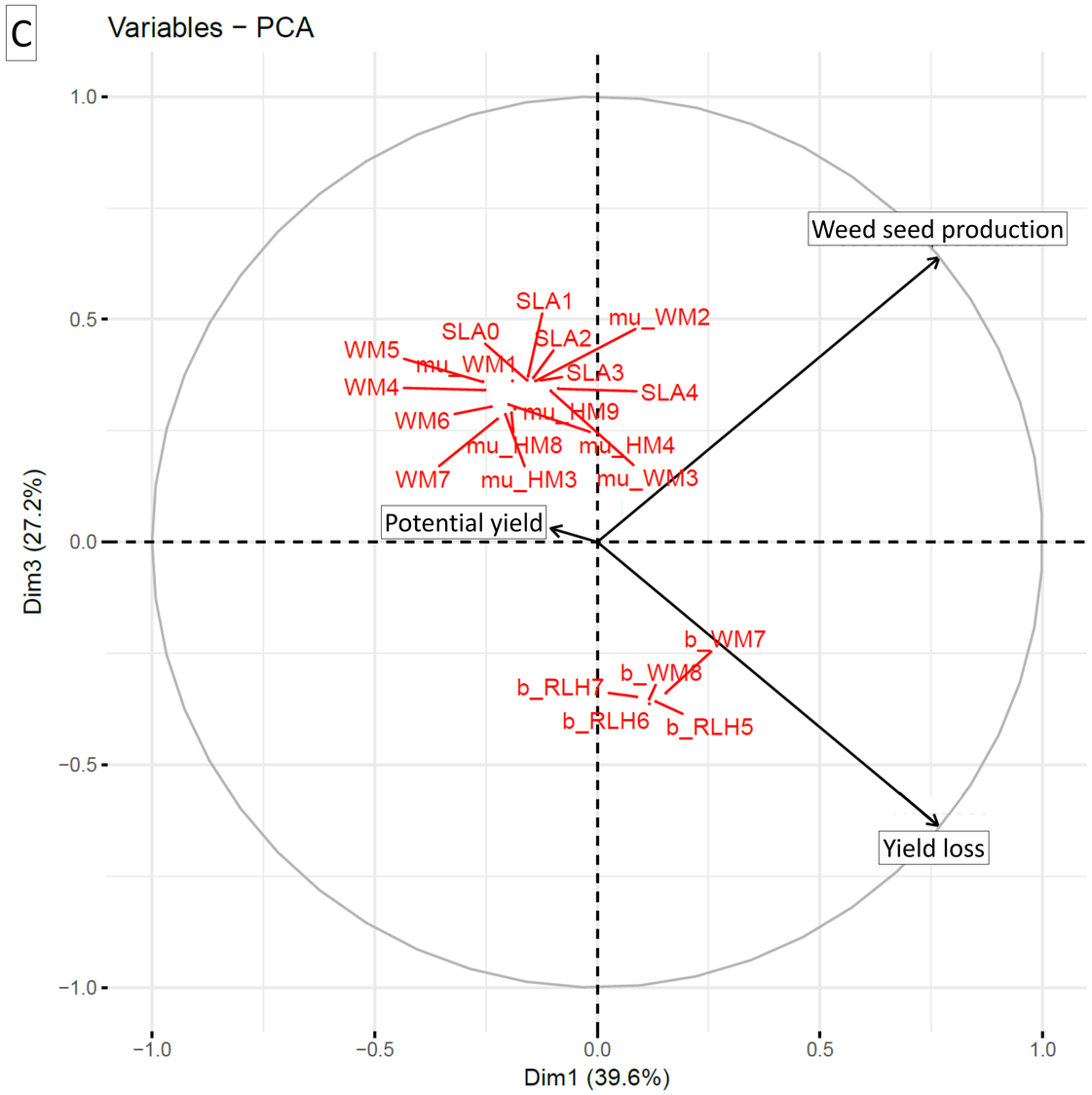
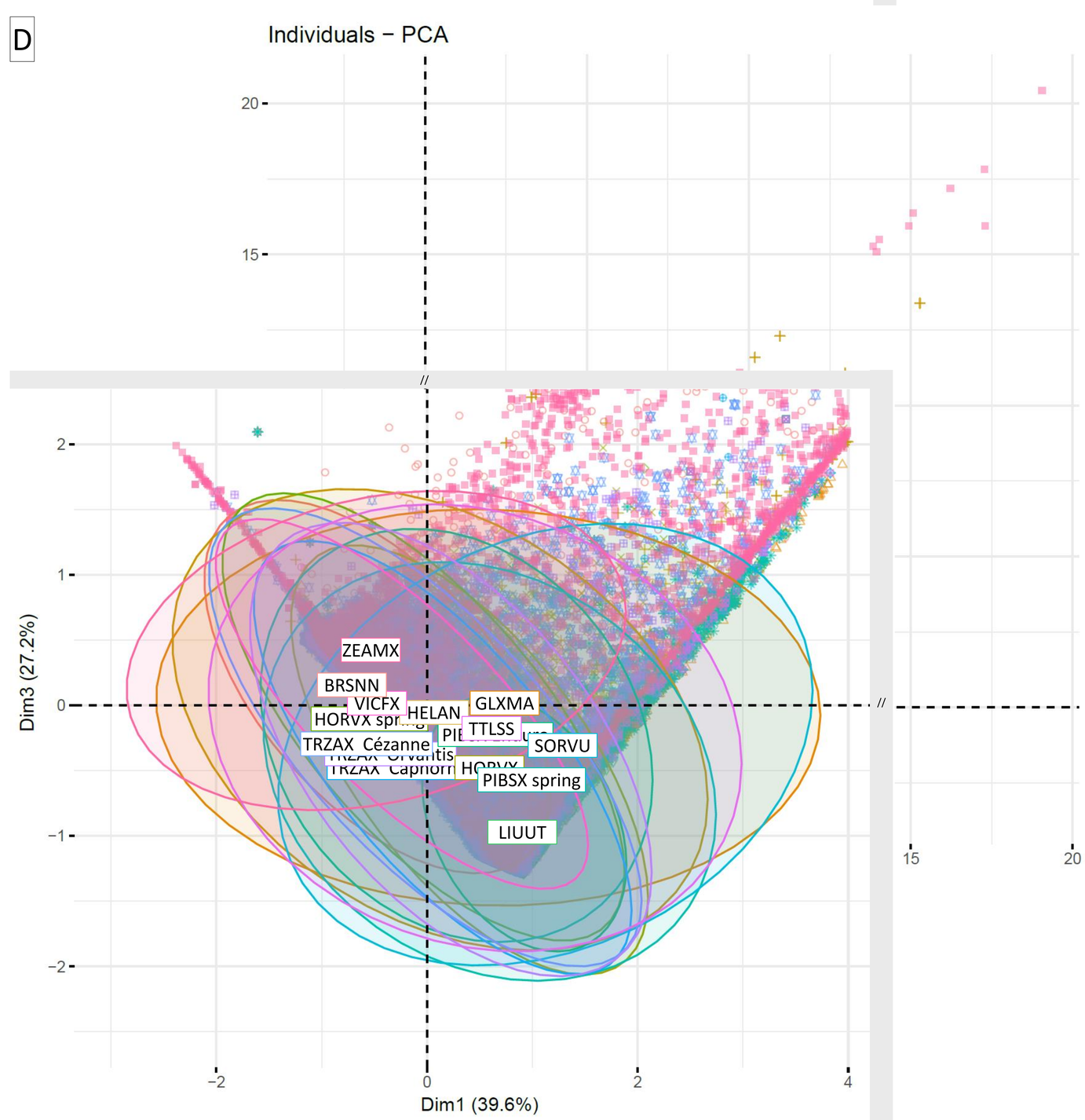
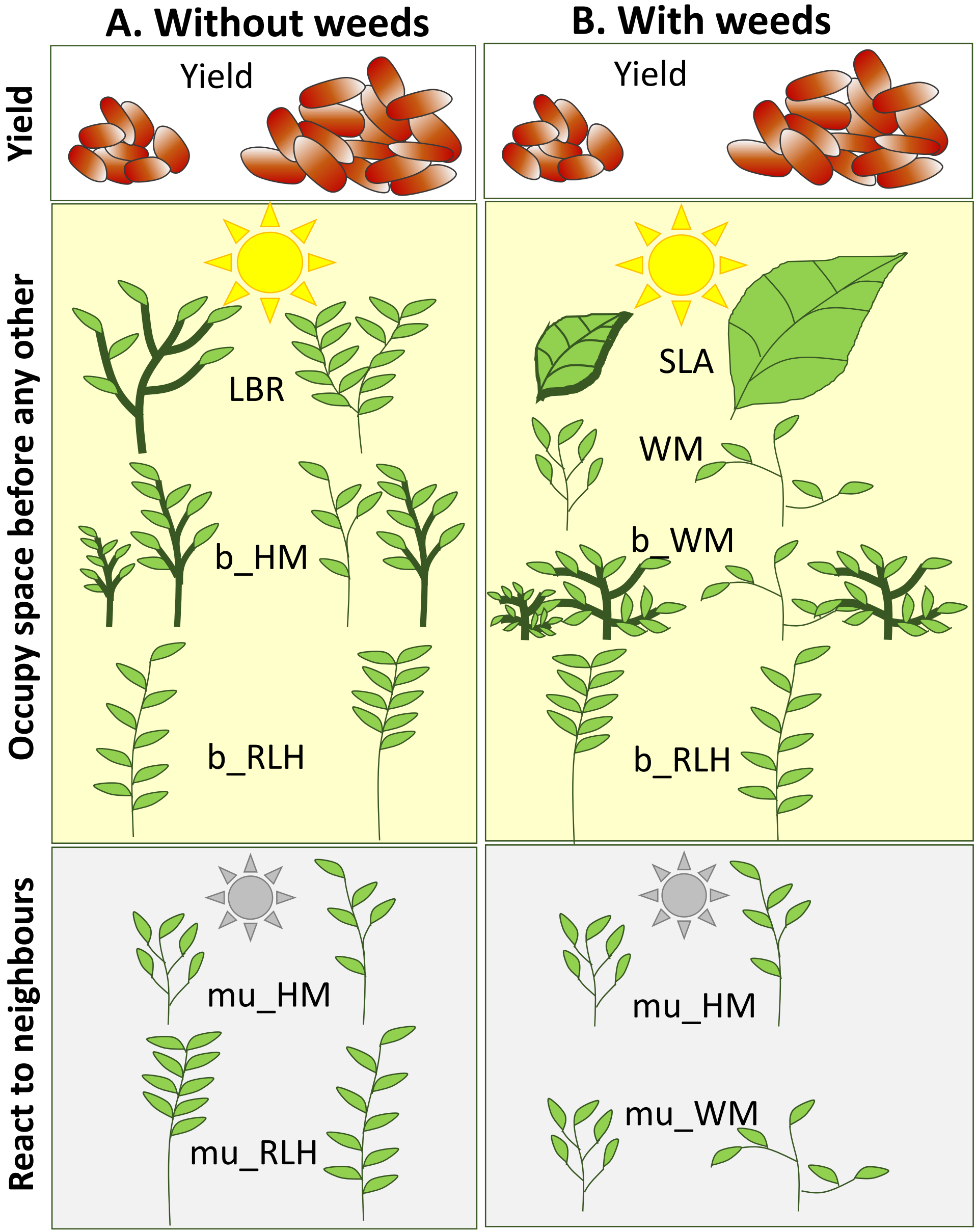
SLA6
RLH4
RLH5
SLA5
SLA3
SLA4

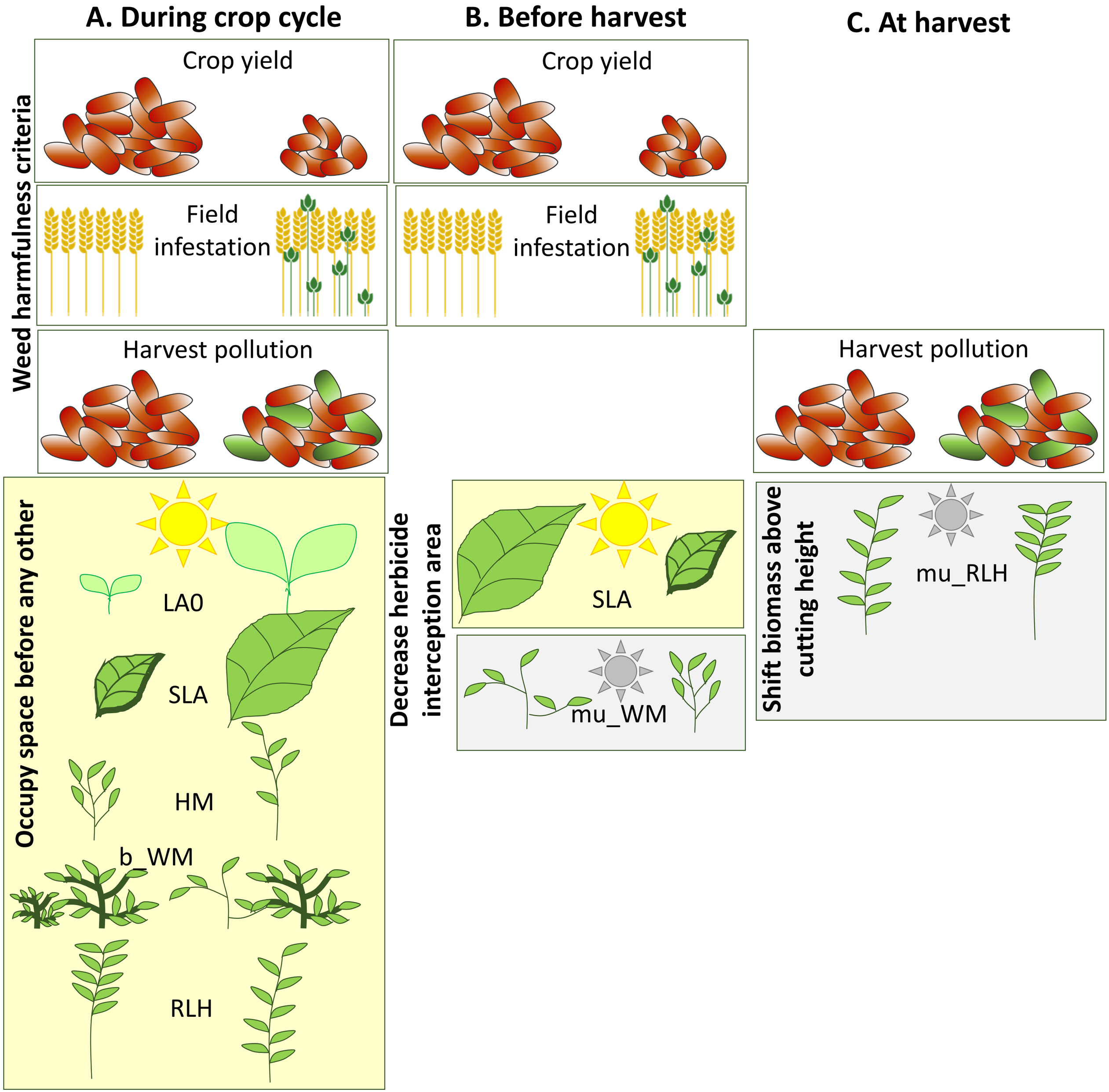

A
Variables – PCA
Potential yield
Yield loss
Weed seed production
LBR3
LBR4
LBR2
LBR0
b_RLH9
LBR1
b_RLH10
mu_HM7
b_RLH8
mu_HM6
mu_HM8
mu_HM5
b_WM0
mu_RLH2
mu_RLH3
RLH5
b_HM8
mu_RLH10
b_HM9
mu_RLH1
b_HM10
mu_RLH0
Dim2 (33.3%)
Dim1 (39.6%)


B
Individuals – PCA
TRZAX_Orvantis
TRZAX_Cézanne
TRZAX_Caphorn
HELAN
ZEAMX
VICFX
TTLSS
SORVU
PIBSX Enduro
BRSNN
PIBSX spring
HORVX spring
GLXMA
HORVX
LIUUT
Dim2 (33.3%)
Dim1 (39.6%)


C
Variables – PCA
Weed seed production
Potential yield
Yield loss
SLA1
SLA0
mu_WM2
SLA2
WM5
mu_WM1
SLA3
WM4
SLA4
WM6
mu_HM9
mu_HM8
mu_HM4
WM7
mu_HM3
mu_WM3
b_WM7
b_WM8
b_RLH7
b_RLH6
b_RLH5
Dim3 (27.2%)
Dim1 (39.6%)


D
Individuals – PCA
ZEAMX
BRSNN
VICFX
HELAN
GLXMA
TTLSS
SORVU
TRZAX_Cézanne
PIBSX spring
LIUUT
Dim3 (27.2%)
Dim1 (39.6%)


A. Without weeds
B. With weeds
Yield
Yield
Yield
Occupy space before any other
React to neighbours
LBR
b_HM
b_RLH
SLA
WM
b_WM
b_RLH
mu_HM
mu_RLH
mu_HM
mu_WM


A. During crop cycle
B. Before harvest
C. At harvest
Weed harmfulness criteria
Crop yield
Crop yield
Field infestation
Field infestation
Harvest pollution
Harvest pollution
Occupy space before any other
LA0
SLA
HM
b_WM
RLH
Decrease herbicide interception area
SLA
mu_WM
Shift biomass above cutting height
mu_RLH