Modelling the persistence of weed populations

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Chapter 9: Modelling the persistence of weed populations

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Abstract

One of the adaptations of weeds to highly disturbed environments is a persistent seedbank meaning there can often be a lag of several years in the response of a weed flora to a change in management. This buffering effect of the seedbank is a challenge to understanding weed dynamics through empirical field experiments that tend to be short lived. One solution is to simulate the response of weed populations to management in a computer model. Two approaches to modelling are discussed. The first draws on fundamental theory of plant ecological strategies to predict the shift in the distribution of weed functional traits under different management scenarios. Secondly, a detailed, process-based model of weed population dynamics is described with a worked case study example. This second approach also uses plant traits to parameterize the model and predict the function of emergent weed communities but has a more intensive requirement for parameterization. Models have a crucial role to play in predicting the persistence of weed populations in a field but care should be taken in investing too much confidence in predictions of absolute weed numbers. Rather, models are a powerful tool for testing the relative efficacy of contrasting weed management scenarios.

Key words
Functional traits, process-based model, weed management, parameterisation

9.1. Why do we need models to predict weed persistence?

Weeds are adapted to highly disturbed environments characterised by ephemeral, short-lived opportunities for growth and reproduction. They tend, therefore, to be inherently persistent, with long lived seed banks that enable populations to survive periods of unfavourable growing conditions. This means there is a significant time lag in the response of weed populations to a change in management (such as a new herbicide or tillage practice) which presents a significant challenge to research approaches based on short term field experimentation that seek inform sustainable weed management strategies. While the experimental response of weed to contrasting management treatments over one or more years will be indicative of trends in community dynamics, in the context of 'real world' farming systems, data of this kind cannot be relied upon to predict long term community dynamics. This is especially true when seeking to understand the impact of environmental change which generally occurs over decadal time scales (Varanasi et al., 2016). One way to meet this challenge is to attempt to capture the effects of management and environmental on weeds in a computer model that simulates changes in populations over many years. These so-called population dynamics models all generally have a similar structure based on the life cycle of an annual weed (Holst et al. 2007) that can be thought of as having four 'states': seeds in the seedbank, seedlings, mature plants and fresh seed either still on the maternal plant or on the soil surface (Figure 9.1).
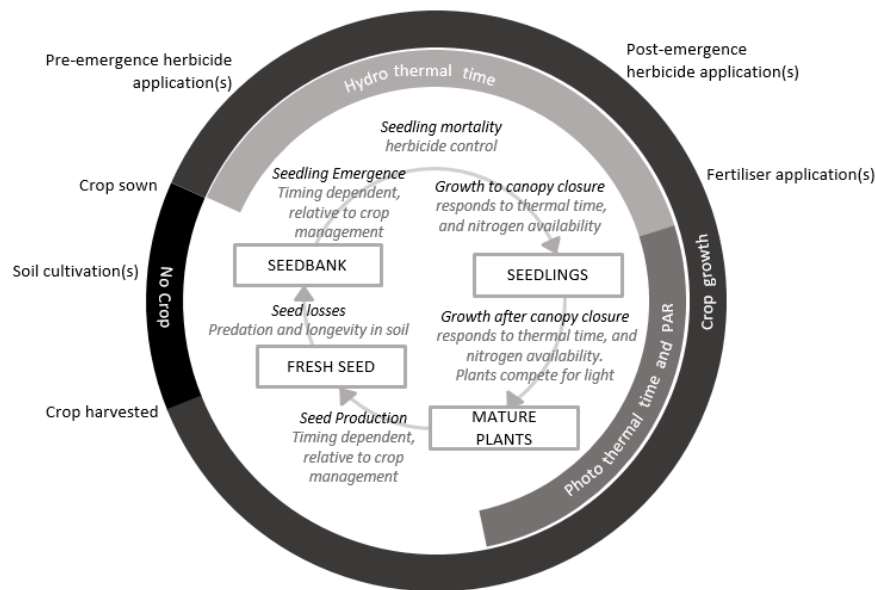
Figure 9.1. Schematic of the system that needs to be captured in models of weed population dynamics and persistence (based on model discussed in section 9.2.3). Weed species will vary in their response to management through the cropping season (outer ring and text) and environmental conditions (inner ring). Transitions between different states (boxes in inner circle) will be determined by processes that may be regulated by the environment, management or biological interactions. Models will vary in the complexity with which they simulate the system; from models that derive empirical relationships that describe transitions between states in a range of 'static' conditions to 'process based' approaches that attempt to capture all management x environment x biological interactions dynamically. Environmental variables are usually included in models as some measure of 'biological time' that reflects the amount of temperature, moisture, Photosynthetically Active Radiation (PAR) or daylight hours over the cropping season, for example thermal time (temperature), hydro-thermal time (temperature and moisture) or photo thermal time (temperature and daylength).

Any weed individual in a field will be in one of these four states. Models attempt to predict the transition of populations between states in response to environmental variables or management options. For example, the proportion of the seedbank that will germinate in a given year will be a product of the moisture and temperature of the soil, the depth it has been buried by previous cultivation and the timing of any soil disturbance. A model consists of a series of equations that predict these relationships with 'parameters' that may be specific to individual species; for example, the base temperature below which seeds do not germinate. Modelling transitions between states can either be based on 'empirical' relationships between management explanatory and weed response variables (for example the relationship between depth of seed burial and probability of a seed germinating) or 'process based' (for example modelling the growth rate of the hypocotyl in response to soil moisture and temperature). These approaches tend to lie along a 'tractability – prediction' continuum with trade-offs between the amount of data required to parameterise the model and the resolution in the response of the weeds.

9.1.1. The challenge of modelling weed persistence

Whether or not a weed species can persist in a cultivated field will largely be determined by the properties of the soil seedbank. This chapter will, therefore, focus on the challenge of modelling seedbank dynamics and early growth stages. Whether or not a new seed shed onto the soil surface survives and emerges to produce a following generation will depend on: the survival of the embryo against ageing, avoidance of predation by arthropods or vertebrates, survival of pathogen attacks and its dormancy profile in the context of opportunities for germination and

emergence as well as the ability of the emerged plant to capture resources and survive weed control. These processes will be affected differently by the management operations performed in arable fields and be dependent on the local environment. For example, tillage can bury seeds and protect them from predation, but it can also reduce the probability of successful germination and emergence if buried too deep. The challenge facing modellers that aim to explain variation in weed persistence between fields and predict the impact of change is to integrate these factors in sufficient detail to retain the power to discriminate between the response of contrasting species while avoiding the need for derive values for excessive numbers of parameters.

In this chapter, we present contrasting approaches to meeting the challenge of modelling weed persistence that lie at different points along this 'tractability – prediction' continuum. Firstly, a 'broad-brush', largely empirical approach is described that applies ecological strategy theory to weed communities to predict the impact of management on broad functional groups based on morphological and phenological traits available in the literature for all weed species. This approach is largely based on quantifying empirical relationships between management and the distributions of these traits. Secondly, we discuss a mechanistic, process-based model that predicts the impact of the local environment and management on the behaviour of the weed seedbank at the level of the species. Traits are, again, used in this this example but this time they are used to derive species-specific parameters in the model and have been measured experimentally for a sub-set of weeds. We do not present a comprehensive description of the models here but, rather, use them to illustrate different approaches to predicting weed persistence and the central importance of having an underlying detailed understanding of weed biology that is explored in other chapters.

9.2. 'Broad-brush' ecological approaches to modelling weed persistence

9.2.1. Ecological strategies of weeds

Predicting the persistence of weeds in cultivated fields is a specific example of the broader challenge of understanding the assembly of plant communities in contrasting habitats. One promising approach to meeting this challenge is to characterise plant communities based on the distribution of plant traits as opposed to traditional metrics of species diversity. Central to this discipline of functional ecology is the concept of the 'Plant Ecological Strategy Scheme' (PESS) that assumes trade-offs and synergies between traits that reflect contrasting evolutionary solutions to environmental constraints. One approach to modelling the impact of the environment and management on the persistence of weed communities would be to quantify the relative response of these different strategies ('functional groups') or the individual traits that underlie them.

The most widely accepted PESS is that introduced by Grime (1974) who identified three contrasting strategies at the extremes of a triangle based on species adaptation to gradients of soil fertility and disturbance. 'Competitors' (C) are characterised by traits that make them effective at resource acquisition, such as a fast growth rate and tall stature and are adapted to high fertility environments with low disturbance. 'Stress tolerators' (S) are adapted to low fertility environments with low disturbance and have traits that conserve nutrients in the plant such as long leaf life span. Finally, 'ruderals' (R) are typically found in habitats with high disturbance and high fertility with a short life span and fast growth rate. So-called 'regenerative traits', for example, seed mass, flowering, and seedbank persistence vary between the strategies and reflect fundamental ecological trade-offs such as that between competition and colonisation

(mediated via seed mass) (Moles and Westoby, 2004). All species can be assigned to one of these, or an intermediate, functional group (for example, competitive-ruderals, CR).

In the context of the C-S-R ecological strategy scheme, cropped fields with regular cultivation and application of nutrients, either as inorganic fertilizers or manure, represent a habitat at the extreme of the soil fertility and disturbance gradient. Consequently, weed floras are dominated by R species; they are predominantly annuals with a short life cycle, rapid growth rate and high seed production (Gaba et al., 2017). These traits enable weeds to complete their life cycle between disturbance events and rapidly capture applied nutrients. A recent trait-based analysis of two national weed floras (in the UK and France) compared arable weeds to equivalent floras found in grassland habitats to identify traits that typified adaptation to arable fields (Bourgeois et al., 2019). As a group, weeds occupied an extreme 'ruderal trait space' and this was reflected in significant differences in key traits when compared to the grassland flora. Particularly relevant to this discussion on weed persistence was the finding that weeds tend to flower earlier and for longer, meaning they are able to produce seed opportunistically avoiding the selection pressure of soil disturbance and herbicides.

9.2.2. Ecological strategies and the historical effect of management on weed floras

While the contemporary weed flora is characterised by extreme R strategies reflecting the dominance of ploughed systems and high inputs of inorganic fertilisers and herbicides, this has not always been the case and one might expect changes in cropping system management to be reflected in shifts in the functional characteristics of the weed flora. That is, traits that meant weed species could persist in past management scenarios may be selected against in current systems. These insights are important for predicting the potential impact of new management options on the weed flora and identifying traits that respond to management change. Several studies of this type exist in the literature.

Storkey et al. (2010) compared the traits of the common weed flora in the UK to a group of species that had declined since the 1960s owing to the increase in nitrogen fertiliser and herbicide use. The combination of short stature, late flowering and large seed emerged as a combination of traits that had been selected against by modern crop management – a so-called 'rare weed trait syndrome'. Examples include *Scandix pecten-veneris* and *Agrostemma githago*. These trends can be related to the large seeded species being better adapted for competition for nutrients, an advantage in fields with lower fertilizer applications. However, large seeded species tend to have shorter seedbank persistence (Thompson et al., 1993) and have a limited capacity to buffer against high herbicide mortality (owing to lower seed production per plant). The decline of this functional group can, therefore, be attributed to the increased use of herbicides and inorganic fertiliser (Storkey et al., 2012). A study of changes in the functional characteristics of weed floras in France over a similar period also identified shifts in traits that explain the relative persistence of contrasting weed species (Fried et al., 2012). Again, regenerative traits emerged as being important in explaining changes in community composition. 'Successful' species under current management tended to have a smaller seed size (high seedbank persistence and fecundity) and the ability to germinate and flower all year round – a generalist strategy that enables seed set across a range of crop types and the 'avoidance' of herbicide applications. Although there was also some evidence for a shift in traits in response to reduced disturbance under minimum tillage systems (towards a perennial life cycle and larger seed), crop type appeared to be the dominant management option driving weed functional traits in this and other studies (Gunton et al., 2011). One interesting result from the Gunton et al.

(2011) study was the shift in C-S-R strategies in different crop types related to their architecture, with a shift towards more competitive species in taller crops such as sunflower and maize.

9.2.3. Modelling future changes in the functional composition of weed seedbanks

Can we use new knowledge on the past effects of management on the change in distribution of 'persistence traits' to develop methodologies for predicting the effect of future management on weed communities? Meeting this challenge will require a life cycle model of weeds (Figure 9.1) that operates at the level of traits or functional group (as opposed to individual species). This approach represents a departure from traditional weed life cycle models that are developed for individual species (for example, Freckleton and Watkinson, 1998 for *Chenopodium album* in sugar beet) and are underpinned by empirical data measured at the species level. Rather, it identifies weed functional groups or ideotypes that reflect trade-offs between traits and contrasting ecological strategies. Such a model will be positioned at the interface between functional plant ecology and weed science and seeks to integrate data from functional trait databases of national floras with detailed weed life cycle data. The approach assumes that concepts developed in theoretical ecology to do with the processes underpinning community assembly and plant co-existence are useful for understanding the response of weed in cropped fields. It also relies on the existence of data that explicitly link the ecology of weeds to the dynamic response of their populations to management.

Metcalfe et al. (2020) have published a model of this type that is founded on the principle of identifying relationships between functional traits in large ecological databases and life cycle parameters that predict shifts between demographic states (e.g. seedbank to emerged seedlings) under contrasting management scenarios. Here, we illustrate the approach using the example trait of seedbank persistence. In his compilation of the seedbank characteristics of a national flora, Thompson et al. (1997) identified three categories of seedbank persistence for UK plants: transient, short term persistent and long term persistent and published these ecological data for the UK flora, including weeds. For a small subset of common weed species, including *Galium aparine* (short term persistent) and *Papaver rhoeas* (long term persistent), the decline of the weed seedbank in cultivated fields has been well-characterised (Lutman et al., 1993). By assigning each of the three categories (identified by Thompson et al., 1997) - transient, short term and long term persistent - an average value for weed seedbank decline (according to the data from Lutman et al., 1993) it is possible to estimate the survival rate of all weeds in each of the persistence categories (Figure 1a). This parameter will determine the decline of the seedbank under contrasting strategies and, although an intensive weed seedbank decline study cannot be done for every weed species, the whole flora can be modelled at the level of the seed persistence category. The behaviour of the different persistence categories under contrasting tillage (Figure 1b) can be predicted using a whole life cycle model that relies on a similar 'broad-brush' ecological approach to modelling transitions between the remaining life cycle stages (Storkey et al., 2015, Metcalfe et al., 2020).

Using the impact of different tillage regimes on an observed local species pool in a field on a research farm as a worked example, following 30 years of simulation with continuous inversion tillage the proportion of the seedbank made up of weeds in the "long-term persistent" seed bank category was predicted to reduce and there was a predicted increase in "short-term persistent" seed bank types (Figure 9.2). As germination is prevented when seeds are moved deep into the soil profile, tillage is an important weed management tool and it can change the functional composition of the weed community according the to the seedbank type. While having limited power to predict the change in absolute numbers of individual weed species, this

approach is useful for giving an insight into how a change in practice might influence the functional composition and absolute abundance of weeds. By aiming to predict changes in trait distributions across the whole regional species pool, as opposed to the dynamics of individual species, this model is restricted to using functions that can be related to traits widely reported in the literature. The following section shows how a similar approach to relating traits to model parameters can be used in a 'process based', mechanistic model developed using novel data on traits not routinely measured in the ecological literature.
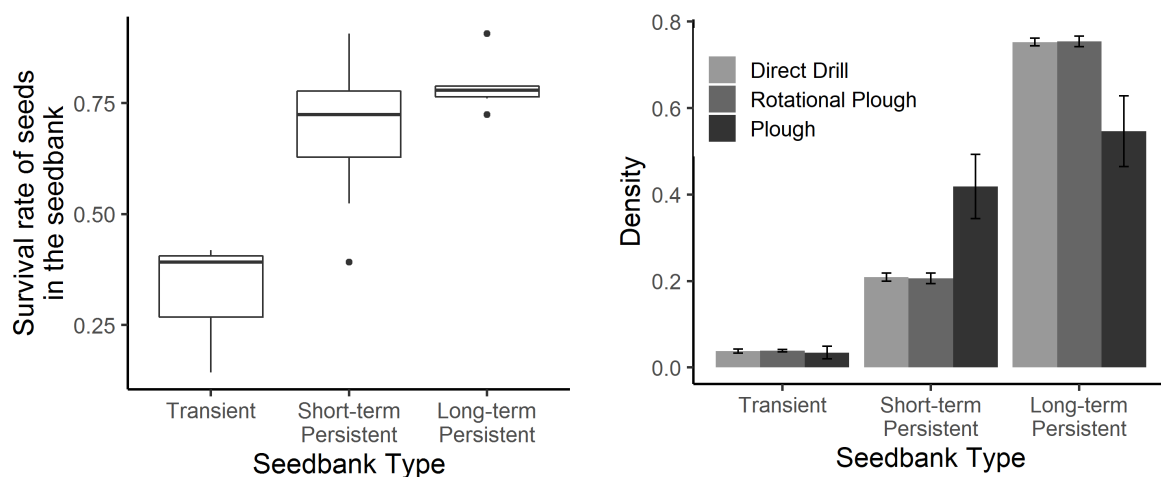

Figure 9.2. a) Functional group categorisation of weeds in terms of seedbank persistence, based on empirical data of seed survival at the level of individual weed species b) the proportion of the seedbank in each seedbank category in contrasting tillage scenarios, continuous direct drill (no inversion), rotational ploughing (three seasons direct drill followed by one season plough) and continuous ploughing (full inversion). Results are specific to the functional characteristics of the initial species pool; in this case, the field has low initial abundance of transient species meaning the contrasting response to management for this group is less clear.

9.3 A process-based approach to modelling weed persistence

Arable fields often have a wide range of weed species in the seedbank with continuous shifts in weed communities in response to changes in cropping systems in the medium and in the long term (see section 9.2.2). The approach described above to predicting these shifts, assigns weeds to functional groups based on broad categories of 'seedbank persistence' using online trait databases and predicts contrasting responses using parameters estimated at the level of the functional group. While this pragmatic approach can capture the effect of management on the functional composition of communities, it is less powerful in terms of predicting the response of individual species. Modelling the diversity of behaviours at the species level requires a tailored approach that captures the interactions between management, environment and biological processes (Figure 9.1). When considering the dynamics of the seedbank, these processes include the induction and release of seed dormancy, mortality of seeds through predation and rotting, germination, seedling growth and emergence. This alternative mechanistic, process-based approach to modelling weed communities represents a powerful tool for continuously synthesizing biological knowledge (Colbach, 2010). However, in the context of the 'tractability – prediction' trade-off, it also requires large numbers of parameters, which hinders the addition of new species to the model.

Previously, multi-species weed dynamics models of this type relied on the aggregation of independent single-species models, with a species-specific structure and a species-specific set of parameters (with the associated experimental overhead). To simplify the addition of new species, a generic model has been developed using the *same structure for all species* whose parameters are estimated from species traits. This model, parts of which are described in the following sections, is called FLORSYS (weed <u>flora</u> and cropping <u>sys</u>tem) and simulates the effects of cropping systems, in interaction with climatic and soil conditions, on the dynamics of a multi-species weed flora composed of annual species. Following the general structure of weed populations dynamic models (Figure 9.1), FLORSYS is based on the representation of the weed life cycle by a succession of key life-stages linked by demographic processes that are regulated by the cropping system, in interaction with the climatic and soil conditions. In the following discussion, the development of the seedbank part of the model and the approaches taken to deriving parameters for multiple species are reviewed with reference to a progression of published studies. To estimate the required parameters for a large number of weeds, they were, where possible, related to easier to measure species traits (*sensu* Violle et al., 2007), for example seed mass. However, as opposed to relying on published values in online trait databases (see section 9.2.3), the relationships between traits and parameters were quantified from a series of bespoke experiments (Gardarin et al., 2012). Below, we present this approach for the processes determining seedbank persistence: seed survival in the soil (or mortality), dormancy and germination.

9.3.1. Modelling seed mortality processes

In situ seed mortality includes any seed disappearance caused by age, diseases or microscopic predators (chapter 13), but excludes any seed bank decrease due to germination (chapter 6). In FLORSYS, predation by macro-organisms (vertebrates and arthropods) is not taken into account because it is assumed to be negligible for buried seeds (Westerman et al., 2006); this assumption would, therefore, be valid for regularly tilled systems. To measure seed mortality, a parameter in the FLORSYS model, an experiment was done in which seeds of 13 weed species were buried 30 cm deep in a field and recovered regularly for two years to measure their viability (germination tests followed by seed crushing tests). Seed viability decreased during the second year of burial, with mortality rates ranging from 0.01 to 0.63 y^{-1}, depending on the species. More than 75% of the seeds of *Galium aparine* disappeared whereas more than 80% of *Amaranthus hybridus* or *Polygonum lapathifolium* seeds were still viable. To facilitate including additional species in the model without having to run the field experiment for every species, the mortality parameter was related to seed traits which could be more easily measured. Among the studied trait-mortality relationships, it was found that seed mortality decreased with increasing seed coat thickness (Figure 9.3). This was measured using X-ray images (Figure 9.4). Seed mortality was higher for seeds with thin seed coats (e.g. *Geranium dissectum* and *Digitaria sanguinalis*) and lower for seeds with thick seed coats (e.g. *Fallopia convolvulus* and *Datura stramonium*). This relationship explained half the between-species variability in mortality rate (Gardarin et al., 2010).
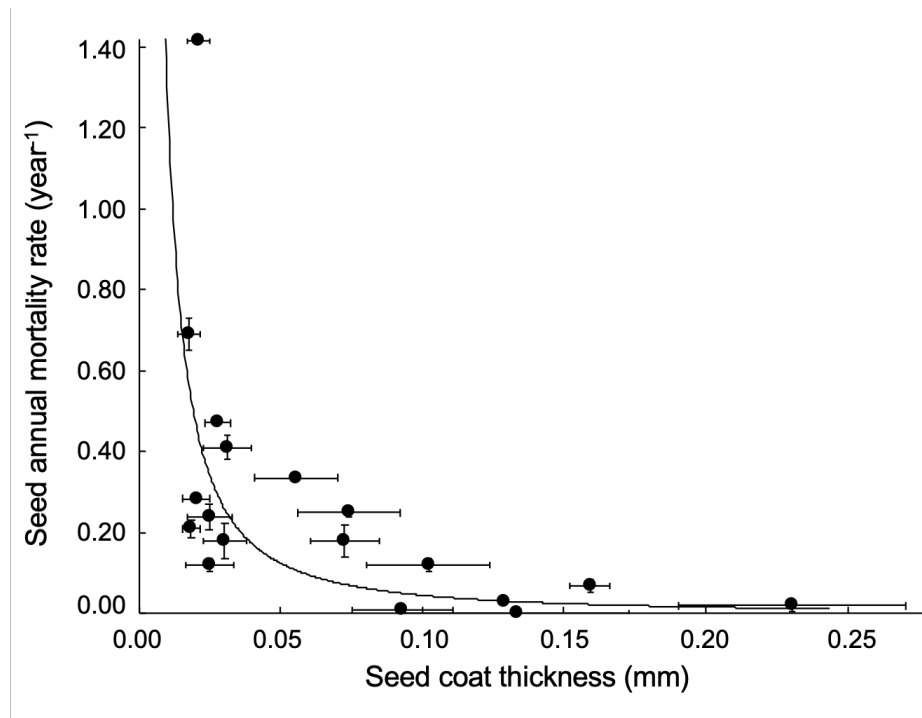
Figure 9.3. Annual seed mortality rate of seeds buried deep in the soil as a function of seed coat thickness (± standard deviation). A mortality rate exceeding 1 means that all the seeds lost their viability in less than 1 year. Data from Gardarin et al. (2010).

Despite its importance in governing several processes in seed bank dynamics, seed coat thickness has rarely been reported in the weed science literature. Seminal envelopes, such as the seed coat or the achene wall, provide a mechanical and chemical barrier, protecting the seed and embryo from parasitic attacks, predation and wide variations in temperature and humidity. Seeds with thick seminal envelopes (e.g. *Ambrosia artemisiifolia* and *Polygonum spp.*) have lower mortality. The biochemical composition of the seed shells and reserves, which may contain phenolic compounds and alkaloids with antibacterial and antifungal properties, may also contribute to seed protection and maybe affect predator preferences.
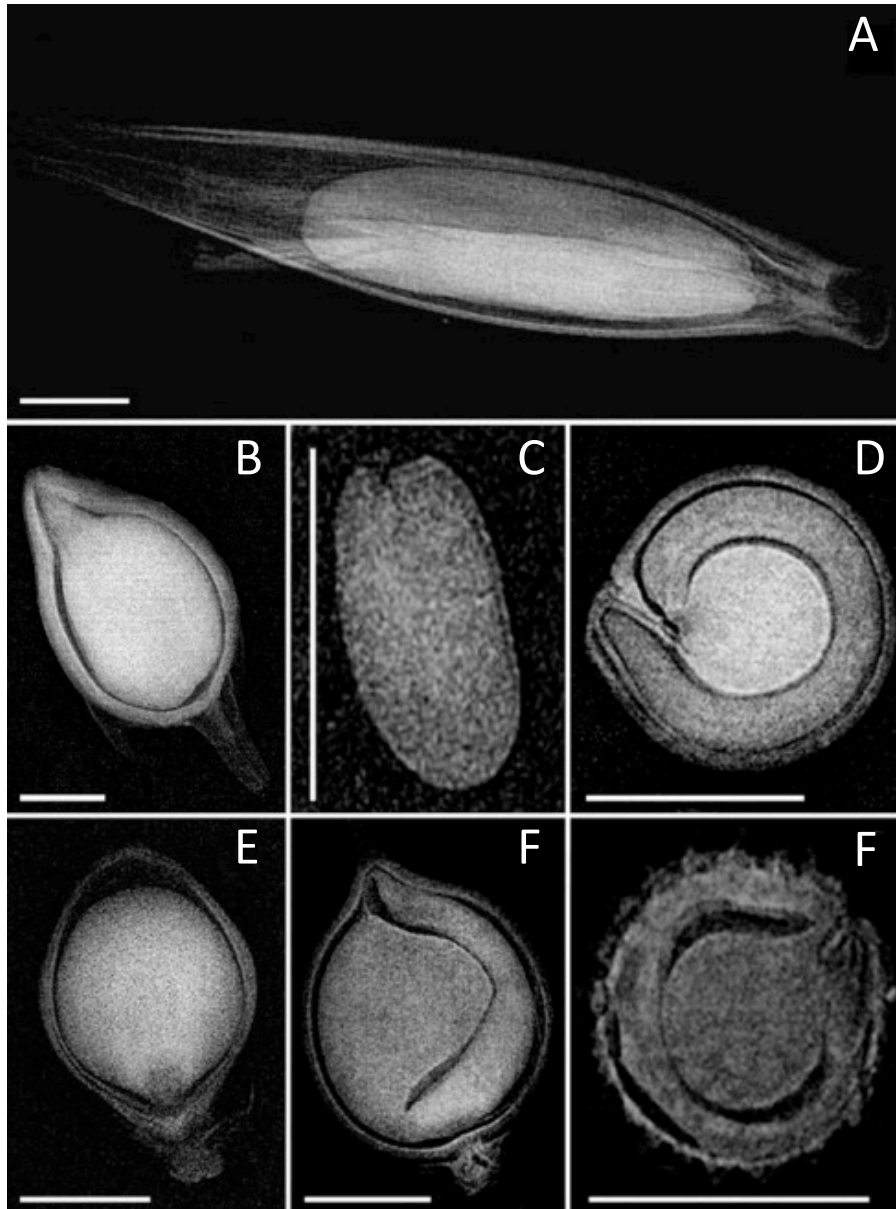
Figure 9.4. X-ray images of seeds of nine weed species with contrasted seed coat thickness. (A) *Avena fatua*; (B) *Ambrosia artemisiifolia*; (C) *Capsella bursa-pastoris*; (D) *Chenopodium album*; (E) *Echinochloa crus-galli*; (F) *Polygonum lapathifolium*; (G) *Stellaria media*. Scale bars represent 1 mm.

9.3.3. Modelling seed dormancy processes

Most weed species display cyclic dormancy, being dormant in one season and non-dormant in another, thus optimising their chance to establish and reproduce in a favourable environment (chapter 3). Variation in seed dormancy can be modelled using a broken-stick linear model which is essentially a series of regression lines that predict the dynamics of dormancy in time (Figure 9.5). The proportion of non-dormant seeds varies within the season, between a minimum and maximum level. Four timing parameters define the dates of dormancy induction (onset and end) and release (onset and end). In the first year after seed production, the dormancy levels may differ from the subsequent ones due to primary dormancy acquired while on the maternal plant. To quantify dormancy level-trait relationships, data were collected on seasonal seed dormancy fluctuations obtained after seed burial experiments under comparable germination conditions, in terms of temperature and light. Together with data from new

experiments, the dataset comprised information on dormancy fluctuations for 29 weed species from 32 literature sources. Again, these parameters were related to seed traits to allow species outside of the germination dataset to be included in the model.
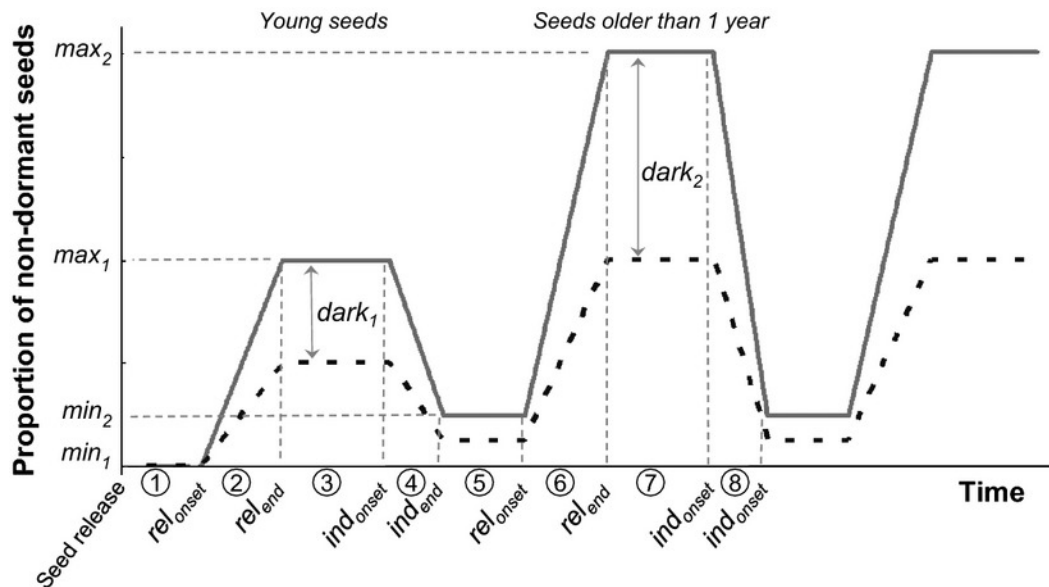

Figure 9.5. Representation of the parameters used in a model of the change in seed dormancy through a season. In the light (solid line), the proportion of non- dormant seeds vary between min_1 and max_1 for young seeds, and between min_2 and max_2 for seeds aged more than 1 year. In the dark (dotted line), these proportions were proportionally reduced by a factor of $dark_1$ and $dark_2$, respectively for young and old seeds. Dormancy release occurs between rel_{onset} and rel_{end} dates, and dormancy is induced from day ind_{onset} to day ind_{end} (Gardarin and Colbach, 2015).

Minimum (when dormancy was low) and maximum (when dormancy was high) proportions of non-dormant seeds in the first and the second years of burial were almost always explained by the same seed traits. Both minimum and maximum dormancy significantly increased with the seed shape index (the variance of the relative seed dimensions, ranging from nearly zero for spherical seeds to nearly 1 for elongated or flattened seeds), with a lower dormancy level for elongated seeds, even when accounting for phylogenetic relatedness between species (Gardarin and Colbach, 2015). From an evolutionary point of view, natural burial of spherical seeds is easier than for flattened seeds, the latter tending to remain on the soil surface (Benvenuti, 2007). Seeds located on the surface are more prone to predation than buried ones (Hulme and Borelli, 1999) and may have been selected for lack of dormancy and immediate germination to limit such mortality risks (Grime et al., 1981). The seed dormancy of each species also increased with increasing coat thickness or dry mass, which were all correlated (Gardarin and Colbach, 2015). The seed coat represents a physical and maybe chemical barrier. We observed in our data set that the thicker the coat, the larger this barrier effect, resulting in coat-imposed dormancy and a lower germination proportion.

Seed morphological traits (mass, shape, coat thickness) traits explained 38–56% of the variability in the level of seed dormancy, while no relation was found with seed lipid or protein content. The unexplained variability was a product of the interaction with environmental factors; a large proportion of the variability in the level of dormancy is not species specific but results from prevailing conditions experienced by the maternal plant during seed production including heat and moisture stress (chapters 3 and 4). As for the dates of dormancy fluctuations, they were not related to any trait but could be related to average weed emergence periods (with

a 10-day time scale) using emergence calendars for each species. This kind of information can be obtained by questioning agricultural botanists with a long experience of weed emergence surveys in field conditions or interrogating the literature. It is also possible to group species into categories defined by the periodicity of emergence (Storkey et al., 2015) – this is the approach that was taken in the trait-based approach to modelling weed persistence (section 9.2.3). The dates of dormancy induction are positively correlated with the date of the end of emergence of each species, that is the later the end of the average emergence period, the later the dormancy induction period. The dates of dormancy release increased with the date of the onset of emergence in the field. It was therefore possible to estimate dates of dormancy induction and release for a wide range of species by knowing the usual approximate dates of weed emergence onset and end in the field (Figure 9.5).

9.2.4. Modelling seed germination processes

In the field, germination can be triggered when tillage is performed in a moist soil or when precipitations moisten a dry soil layer. Germination only occurs when the soil temperature and soil water potential exceed the base values for a given species. Modelling the date and rate of germination is essential as it determines the date of seedling emergence relative to the crop, crop-weed competitive interactions and the ability of the weed to replenish the seedbank. Below, we again describe the parameters used in the FLORSYS model and present the analysis of the traits associated with these germination dynamics.

A dataset of 185 germination time courses covering 25 weed species under optimal germination conditions was used to quantify the following model parameters: the germination lag-time (time from imbibition to the first germinated seed), the time to mid-germination (time to reach 50% of the final germination percentage) and the maximal rate (slope of the germination curve at mid-germination). The correlations between seed germination parameters and morphological, chemical and physiological seed traits were then analysed, using seed dormancy level as a covariate (section 9.2.3) since germination occurred earlier and was faster in non-dormant seed lots. Seed traits, together with dormancy level (final germination rate) explained 41 to 59% of the variability in germination speed parameters (Gardarin et al., 2011). Germination was more rapid in species with a high base temperature for germination; a trait that is often available in the literature. This relationship indicates that species requiring high temperature germinate faster than those germinating earlier at low temperatures. Thus, both types of species achieve germination and subsequently grow and develop in a similar time considering the range of temperatures in which they each germinate in field conditions.

Lipid-rich seeds (exceeding 30% lipid content) also had earlier and more rapid germination (Gardarin et al., 2011). This effect was found for species with a wide range of seed lipid contents, varying from 3.5% (*Fallopia convolvulus*) to 43.6% (*Papaver rhoeas*) and was a novel finding as a reverse correlation was expected between seed lipid content and germination rate. The reactivation of metabolism at seed imbibition is associated with the beginning of the mobilization of reserves. The use of lipid reserves requires a greater quantity of oxygen, which makes the germination of lipid rich species more sensitive to partial oxygen pressure (Al-Ani et al., 1985, Raymond et al., 1985), which can thus slow the rate of germination. The last trait that was found to affect germination was the surface area to mass ratio which was positively related to the germination lag (Gardarin et al., 2011). It was hypothesized that germination timing partly depends on the time required for seed imbibition. Imbibition should be faster in seeds with a large area for water to enter relative to seed water

demand, probably linked to seed mass. However, although logical, the present correlation only explains a small proportion of the variability in the germination rate and remains to be confirmed on a larger number of species.

9.3 Integrating seedbank processes into the multi-annual weed dynamics model

Modelling seed germination and pre-emergent growth alone is not enough to predict the persistence of weeds in fields. The processes regulating seedbank dynamics, described in sections 9.2.2 – 9.2.4, have been aggregated with other sub-models to complete the life-cycle of annual weeds (Munier-Jolain et al., 2013, Colbach et al., 2014b, Colbach et al., 2014c, Mézière et al., 2015). The resulting model, FLORSYS, can be visualised as a virtual field on which cropping systems can be tested with different pedoclimates and weed floras in terms of crop production and weed (dis)services (Colbach et al., 2014a). 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, more feasible, estimated from regional flora assessments (Colbach et al., 2016). Parameters have been estimated for 25 frequent and contrasting annual weed species and 33 cash and cover crop species, using relationships with traits where necessary. The input variables influence the annual life cycle of annual weeds and crops, with a daily time-step. Pre-emergent stages are described in section 5.2. After emergence, the crop-weed canopy is simulated in 3D to account for heterogeneous canopies in terms of species and emergence cohorts, with a simplified representation of each crop and weed plant. A series of post-emergence processes (e.g. photosynthesis, respiration, growth, shade response), driven by light availability and air temperature, are modelled at the level of the individual plant. At plant maturity, weed seeds are added to the soil seed bank and crop seeds are harvested to determine crop yield. As for the pre-emergence submodel, functional relationships were established to estimate difficult-to-measure parameters from more easily measured or accessible species traits and characteristics (Colbach et al., 2019).
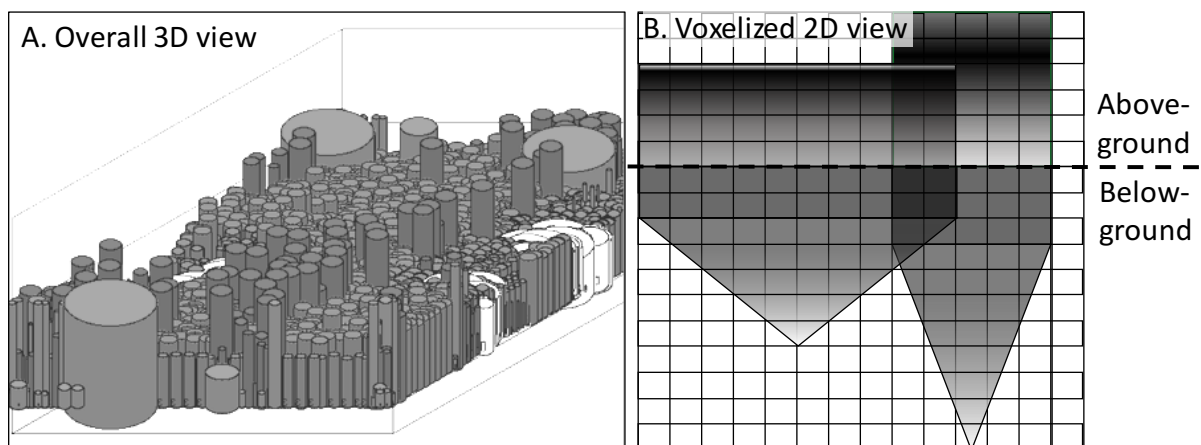

Figure 9.6. 3D individual based representation of multispecies canopy in FLORSYS. A. 3D above-ground view of a sample of a simulated field of 3 x 6 m² where each crop and weed plant is represented as a cylinder. B. 2D view of two plants, detailing above and below-ground plant volume (with leaf area and root biomass distributed along layers) and space discretized with voxels (3D pixels) to simulate light trickling down in the above ground part of the canopy and over lapping root systems competing for soil resources (Nathalie Colbach © 2020).

This thorough simulation of the whole weed life cycle produces very detailed outputs, at a daily time step and in 3D. These virtual measurements are essential to provide a mechanistic understanding of why a given technique or cropping system results in a given weed seedbank community. To simplify the comparison of different cropping systems, the detailed outputs are translated into indicators of weed impact on crop production and the environment (Mézière et al., 2015). For instance, crop yield loss due to weeds is the relative difference in yield of simulations with versus without weeds. Other indicators use a trait-based approach (i.e. community-weighted mean of trait) to assess weed services (e.g. potential trophic resources for carabids), weighting weed state variables (e.g. weed seeds on soil surface during insect activity season) by species traits reflecting the contribution to the service (e.g. seed lipid content) (Mézière et al., 2015).

5.3.1 Case study using the process-based model

In this section, a simulation with FLORSYS is presented to illustrate the power of the model to simulate the effect of management on weed persistence and show an example of the kind of output the models can produce, capturing the time lag in the response of weeds to management that is inherent in their population dynamics.

Weed seed persistence is the reason why a management decision in a given year can have consequences for many years to come. To illustrate this, we assessed the effect of cover and companion crops in winter wheat (*Triticum aestivum* L.) on weed persistence in a wheat/barley/oilseed rape rotation in three virtual fields whose management only differs during the first year (Figure 9.6). During that year, one field was grown only with wheat, one had a cover crop during summer fallow and the third one associated wheat with a companion crop. Cover and companion crops are grown to occupy the soil surface and leave no available niches for weeds. Simulations using FLORSYS show that these solutions, particularly the companion crop, are indeed efficient in reducing weed densities in the cash crop grown during the year the solutions are tested, compared to a sole wheat crop (Figure 9.6). However, the beneficial effect of the companion crop was also still visible intermittently during the next 9 years, even though the three fields were managed identically during that time. More importantly, weed densities increased in the field with the initial cover crop compared to the control. This was a consequence of the cover crop restricting opportunities for controlling weeds in false seed beds, resulting in a denser seed bank than in the control. These seeds emerged during the third year, with a nefarious effect still visible in the tenth year. This case study illustrates the necessity of long term modelling approaches to capture the impact of interacting management effects that would not be possible using conventional field experimentation approaches.
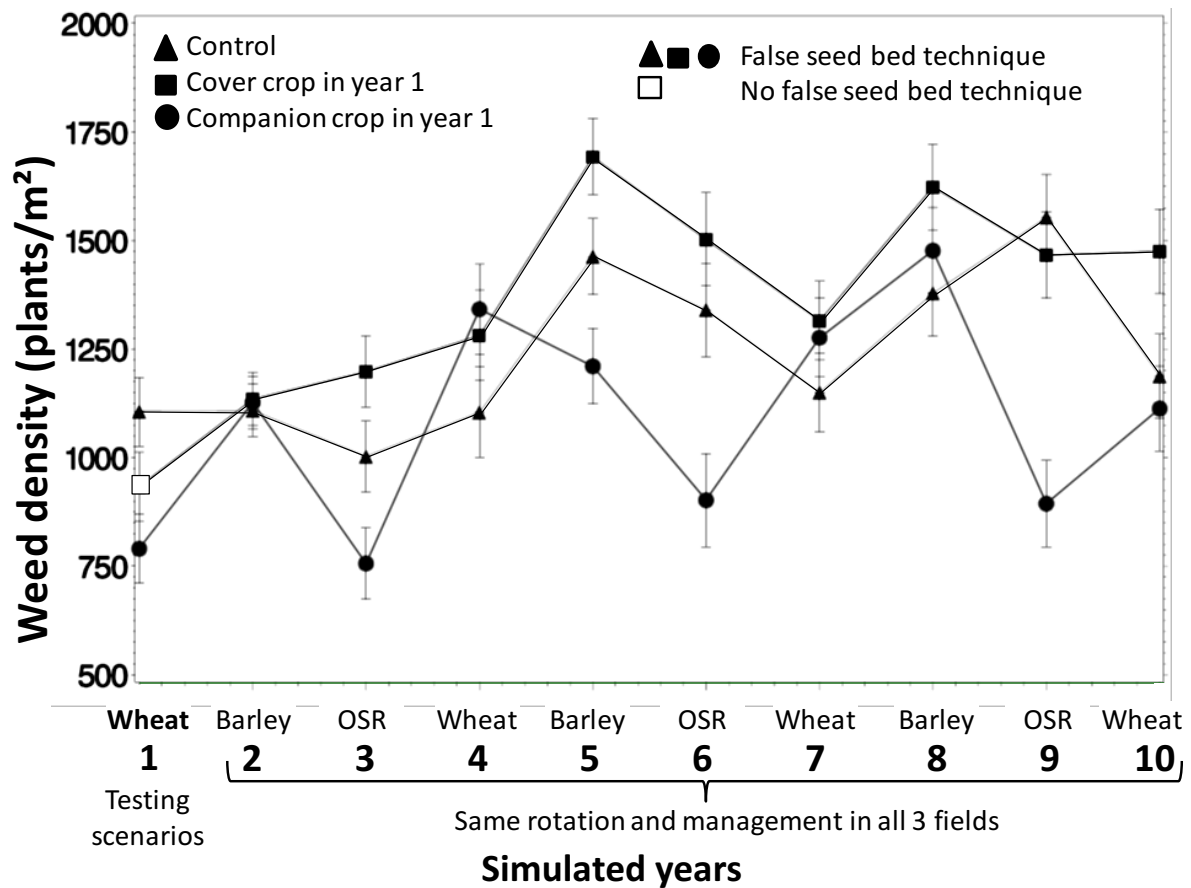
Figure 9.6. Long-term effects of cover (mustard) and companion crops (field bean) and the associated management practices in the wheat grown in year 1 on multispecies weed dynamics over 10 years. Mean and standard-deviation of the maximum weed density in the cash crop of 10 weather repetitions from Burgundy (data from Colbach et al., 2014a) (Nathalie Colbach ©).

9.4. The weed seed traits selected by management practices

A central theme running through this chapter has been the value of understanding how the traits of weed species can be used to predict model parameters and the response of their population dynamics under contrasting management scenarios. Identifying which traits should be targeted in these analyses largely relies on a knowledge of the underlying biology or evidence from the published literature. However, it is also possible to use models to identify the extent to which management discriminates between, or acts, on different traits related to their persistence. Models such as FLORSYS can be used to ask this kind of theoretical question by establishing multiple scenarios covering contrasting pedoclimates and cropping systems (Colbach and Cordeau, 2018). The simulated data are analysed similarly to data collected in actual fields (Colbach et al., 2014d) but allows the coverage of considerably more situations and measurements and can be used to better understand underlying processes and trends.

The example of Colbach and Cordeau (2018), Table 9.1, shows an example of such an analysis. In this case, the two weed species traits determining the timing of germination and emergence (section 9.2.4), i.e. base temperature and base water potential, were those that the most interacted with management practices in average over all regions, weather conditions and cropping systems. Species that require a warmer soil were rarer in longer rotations (negative correlation for base temperature in line [1] in Table 9.1) consisting of many different species or varieties [4], and comprising long cover crops [3] as well as frequent winter crops [5]. They are

also disadvantaged by frequent [9-11] and deep tillage [8] but favoured by rare mouldboard ploughing [13]. Conversely, seed traits that are related to persistent seeds, i.e. thick seed coats, small seed areas per seed mass and round seeds were better adapted to long crop covers as well as deep and frequent tillage.

Table 9.1. Which weed species traits related to seed bank persistence are selected by management practices? Relationships identified by fourth-corner analyses on 272 cropping systems from 7 French and Spanish regions simulated over 28 years and 10 weather repetitions (method from Colbach et al., 2014d, data from Colbach and Cordeau, 2018). Pearson correlation coefficients between practices and species traits/parameters, showing only coefficients exceeding 0.20 in absolute values and significant at p<0.001 (positive relationships indicated with bold outlines and negative relationships with shaded boxes). Fourth-corner analyses investigate correlations between three matrixes consisting of management practices in fields, weed species densities in these same fields and weed species traits/parameters, using permutations to test the null hypothesis that species are distributed independently of scenarios and traits/parameters. Here, practices and weed densities were averaged over 27 years.

Cropping system components	Seed traits					
	Area/ mass	Coat thickness	Shape[§]	Mass	Base Tempe-rature	Base Water potential
[1] Rotation length (years)					-0.21	
[2] % cover crops during fallow		0.20				
[3] Duration of crop cover (moths/year)					-0.24	
[4] Number of crops or varieties in rotation					-0.22	
[5] % winter crops					-0.30	-0.20
[6] Sowing date of winter crops					-0.24	
[7] Harvest date of winter crops					-0.29	-0.21
[8] Mean tillage depth (cm)	-0.27		-0.34		-0.29	-0.27
[9] Superficial tillage (operations/year)			-0.29		-0.40	-0.34
[10] Superficial tillage (April-Sept)			-0.29		-0.39	-0.32
[11] Superficial tillage (Oct-March)					-0.28	-0.26
[12] Days from harvest to 1st till	-0.24			0.24		
[13] Years between ploughing			0.20		0.20	0.20
[14] Days from ploughing to sowing					-0.23	-0.24
[15] Rolling operations/year					-0.27	-0.22
[16] Days from harvest to rolling					-0.21	
[17] Non-systemic herbicides/year					-0.22	

[§] Elongated and flattened seeds have a high shape index, round seeds a small index value.0

Knowing the weed density or the frequency of key weed traits in a field or a cropping system is not enough to assess whether the weed flora is harmful for crop production or beneficial for the agroecosystem. Thanks to its weed-impact indicators, FLORSYS allows the weed traits that drive weed (dis)services to be determined, using the same methods as for investigating the links between management practices and species traits (i.e. running a virtual field network with FLORSYS and analysing the correlations between weed species densities, traits and (dis)services). For instance, weed contribution to reducing nitrate leaching during summer fallow was shown to increase in species with a high seed lipid content and a large seed area per mass. Both traits result in fast and early germination, which is crucial to ensure that weeds take up nitrogen fast enough to keep it from leaching to groundwater. Similarly, weeds with thinner seed coats protected the soil more against erosion as such seeds are less dormant and can emerge during fallow.

9.5. Conclusion

The need to understand the complex, interacting effects of the environmental, management and biological components of an arable field on the persistence of weeds (Figure 1) means that weed population modelling will continue to make an important contribution to sustainable weed management. However, precisely because of this complexity and associated uncertainty, care should be taken in how models are presented and interpreted (Holst et al., 2007). It is unlikely that any model, regardless of its complexity, will be able to accurately predict the change in absolute numbers of weed seeds of a given species under contrasting management scenarios. However, as illustrated above, models do have the power to ask 'what-if' questions to do with the relative response of different weed species or the likelihood of a management change to reduce overall abundance or functional composition of the community. When applied in this 'hypothesis generation and testing way', they have an important role to play in exploring future trajectories of weed communities under future, novel, environmental and management conditions.

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