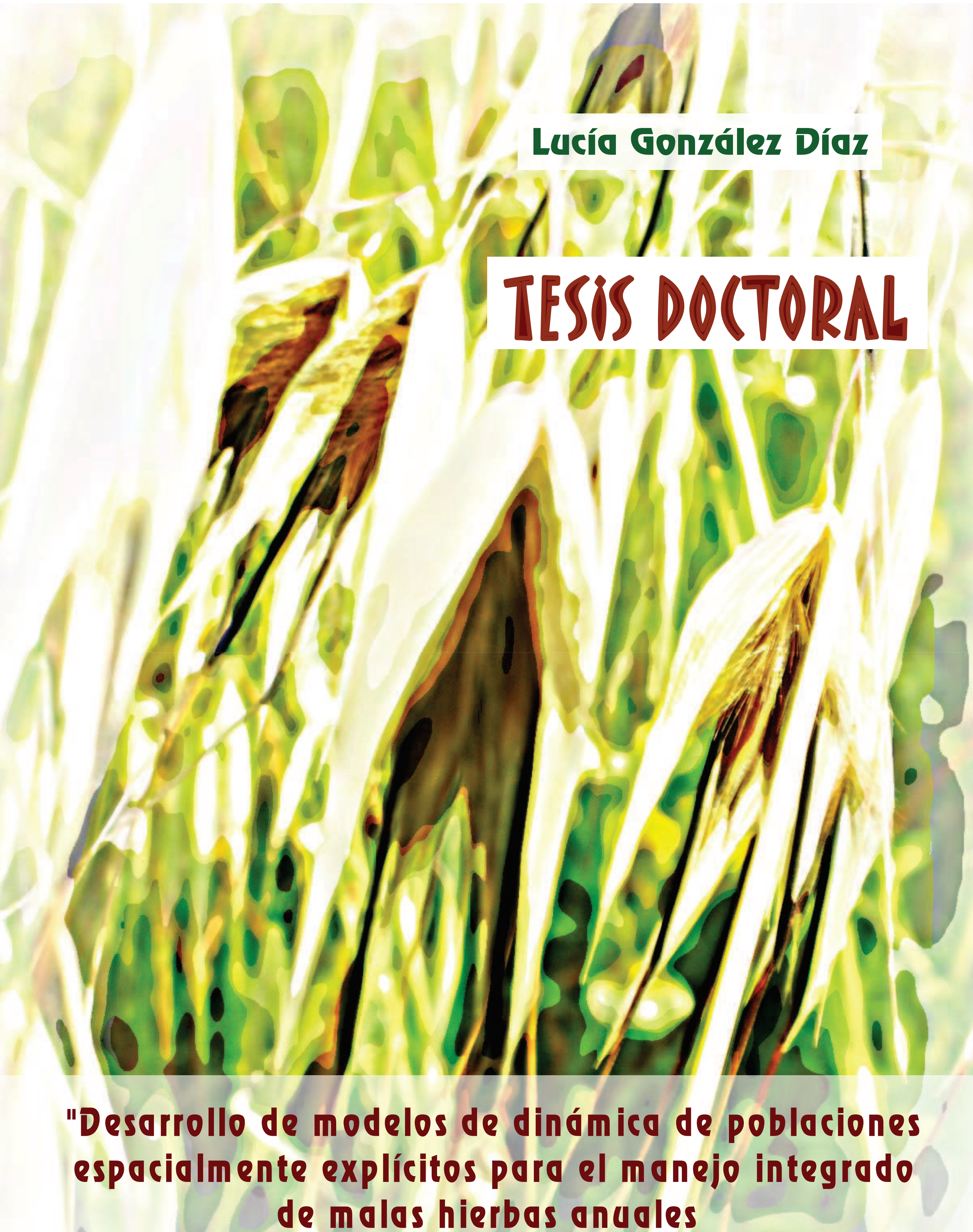

Lucía González Díaz

TESIS DOCTORAL

"Desarrollo de modelos de dinámica de poblaciones espacialmente explícitos para el manejo integrado de malas hierbas anuales a diferentes escalas espaciales"

Córdoba, 2012

TITULO: *Desarrollo de modelos de dinámica en poblaciones espacialmente explícitos para el manejo integrado de malas hierbas anuales a diferentes escalas espaciales*

AUTOR: *LUCIA GONZALEZ DIAZ*

© Edita: Servicio de Publicaciones de la Universidad de Córdoba.
Campus de Rabanales
Ctra. Nacional IV, Km. 396 A
14071 Córdoba

www.uco.es/publicaciones
publicaciones@uco.es

UNIVERSIDAD DE CÓRDOBA

CSIC
CONSEJO SUPERIOR DE INVESTIGACIONES CIENTÍFICAS

INSTITUTO DE AGRICULTURA SOSTENIBLE
IAS

TESIS DOCTORAL

Desarrollo de modelos de dinámica de poblaciones espacialmente explícitos para el manejo integrado de malas hierbas anuales a diferentes escalas espaciales

AUTORA:

Lucía González Díaz

DIRIGIDA POR:

Dr. José Luis González Andújar

Dr. Antonio J. Pujadas Salvà

Córdoba, septiembre de 2012

TESIS DOCTORAL

Desarrollo de modelos de dinámica de poblaciones espacialmente explícitos para el manejo integrado de malas hierbas anuales a diferentes escalas espaciales

Memoria redactada para optar al grado de Doctor por la Universidad de Córdoba, por la Ingeniera Agrónoma:

Lucía González Díaz

Visto Bueno:

Directores de tesis

Dr. José Luis González Andújar
Investigador Científico
Instituto de Agricultura Sostenible, CSIC

Dr. Antonio J. Pujadas Salvà
Profesor titular
Universidad de Córdoba

Córdoba, septiembre de 2012

TÍTULO DE LA TESIS: Desarrollo de modelos de dinámica de poblaciones espacialmente explícitos para el manejo integrado de malas hierbas anuales a diferentes escalas espaciales

DOCTORANDA: Lucía González Díaz

INFORME RAZONADO DE LOS DIRECTORES DE LA TESIS

(se hará mención a la evolución y desarrollo de la tesis, así como a trabajos y publicaciones derivados de la misma).

D. JOSÉ LUIS GONZÁLEZ ANDÚJAR, Investigador Científico del Departamento de Protección de Cultivos, Instituto de Agricultura Sostenible, CSIC, y **D. ANTONIO J. PUJADAS SALVÀ**, Profesor titular del Departamento de Ciencias y Recursos Agrícolas y Forestales, ETSIAM, UCO, directores de la presente Tesis Doctoral

Informan:

Que el trabajo que lleva por título "**Desarrollo de modelos de dinámica de poblaciones espacialmente explícitos para el manejo integrado de malas hierbas anuales a diferentes escalas espaciales**" ha sido realizado bajo nuestra supervisión por la Ingeniera Agrónoma, D. Lucía González Díaz, y consideramos que reúne los méritos suficientes para optar al grado de Doctor.

Que dicha Tesis Doctoral se va a presentar como un compendio de capítulos donde se recogen los objetivos perseguidos y cumple con los requisitos de indicios de calidad (Art. 25 de la Normativa Reguladora de los Estudios de Doctorado, propuesta por la Comisión de Másteres y Doctorado de 14 de diciembre de 2011 y aprobada por Consejo de Gobierno de 21 de diciembre de 2011). En cumplimiento de este artículo se presenta un artículo científico correspondiente al Capítulo III de la presente Tesis Doctoral.

González-Díaz, L.; van den Berg, F.; van den Bosch, F.; González-Andújar, J. L. (2012) Controlling annual weeds in cereals by deploying crop rotation at the landscape scale: *Avena sterilis* as an example. Ecological Applications 22, 982-992.

Ecological Applications, de difusión internacional, cuenta con un índice de impacto de 5.102 ocupando la posición 10/205 (primer cuartil) en el descriptor 'Environmental Sciences' y la posición 14/131 (primer cuartil) en el descriptor 'Ecology' del ISI-JCR.

Los resultados relativos a los capítulos II y IV se encuentran pendiente de envío a revistas de difusión internacional del ISI-JCR. Otras publicaciones derivadas de la presente tesis son dos contribuciones a congresos de ámbito nacional y una patente nacional

Contribuciones a congresos:

González-Díaz, L.; van den Berg, F.; van den Bosch, F.; González-Andújar, J. L. (2011) Sincronización de rotaciones a nivel de paisaje como una estrategia de manejo de *Avena sterilis* en cereales. En: Plantas invasoras, resistencias a herbicidas y detección de malas hierbas (Eds. J. R. Arévalo, S. Fernández, F. López, J. Recasens, E. Sobrino) pp. 361-364. ISBN 978-84-615-4903-0. Universidad de La Laguna. San Cristóbal de La Laguna, España.

González-Díaz, L.; González-Andújar, J. L. (2011) Modelo bioeconómico y espacial de *Lolium rigidum* y estrategias para su control en cereales. En: Plantas invasoras, resistencias a herbicidas y detección de malas hierbas (Eds. J. R. Arévalo, S. Fernández, F. López, J. Recasens, E. Sobrino) pp. 357-360. ISBN 978-84-615-4903-0. Universidad de La Laguna. San Cristóbal de La Laguna, España.

Patente nacional:

González Díaz, L.; González Andújar, J. L. (2012) Programa de ordenador WeedRESIST: modelo espacial a escala de paisaje sobre la evolución de las poblaciones de malas hierbas anuales resistentes a herbicidas y estrategias para su control. Nº protocolo Acta de Depósito Notarial 819/2012.

La doctoranda, además, ha complementado su formación con estancias de dos meses de duración en tres centros internacionales de prestigio en su especialidad y bajo la supervisión de prestigiosos investigadores:

Julio-agosto 2009. Department of Land Resources and Environmental Sciences (Montana State University, EEUU) bajo la supervisión del Dr. Bruce Maxwell.
Junio-julio 2010. Department of Biomathematics and Bioinformatics (Rothamsted Research, UK) bajo la supervisión del Dr. Frank van den Bosch.
Junio-julio 2011. School of Life Sciences (University of Warwick, UK) bajo la supervisión del Dr. Paul Neve.

Por todo ello, se autoriza la presentación de la tesis doctoral.

Córdoba, 5 de septiembre de 2012

Firma de los directores

Fdo.: José Luis González Andújar

Fdo.: Antonio J. Pujadas Salvà

Esta tesis doctoral ha sido realizada gracias a una beca JAE-PRE del Consejo Superior de Investigaciones Científicas (CSIC) y se ha llevado a cabo en las instalaciones del Instituto de Agricultura Sostenible (CSIC) en Córdoba. La tesis ha contado con financiación de los fondos FEDER y del Ministerio de Ciencia e Innovación a través de los proyectos del Plan Nacional I+D+i AGL2008-00544 (Bases ecológicas del paisaje agrícola para el manejo de la flora arvense: biodiversidad, dispersión de semillas y modelización espacial) y AGL2009-07883 (Influencia de la estructura del paisaje agrícola cerealista sobre la composición y dinámica espacial de las poblaciones de plantas arvenses y su manejo).

A mi familia,
especialmente a Manuela

“La vida tiene profundidades que las palabras no alcanzan a sondar”

Carlos González

Agradecimientos

A mis directores de tesis por su paciencia, apoyo y supervisión del trabajo desarrollado.

A mis supervisores en las estancias realizadas, por su dedicación, amabilidad e interés en el trabajo que se estaba desarrollando.

A mis compañeras/os de laboratorio, que más que compañeras/os son amigas/os. Por tantas preguntas y respuestas, desayunos, vivencias y complicidades compartidas.

A mis amigos de aquí y de allá. Porque siempre están ahí, aunque en los últimos años no les haya dedicado suficiente atención.

A mi familia, por su incondicional apoyo y comprensión, por el ánimo que me infunden en cada momento y por su inmensurable paciencia durante todo este tiempo.

A los que no están y les hubiera gustado participar en esta etapa de mi vida. Ellos saben cuánto siento su apoyo. Gracias.

A Carlos y a Manuela, que son el empuje que diariamente me hace seguir adelante e intentar mejorar.

Y a todas aquellas personas que de alguna forma han participado en el desarrollo de esta tesis y por olvido no menciono.

Resumen

Las malas hierbas, como las especies dominantes de los cereales de secano españoles *Avena sterilis* L. (avena loca) y *Lolium rigidum* Gaudin (vallico), compiten con el cultivo y reducen significativamente su producción. La proximidad fisiológica y morfológica de estas malas hierbas con el cereal dificulta su control basado principalmente en el uso de herbicidas, lo que genera problemas medioambientales y de resistencia. Por ello, es necesario desarrollar nuevas estrategias de manejo que minimicen dichos problemas. El desarrollo de nuevas estrategias requiere experimentación a largo plazo con un elevado coste económico y de tiempo. Una herramienta idónea para el estudio a largo plazo de estrategias de manejo son los modelos de dinámica de poblaciones. Dichos modelos permiten evaluar y comparar múltiples estrategias de manejo y ayudan a elegir las más eficientes.

Hasta la fecha, la mayoría de los modelos se han centrado en la evolución temporal de las poblaciones de las malas hierbas y con menor incidencia en su dinámica espacial, a pesar de que toda relación ecológica requiere un marco espacial. Bajo este contexto, en el presente trabajo se han desarrollado tres modelos espacialmente explícitos a diferentes escalas espaciales (uno a escala de parcela y dos a escala de paisaje) basados en la dinámica espacial y temporal de las poblaciones de *A. sterilis* y *L. rigidum*. Estos modelos se han utilizado en la búsqueda de estrategias de manejo efectivas y rentables y con menor riesgo de desarrollo y expansión de la resistencia a los herbicidas en las poblaciones de las malas hierbas estudiadas.

El primer modelo, desarrollado a escala de parcela, comparó la eficacia y la rentabilidad de estrategias de manejo químicas y culturales en el control de *L. rigidum* en cereales. El modelo fue parcialmente validado con datos experimentales, mostrando una distribución similar en las tasas de crecimiento poblacional en las parcelas reales y simuladas. De las estrategias estudiadas, los programas de manejo integrado que engloban estrategias culturales y la aplicación de herbicida a dosis completa fueron los que consiguieron mejores resultados. La aplicación de dosis reducida de herbicida y el uso exclusivo de estrategias de manejo culturales fueron menos exitosas en el control de las poblaciones de *L. rigidum*, aunque en algunos casos la aplicación de dosis reducida de herbicida fue más rentable económicamente que la aplicación de dosis completa. En todos los casos las estrategias de manejo mostraron retornos económicos negativos, lo que pone de manifiesto la necesidad de aplicar estrategias basadas en bajos inputs para conseguir mayor rentabilidad en un cultivo que presenta un bajo retorno económico. El banco de semilla de *L. rigidum* mostró una alta sensibilidad al porcentaje de control y a la fecundidad. Los retornos económicos fueron especialmente sensibles a la fecundidad y a la supervivencia de las plántulas para las estrategias de control culturales. Las estrategias que incluyeron la aplicación de herbicidas fueron más sensibles al precio de venta del cereal y al porcentaje de control.

El segundo modelo fue desarrollado a escala de paisaje para evaluar el potencial de las rotaciones de dos y tres cultivos en el control de *A. sterilis*. Las rotaciones mostraron ser un método eficaz de control de las poblaciones de *A. sterilis*, siendo las rotaciones de tres cultivos más eficaces que las rotaciones de dos cultivos. El control de las malas hierbas podría ser aún más eficaz si se evitasen dos años consecutivos de los cultivos menos competitivos con la mala hierba y si los cultivos, dentro del ciclo de la rotación, se distribuyesen creando un gradiente creciente de control de las poblaciones de *A. sterilis*. El modelo también sugiere que un mayor intercambio de semillas de *A. sterilis* entre parcelas incrementa el banco de semillas a nivel de paisaje y que un paisaje agrícola homogéneo, compuesto por un solo cultivo un determinado año, favorece un control más eficaz de las poblaciones de la mala hierba que paisajes con varios cultivos presentes y en proporciones relativamente iguales. En este contexto se pueden describir dos marcos de actuación: el primero encaminado a reducir la dispersión de semillas entre parcelas a través de la limpieza de los aperos de labranza y de la cosechadora, y el segundo a través de la cooperación de los agricultores por medio de la agregación espacial de las parcelas según el tipo de cultivo y/o la creación de paisajes con una proporción relativa de cultivos desigual y con independencia de su disposición espacial.

El tercer modelo se desarrolló a escala de paisaje para la evaluación de estrategias de manejo en el desarrollo y la dispersión de la resistencia a herbicidas en poblaciones de *L. rigidum*. El modelo predice la aparición de poblaciones resistentes de esta especie a nivel de paisaje a partir del tercer año de aplicaciones repetidas de un herbicida con igual modo de acción. Las parcelas bajo un sistema de cultivo basado en el monocultivo de cereal desarrollaron antes poblaciones resistentes que aquéllas bajo un sistema de rotación de cultivos (i. e., cereal-girasol). En aquéllos paisajes donde existen individuos de *L. rigidum* resistentes establecidos, las estrategias de manejo encaminadas a reducir la dispersión de las semillas entre las parcelas no obtuvieron buenos resultados, siendo el uso de las rotaciones de cultivos y/o la rotación de herbicidas con distintos modos de acción las estrategias más eficaces. El polen fue el principal responsable de la dispersión de la resistencia en el paisaje aunque junto con la dispersión de las semillas de la mala hierba debido a la siembra de cereal contaminado y al movimiento de la cosechadora entre las parcelas, produjo un efecto sinérgico positivo en la expansión de las poblaciones resistentes de *L. rigidum*. La siembra de semilla certificada o limpia y un movimiento menos aleatorio de la cosechadora en el paisaje durante la cosecha del cereal frenaron de manera notable la expansión de la resistencia.

Los modelos desarrollados en la tesis suponen una aproximación original al estudio de las malas hierbas, con utilización de herramientas y conceptos novedosos dentro de la Malherbología. Este trabajo proporciona un conocimiento más profundo de la dinámica de poblaciones de las malas hierbas a diferentes escalas espaciales y muestra la importancia de un análisis económico y la

consideración del espacio en el estudio de estrategias de manejo. Un manejo efectivo de las malas hierbas requiere una combinación de actuaciones a diferentes escalas espaciales.

Palabras clave: análisis de sensibilidad, *Avena sterilis*, heterogeneidad espacial y temporal, *Lolium rigidum*, resistencia a herbicidas, rotación de cultivos, validación, vectores de dispersión.

Summary

Weeds, as *Avena sterilis* L. (wild oat) and *Lolium rigidum* Gaudin (ryegrass) the dominant species in Spanish dry cereals, compete with crops and decrease the yield. Their control is difficult due to a clear physiological and morphological similarity with the crop and is mainly based on herbicide applications, implying important environmental and herbicide-resistance problems. New management strategies are needed to reduce the risk related to herbicide applications. Such strategies imply long-term experimentation with high economic cost and time consumption. Population dynamic models are suitable tools to explore and compare long-term management strategies for weed control.

To date, most weed population models focus on temporal evolution more than on spatial despite of ecological relationships require a spatial framework. In this context, three spatially explicit models about *A. sterilis* and *L. rigidum* at different spatial scales (i.e., one at field scale and the others at landscape scale) have been developed. These models were used to achieve effective and profitable management strategies with a low risk for the evolution and spread of resistance.

The first model was developed at field scale to compare chemical and cultural management strategies on the *L. rigidum* control in cereals. The model was partially validated with independent experimental data, the growth rate distribution was similar on the observed and simulated plots. The best management strategies were the integrated management programs implying cultural methods and herbicide application at full rate. Herbicide application at half rate and cultural control methods were less profitable on the *L. rigidum* control although occasionally herbicide application at half rate was more profitable than herbicide application at full rate. The economic return were negative in all management strategies simulated. It evidences the necessity of management strategies based on low inputs to increase the profitability of Spanish cereals. *L. rigidum* seed bank was sensitive to the fecundity and the weed control strategies. Economic returns were especially sensitive to the fecundity and weed seedling survival for cultural control methods, and the cereal sale price and the control rate for strategies involving herbicide application. The model was not sensitive to the seed dispersal for all management strategies simulated.

The second model was developed at landscape scale to evaluate the control exerted in *A. sterilis* by the use of two and three crop species rotations. Crop rotation had great potential to control *A. sterilis* populations. Three crop species rotations decreased the weed population more than two crop species rotations and extra control could be achieved avoiding two consecutive years of crops with a low weed competitive ability and if the crop order within a crop rotation is such that crops are deployed in order of increasing level of *A. sterilis* control. Weed seed densities increased in landscapes with increasing similarity *A. sterilis* seed interchange between fields and homogeneous landscapes whereby one crop was present each year, achieved better weed control than landscapes whereby more than one crop was present and with all crops in equal proportions. In this context two practical approaches were derived: the first was to decrease the weed dispersal at landscape level through cleaning procedures of tillage and harvesting equipment and the latter was the coordination between farmers with regards to crop allocation according to the crop type and/or unequal crop proportions independently of their specific allocation.

The third model was developed at landscape scale to evaluate the efficacy of management strategies slowing and decreasing the resistance evolution and spread in *L. rigidum* populations. The model predicted herbicide-resistant weed populations in the landscape beyond three years whereby equal herbicide modes of action was applied every year. Cropping systems based on cereal monoculture developed herbicide resistance before than crop rotations (i. e., cereal-sunflower). Management strategies such as the use of crop rotations and/or rotation of different herbicide modes of action were more efficient decreasing the resistance evolution than strategies based on decreasing the weed seed dispersal between fields in landscapes with established herbicide-resistant weed populations. The pollen flow was the dispersal vector which mainly drove the resistance spread and in conjunction with the seed dispersal ought to weed-contaminated cereal seeds sowing and harvester movement over the landscape produced a positive synergistic effect in the spread of herbicide-resistant *L. rigidum* populations. The sowing of certified or cleaned crop seeds and a less randomised movement of the harvester at harvest timing helped to decrease the resistance spread.

The models developed along this thesis are original approaches in weed science based on new concepts and tools. The present work improved the knowledge about weed population dynamic at different spatial scales and how important the economic analysis and the spatial aspect are in the study of the weed management strategies. An effective weed control would require a combination of management approaches at different spatial scales.

Key words: *Avena sterilis*, crop rotation, dispersal vectors, herbicide resistance, *Lolium rigidum*, sensitivity analysis, spatial and temporal heterogeneity, validation.

ÍNDICE GENERAL

CAPÍTULO I

Introducción general y Objetivos

CAPÍTULO I: INTRODUCCIÓN GENERAL Y OBJETIVOS

I. 1. INTRODUCCIÓN GENERAL

I. 1. 1. CEREALES DE SECANO ESPAÑOLES Y ANDALUCES

Los cereales presentan una amplia distribución geográfica en torno al 16% de la superficie agraria útil mundial, lo que equivale a la mitad de las tierras arables de nuestro planeta. La Unión Europea es uno de los principales productores con una superficie sembrada de cereal en torno al 27.5% de la superficie agraria útil. En España la producción de cereales asciende a $221.7 \cdot 10^6$ t con una superficie en torno a las $5.9 \cdot 10^6$ ha, de las cuales el 90% corresponden a cereales de invierno (MAGRAMA, 2012). La superficie dedicada al cultivo de estos cereales muestra una tendencia decreciente a lo largo del tiempo, con algunas excepciones en años concretos, como el año 2008, donde se produjo un pico de crecimiento de la superficie sembrada (Fig. 1) debido principalmente al aumento del precio en la comercialización del grano. Esta tendencia, sin embargo, no se ve reflejada en la producción de grano donde se aprecia un comportamiento oscilante y no siempre asociado a una mayor superficie sembrada (Fig. 1). Una de las causas de estas fluctuaciones es a consecuencia de unas condiciones climáticas variables que marcan en gran medida las producciones de unos cultivos sembrados bajo régimen de secano en su mayoría, cerca del 90%, y que dependen íntegramente de ellas.

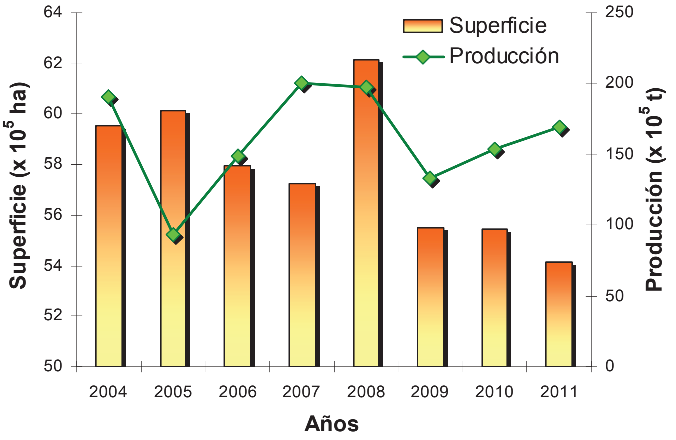

Figura 1. Evolución de la superficie y la producción de cereales de invierno sembrados en España (MAGRAMA, 2012).

Los cultivos cerealistas constituyen un elemento esencial en la agricultura de muchas regiones españolas, especialmente en las comunidades autónomas de Castilla-La Mancha y Castilla y León (Fig. 2). Les sigue en importancia Andalucía, principalmente en las provincias de Sevilla, Córdoba y Cádiz.

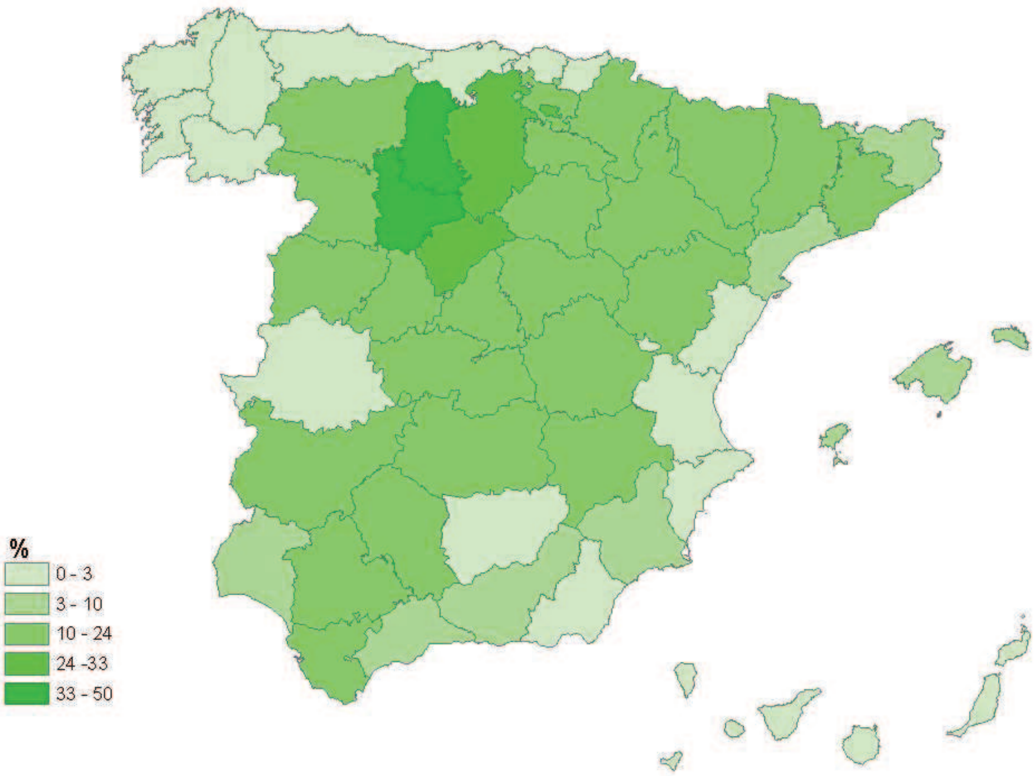

Figura 2. Superficie de cereales respecto a la superficie geográfica provincial (MAGRAMA, 2012).

En Andalucía, los cereales entran en rotación con girasol y leguminosas en la zona oeste, donde los suelos son más fértiles, siendo el monocultivo de cereal y las rotaciones de cereal-barbecho los sistemas de cultivo predominantes en las zonas más pobres situadas en la parte este y consecuentemente con producciones mucho más bajas (Saavedra et al., 1989).

La amplia superficie dedica al cultivo de cereales es una de las grandes razones, pero no la única, que hacen de este cultivo un elemento base de la agricultura española. Su importancia económica y social junto con la función ecosistémica que realiza, le confieren un papel muy importante en la vida rural y lo hacen difícilmente sustituible. Así, el cereal es un alimento energético muy importante en la dieta humana y animal. En los países desarrollados el consumo de cereales es menor que en los países en desarrollo, si bien, su destino es diferente, siendo en el primer caso la alimentación animal la principal demandante y en el segundo, la alimentación humana (FAO, 2012). Aparte de su función alimentaria, el cereal es también utilizado para semilla, en las camas del ganado, o como acolchado de cubiertas vegetales, sin olvidar su aprovechamiento energético como biomasa. Además ofrece un hábitat propicio para una gran número de especies que están adaptadas a estos paisajes de secano y cuya supervivencia depende de la conservación de los mismos (Delgado y Moreira, 2000).

I. 1. 2. MALAS HIERBAS DE LOS CEREALES DE SECANO

La producción de cereales se ve afectada por una serie de agentes que interaccionan con el cultivo y disminuyen su producción. Uno de los más importantes es la presencia de las malas hierbas, como puede verse reflejado en la Fig. 3, donde se muestra que el nivel de facturación a nivel español de productos herbicidas empleados para el control de las malas hierbas es mayor que para cualquiera de los productos fitosanitarios empleados para el control de otras plagas y enfermedades. En España se alcanzó en el año 2010 un nivel de facturación de herbicidas en torno a los $217 \cdot 10^6$ €, lo que pone de manifiesto la importancia económica que supone la presencia de las malas hierbas en los cultivos y el gran esfuerzo que se emplea en controlarlas.

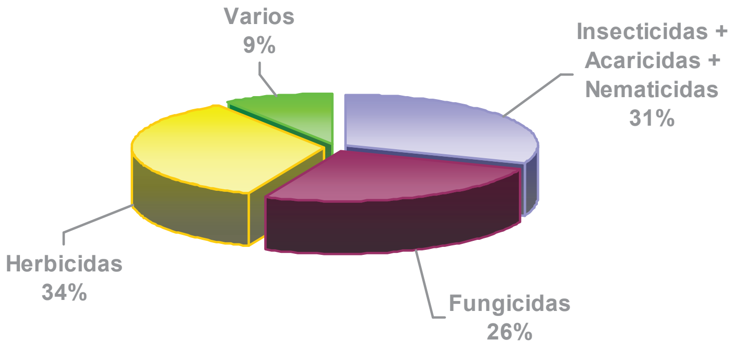

Figura 3. Importancia relativa de las ventas de productos fitosanitarios en el mercado español (AEPLA, 2011).

Son muchas las definiciones que podemos encontrar sobre el concepto de mala hierba, si bien, este tiene una gran connotación antropocéntrica y por tanto es muy subjetivo, ya que no existe ninguna característica morfológica o fisiológica que permita catalogar de forma objetiva una mala hierba como tal. Pujadas y Hernández (1988) hicieron una revisión de este concepto para definirlo finalmente como: “Planta que crece siempre o de forma predominante en situaciones marcadamente alteradas por el hombre y que resulta no deseable por él en un lugar y momento determinados”. Esta definición soslaya un concepto de mala hierba con una clara acepción negativa que podría variar dependiendo del enfoque y del objetivo del trabajo. Por ello, es necesario encuadrar el concepto dentro del contexto donde se trata, en nuestro caso, los cereales de invierno.

Las malas hierbas que se encuentran presentes en los campos de cereales pueden producir una serie de problemas diversos, entre ellos tenemos la competencia con los cultivos por los nutrientes, la luz, el agua y el espacio o los posibles efectos de alelopatía. Además, son posibles hospedantes de otras plagas y enfermedades que pueden afectar negativamente al cultivo. También pueden producir problemas de recolección, en casos de altas infestaciones, y pérdidas económicas derivadas de la menor la calidad del producto cosechado debido a la contaminación de las semillas del cultivo con las semillas de las malas hierbas (Pérez-García, 2006; Fernández-Quintanilla y Saavedra, 1991) e incrementos en los costes de producción derivados de la implementación de los programas de manejo para su control (Fernández-Quintanilla y Saavedra, 1991). Si bien, hay que recordar el papel que ejercen las malas hierbas en las grandes extensiones de cereal como proveedoras de servicios ecosistémicos y con un papel importante como fuente de biodiversidad (Marshall et al., 2003).

Las malas hierbas presentes en los cultivos de cereales pueden variar de unas regiones a otras debido a los factores climáticos y edáficos de la zona (Cimalova y Lososova, 2009), a los factores de manejo (José-María et al., 2011) y a la posible influencia de la complejidad del paisaje circundante (Roschewitz et al., 2005). Un estudio desarrollado por García-Baudín (1984) sobre las malas hierbas gramíneas más importantes de los cereales españoles en base a encuestas realizadas a los agentes de extensión agraria, cita el género *Avena* y dentro de éste *Avena sterilis* L., como la especie más abundante, seguido de los géneros *Lolium*, *Phalaris* y *Bromus*. Dentro del género *Lolium*, la especie *Lolium rigidum* Gaudin es la más abundante, y junto con *A. sterilis* están ampliamente distribuidas por la mayoría de las regiones cerealistas. El género *Phalaris*, de menor importancia en cuanto a la superficie que ocupa, se encuentra principalmente distribuido en Extremadura y Andalucía, y el género *Bromus*, también de escasa incidencia, lo encontramos principalmente en Cataluña, aunque la importancia de este último ha crecido en los últimos años como consecuencia de la implantación de los sistemas de agricultura de conservación. Otros estudios posteriores (Saavedra et al., 1989; Taberner, 1996; Chamorro et al., 2007; Romero et al., 2008; Cirujeda et al., 2011) desarrollados en Cataluña, Aragón y Andalucía señalan a las gramíneas adventicias como las malas hierbas con mayor presencia en los cereales, si bien, en algunos casos el orden de importancia es diferente. *L. rigidum* fue la mala hierba más distribuida y abundante en Aragón y Cataluña siendo *A. sterilis* la siguiente especie en orden de importancia. En Andalucía *A. sterilis* mostró una mayor incidencia con *L. rigidum* presente en áreas más localizadas. La tercera mala hierba con mayor presencia en Andalucía, aunque concentrada en áreas más fértiles y húmedas, fueron especies del género *Phalaris*. El género *Bromus* queda relegado en zonas concretas de mayor altitud de Andalucía pero con presencia significativa en Cataluña. Como especies dicotiledóneas, y de menor frecuencia que las gramíneas más comunes, se encontraron las especies *Papaver rhoeas* L., considerada problemática por su difícil control y por presentar resistencia a los herbicidas, y *Convolvulus arvensis* L. en Cataluña y Aragón. Otras especies dicotiledóneas anuales como *Fumaria* spp. y *Polygonum aviculare* L. también estuvieron presentes con una frecuencia más baja y con un menor impacto en el cultivo ya que son menos competitivas, al igual que C. *arvensis*, debido a su emergencia tardía.

Estudios comparativos de las principales malas hierbas encontradas actualmente en los campos de cereales con estudios realizados hace 30-50 años reflejan una evolución de las especies arvenses de estos cultivos hacia una disminución del número de especies dominantes (Romero et al., 2008), una o dos en la mayoría de los casos (Saavedra et al., 1989) y una mayor presencia de gramíneas (Chamorro et al., 2007; Cirujeda et al., 2011), que debido a su proximidad fisiológica y morfológica con el cultivo dificultan aún más su control. Esta inversión de la flora posiblemente ha sido influenciada por la utilización indiscriminada de herbicidas fenoxiácidos frente a los que las especies anuales dicotiledóneas muestran sensibilidad y por una adaptación a los factores de manejo imperantes en las distintas épocas (García-Baudín, 1984). Cirujeda et al. (2011) encontraron una evolución de la comunidad arvense hacia especies adaptadas al mínimo laboreo, y Chamorro et al. (2007) y Romero et al. (2008) encontraron una mayor presencia de especies dicotiledóneas en cultivos bajo sistemas de producción ecológica.

I. 1. 2. 1. *Avena sterilis* L. y *Lolium rigidum* Gaudin

Como se ha mencionado anteriormente, las especies de malas hierbas dominantes en los cereales españoles son *A. sterilis* y *L. rigidum*, ambas pertenecientes a la familia Poaceae. La dinámica de poblaciones de ambas especies que engloba las características biológicas, los mecanismos de dispersión y las estrategias de manejo empleadas para el control de sus poblaciones son detalladas a continuación.

I. 1. 2. 1. 1. Características biológicas y distribución de las especies

El género ***Avena*** ha sufrido diferentes tratamientos taxonómicos, por lo que el número de especies y de subespecies considerado varía según el autor. Bolòs y Vigo (2001) hablan de 30 especies distribuidas por las regiones templadas, las montañas de las zonas tropicales y la región mediterránea. Las especies adventicias de este género más frecuentes en Andalucía son: *A. sterilis*, *A. fatua* L., *A. barbata* Link, *A. eriantha* Durieu, en la zona oriental y *A. longiglumis* Durieu en la zona occidental (Romero-Zarco, 1987; 2011), siendo *A. sterilis* la especie con mayor incidencia en los cereales de secano españoles. *A. sterilis* presenta dos subespecies (*A. sterilis* subsp. *ludoviciana* (Durieu) Gillet & Marget y *A. sterilis* L. subsp. *sterilis*) ampliamente extendidas en la península (Fig. 4) y con una distribución espacial bastante diferenciada, aunque coexistiendo en ciertas áreas donde la hibridación de las dos especies puede ser posible dando lugar a diversas formas intermedias (Fernández-Quintanilla et al., 1997). Ambas especies están adaptadas al clima mediterráneo, pero la subsp. *ludoviciana* se encuentra principalmente en zonas templadas y la subsp. *sterilis* es más abundante en las zonas más cálidas (Aibar, 1990).

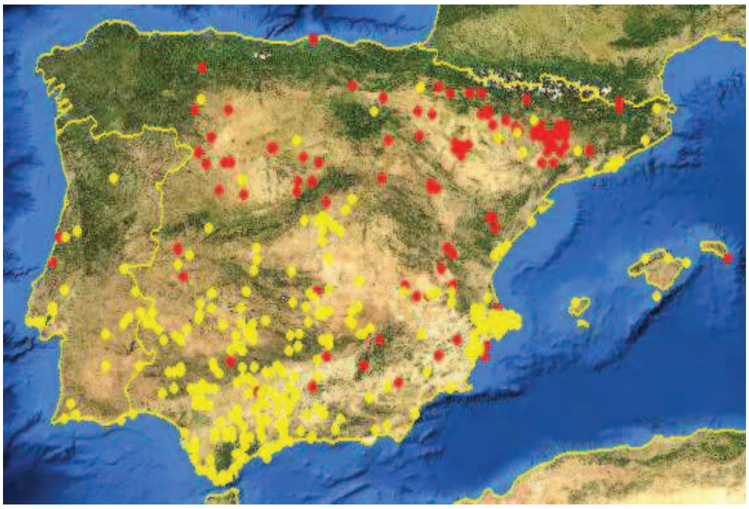

Figura 4. Distribución de *A. sterilis* subsp *sterilis* (en amarillo) y subsp. *ludoviciana* (en rojo) en la península ibérica y Baleares (ANTHOS, 2012).

A. sterilis es una planta anual hexaploide (6n = 42) (Aibar, 1990), lo que le confiere una mayor plasticidad y variabilidad genética que, quizás, explica la agresividad de esta especie. Los tallos, glabros, erectos o geniculados, pueden llegar a medir 150 cm, con hojas planas y alargadas de hasta 60 cm de longitud y 17 mm de ancho, glabras o setosas. La panícula de 5-30 cm posee espiguillas con 2-4 flores no articuladas entre sí que permanecen unidas en la madurez y se desprenden juntas (Romero-Zarco, 1987; 2011) (Fig. 5).

Figura 5. *Avena sterilis*. a) Plantas adultas creciendo en campo (Fuente: Infoagro, 2012) y b) espiguillas (Fuente: Pan-Sande, 2006).

Esta especie tiene un ciclo de vida muy adaptado al cereal con el que convive (Fernández-Quintanilla et al., 1997). El periodo de emergencia abarca desde finales de octubre hasta mediados de abril (Fernández-Quintanilla et al., 1986; Aibar et al., 1991) con un pico de emergencia en noviembre-diciembre (Fernández-Quintanilla et al., 1997) y alcanzando el 75% del total de la emergencia en las primeras nueve semanas (Aibar et al., 1991). Se ha visto una estrecha relación de la emergencia con la temperatura y con el régimen de precipitaciones (Leguizamon et al., 2005). Estos factores, entre otros, también afectan a la capacidad de dormición de la especie (Quail y Carter, 1969) aunque otros estudios apuntan a una dormición endógena como la principal responsable de la persistencia de esta especie (Sánchez del Arco et al., 1995) que es capaz de permanecer viable en el suelo, aunque en baja proporción, por un periodo de tiempo superior a dos campañas de cultivo (Quail y Carter, 1968; Sánchez del Arco et al., 1995). Alrededor de un 35% de las plántulas emergidas no consiguen llegar al estado adulto (Aibar et al., 1991), principalmente aquéllas provenientes de las emergencias más tardías. Del mismo modo, una emergencia tardía además de afectar a la capacidad competitiva de la especie, afecta a la capacidad reproductiva, donde el número de semillas por planta se ve reducido considerablemente respecto a las emergencias tempranas (Fernández-Quintanilla et al., 1986). Las plantas adultas, en competencia con cereal, poseen una baja fecundidad media en torno a las 13-21 semillas/planta que muestra un efecto dependiente de la densidad (Fernández-Quintanilla et al., 1986), es decir, se ve influenciada por la densidad de adultos presentes de acuerdo a una función hiperbólica (González-Andújar y Fernández-Quintanilla, 1991).

El género ***Lolium*** se extiende por las zonas templadas de Europa y Asia y el norte de África, representado en una docena de especies (Bolòs y Vigo, 2001). En Andalucía están presentes las especies: *L. rigidum*, *L. multiflorum* Lam., *L. temulentum* L., *L. perenne* L. (Devesa, 1987), siendo *L. rigidum* la especie infestante de los cereales españoles casi de forma exclusiva (Taberner, 1996). Esta especie se encuentra presente en los países ribereños del Mediterráneo, con una amplia distribución en la península (Fig. 6) donde tiene una incidencia especialmente importante en la región del Duero y Cataluña (Taberner, 1996; Recasens et al., 1997).

L. rigidum es una gramínea anual, e incluso bienal (Romero, 2011), con polinización cruzada y diploide (2n = 14) (Devesa, 1987). Es una planta muy polimorfa y a veces difícil de distinguir de otras especies del género con las que puede hibridar (Romero, 2011). Los tallos, glabros y estriados, pueden llegar a medir 100-120 cm, con hojas alargadas de hasta 28 cm de longitud y 2-9 mm de anchura, planas y con un nervio medio más marcado. La espiga que raramente sobrepasa los 33 cm tiene el raquis cilíndrico y glabro con las espiguillas elípticas o lanceoladas insertas en las excavaciones del raquis y con 4-11 flores (Devesa, 1987; Romero, 2011) (Fig. 7).

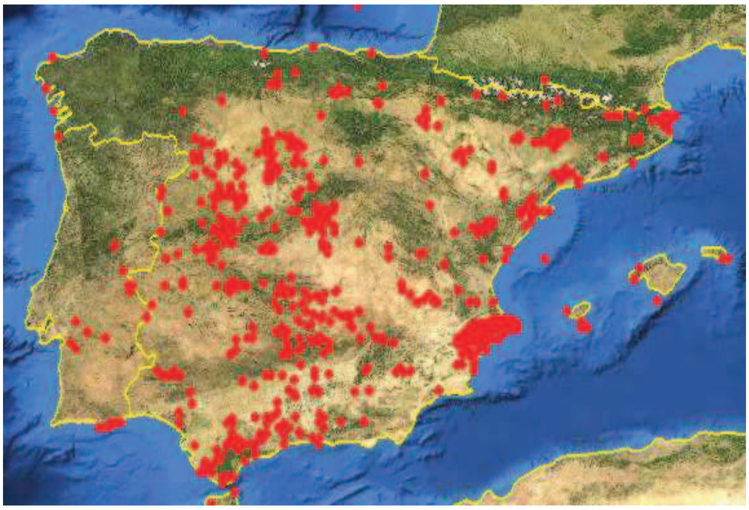

Figura 6. Distribución de *Lolium rigidum* (en rojo) en la península ibérica y Baleares (ANTHOS, 2012).

Esta especie muestra un retraso fenológico respecto al cereal con el que convive, especialmente acusado en las primeras etapas del desarrollo (Recasens et al., 1997). El periodo de emergencia se centra principalmente desde finales de otoño hasta mediados de invierno (Recasens et al., 1997) aunque generalmente se da lugar en un corto periodo de tiempo tras la siembra del cereal y directamente relacionado con el contenido de humedad en el suelo (Fernández-Quintanilla et al., 2000). Las semillas no germinadas pueden inducir una dormición secundaria y permanecer en el suelo por un periodo de tiempo no mayor de dos años, ya que a partir de entonces su viabilidad es muy baja (Taberner, 1996). Una alta proporción de las semillas germinadas, alrededor del 78-95%, consiguen alcanzar el estado adulto (Fernández-Quintanilla et al., 1997) siendo la mortalidad más acusada en las etapas finales del desarrollo y sin que se aprecie en este patrón un efecto claro de las variables climáticas (Fernández-Quintanilla et al., 1997). La fecundidad de las plantas adultas, sin embargo, sí está muy influenciada por el régimen de precipitaciones a lo largo del ciclo de vida y por tanto, muestra un patrón muy variable que puede oscilar desde 7 a 237 semillas/planta (Fernández-Quintanilla et al., 2000), aunque se han citado producciones de semilla en torno a las 1000 semillas/planta (Taberner, 1996). Esta capacidad reproductiva también se ve influenciada por la competencia inter e intraespecífica que muestra esta especie (Fernández-Quintanilla et al., 2000) y que se puede ajustar a una función hiperbólica (González-Andújar y Fernández-Quintanilla, 2004).

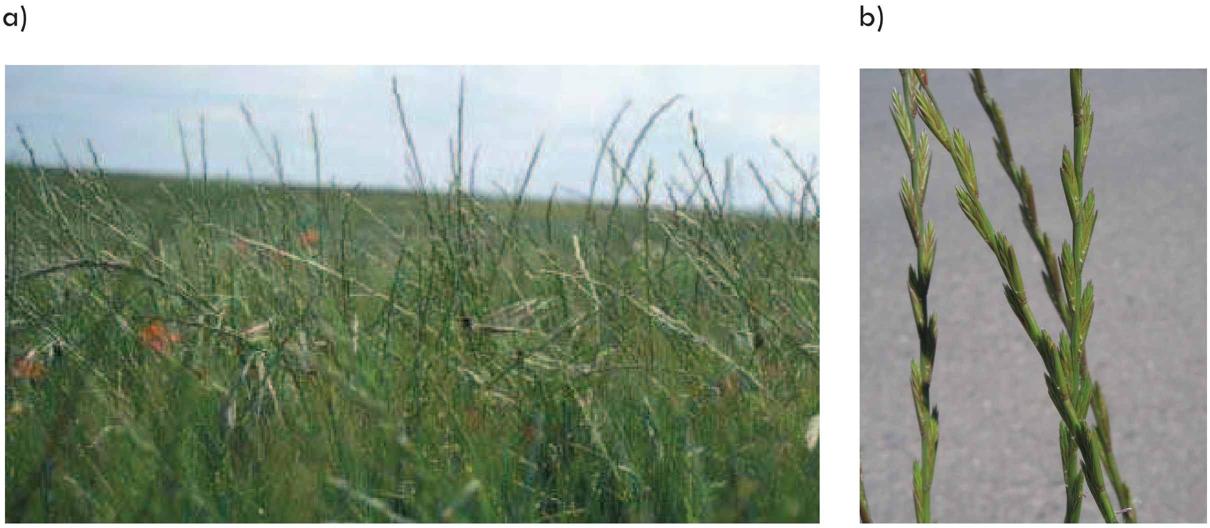

Figura 7. *Lolium rigidum*. a) Plantas en estado en estado adulto creciendo en campo (Fuente: Recasens, 2012) y b) inflorescencia (Fuente: Pan-Sande, 2006).

I. 1. 2. 1. 2. Mecanismos de dispersión

Las malas hierbas aseguran su persistencia en el tiempo a través de los mecanismos de dormición de sus semillas, entre otros, y en el espacio a través de los mecanismos de dispersión de semillas y polen (Thill y Mallory-Smith, 1997). La dispersión de las semillas producidas hace posible la expansión de la mala hierba, consiguiendo una reducción en la competencia intraespecífica por los recursos y aumentando la probabilidad de supervivencia de la especie. *A. sterilis* y *L. rigidum* presentan una dispersión natural limitada alrededor de la planta madre en torno a 1.5 m (Barroso et al., 2006) aunque si la dispersión ocurre en días ventosos esta distancia puede ser aún mayor. Esta corta distancia de dispersión hace que podamos encontrar poblaciones de *A. sterilis* formando rodales bastante estables en el tiempo (Barroso et al., 2006), no tanto en el caso de *L. rigidum* (Blanco-Moreno et al., 2004).

A estos procesos de dispersión natural o primaria de estas especies hay que añadirle procesos de dispersión secundaria donde las semillas son dispersadas gracias a la ayuda de ciertos vectores, entre los que cabe destacar los animales, especialmente las hormigas, y el hombre, principalmente a través de la maquinaria agrícola (aperos de labranza y cosechadora) y de la siembra de semilla contaminada. Las hormigas, cuya actividad se centra principalmente entre los meses de abril-octubre, son las responsables de una gran pérdida de las semillas producidas por las malas hierbas (Baraibar et al., 2009). En *A. sterilis* puede citarse esta pérdida en un 12% de las semillas producidas (Sánchez del Arco et al., 1995) e incluso un 50% en especies del género *Lolium*, como *L. multiflorum* (Baraibar et al., 2009). Si bien, no se sabe explícitamente la cantidad de semillas que son consumidas por estos invertebrados o son almacenadas en sus nidos ayudando con ello a la dispersión de la especie. Los aperos de labranza, además de una distribución vertical de las semillas en el suelo, producen una distribución horizontal que en *A. sterilis* se ha cifrado en torno a los 2-3 m en la dirección de avance de la maquinaria (Barroso et al., 2006). Además de esta dispersión a corta distancia, las semillas pueden ser desplazadas largas distancias adheridas a los aperos, especialmente si el suelo se encuentra con gran contenido de humedad (Thill y Mallory-Smith, 1997). Otros vectores importantes en la dispersión de semillas a larga distancia son las cosechadoras que pueden dispersar semillas dentro y entre campos de cultivo (McCanny y Cavers, 1988). La cantidad de semillas dispersadas a través de este mecanismo dependerá de las semillas que permanecen en la planta en el momento de la cosecha del cereal, que a su vez depende de las condiciones climáticas imperantes. En general, *A. sterilis* suele dispersar la mayoría de sus semillas antes de la cosecha y *L. rigidum*, sin embargo, presenta un gran porcentaje de semillas en la planta que son cosechadas junto con el cereal (Blanco-Moreno et al., 2004). La mayor parte de las semillas de las malas hierbas cosechadas se expulsan por la cosechadora junto con la paja llegándose a encontrar semillas de *A. sterilis* a más de 30 m (Barroso et al., 2006) y de *L. rigidum* a más de 18 m (Blanco-Moreno et al., 2004) del foco de infestación inicial. Aproximadamente, un 3% de las semillas de *A. sterilis* (Barroso et al., 2006) y un 7% de las semillas de *L. rigidum* (Matthews et al., 1996) cosechadas son retenidas por la cosechadora y mezcladas con el grano. Si el grano cosechado contaminado con las semillas de las malas hierbas no es sometido a ningún tipo de proceso de limpieza y se utiliza como semilla de siembra en la siguiente campaña, se producirá una contaminación uniforme e importante en todas las parcelas sembradas con esa simiente (Thill y Mallory-Smith, 1997; Michael et al., 2010).

Otros vectores de dispersión de las semillas de las malas hierbas a tener en cuenta son el empleo de semillas contaminadas para la alimentación del ganado, el uso de paja contaminada para el ganado o cubiertas vegetales, el empleo de estiércol contaminado o el propio ganado en sus desplazamientos dentro y entre parcelas, ya que las semillas de las malas hierbas pueden permanecer adheridas a estos animales (Aibar, 1990).

Todos los vectores de dispersión repercutirán más o menos en la expansión de las especies arvenses en la medida en que éstas se encuentren en una mayor o menos densidad en las parcelas (Thill y Mallory-Smith, 1997). Por ello, mantener las malas hierbas a un nivel adecuado, además de mejorar los rendimientos del cultivo (Torner et al., 1991), ayuda a frenar la expansión de las poblaciones de las malas hierbas.

I. 1. 2. 1. 3. Manejo de las poblaciones

Las poblaciones de *A. sterilis* y *L. rigidum* son controladas principalmente a través del uso de herbicidas (Saavedra et al., 1989; Aibar, 1990; Taberner, 1996; Cirujeda y Taberner, 2010). Cirujeda et al. (2011) señalan las estrategias de manejo basadas en la siembra de semilla de cereal limpiada previamente y el uso de cultivos competitivos como estrategias usuales en Aragón, estando la aplicación de herbicidas relegada a zonas donde el cultivo representa valores económicos más rentables y donde el regadío y el uso de rotaciones y fertilizantes son también más comunes. Esta misma tendencia se aprecia en Andalucía, con aplicaciones de herbicidas en las zonas más productivas y manejos basados en bajos inputs, como rotaciones de cereal-barbecho, en las zonas con producciones poco rentables (Saavedra et al., 1989). Encuestas realizadas a los agricultores mostraron que los métodos de control en preemergencia están principalmente basados en métodos de lucha no química, como el laboreo del suelo, y los estrategias de control en postemergencia, una vez que el cultivo está establecido, se basan en métodos de lucha química durante los primeros estadios de la mala hierba (Taberner, 1996).

Numerosos trabajos se han centrado en estudiar el efecto que determinadas estrategias de manejo culturales, preventivas y químicas tienen sobre las poblaciones de las malas hierbas. Las estrategias culturales basadas en el laboreo del suelo propician una distribución más homogénea de las semillas en el perfil del suelo y un patrón en la germinación y mortalidad de las semillas de las malas hierbas. En el caso de *A. sterilis*, las semillas más profundas mostraron una mortalidad mayor y una emergencia menor que las semillas localizadas más superficialmente (Sánchez del Arco et al., 1995). En las poblaciones de *L. rigidum*, los sistemas de cultivo bajo no laboreo redujeron el número de plántulas emergidas y aumentaron la mortalidad de las semillas en el suelo (Chauhan et al., 2006) frente a los sistemas bajo mínimo laboreo o los sistemas de laboreo tradicional. Si bien, Cirujeda y Taberner (2009) obtuvieron una buena eficacia en el control de las poblaciones de *L. rigidum* con laboreos profundos de inversión del suelo aunque mostraron ser muy dependientes de las características edáficas de la zona.

El aumento de la densidad de siembra y el retraso de la fecha de siembra del cereal han sido otros factores tenidos en cuenta a la hora de controlar las malas hierbas (Paynter y Hills, 2009). Sin embargo, los resultados obtenidos han sido muy variables. Varios autores (Torner et al., 1991; Izquierdo et al., 2003; Cirujeda y Taberner, 2009) no encontraron un efecto claro en el control de las poblaciones de las especies arvenses y/o en el porcentaje de pérdida que éstas causaron en la producción del cereal debido probablemente a que los factores ambientales produjeron una gran variabilidad en sus resultados

Otras prácticas de manejo culturales basadas en la implementación de rotaciones de cultivo y el uso de cultivares más competitivos o tolerantes a las malas hierbas han mostrado ser efectivas en el control de las poblaciones de *A. sterilis* (Fernández-Quintanilla et al., 1984; Torner et al., 1984). En el caso de *L. rigidum* los resultados han sido más contradictorios (Lemerle et al., 1995; Cousens y Mokhtari, 1998) al verse altamente influenciados por las condiciones climáticas interanuales y la localización espacial de las poblaciones. Cirujeda y Taberner (2009) llegaron a la conclusión de que el uso exclusivo de este tipo de estrategias, tanto de forma individualizada como de forma conjunta, no fueron suficientes para alcanzar un control aceptable de las poblaciones de la mala hierba. En contraposición, Gill y Holmes (1995) propusieron que un plan de acción basado en la integración de estrategias culturales debidamente planeado puede alcanzar buenos niveles de control.

En Australia se ha desarrollado una técnica basada en lo que denominan “seed catching” (captura de semilla) para reducir las poblaciones de *L. rigidum* en las parcelas y limitar su expansión. La técnica se basa en la disposición de un remolque acoplado a la cosechadora que recoge la paja y las semillas que ésta van depositando en el suelo. Con estos dispositivos se logra reducir considerablemente la cantidad de semillas de malas hierbas que de otra forma serían incorporados en las parcelas siguiendo el movimiento de la cosechadora (Gill y Holmes, 1995; Matthews et al., 1996).

Además de las estrategias de manejo culturales señaladas, la aplicación de medidas preventivas como la limpieza de aperos y de la cosechadora cuando se desplazan de unas parcelas a otras, o el uso de semilla certificada o previamente limpiada para la siembra del cereal, pueden mejorar el control de las poblaciones tanto de *L. rigidum* como de *A. sterilis* en cereales (Thill y Mallory-Smith, 1997; Michael et al., 2010).

Los estudios experimentales basados en el uso de estrategias químicas para el control de las gramíneas dominantes en los cereales abundan en la literatura (Fernández-Quintanilla et al., 1987; Barroso et al., 2009; Cirujeda y Taberner, 2010). El efecto que los herbicidas producen en las poblaciones arvenses varía afectando a diferentes etapas del ciclo de vida de la mala hierba y en general reduciendo substancialmente su banco de semilla. A pesar de ello, las poblaciones remanentes en el suelo son aún elevadas y junto con los problemas de resistencia debido al uso reiterado de herbicidas que están apareciendo de manera alarmante desde la década de los noventa con resistencias múltiples y cruzadas en muchos casos (de Prado et al., 2005; Cirujeda y Taberner, 2010) hace que la necesidad de otras técnicas de control integrado sean necesarias (Fernández-Quintanilla et al., 1987; Cirujeda y Taberner, 2010). Estrategias químicas basadas en aplicaciones de herbicidas a dosis reducidas, en un intento de búsqueda de estrategias más sostenibles con el medio ambiente y a la vez más rentables económicamente, han sido estudiadas tanto en *A. sterilis* como *L. rigidum* (Fernández-Quintanilla et al., 1998; Barros et al., 2005; González-Andújar et al., 2011) e incluso a nivel espacial (Barroso et al., 2004) y, aunque en general controlaron eficazmente las poblaciones, resultaron ser muy dependientes de las condiciones climáticas y del momento de la aplicación (Fernández-Quintanilla et al., 1998; Barros et al., 2005; 2008). Si bien, aunque estas prácticas podrían parecer deseables, diversos estudios han mostrado que favorecen la expresión de genes menores que contribuyen al rápido desarrollo de resistencia a herbicidas (Neve y Powles, 2005; Busi y Powles, 2009; Manalil et al., 2011).

Finalmente, las prácticas de manejo también han sido estudiadas mediante modelos de simulación de las poblaciones de *A. sterilis* y *L. rigidum* para ver su evolución a medio y a largo plazo (González-Andújar y Fernández-Quintanilla, 1991; González-Andújar y Fernández-Quintanilla, 2004). Los resultados de las simulaciones mostraron que los programas de manejo integrado que incluyeron una mezcla de prácticas culturales y aplicaciones de herbicidas obtuvieron, en general, el mejor nivel de control en las poblaciones de las malas hierbas a largo plazo (González-Andújar y Fernández-Quintanilla, 1991) aunque no siempre estas estrategias mostraron los mejores resultados económicos (González-Andújar y Fernández-Quintanilla, 1993). Algunos autores, basados en los modelos de simulación, han desarrollado Sistemas de Soporte a la Decisión (SSD) para ambas especies como herramientas de ayuda en la toma de decisiones por agricultores y técnicos. En Australia, Pannell et al. (2004) han desarrollado un SSD para el establecimiento de programas de manejo óptimos de acuerdo a las características de las explotaciones, incluso, con aplicaciones en la búsqueda de alternativas efectivas para controlar poblaciones de *L. rigidum* resistentes a herbicidas. En nuestro país se han desarrollado SSDs para el manejo integrado de ambas especies basados en criterios económicos (González-Andújar et al., 2010; González-Andújar et al., 2011).

I. 1. 3. ESTUDIO DE LAS POBLACIONES DE MALAS HIERBAS A TRAVÉS DE MODELOS DE DINÁMICA DE POBLACIONES

El estudio de la dinámica poblacional de las malas hierbas bajo diferentes condiciones ambientales y de manejo ha sido abordado tradicionalmente a través de experimentos en campo (Chauhan et al., 2006; Barroso et al., 2009) y/o en invernadero (Taberner, 1996; González-Ponce, 1998). Estos estudios, básicamente desarrollados a corto plazo, no permiten explorar la dinámica poblacional de las malas hierbas a medio y largo plazo (Holst et al., 2007), que son horizontes necesarios para explorar sistemas de manejo de índole estratégico. Otra alternativa, y a su vez complementaria a la anterior, es el uso de modelos de simulación. Estos modelos nos proporcionan la posibilidad de analizar escenarios de manejo tanto a medio como a largo plazo, incluso nos permite estudiar situaciones de difícil abordaje a través de los clásicos métodos experimentales. Los modelos han mostrado ser útiles en dos ámbitos generales de la Malherbología (Holst et al., 2007), (1) el teórico, explorando nuevos conceptos e ideas, y (2) el práctico, explorando a medio y largo plazo estrategias de manejo bajo escenarios del tipo IF-THEN.

De manera amplia podemos clasificar los modelos en empíricos y mecanicistas, aunque es usual encontrar modelos híbridos (semi-empíricos) formados por ambos tipos de modelos. Los primeros establecen relaciones funcionales mediante el uso de modelos estadísticos. Ejemplos de estos modelos son las curvas dosis-respuesta y los modelos de emergencia de plántulas. Los modelos mecanicistas tratan de conocer los procesos fisiológicos y morfológicos subyacentes en los sistemas biológicos y establecen relaciones funcionales basándose en este conocimiento (Maxwell y O'Donovan, 2007). Ejemplo de estos modelos son los modelos tipo CERES de crecimiento de los cultivos. Los modelos mecanicistas son más exactos a la hora de realizar predicciones, si bien, la complejidad de los mismos y la gran cantidad de información requerida para su implementación han hecho que sean los modelos empíricos o semi-empíricos los más utilizados en Malherbología.

En el contexto de los modelos empíricos o semi-empíricos encontramos los modelos de dinámica de poblaciones. Estos modelos establecen relaciones funcionales entre las distintas etapas del ciclo de vida de la mala hierba. Un diagrama idealizado del ciclo de vida de una mala hierba anual puede verse esquematizado en la Fig. 8. El ciclo de vida se caracteriza por una serie de estados funcionales y de tasas de transferencia entre ellos. Como estados funcionales principales se destaca el banco de semilla, el estado de plántula, el estado de planta adulta y la lluvia de semillas producida (González-Andújar, 2008). Cada estado puede estar a su vez caracterizado por estructuras más complejas en función de los objetivos perseguidos, algunos ejemplos son la estratificación del banco de semilla en diferentes profundidades del suelo o la consideración de cohortes de plántulas. El paso de un estado funcional a otro se realiza a través de procesos demográficos (tasas de transferencia) cuantificados por medio de la germinación de las semillas, la supervivencia de plántulas (establecimiento de adultos), la producción de semillas o fecundidad y la mortalidad de semillas en el suelo (Fig. 8). Estos procesos pueden ser simples tasas de transferencia o relaciones funcionales más complejas como, por ejemplo, las derivadas de procesos dependientes de la densidad que pueden actuar a diferentes niveles dentro del ciclo de vida de la mala hierba (Freckleton et al., 2008).

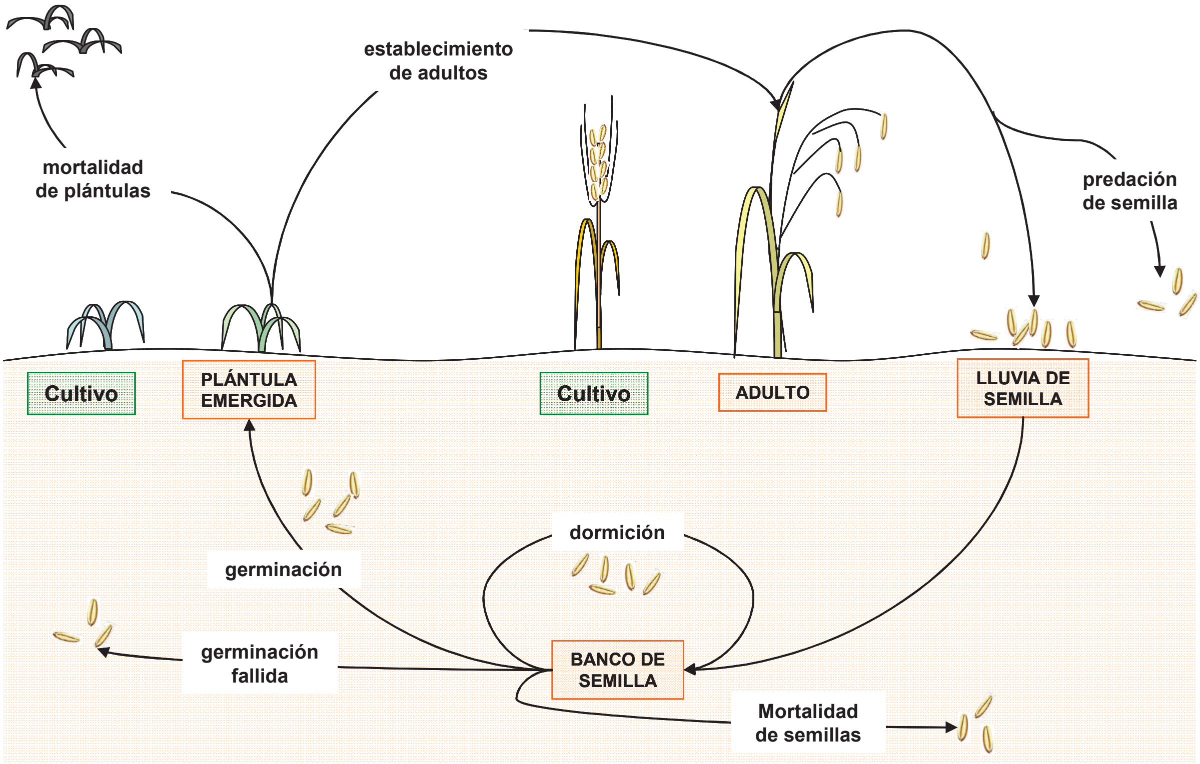

Figura 8. Ciclo de vida de una de mala hierba anual creciendo en un cultivo de cereal.

Los modelos de dinámica de poblaciones pueden ser fácilmente modificados para introducir estrategias de control. Las estrategias de manejo tanto químicas como culturales encaminadas a controlar las poblaciones de malas hierbas son normalmente introducidas en el modelo de forma explícita a través de parámetros de control (Colbach y Debaeke, 1998) que reducen las tasas de transferencia entre los estados funcionales (e. g., incremento en la mortalidad de las plántulas).

El modelo conceptual presentado en la Fig. 8 permite su implementación matemática fácimente y la simulación de las poblaciones de las malas hierbas en el tiempo pero no considera la escala espacial como un componente del mismo. Las malas hierbas tienen una disposición agregada en el espacio, formando en muchos casos rodales definidos (Barroso et al., 2004; Blanco-Moreno et al., 2006). Esto es debido a la heterogeneidad de los factores ambientales, a la biología de las especies arvenses y a su manejo (Holst et al., 2007). La consideración de la dimensión espacial en los modelos poblacionales permite crear modelos más reales (Zavala et al., 2006), ya que los agro-ecosistemas son sistemas espacio-temporales. Esto es especialmente importante en el estudio de la dinámica de las malas hierbas ya que su control y los procesos de dispersión de sus semillas tienen lugar a diferentes escalas espaciales (desde la parcela al paisaje) debido a las operaciones de manejo de los sistemas agrarios (Petit et al., 2012).

I. 1. 3. 1. Modelos espaciales

Como se ha expuesto en el apartado anterior, el desarrollo de modelos poblacionales más realistas requieren la consideración del espacio dentro de los mismos. El componente espacial puede introducirse en los modelos de dinámica de poblaciones a través de los procesos de dispersión de individuos/polen y la definición de un marco espacial donde se mueva la población.

El uso de modelos espacio-temporales de la dinámica de poblaciones arvenses no ha sido muy habitual en Malherbología, si bien, han existido algunos trabajos pioneros a finales de los 80s y principios de los 90s (Ballaré et al., 1987; Perry y González-Andújar, 1993), extendiéndose en años posteriores gracias, entre otros factores, a las facilidades informáticas para su desarrollo. El ámbito de aplicación de estos modelos ha sido variado destacando su uso en el estudio de escenarios de manejo (Paice et al., 1998; Blanco-Moreno, 2004; van Mourik et al., 2008) y la expansión de la resistencia a herbicidas (Roux et al., 2008; Dauer et al., 2009). También se han utilizado para alcanzar un mayor entendimiento de los procesos espaciales y sus consecuencias sobre las poblaciones arvenses (Ballaré et al., 1987; González-Andújar y Perry, 1995).

Los modelos desarrollados en tales estudios varían en la metodología seguida. Según Cousens et al. (2008) podemos clasificar los modelos en función de la forma en que éstos tratan el tiempo y el espacio. Hay modelos que consideran el tiempo y el espacio continuo, como los modelos de reacción-difusión, modelos que consideran el espacio continuo y el tiempo discreto, como los modelos integro-diferenciales y, finalmente, modelos que consideran el tiempo y el espacio discretos, como los modelos celulares. Los dos primeros tipos de modelos tienen la ventaja de que pueden ser abordados a través de métodos analíticos. A pesar de esta ventaja, los modelos de reacción-difusión no son adecuados para describir las poblaciones de plantas ya que los procesos de dispersión y crecimiento son procesos discretos en el tiempo más que continuos. Los modelos integro-diferenciales son más adecuados y han sido utilizados en algunos estudios (Allen et al., 1996; Woolcock y Cousens, 2000). Aunque la posibilidad de obtener soluciones analíticas es atractiva, estos modelos están muy limitados a medida que introducimos complejidad en el sistema. Para estudios donde se requieran mayores niveles de complejidad, de realismo y de detalle (e.g., la consideración de heterogeneidad espacial o la fragmentación del espacio) los modelos celulares son más adecuados (Cousens et al., 2008). En estos modelos el espacio se considera dividido en unidades discretas de igual tamaño denominadas celdas o células que adoptan un determinado estado (en sentido matemático) en cada instante de tiempo. Este estado va cambiando según una regla de transición de índole local, es decir, cada celda está asociada a otras que conforman su vecindad, de modo que el estado de una de ellas en el instante $t + 1$ depende de los estados en los que estaban sus vecinas en el instante anterior t. Las celdas normalmente adoptan una forma cuadrada (Paice et al., 1998; Roux et al., 2008), dada la mayor facilidad de programación y visualización de estas estructuras, aunque celdas hexagonales también se han utilizado en algunos trabajos (González-Andújar y Perry, 1995; González-Andújar et al., 1999). Las celdas hexagonales presentan la ventaja de estar separadas desde su centro a igual distancia del centro de las celdas vecinas que la rodean, lo que no ocurre en las celdas cuadradas, donde las celdas situadas en sentido diagonal se encuentran separadas a mayores distancias que las celdas situadas con lados adyacentes (Fig. 9). Por otro lado, las celdas cuadradas parecen ser más adecuadas para modelizar procesos de dispersión anisotrópicos (e.g., por cosechadora o aperos de labranza), mientras que las celdas hexagonales presentan mayor facilidad en la modelización de procesos de dispersión natural (Paice et al., 1998).

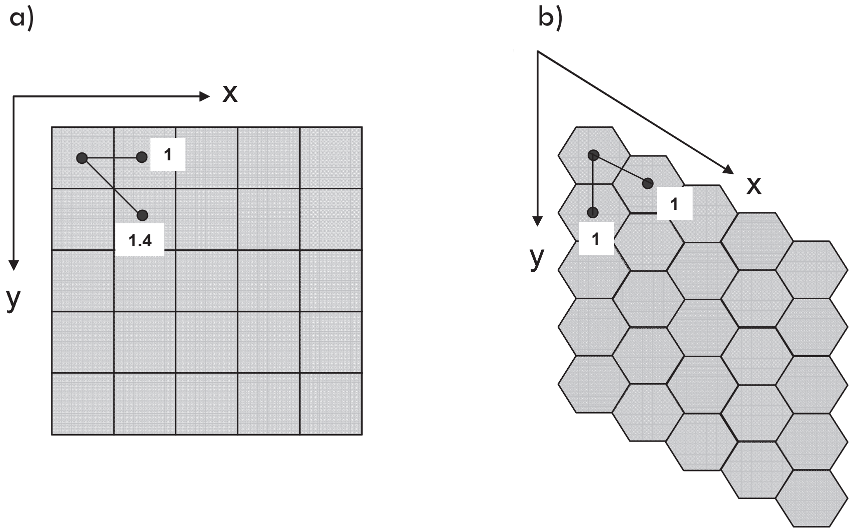

Figura 9. Marco espacial constituido por a) celdas cuadradas y b) hexagonales donde se muestra la distancia equivalente entre celdas vecinas.

Los modelos celulares pueden a su vez dividirse en autómatas celulares y en modelos de mallas de mapas acoplados (“couple map lattice”). En los primeros, cada celda contiene sólo un individuo, mientras que en los segundos la variable de estado es la densidad local de plantas o semillas. En cada una de estas celdas se desarrolla el ciclo de vida de la mala hierba (Fig. 8) y las celdas se interrelacionan a través de procesos de dispersión de semilla (o propágulos) y de polen. La dispersión de semilla entre celdas dependerá de la cantidad de semilla producida, de las características de la semilla y de los vectores de dispersión (ver sección I. 1. 2. 1. 2. Mecanismos de dispersión) que gobiernen la dispersión de semilla en el espacio (Ghersa y Roush, 1993) a la escala considerada. El flujo de semilla entre celdas es usualmente definido a través de funciones de densidad de probabilidad que responden a los conocimientos de la especie de mala hierba y a sus mecanismos de dispersión para esa escala (Cousens et al., 2008).

I. 1. 3. 1. 1. La elección del tamaño de celda y de la escala

Centrándonos en los modelos celulares, una decisión clave es la elección del tamaño de celda. El tamaño debe ser aquél que describa adecuadamente los procesos de dispersión a estudiar y la escala de estudio requerida; tamaños de celdas pequeños aproximarán el espacio de estructura discreta a un sistema continuo y por tanto los errores serán menores (Cousens et al., 2008) aunque el coste computacional para el estudio de escalas espaciales grandes puede ser muy elevado. Si por el contrario el tamaño de celda a emplear es demasiado grande para el mecanismo de dispersión de la especie, la dispersión de las semillas quedará relegada a unas pocas celdas alrededor de la celda fuente, lo que puede suponer una descripción limitada y sesgada del proceso de dispersión. Además, la dispersión de semillas en celdas más alejadas será nula (la dispersión está limitada), al contrario que ocurriría en los modelos que consideran el espacio continuo y donde las funciones de densidad de probabilidad poseen unas colas infinitas y permiten eventos de dispersión a larga distancia (Woolcock y Cousens, 2000).

A veces, el tamaño de la celda es elegido en función del tamaño de marco empleado en el muestreo experimental de donde se obtuvieron los parámetros del modelo, que a menudo es arbitrario (Cousens et al., 2008). Otras veces, el tamaño de celda a emplear ha sido estudiado en trabajos de campo o a través de los propios modelos variando el tamaño de celda en base a la función de distribución a emplear y a tasas de dispersión conocidas. Blanco-Moreno et al. (2006) a través de un estudio experimental concluyeron que el efecto de la cosechadora en la dispersión de las semillas de *L. rigidum* y *A. sterilis* podría ser descrito a distancias de centímetros, mientras que el efecto de la dispersión natural de estas especies podría ser descrito a distancias de un metro o menos. Collingham y Huntley (2000) examinaron el tamaño de celda adecuado a través de simulaciones con su modelo espacial para conseguir tasas de migración de semillas acordes a los datos experimentales conocidos para la especie *Tilia cordata* Mill.

Por otro lado, hay que tener en cuenta que los resultados obtenidos en cuanto a la dinámica de las especies arvenses puede variar de acuerdo a la escala espacial considerada.

A escalas mayores una mala hierba puede parecer localizada en rodales estables dentro del cultivo, sin embargo, a escalas menores estos rodales pueden ser altamente móviles debido a procesos de dispersión que operan a escalas más pequeñas (Woolcock y Cousens, 2000). Por tanto, la elección de la escala espacial debe responder a los objetivos que se quieren estudiar o predecir, y en base a esto y a la disponibilidad de recursos, se debe seleccionar el tamaño de celda.

I. 1. 3. 1. 2. Heterogeneidad espacial

Los agro-ecosistemas no son espacialmente homogéneos, sino que presentan una gran variabilidad en sus componentes (nutrientes, temperatura, densidad de poblaciones, etc.). Esta heterogeneidad espacial es la que permite la expresión de procesos ecológicos como la coexistencia de especies, a pesar de la mayor habilidad competitiva de unas sobre otras (Zavala y Zea, 2004). Por ejemplo, Ruiz et al. (2008) comprobaron, a través de ensayos experimentales en campo, que el efecto competitivo mala hierba-cultivo era variable en el espacio y dependía de las características de la zona. Por ello, la consideración de la heterogeneidad espacial en los modelos va a permitir una descripción más realista del agro-ecosistema.

Los modelos celulares nos permiten considerar la heterogeneidad espacial de manera sencilla asignando características específicas del hábitat (Cousens et al., 2008), de las malezas y/o de manejo a celdas concretas del marco espacial de tal manera que consigan variaciones espaciales en los parámetros demográficos (González-Andújar y Perry, 1995), genéticos (Richter et al., 2002; Peck et al., 1999) y/o de control (Byers y Castle, 2005; Roux et al., 2008) de la mala hierba. La forma de considerar la heterogeneidad espacial en la literatura ha sido muy variada y dependiente de los objetivos de la investigación. Pero se puede enmarcar en dos grandes grupos (Cousens et al., 2008). El primero considera las celdas de manera cualitativa, considerando si son adecuadas o no para el crecimiento de la especie. El segundo grupo considera la cuantificación de alguna/s variable/s que influyan en el crecimiento de la mala hierba dentro de cada celda. La asignación del valor de la variable a cada celda pueden ser definida aleatoriamente en el espacio, ser derivada de la geometría de fractales (Collingham y Huntley, 2000), de experimentos en campos, de imágenes de satélites (Dauer et al., 2009) o creada artificialmente para describir diferentes escalas en función del "tamaño de grano" (agrupación de celdas) (Roux et al., 2008).

I. 1. 3. 2. Limitaciones de los modelos

Un modelo es una simplificación o abstracción de un sistema real y nos ayuda a interpretarlo (Fig. 10). Aunque los modelos son esquemas o bocetos de la realidad, pueden conservar, si son correctos en su desarrollo y posiblemente de una forma distorsionada, las características más relevantes del problema real. Podemos decir, de una manera general, que los modelos son siempre incorrectos aunque muchos de ellos son muy útiles.

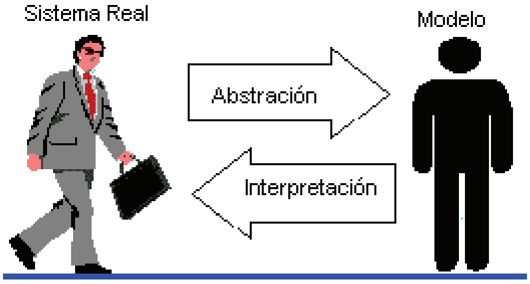

Figura 10. Esquema conceptual de un modelo.

Una etapa básica del proceso de modelización es un análisis de la calidad del modelo, esencial para conocer la confianza que podemos tener en su aplicación (Wallach y Goffinet, 1989). A este proceso se le conoce como proceso de "validación" y consiste en comprobar la similitud entre las observaciones reales y las predicciones del modelo (Holst et al., 2007). Las observaciones deben provenir de datos independientes, es decir, diferentes de aquéllos usados en la calibración o parametrización del modelo. El proceso de validación es, la mayoría de las veces, una técnica subjetiva (e.g., verificación visual) que comprueba el comportamiento del modelo dentro de unos límites reales. Sin embargo, sería más recomendable una aproximación más objetiva a través de unos criterios matemáticos y estadísticos (Smith y Rose, 1995; Piñeiro et al., 2008). En Malherbología pocos modelos espaciales presentan un proceso de validación basado en criterios objetivos (Dicke et al., 2007).

Los modelos son creados para responder a objetivos muy diversos y en base a estos se desarrolla la estructura del mismo. Por ello, hay que tener en cuenta que un modelo no puede usarse fuera del contexto ni más allá de los límites dentro de los cuales el modelo fue creado, de otro modo podríamos generar resultados erróneos. Si bien, es imposible que un modelo con una estructura definida, pueda describir un sistema natural, que es un sistema abierto, por lo que diferentes estructuras de un modelo pueden caracterizar el comportamiento de una misma población o de un mismo sistema (Freckleton et al., 2008). Existe consecuentemente una incertidumbre en la elección de la estructura del modelo, sus variables y sus parámetros, así como en los propios valores de los parámetros (Monod et al., 2006) debido a la propia complejidad del sistema y/o a la forma en que los valores han sido obtenidos (Massada y Carmel, 2008). Es importante conocer qué tipo de incertidumbre existe en nuestro modelo para interpretar correctamente los resultados. Para ello se usan los análisis de incertidumbre y de sensibilidad (Monod et al., 2006). Con el análisis de incertidumbre se evalúa cuantitativamente la variabilidad de los componentes del modelo para una situación dada y así obtener una distribución de incertidumbre en los resultados del modelo. Posteriormente un análisis de sensibilidad determina la sensibilidad de los resultados del modelo a los componentes del modelo que presentan variabilidad. Estos análisis son necesarios en el proceso de modelización, ya que cuando una alta incertidumbre coincide con una alta sensibilidad las predicciones del modelo pueden tener una fiabilidad muy baja (Massada y Carmel, 2008).

I. 2. ESTRUCTURA DE LA MEMORIA DE TESIS

La presente memoria de tesis se ha organizado en capítulos con formato de artículos científicos.

Al capítulo introductorio (**Capítulo I**), le siguen los **Capítulos II, III** y **IV** que se corresponden con artículos publicados o pendientes de envío a diferentes revistas científicas de difusión internacional, por lo que se presentan en inglés y con sus respectivas secciones de resumen, introducción, materiales y métodos, resultados, discusión y referencias, precedido por un resumen en castellano. El último capítulo (**Capítulo V**) presenta las conclusiones de la Tesis Doctoral.

Breve descripción del contenido de los capítulos principales

Capítulo II: se desarrolla un modelo bioeconómico espacialmente explícito de *L. rigidum* en cereales que consiste en un modelo de mallas de mapas acoplados (coupled map lattice) compuesto por celdas hexagonales. Cada celda representa un área de 0.86 m^2 dentro de una parcela de 1 ha. En cada celda se desarrolla un modelo bioeconómico formado por la integración de tres submodelos: un submodelo de dinámica de poblaciones, un submodelo de competencia mala hierba-cultivo y un submodelo económico. El submodelo de dinámica de poblaciones cuenta con un banco de semillas clasificado en clases de edad y con un proceso denso-dependiente de producción de semillas. El submodelo de competencia consiste en un modelo hiperbólico que establece la relación funcional entre la producción y la densidad de *L. rigidum*. Finalmente, el submodelo económico es un sencillo modelo de ingresos y gastos. Todas las celdas están conectadas por un proceso de dispersión de semillas. El modelo es utilizado, mediante simulación, para la evaluación de diversas estrategias de control integrado y para analizar la sensibilidad del modelo a diferentes parámetros demográficos y económicos.

Capítulo III: se desarrolla un modelo espacialmente explícito de la dinámica de poblaciones de *A. sterilis* en cereales que consiste en un modelo de mallas de mapas acoplados (coupled map lattice) compuesto por celdas cuadradas. Cada celda representa un área de 1 ha dentro de un paisaje agrícola de 10000 ha. En cada celda se desarrolla una población de avena loca que cuenta con un banco de semillas y con un proceso denso-dependiente de producción de semillas. El paisaje está conectado por la dispersión de semillas entre las celdas. El modelo es utilizado para explorar el efecto de las rotaciones de cultivo sobre el control de *A. sterilis* y la interacción de esta práctica de control con la capacidad de dispersión de la especie y la distribución espacial de los cultivos presentes. Se analizaron rotaciones de diferente longitud de ciclo y secuencia de cultivos bajo varios supuestos de fracciones de dispersión de la mala hierba en paisajes con diferente abundancia relativa de los cultivos presentes.

Capítulo IV: se desarrolla un modelo espacialmente explícito que contempla la dinámica de poblaciones y la evolución de la resistencia a herbicidas de *L. rigidum* en cereales. El modelo consiste en un modelo de mallas de mapas acoplados (coupled map lattice) compuesto por celdas cuadradas de 1 ha. Estas celdas están agrupadas formando parcelas de diferentes tamaños y que se encuentran dispuestas aleatoriamente en un paisaje agrícola de 10000 ha En cada celda del modelo se desarrolla un submodelo poblacional y un submodelo genético. El submodelo poblacional cuenta con un banco de semilla estratificado en diferentes capas del suelo y un estado de plántula estructurado en cohortes en función del momento de la germinación de la semilla. La producción de semilla responde a un proceso denso-dependiente. El modelo genético caracteriza el genotipo de las poblaciones de las malas hierbas de forma explícita en cada una de las celdas del paisaje. Entre las celdas del paisaje se producen procesos de dispersión de polen y de semillas, este último debido a procesos relacionados con la intervención humana como la siembra y la cosecha del cereal. El modelo fue usado en la búsqueda de estrategias de manejo que retrasen el desarrollo de la resistencia a herbicidas a escala de paisaje, así como analizar los vectores de dispersión más influyentes en la expansión de la resistencia. Se realizó un análisis de sensibilidad para establecer los parámetros más influyentes en el modelo bajo las condiciones iniciales consideradas.

Capítulo V: se presentan las conclusiones finales de la Tesis Doctoral.

I. 3. OBJETIVOS DE LA TESIS

El objetivo general de la tesis es mejorar el conocimiento sobre la dinámica poblacional de algunas de las especies arvenses más problemáticas de los sistemas cerealistas de secano españoles a diferentes escales espaciales y su manejo, mediante el desarrollo de modelos espacialmente explícitos y con el fin último de hacer dichos sistemas más sostenibles y rentables económicamente.

Objetivos específicos

- Desarrollar modelos de dinámica de poblaciones espacialmente explícitos para *Avena sterilis* (avena loca) y *Lolium rigidum* (vallico) a diferentes escalas espaciales (de parcela, Capítulo II y de paisaje, Capítulos III y IV).

- Estudiar el efecto de diferentes escenarios de manejo integrado en el control de estas especies arvenses a la escala espacial considerada en cada caso (Capítulo II, III y IV).

- Estudiar el desarrollo de la resistencia a los herbicidas y su velocidad de expansión en las poblaciones de las malas hierbas sometidas a diferentes estrategias de manejo (Capítulo IV).

- Determinar los factores biológicos, genéticos y de manejo más influyentes en el crecimiento de las poblaciones de las malas hierbas (Capítulos II, III y IV) y en el retorno económico de los sistemas cerealistas (Capítulo II) a la escala considerada en cada caso.

I. 4. REFERENCIAS

AEPLA (2011), Asociación Empresarial para la Protección de las Plantas. http://www.aepla.es. Visitada: 20/05/2012.

Aibar, J. (1990) Biología y control de la avena loca (*Avena fatua* L. y *A. sterilis* subsp. *ludoviciana* (Dur.) Nym.) en Aragón. ED INIA, España.

Aibar, J.; Ochoa, M. J.; Zaragoza, C. (1991) Field emergente of *Avena fatua* L. and *A. sterilis* ssp. *ludoviciana* (Dur.) Nym. in Aragón, Spain. Weed Research 31, 29-32.

Allen, L. J. S.; Allen, E. J.; Ponweera, S. (1996) A mathematical model for weed dispersal and control. Bulletin of Mathematical Biology 58, 815-834.

ANTHOS (2012) Sistema de información sobre las plantas de España. http://www.anthos.es. Visitada: 03/03/2012.

Ballaré, C. L.; Scopel, A. L.; Ghersa, C. M.; Sánchez, R. A. (1987) The population ecology of *Datura ferox* in soybean crops. A simulation approach incorporating seed dispersal. Agriculture, Ecosystems and Environment 19, 177-188.

Baraibar, B.; Westerman, P. R.; Carrión, E.; Recasens, J. (2009) Effects of tillage and irrigation in cereal fields on weed seed removal by seed predators. Journal of Applied Ecology 46, 380-387.

Barros, J. F. C.; Basch, G.; de Carvalho, M. (2005) Effect of reduced doses of a post-emergence graminicide mixture to control *Lolium rigidum* G. in winter wheat under direct drilling in Mediterranean environment. Crop Protection 24, 880-887.

Barros, J. F. C.; Basch, G.; de Carvalho, M. (2008) Effect of reduced doses of a post-emergence graminicide to control *Avena sterilis* L. and *Lolium rigidum* G. in no-till wheat under Mediterranean environment. Crop Protection 27, 131-1037.

Barroso, J.; Fernández-Quintanilla, C.; Ruiz, D.; Hernaiz, P.; Rew, L. J. (2004) Spatial stability of *Avena sterilis* ssp. *ludoviciana* populations under annual applications of low rates of imazamethabenz. Weed Research 44, 178-186.

Barroso, J.; Navarrete, L.; Sánchez del Arco, M. J.; Fernández-Quintanilla, C.; Lutman, P. J. W.; Perry, N. H.; Hull, R. I. (2006) Dispersal of *Avena fatua* and *Avena sterilis* patches by natural dissemination, soil tillage and combine harvesters. Weed Research 46, 118-128.

Barroso, J.; Ruiz, D.; Escribano, C.; Barrios, L.; Fernández-Quintanilla, C. (2009) Comparison of three chemical control strategies for *Avena sterilis* ssp. *ludoviciana*. Crop Protection 28, 393-400.

Blanco, J. M. (2004) Effects of dispersal and competition with *Avena sterilis* L. on the spatial structure and dynamics of *Lolium rigidum* Gaudin in dryland cereal fields. Tesis doctoral. Universidad de Barcelona, España.

Blanco-Moreno, J. M.; Chamorro, L.; Masalles, R. M.; Recasens, J.; Sans, F. X. (2004) Spatial distribution of *Lolium rigidum* seedlings following seed dispersal by combine harvesters. Weed Research 44, 375-387.

Blanco-Moreno, J. M.; Chamorro, L.; Sans, F. X. (2006) Spatial and temporal patterns of *Lolium rigidum*–*Avena sterilis* mixed populations in a cereal field. Weed Research 46, 207–218.

Bolòs, O.; Vigo, J. (2001) Flora dels Països Catalans Vol. IV. Editorial Barcino, España.

Busi, R.; Powles, S. B. (2009) Evolution of glyphosate resistance in a *Lolium rigidum* population by glyphosate selection at sublethal doses. Heredity 103, 318-325.

Byers, J. A.; Castle, S. J. (2005) Areawide models comparing synchronous versus asynchronous treatments for control of dispersing insect pests. Journal of Economic Entomology 98, 1763-1773.

Chamorro, L.; Romero, A.; Masalles, R. M.; Sans, F. X. (2007) Cambios en la diversidad de las comunidades arvenses en los cereales de secano en Cataluña. XI Congreso de la Sociedad Española de Malherbología, 51–55. Albacete, España.

Chauhan, B. S.; Gill, G.; Preston, C. (2006) Influence of tillage systems on vertical distribution, seedling recruitment and persistence of rigid ryegrass (*Lolium rigidum*) seed bank. Weed Science 54, 669-676.

Cimalova S.; Lososova Z. (2009). Arable weed vegetation of the northeastern part of the Czech Republic: effects of environmental factors on species composition. Plant Ecology 203, 45-57.

Cirujeda, A.; Aibar, J.; Zaragoza, C. (2011) Remarkable changes of weed species in Spanish cereal fields from 1976 to 2007. Agronomy for Sustainable Development 31, 675-688.

Cirujeda, A.; Taberner, A. (2009) Cultural control of herbicide-resistant *Lolium rigidum* Gaud. populations in winter cereal in Northeastern Spain. Spanish Journal of Agricultural Research 7, 146-154.

Cirujeda, A.; Taberner, A. (2010) Chemical control of herbicide-resistant *Lolium rigidum* Gaud. in north-eastern Spain. Pest Management Science 66, 1380-1388.

Colbach, N.; Debaeke, P. (1998) Integrating crop management and crop rotation effects into models of weed population dynamics: a review. Weed Science 46, 717-728.

Collingham, Y. C.; Huntley, B. (2000) Impacts of fragmentation and patch size upon migration rates. Ecological Applications 10, 131-144.

Cousens, R. D.; Dytham, C.; Law, R. (2008) Dispersal in plants: a population perspective. Oxford University Press, USA.

Cousens, R. D.; Mokhtari, S. (1998) Seasonal and site variability in the tolerance of wheat cultivars to interference form *Lolium rigidum*. Weed Research 38, 301-307.

Delgado, A.; Moreira, F. (2000) Bird assemblages of an Iberian cereal steppe. Agriculture, Ecosystems and Environment 78, 65-76.

de Prado, J. L.; Osuna, M. D.; Heredia, A.; de Prado, R. (2005) *Lolium rigidum*, a pool of resistance mechanisms to ACCase inhibitor herbicides. Journal of Agricultural and Food Chemistry 53, 2185-2191.

Dauer, J. T.; Luschei, E. C.; Mortensen, D. A. (2009) Effects of landscape composition on spread of an herbicide-resistant weed. Landscape Ecology 24, 735-747.

Devesa, A. (1987). *Lolium* L. En: Flora Vascular de Andalucía Occidental Vol. III (Eds.Valdés, B.; Talavera, S. y Fernández-Galiano, E.) pp. 284-286. Ketrés Editora S. A., España.

Dicke, D.; Gerhards, R.; Büchse, A.; Hurle, K. (2007) Modeling spatial and temporal dynamics of *Chenopodium album* L. under the influence of site-specific weed control. Crop Protection 26, 206-211.

FAO (2012) Organización de las Naciones Unidas para la Alimentación y la Agricultura. http://www.fao.org. Visitada: 20/05/2012.

Fernández-Quintanilla, C.; Barroso, J.; Recasens, J.; Sans, X.; Torner, C.; Sánchez del Arco, M. J. (2000) Demograhpy of *Lolium rigidum* in winter barley crops: analysis of recruitment, survival and reproduction. Weed Research 40, 281-291.

Fernández-Quintanilla, C.; Navarrete, L.; González-Andújar, J. L.; Fernández, A.; Sánchez, M. J. (1986) Seedling recruitment anda ge-specific survivorship and reproduction in populations of *Avena sterilis* L. ssp. *ludoviciana* (Durieu) Nyman. The Journal of Applied Ecology 23, 945-955.

Fernández-Quintanilla, C.; Navarrete, L.; Torner, C. (1984) The influence of crop rotation on the popultaion dynamics of *Avena sterilis* (L.) ssp. *ludoviciana* Dur., in Central Spain. Proceeding of the 3rd EWRS Symposium on weed problems in the Mediterranean area, 9-15. Oeiras, Portugal.

Fernández-Quintanilla, C.; Naverrete, L.; Torner, C.; Andújar, J. L. (1987) Influence of herbicide treatments on the population dynamics of *Avena sterilis* ssp. *ludoviciana* (Durieu) Nyman in winter wheat crops. Weed Research 27, 375-383.

Fernández-Quintanilla, C.; Navarrete, L.; Torner, C.; Sánchez del Arco, M. J. (1997). *Avena sterilis* L. en cultivos de cereales. En: Biología de las malas hierbas de España (Eds. Sans, X. F. y Fernández-Quintanilla, C.) pp. 11-23. PHYTOMA-España y Sociedad Española de Malherbología, España.

Fernández-Quintanilla, C.; Saavedra, M. (1991). Malas hierbas: conceptos generales. En: Fundamentos sobre malas hierbas y herbicidas (Eds. García-Torres, L. y Fernández-Quintanilla, C.) pp. 27-48. Mundi-prensa Editores S. A., España.

Fernández-Quintanilla, C.; González-Andújar, J. L.; González Ponce, R.; de Lucas, C.; Navarrete, L.; Recasens, J.; Sánchez del Arco, M. J.; Taberner, A.; Tiebas, M. A.; Torner, C. (1998). Using the low rate concept (LRC) for control of grassweeds in cereals under Mediterranean conditions. Proceedings of the 6th EWRS Mediterranean Symposium, 353-359. Montpellier, France.

Freckleton, R. P.; Sutherland, W. J.; Watkinson, A. R.; Stephens, P. A. (2008) Modelling the effects of management on population dynamics: some lessons from annual weeds. Journal of Applied Ecology 45, 1050-1058.

García-Baudín, J. M. (1984) Gramíneas adventicias en los cereales de invierno (trigo y cebada) españoles. Revista de Extensión Agraria 1, 18-20.

Ghersa, C. M.; Roush, M. L. (1993) Searching for solutions to weed problems. BioScience 43, 104-109.

Gill, G. S.; Holmes, J. E. (1995) Efficacy of cultural control methods for combating herbicide-resistant *Lolium rigidum*. Pesticide Science 51, 352-358.

González-Andújar, J. L. (2008) Weed Control Models. En: Population Dynamics, Encyclopedia of Ecology Vol. V (Eds. Jørgensen, S. E. y Fath, B. D.) pp. 3776-3780. Elsevier, UK.

González-Andújar, J. L.; Fernández-Quintanilla, C. (1991) Modelling the population dynamics of *Avena sterilis* under dry-land cereal cropping systems. The Journal of Applied Ecology 28, 16-27.

González-Andújar, J. L.; Fernández-Quintanilla, C. (1993) Strategies for the control of *Avena sterilis* in winter wheat production systems in central Spain. Crop Protection 12, 617-623.

González-Andújar, J. L.; Fernández-Quintanilla, C. (2004) Modelling the population dynamics of annual ryegrass (*Lolium rigidum*) under various weed management systems. Crop Protection 23, 723-729.

González-Andújar, J. L.; Fernández-Quintanilla, C.; Bastida, F.; Calvo, R.; González-Díaz, L.; Izquierdo, J.; Lezaun, J. A.; Perea, F.; Sánchez del Arco, M. J.; Urbano, J. M. (2011) Field evaluation of a decision support system for herbicidal control of *Avena sterilis* ssp. ludoviciana in winter wheat. Weed Research 50, 83–88.

González-Andújar, J. L.; Fernández-Quintanilla, C.; Bastida, F.; Calvo, R.; Izquierdo, J.; Lezaun, J. A. (2011) Assessment of a decision support system for chemicals control of annual ryegrass (*Lolium rigidum*) in winter cereals. Weed Research 51, 304-309.

González-Andújar, J. L.; Perry, J. N. (1995) Models for the herbicidal control of the seed bank of *Avena sterilis*: the effects of spatial and temporal heterogeneity and of dispersal. Journal of Applied Ecology 32, 578-587.

González-Andújar, J. L.; Perry, J. N.; Moss, S. R. (1999) Modelling effects of spatial patterns on the seed bank dynamics of *Alopecurus myosuroides*. Weed Science 47, 697-705.

González-Ponce, R. (1998) Competition between barley and *Lolium rigidum* for nitrate. Weed Research 38, 453-460.

Holst, N.; Rasmussen, I. A.; Bastiaans, L. (2007) Field weed population dynamics: a review of model approaches and applications. Weed Research 47, 1-14.

Infoagro (2012) Portal temático sobre Agricultura. http://www.infoagro.com. Visitada: 20/06/2012.

Izquierdo, J.; Recasens, J.; Fernández-Quintanilla, C.; Gill, G. (2003) Effects of crop and weed densities on the interactions between barley and *Lolium rigidum* in several Mediterranean locations. Agronomy for Sustainable Development 23, 529-536.

José-María, L.; Blanco-Moreno, J. M.; Armengot, L.; Sans, F. X. (2011) How does agricultural intensification modulate changes in plant community composition? Agriculture, Ecosystems and Environment 145, 77-84.

Lemerle, D.; Verbeek, B.; Coombes, N. (1995) Losses in grain yield of winter crops from *Lolium rigidum* competition depend on crop species, cultivars and season. Weed Research 35, 503-509.

MAGRAMA (2012) Ministerio de Agricultura, Alimentación y Medio Ambiente. http://www.magrama.gob.es. Visitada: 05/04/2012.

Manalil, S.; Busi, R.; Renton, M.; Powles, S. B. (2011) Rapid evolution of herbicide resistance by low herbicide dosages. Weed Science 59, 210-217.

Marshall, E. J. P.; Brown, V. K.; Boatman, N. D.; Lutman, P. J. W.; Squire, G. R.; Ward, L. K. (2003) The role of weeds in supporting biological diversity within crop fields. Weed Research 43, 77-89.

Massada, A. B.; Carmel, Y. (2008) Incorporating output variance in local sensitivity analysis for stochastic models. Ecological Modelling 213, 463-467.

Matthews, J.; Llewellyn, R.; Jaeschke, R.; Powles, S. (1996) Catching weed seeds at harvest: a method to reduce annual weed populations. Proceedings of the 8th Australian Agronomy Conference, 684-685. Toowoomba, Queensland.

Maxwell, B. D.; O'Donovan, J. (2007) Understanding weed-crop interactions to manage weed problems. En: Non-chemical weed management: principles, concepts and technology (Eds. Upadhayaya, M. K. y Blackshaw, R. E.) pp. 17-33. CAB International, UK.

McCanny, S. J.; Cavers, P. B. (1988) Spread of proso millet (*Panicum miliaceum* L.) in Ontario, Canada. II. Dispersal by combines. Weed Research 28, 67-72.

Michael, P. J.; Owen, M. J.; Powles, S. B. (2010) Herbicide-resistant weed seeds contaminate grain sown in the western Australian Grainbelt. Weed Science 58, 466-472.

Monod, H.; Naud, C.; Makowski, D. (2006) Uncertainty and sensitivity analysis for crop models: evaluation, analysis, parameterization and applications. En: Working with dynamic crop models (Eds. Wallach, D.; Makowski, D. y Jones, J. W.) pp 55-100. Elsevier B. V., The Netherlands.

Neve, P.; Norsworthy, J. K.; Smith, K. L.; Zelaya, I. A. (2010) Modelling evolution and management of glyphosate resistance in *Amaranthus palmeri*. Weed Research 51, 99–112.

Neve, P.; Powles, S. (2005) Recurrent selection with reduced herbicide rates results in the rapid evolution of herbicide resistance in *Lolium rigidum*. Theoretical and Applied Genetics 110, 1154-1166.

Paice, M. E. R.; Day. W.; Rew, L. J.; Howard, A. (1998) A stochastic simulation model for evaluating the concept of patch spraying. Weed Research 38, 373-388.

Pannell, D. J.; Stewart, V.; Bennett, A.; Mojardino, M.; Schmidt, C.; Powles, S. B. (2004) RIM: a bioeconomic model for integrated weed management of *Lolium rigidum* in western Australia. Agricultural Systems 79, 305-325.

Pan-Sande, I. (2006) Diseño de un sitio web sobre las malas hierbas de Córdoba. Proyecto Fin de Carrera. ETSIAM, Universidad de Córdoba, España.

Paynter, B. H.; Hills, A. L. (2009) Barley and rigid ryegrass (*Lolium rigidum*) competition is influenced by crop cultivar and density. Weed Technology 23, 40-48.

Peck, S. L.; Gould, F.; Ellner, S. P. (1999) Spread of resistance in spatially extended regions of transgenic cotton: implication for management of *Heliothis virescens* (Lepidoptera: Noctuidae). Journal of Economic Entomology 92, 1-16.

Pérez-García, J. J. (2006) Malas hierbas gramíneas y su control en cereales de invierno. Vida rural 222, 48-50.

Perry, J. N.; González-Andújar, J. L. (1993) Dispersal in a metapopulation neighbourhood model of an annual plant with a seedbank. The Journal of Ecology 81, 453-463.

Petit, S.; Alignier, A.; Colbach, N.; Joannon, A.; Le Coeur, D.; Thenail, C. (2012) Weed dispersal by farming at various spatial scales. A review. Agronomy for Sustainable Development. DOI: 10.1007/s13593-012-0095-8. Visitada: 30/06/2012.

Piñeiro, G.; Perelman, S.; Guerschman, J. P.; Paruelo, J. M. (2008) How to evaluate models: Observed vs. predicted or predicted vs. observed? Ecological Modelling 216, 316-322.

Pujadas, A. J.; Hernández, J. E. (1998). Concepto de mala hierba. ITEA 75, 47-56.

Quail, P. H.; Carter, O. G. (1968) Survival and seasonal germination of seeds of *Avena fatua* and *A. ludoviciana*. Australian Journal of Agriculture Research 19, 721-729.

Quail, P. H.; Carter, O. G. (1969) Dormancy in seeds of *Avena ludoviciana* and *A. fatua*. Australian Journal of Agriculture Research 20, 1-11.

Recasens, J. (2012) Herbario digital de malas hierbas, Universitat de Lleida. http://www.malesherbes.udl.cat. Visitada: 20/06/2012.

Recasens, J.; Taberner, A.; Izquierdo, J. (1997). *Lolium rigidum* Gaud. en cultivos de cereales. En: Biología de las malas hierbas de España (Eds. Xavier Sans, F. y Fernández-Quintanilla, C.) pp. 49-64. PHYTOMA-España y Sociedad Española de Malherbología, España.

Richter, O.; Zwerger, P.; Böttcher, U. (2002) Modelling spatio-temporal dynamics of herbicide resistance. Weed research 42, 52-64.

Romero, A. T. (2011) *Lolium* L. En: Flora Vascular de Andalucía Oriental (Eds. Blanca, G., Cabezudo, B.; Cueto, M.; Morales-Torres, C. y Salazar, C.) pp. 322-323. Universidades de Almería, Granada, Jaén y Málaga, Granada, España.

Romero, A.; Chamorro, L.; Sans, F. X. (2008) Weed diversity in crop edges and inner fields of organic and conventional dryland winter cereal crops in NE Spain. Agriculture, Ecosystems and Environment 124, 97-104.

Romero Zarco, C. (1987) *Avena* L. En: Flora Vascular de Andalucía Occidental Vol. III (Eds. Valdés, B.; Talavera, S. y Fernández Galiano, E.) pp. 302-308. Ketrés Editora S. A., España.

Romero Zarco, C. (2011) *Avena* L. En: Flora Vascular de Andalucía Oriental (Eds. Blanca, G.; Cabezudo, B.; Cueto, M.; Morales-Torres, C. y Salazar, C.) pp. 325-327. Universidades de Almería, Granada, Jaén y Málaga, Granada, España.

Roschewitz, I.; Gabriel, D.; Tscharntke, T.; Thies, C. (2005) The effects of landscape complexity on arable weed species diversity in organic and conventional farming. Journal of Applied Ecology 42, 873-882.

Roux, F.; Paris, M.; Reboud, X. (2008) Delaying weed adaptation to herbicide by environmental heterogeneity: a simulation approach. Pest Management Science 64, 16-29.

Ruiz, D.; Barroso, J.; Hernaiz, P.; Fernández-Quintanilla, C. (2008) The competitive interactions between winter barley and *Avena sterilis* are site-specific. Weed Research 48, 38-47.

Saavedra, M.; Cuevas, J.; Mesa-García, J.; García-Torres, L. (1989) Grassy weeds in winter cereals in southern Spain. Crop Protection 6, 181-187.

Sánchez del Arco, M. J.; Torner, C.; Fernández-Quintanilla, C. (1995) Seed dynamics in populations of *Avena sterilis* ssp. *ludoviciana*. Weed Research 35, 477-487.

Smith, E. P.; Rose, K. A. (1995) Model goodness-of-fit analysis using regression and related techniques. Ecological Modelling 77, 49-64.

Taberner, A. (1996). Biología de *Lolium rigidum* Gaud. como planta infestante del cultivo de cebada. Aplicación al establecimiento de métodos de control. Tesis doctoral. Universidad de Lleida, España.

Thill, D. C.; Mallory-Smith, C. A. (1997) The nature and consequence of weed spread in cropping systems. Weed Science 45, 337-342.

Torner, C.; Fernández-Quintanilla, C.; Navarrete, L. (1984) Tolerance and competitive ability of winter cereal in the presence of *Avena sterilis* L. ssp. *ludoviciana* Dur. Proceeding of the 3rd EWRS Symposium on weed problems in the Mediterranean area, 109-113. Oeiras, Portugal.

Torner, C.; González-Andújar, J. L.; Fernández-Quintanilla, C. (1991) Wild oat (*Avena sterilis* L.) competition with winter barley: plant density effects. Weed Research 31, 301-307.

van Mourik, T. A.; Bianchy, F. J. J. A.; van der Werf, W.; Stomph, T. J. (2008) Long-term management of *Striga hermonthica*: strategy evaluation with a spatio-temporal population model. Weed Research 48, 329-339.

Vinatier, F.; Tixier, P.; Le Page, C.; Duyck, P. F.; Lescourret, F. (2009) COSMOS, a spatially explicit model to simulate the epidemiology of *Cosmopolites sordidus* in banana fields. Ecological Modelling 220, 2244-2254.

Wallach, B.; Goffinet, B. (1989) Mean squared error of prediction as a criterion for evaluating and comparing system models. Ecological Modelling 44, 299-306.

Woolcock, J. L.; Cousens, R. (2000) A mathematic analysis of factors affecting the rate of spreads of patches of annual weeds in an arable field. Weed Science 48, 27-34.

Zavala, M. A.; Díaz-Sierra, R.; Purves, D.; Zea, G. E.; Urbieta, I. R. (2006) Modelos espacialmente explícitos. Ecosistemas 15, 88-99.

Zavala, M. A.; Zea, E. (2004) Mechanisms maintaining biodiversity in Mediterranean pine-oak forests: insights from a spatial simulation model. Plant Ecology 171, 197-207.

CAPÍTULO II

Bioeconomic spatially explicit model for weed management in dryland cereal crops: validation and long-term evaluation of management strategies

CAPÍTULO II: BIOECONOMIC SPATIALLY EXPLICIT MODEL FOR WEED MANAGEMENT IN DRYLAND CEREAL CROPS: VALIDATION AND LONG-TERM EVALUATION OF MANAGEMENT STRATEGIES

RESUMEN

Las condiciones ambientales, las características del suelo o las prácticas de manejo son factores variables en el tiempo y en el espacio que pueden repercutir en la dinámica poblacional de las malas hierbas, en la competencia mala hierba-cultivo e incluso en el control ejercido sobre sus poblaciones. Además, la incorporación del espacio en los modelos poblacionales de las malas hierbas tiene una gran importancia ya que considera la dinámica de la dispersión de estas poblaciones. En este trabajo se ha desarrollado un modelo bioeconómico espacialmente explícito y se ha validado con experimentos de campo. El modelo fue utilizado para comparar estrategias de manejo a largo plazo en el control de *Lolium rigidum* Gaudin (vallico), una mala hierba dominante de los cultivos de cereales en las regiones de clima mediterráneo. Se evaluaron un total de once estrategias de manejo individuales e integradas. Las distribuciones de las tasas de crecimiento observadas y predichas por el modelo fueron similares en las cuatro parcelas experimentales usadas en el proceso de validación. En dos de las parcelas, las tasas de crecimiento predichas por el modelo infravaloraron las tasas de crecimiento observadas y mostraron desviaciones en la distribución espacial de sus residuos. En general, las estrategias de manejo individuales fueron menos eficaces controlando las poblaciones de *L. rigidum* que las estrategias de manejo integradas. Ninguna de las estrategias de manejo individuales logró reducir la densidad inicial de vallico (732 semillas/celda). Las estrategias de manejo que integraron estrategias de control culturales y la aplicación de herbicida a dosis completa fueron las más eficaces controlando las poblaciones a largo plazo. Sin embargo, otras estrategias que fueron menos eficaces controlando las poblaciones de vallico fueron más rentables desde un punto de vista económico, tal como la aplicación de herbicida a dosis completa y algunas estrategias de manejo integrado que incluyeron la aplicación de herbicida a dosis reducida. Los retornos económicos fueron negativos en todas las estrategias simuladas. El análisis de sensibilidad mostró que el banco de semilla de *L. rigidum* fue especialmente sensible a la fecundidad y al porcentaje de control. Los retornos económicos fueron sensibles al porcentaje de control ejercido sobre las malas hierbas y al precio del cereal en aquéllas estrategias que incluyeron aplicación de herbicidas. En el caso de las estrategias que sólo incluyeron métodos de control culturales los retornos económicos fueron especialmente sensibles a la fecundidad y a la supervivencia de las plántulas. El modelo pone en relevancia la importancia de un análisis económico de los resultados cuando se pretende comparar estrategias de manejo y la necesidad de un control de las malas hierbas basado en estrategias de bajos inputs para conseguir rentabilidad en los cereales de secano.

Palabras clave: análisis de sensibilidad, dispersión, heterogeneidad espacial y temporal, *Lolium rigidum*, manejo integrado de las malas hierbas, validación, vallico.

ABSTRACT

Factors such as environmental conditions, soil characteristics or management practices present variability in time and space and may influence weed population dynamics, weed-crop competition and even the level of control exerted on their populations. In addition, the inclusion of a spatial framework in the weed population models has great importance because it allows the dispersal dynamic of the weeds. In this paper a bioeconomic spatially explicit model was developed and validated using field experiments. It was applied to compare long-term management strategies to control *Lolium rigidum* Gaudin (ryegrass), a troublesome weed infesting cereal crops in Mediterranean climate. A total of eleven individual and integrated management strategies were evaluated. The predicted and observed distributions of growth rates were similar for the four experimental plots used in the validation. The predicted growth rates undervalued the observed growth rates in two plots with bias in the spatial distribution of their residuals. Our results showed, in general, that individual management programs were worse controlling *L. rigidum* populations than integrated management programs. None of the individual management programs decreased the initial ryegrass density (732 seeds/cell). The management programs integrating cultural control strategies and herbicide at full rate showed the best long-term control. However, other strategies that were not as efficient decreasing the weed density were more profitable from an economic point of view, such as herbicide application at full rate and an integrated management program implying herbicide application at half rate. Economic returns were negative in all strategies simulated. Sensitivity analysis showed that the seed bank was especially sensitive to the fecundity and the weed control strategies. Economic outcomes were most affected by the control rate and the cereal price under management strategies implying chemical control, and by the fecundity and the seedling survival fraction under management strategies implying only cultural control. Our model simulations put in relevance the benefits of an economic analysis when comparing management strategies and the necessity to control weeds based on strategies of low inputs to make dryland cereals profitable.

Key words: dispersal, integrated weed management, *Lolium rigidum*, sensitivity analysis, spatial and temporal heterogeneity, ryegrass, validation.

II. 1. INTRODUCTION

Factors such as environmental conditions, soil characteristics or management practices present variability in time and space within the agricultural fields and may influence weed population dynamics (González-Andújar and Perry, 1995), weed-crop competition (Izquierdo and Fernández-Quintanilla, 2010) and even the level of control exerted by specific management practices like herbicide applications (Izquierdo et al., 2003). Although this heterogeneity has rarely been considered in the modelling exercise (Holst et al., 2007) it may be affordable through spatially explicit models (Woolcock and Cousens, 2000).

The construction of weed population models has proved useful for integrating the available information on weed growth, evaluating weed control scenarios and identifying critical gaps in research (Holst et al., 2007). While this approach may be sufficient to understand the general dynamic of a species, it may overlook important aspects of the weed's interactions with its surrounding. The inclusion of a spatial framework in the models has great importance in the dispersal dynamic of the weeds and it may affect the control exerted in their populations (Maxwell, 1992; Ghersa and Roush, 1993) especially in those implying management decisions for the long term (Thill and Mallory-Smith, 1997). However, if we want to give useful advices to farmers, it would be necessary to consider economic aspects in the population dynamic models in order to evaluate the economic implications of the management strategies (Doyle et al., 1986; González-Andújar and Fernández-Quintanilla, 1993). This is especially valuable when management scenarios are evaluated in the long term (Colbach and Debaeke, 1998). Bioeconomic models have been developed through the integration of population dynamics, weed-crop competition and economic sub-models with the aim of meet the farmer needs (González-Andújar and Fernández-Quintanilla, 1993). However, to our knowledge, there have been no attempts to develop bioeconomic spatial models to evaluate weed management strategies.

One basic step of any modeling exercise is the model validation in order to produce more robust and accurate models (Peltzer et al., 2008). This process is based on comparing a set of independent data (Cousens et al. 2008) with the results of the modeling process (Piñeiro et al., 2008) according to statistical criteria (Smith and Rose, 1995; Piñeiro et al., 2008; Mesplé et al., 1996). Few pest spatial models present validation processes based on statistical evidence (Dicke et al., 2007; Vinatier et al., 2009) which limits their usefulness.

In the present paper, we developed the first bioeconomic spatially explicit model. The model was parameterized for *Lolium rigidum* Gaudin. *L. rigidum* (annual ryegrass) is a winter annual grass considered to be among the most troublesome weeds of cereal crops in Mediterranean areas (Reeves, 1976; González-Andújar and Saavedra, 2003). Yield losses in cereal crops due to competition with ryegrass can reach up to 80% depending on season and infestation level (Medd et al., 1985; Izquierdo et al., 2003). The main control method of this species is herbicide application (Taberner, 1996; Izquierdo et al., 2003). However, the efficacy of this tactic is currently threatened by the evolution of herbicide-resistant populations (Heap, 2012). Farmers are not able to achieve successful control on such populations using herbicide alone, so the introduction of alternative techniques, integrating herbicide and non-herbicide tactics is required (Mortensen et al., 2000). In order to study the long-term behaviour of management scenarios some non-spatial ryegrass population models have been published (González-Andújar and Fernández-Quintanilla, 2004; Pannell et al., 2004; Mojardino et al., 2003).

In this context, the objectives of our work were to develop a bioeconomic spatially explicit model and to validate it using different statistical criteria. The model was used to compare management strategies integrating different chemical and non-chemical tactics to control *L. rigidum* in cereal crops. Finally, the most influential parameters in the model outcomes were identified through a sensitivity analysis.

II. 2. MATERIALS AND METHODS

II. 2. 1. THE BIOECONOMIC SPATIAL FRAMEWORK

The bioeconomic model was developed for *L. rigidum* growing in barley fields, as this weed is one of the most abundant in Spanish cereals (Saavedra et al., 1989; Romero et al., 2008; Cirujeda et al., 2011). The model was integrated by three sub-models, namely: population dynamics, weed-crop competition and field economic outcomes from specific management tactics imposed on the field.

II. 2. 1. 1. Population dynamic sub-model

The detailed structure of the model has been described elsewhere (Perry and González-Andújar, 1993; González-Andújar and Perry, 1995). Briefly, the sub-model used an annual time step and a two-dimensional grid of sites representing space. The space comprises an array of 100 × 100 hexagons (each hexagon represent an area of 0.87 m^2) of equal size with a distance of 1 m between the centre of adjacent cells, with absorbing edges (i.e., the weed plants growing in the cells located in the edge of the simulated landscape do not spread their seed beyond these limits, reallocating the produced seeds between the other surrounding cells). The size of the simulated arena was big enough in order to avoid edge effects (Wang et al., 2003).

The population of seeds at the start of generation t, denoted by $N_{l,t}[i, j]$, in the cell of row i and column j came from the seeds shed immediately preceding the current generation $(t - 1)$. Three age classes of seed (Recasens et al., 1997) were included in the model, $l = 1 \ldots 3$; one for each of the three preceding generations. Older surviving seeds were included in the final (third) age class, assuming that all seeds older than 3 years have equal biological characteristics as 3-year-old seeds. Age-specific seed mortality was modeled by specifying that only a proportion, s_l in age class l, of those seeds in the seed bank from the previous $(t - 1)$ generation survive into the current t generation. Dormancy was modeled by allowing a different proportion, g_l, of seeds to germinate for each age class, so the total seeds germinating in cell $[i, j]$ during generation t was

$$N_t[i,j] = \sum_{l=1}^{3} s_l g_l N_{l,t}[i,j] \tag{1}$$

We denote by $R_{l,t}[i, j]$ the final number of ungerminated seeds in age class l and cell $[i, j]$ at the end of generation t. Those seeds which survived ungerminated, named $R_{l,t}[i,j] = s_l(1-g_l)N_{l,t}[i,j]$, were carried over to the next (l) age-class; at the end of the next generation t, they moved into the next age class and were added to the newly shed seeds to form the initial seed population for generation $(t + 1)$. Only a proportion v from the germinated seeds developed into adult plants, S,

$$S_t[i,j] = vN_t[i,j] \tag{2}$$

As noted by previous authors (González-Andújar and Fernández-Quintanilla, 2004), reproduction is a density-dependent process. The total produced seeds, T, was given by,

$$T_t[i,j] = \frac{fS_t[i,j]}{1 + aS_t[i,j]} \tag{3}$$

The parameter f is the maximum number of seed produced by an individual plant and a represented within-cell, density-dependent competition, both intraspecific and interspecific. Additionally, we considered spatial heterogeneity (i.e., variability in the nitrogen availability) in the model by simulating a as a random variable with a normal distribution N(0.34, 0.027).

The normal distribution parameters were taken from the González-Andújar and Fernández-Quintanilla (2004).

The use of control measures (chemical and cultural) may result in the alteration of either one or several demographic parameters (Maxwell and O'Donovan, 2007). The control rates were simulated by imposing a reduction in the seedling survival, denoted by c_1 and c_2 (see Table 1), and/or the fecundity parameter f, denoted by c_3 and c_4 (seet Table 1), where $0 \leq c_x \leq 1$ for $x = 1, 2, 3, 4$. Eq. 3 was therefore modified to

$$T_t[i, j] = \frac{(1-c_1)(1-c_2)(1-c_3)(1-c_4)fS_t[i, j]}{1 + aS_t[i, j](1-c_1)(1-c_2)} \tag{4}$$

L. rigidum plants disperse seeds close to the parent plant (Blanco-Moreno, 2004; Rauschert et al., 2009). Dispersal was modelled following a negative exponential function (Eqs 5 and 6) (González-Andújar and Perry, 1995). Seeds were spread between the source cell and up to two surrounding neighbour cells, analogous to other grass weeds which disperse their seeds in similar ways (Barroso et al., 2006). The fraction of seeds falling in the source cell is expressed by (Perry and González-Andújar, 1993; González-Andújar and Perry, 1995; González-Andújar et al., 1999),

$$\frac{1-\exp(-d/2)}{1-\exp(-5d/2)} \tag{5}$$

Where d is the exponential probability distribution parameter.

The rest of seeds were dispersed among neighbouring cells in the first and the second ring around the source cell at distance of 1 and 2 m. We denote r the number of the ring in relation to the position around the source cell (1 or 2). Each ring is composed by $6r$ hexagonal cells receiving each one $1/6r$ of seeds. The dispersed seeds out from the source cell and for each ring ($r = 1, 2$) are given by

$$\frac{\exp[-(2r-1)d/2] - \exp[-(2r+1)d/2]}{1-\exp(-5d/2)} \tag{6}$$

The newly shed seeds in the generation t and cell $[i, j]$, denoted $R_{0,t}[i, j]$, and the seeds which survived ungerminated within the seed bank, $R_{l,t}[i, j]$ with $l = 0, \ldots, 3$, were a continuous-valued, decimal number, representing the expected local seed density, averaged over the several processes of seed mortality, germination, reproduction and dispersal. Perry and González-Andújar (1993) emphasized the need for a process of rounding to an integer as essential to prevent spurious artifacts in population modeling. We therefore adjust $R_{l,t}[i, j]$, $l = 0, ..., 3$, stochastically, to an integer, by adding to it an uniform random number between 0 and 1 and rounding the result down to the nearest integer (Perry and González-Andújar, 1993).

II. 2. 1. 2. Weed-Crop competition sub-model

Competition sub-model was based on the hyperbolic competition model (Cousens 1985),

$$Y_t[i,j] = Y_{0,t}[i,j]\left(1 - \frac{kS_t[i,j]}{1+(k/b)S_t[i,j]}\right) \tag{7}$$

The crop yield (kg/cell) in competition with weeds is denoted by Y, while Y_0 (kg/cell) is the potential crop yield. Y_0 varied spatially according to the spatial variability in nitrogen availability previously cited following a normal distribution $N(2400, 293)$. The normal distribution parameters were derived from a field experiment in Montana (Maxwell, personal communication) and adapted to Spanish barley yield (MAGRAMA, 2009). The parameter k is the slope of the yield reduction as weed density approaches zero, and b is the maximum proportional yield loss at high weed densities.

II. 2. 1. 3. Economic sub-model

The economic output was calculated according to the difference among profits and costs of the different management strategies (Dorr and Pannell, 1992). Net Return (NR, €/cell) calculated over annual period is given by,

$$NR_t[i,j] = Y_t[i,j]P - FC - HD - HA \tag{8}$$

Where P is the price of the crop in €/kg. The costs for herbicide and its application (€/cell) is given by HD and HA respectively. The fixed cost from other inputs was represented by FC (€/cell).

The net return over the long-term (n years) must be transformed in current currency for comparing results from different simulations (González-Andújar and Fernández-Quintanilla, 1993). The Annualized Net Return (ANR, €/cell) is given by the following expression where an annual discount factor h is applied

$$ANR[i,j] = \frac{h\sum_{t=1}^{n} NR_t[i,j](1+h)^{-t}}{1-(1+h)^{-t}} \tag{9}$$

II. 2. 1. 4. Model parameters and initial conditions

Model parameter values were obtained from different sources (Table 1). The average value was used as the default value to simulate the model under the management strategies and the maximum and minimum values of each parameter were used in the sensitivity analysis performed to the outputs of the model (see below).

The initial spatial distribution of *L. rigidum* seed bank used in the model was taken from a survey carried out in Catalonia (Spain) (Izquierdo et al., 2009). The arrayed data were interpolated according to the linear triangulation method (Gerhards et al., 1997; Dicke et al., 2007) to create an initial infestation map of 100 × 100 cells.

II. 2. 1. 5. Management strategies

Different management strategies based on individual control programs and integrated management programs were simulated (Table 2) (Taberner, 1996; González-Andújar and Fernández-Quintanilla, 2004; Barros et al., 2008; Cirujeda and Taberner, 2009).

II. 2. 2. SENSITIVITY ANALYSIS

In the model described previously almost all parameters were assumed to be constant. In practice most of these parameters vary from year to year and between different localities. In order to assess the sensitivity of the model to parameter variation, a sensitivity index was calculated (Pannell, 1997),

$$SI = D_{\max} - D_{\min} \tag{10}$$

Where $D_{\max}$ is the output (i.e., *L. rigidum* seed bank at equilibrium and ANR) when the parameter in question is set at its maximum value and $D_{\min}$ is the result for the minimum parameter value. A large SI indicates that a small variation in such parameter will result in a large modification in the model output. The range of values for parameters were established according to either the extreme values found in the literature or over the standard deviation observed from average experimental data. The maximum and minimum values used for the sensitivity analysis are shown in Table 1.

Table 1. Model parameter values for *L. rigidum* (mean, maximum and minimum values). Note that some parameters are expressed in hectare units instead of cell units.

MODEL PARAMETERS	**Mean**	**Max.**	**Min.**	**References**
Population dynamic sub-model				
Seed bank survival: s_l				
- Age class I	0.93	0.94	0.92	Chauhan et al. (2006)
- Age class II	0.26	0.35	0.20	González-Andújar and Fernández-Quintanilla (2004)
- Age class III	0.12	---	---	Recasens et al. (1997)
Seed bank germination : g_l				
- Age class I	0.64	0.80	0.34	Fernández-Quintanilla et al. (2000)
- Age class II	0.64	0.80	0.34	
- Age class III	0	---	---	
Seedling survival: v	0.76	0.95	0.17	Fernández-Quintanilla et al. (2000)
Fecundity (seeds/plant): f	935	1250	7	González-Andújar and Fernández-Quintanilla (2004) Fernández-Quintanilla et al (2000)
Parameter of the dispersal distribution: d	1.5	10	0.01	Barroso et al. (2006)
Seedling control in the crop rotation: c_1				
- Barley year	0	0	0	González-Andújar and Fernández-Quintanilla (2004)
- Fallow year	0.997	1	0.995	
Herbicide control: c_2 and c_3				
- Full rate				
· Direct effect: c_2	0.90	0.99	0.60	González-Andújar and Fernández-Quintanilla (2004)
· Residual effect: c_3	0.70	0.77	0.47	
- Half rate				Fernández-Quintanilla et al. (1998)
· Direct effect: c_2	0.80	0.92	0.44	Taberner (1996)
· Residual effect: c_3	0.40	0.46	0.22	
High seeding rate control: c_4	0.50	0.80	0	González-Andújar and Fernández-Quintanilla (2004) Lacasta et al. (2008) Gill and Holmes (1997)
Weed-crop competition sub-model				
Parameter k	0.0051	0.0083	0.0019	Izquierdo et al. (2003)
Parameter b	0.95	1	0.79	
Economic sub-model				
Barley price (€/kg): P	0.16	0.21	0.13	MAGRAMA (2009)
Fixed cost (€/ha): FC				
- Normal seeding rate	317	351	281	Lacasta and Meco (2006)
- High seeding rate	353	387	317	Aragon Agriculture Department (2009)
Herbicide spraying cost (€/ha): HA	8.4	8.86	7.98	Lacasta and Meco (2006) Aragon Agriculture Department (2009)
Herbicide cost (€/ha): HD	38	39	4	Barroso et al. (2009) Ruiz et al. (2006) Herbicide Supplier, personal communication
Annual discount factor: h	0.05			

Table 2. Management strategies simulated to control *L. rigidum* population.

MANAGEMENT STRATEGIES	Abbreviations
Without control	CON
Individual management programs	
Herbicide: full rate	FRH
Herbicide: half rate	HRH
Crop rotation: barley-fallow*	ROT
Higher seeding rate	HSR
Integrated management programs	
Herbicide (half rate) + higher seeding rate	IMP1
Crop rotation + higher seeding rate	IMP2
Crop rotation + herbicide (full rate)	IMP3
Crop rotation + herbicide (full rate) + higher seeding rate	IMP4
Crop rotation + herbicide (half rate)	IMP5
Crop rotation + herbicide (half rate) + higher seeding rate	IMP6
Herbicide (full rate) + higher seeding rate	IMP7

* Two-year rotation length. In each weed growing season only the barley or the fallow appears in the cell.

II. 2. 3. MODEL VALIDATION

The model predictions were tested against real and independent data from field observations of *L. rigidum* seedlings carried out in cereals fields in Northeast Spain (Blanco-Moreno et al., 2006). The detailed indication of the sampling procedure has been described by Blanco-Moreno et al. (2006). Briefly, the sampling consisted in four nearby plots (named hear Plot_01, Plot_02, Plot_03 and Plot_04) of 100 m^2 each one whereby *L. rigidum* seedlings were counted over three years (2001, 2002 and 2003) before herbicide application in a grid of 21 rows × 21 columns where the unit cell was 0.5 × 0.5 m^2. Data were aggregated and extended in order to define an area of 10 rows × 10 columns, similar to the simulated area. The herbicide application at full rate was carried out only in 2002 and it was not efficient controlling the *L. rigidum* populations in all plots (a herbicide control rates of $c_2 = 0.44$ and $c_3 = 0.22$ were used in the model validation).

We followed several approaches to validate the model:

1) We compared the observed vs. simulated data via linear regression (Piñeiro et al., 2008; Mesplé et al., 1996). This relation was tested by the determination coefficient r^2, line 1:1 and intercept = 0. To complete this analysis other authors suggested methods focused on quantifying the errors of different sources in the unexplained variance (Wallach and Goffinet, 1989; Smith and Rose, 1995; Mesplé et al., 1996; Piñeiro et al., 2008). We chose the Root Mean Squared Deviation (RMSD) proposed by Piñeiro et al. (2008) and calculated the Theil's

coefficients (U) (Paruelo et al., 1998), when applicable. The latter method separates the total error of predictions in different components: U_{bias} (associated to mean differences between observed and predicted values), U_{slope} (associated to mean differences between the slope of fixed model and the line 1:1) and U_{error} (associated to unexplained variance).

2) To compare the predicted growth rates to those which have been observed in the field, we used a Kolmogorov-Smirnov's test (Vinatier et al., 2009).

3) Spatial distribution of residuals were also calculated and represented by graphs. As the errors approach normal distribution with a mean equal to zero, the predictions are less biased (Aguilar et al., 2005). Besides, the errors must be distributed at random around the space without a clear spatial pattern and avoiding spatial autocorrelation.

II. 3. RESULTS

II. 3. 1. MODEL VALIDATION

Initial weed infestations in the four observed plots were spatially homogeneous showing a mean around of 90-400 seeds/cell. Some data belonging to Plot_01 and Plot_03 were not considered in the validation because their values were far lower than the average and they behaved as outliers in the analysis.

The observed vs. predicted growth rates for each cell within each plot were fitted to a regression model in all cases (Fig. 1). The r^2 of the models ranged over 0.75-0.89. This showed that a high linear variation of the observed values was explained by the variation of the predicted values and a high proportion of observed variance was explained by the regression model.

Comparisons between the parameters of the regression lines fitted to the data and the hypothesis of slope = 1 and y-intercept = 0 were only fulfilled for Plot_02 (Table 3). In this case the predicted data were consistent with the observations and the disagreement between them was due to the unexplained variance (Table 3) as seen in the high percentage of U_{error}. The RMSD between simulated and predicted values for Plot_02 was 0.33.

The regression lines fixed in Plot_01, Plot_03 and Plot_04, had parameters that were significantly different to the hypothetical ones (Table 3). Therefore, the growth rates observed in such plots were not consistent with those predicted in the model. In Plot_03 and Plot_04 the model underestimated the observed growth rates for almost the entire range of values (Fig. 1).

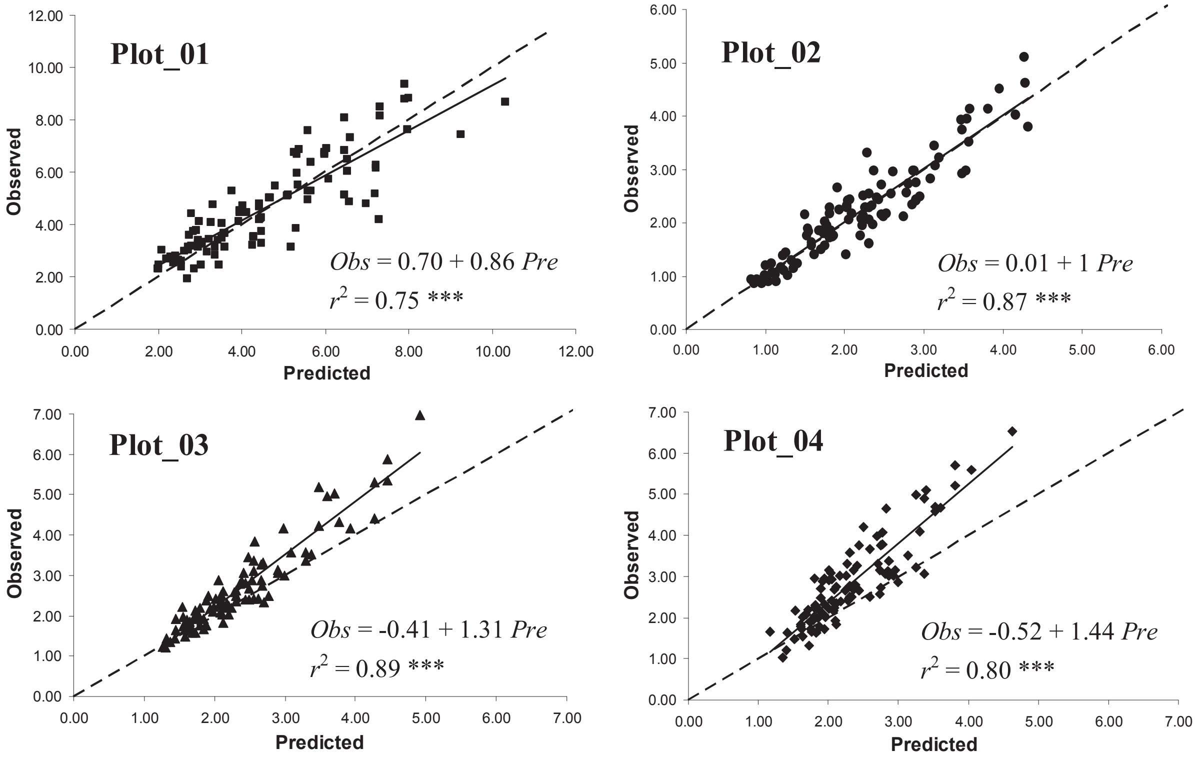

Figure 1. Observed vs. predicted grow rates for each plot. The solid line is the regression line best fitted to data set and dotted line is the line 1:1. Where *Obs* is the observed growth rate in the field and *Pre* is the predicted growth rate by the model.

Table 3. Parameters of the regression lines and their significance for the all four plots studied (Plot_01, Plot_02, Plot_03, Plot_04). The Theil's coefficients (U_{bias}, U_{slope} y U_{error}) and RMSD were calculated when applicable.

	Plot_01	Plot_02	Plot_03	Plot_04
Slope^{a}	0.86^{**}	1^{NS}	1.31^{***}	1.44^{***}
Intercept^{a}	0.73^{**}	0.01^{NS}	-0.41^{**}	-0.52^{**}
U_{bias} (%)		0.002		
U_{slope} (%)		0		
U_{error} (%)		0.998		
RMSD^{b}		0.330		

^{a} ^{NS} $p \geq 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

^{b} RMSD: Root Mean Squared Deviation.

In all plots the observed and predicted distributions of the population growth rates showed no significant difference according to the Kolmogorov-Smirnov test.

The spatial distribution of the residuals presented means close to zero in the first two plots (Plot_01 and Plot_02), but only in the Plot_02 the residuals followed a normal distribution (results not shown). The Plot_01 showed a residual distribution without a clear random pattern (Fig. 2) and the residual distribution in Plot_02 was concentrated around zero but this value was increased at either end of the plot (Fig. 2). The Plot_03 and Plot_04 both showed positive residuals in most of the points resulting in predictions that underestimated the observed data in the field (Fig. 2).

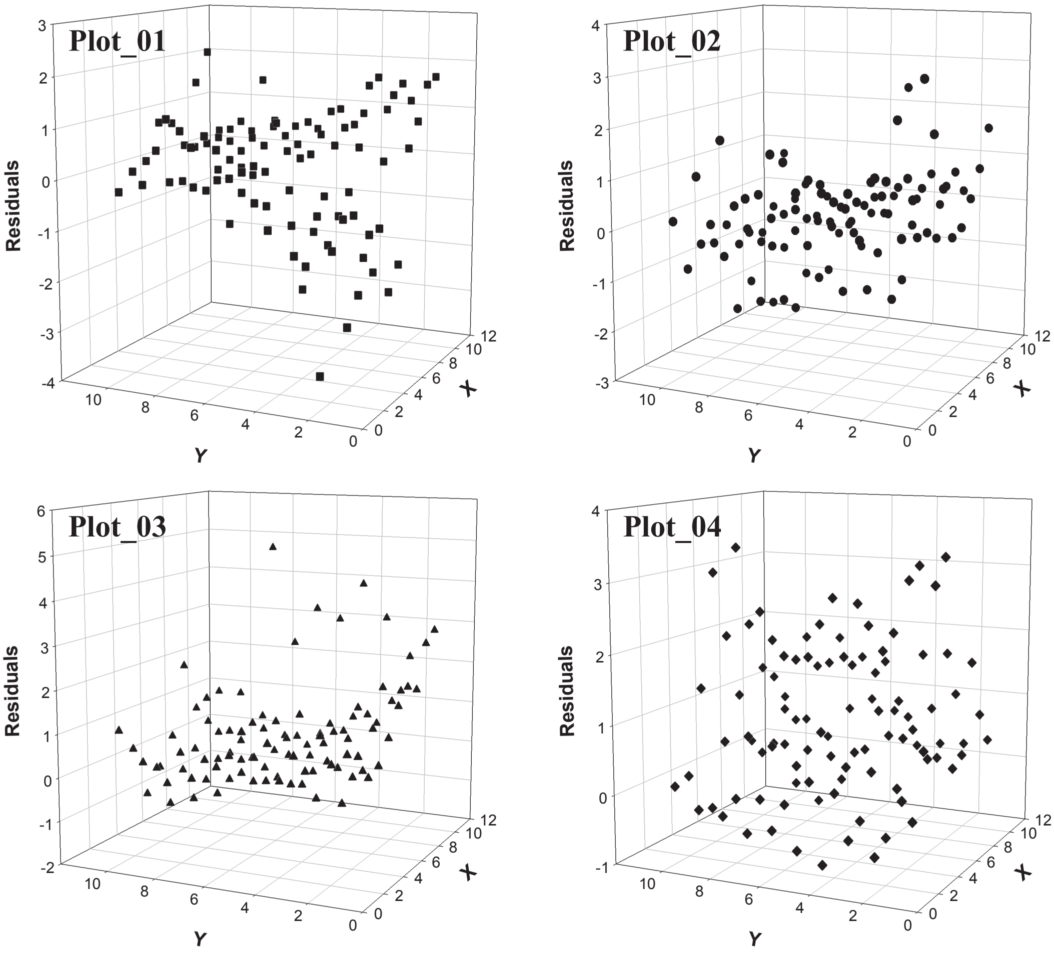

Figure 2. Residual spatial distributions for each plot (Plot_01, Plot_02, Plot_03 and Plot_04).

II. 3. 2. MANAGEMENT STRATEGIES

The simulated management strategies showed different ranking based on the outcomes for each established sub-model (Table 4).

II. 3. 2. 1. *Lolium rigidum* seed bank density

In absence of control measures, *L. rigidum* seed bank is projected to rise from 732 seeds/cell to an equilibrium population of 3758 seeds/cell in three years (Table 4). This high density of ryegrass in association with barley can be considered to be the carrying capacity of the system under the specified set of conditions. As could be expected, the management strategies reduced the equilibrium density between 12% (rotation barley-fallow) and 87% (strategy IMP7) (Table 4).

Table 4. *L. rigidum* seed bank at equilibrium, barley yield and annualized net return for the management strategies evaluated.

MANAGEMENT STRATEGIES	***L. rigidum* seed bank (Seeds/cell year)**	**Barley yield* (kg/ha year)**	**Annualized net return* (€/ha)**
Without control	3758	397	-524
Individual management programs			
Herbicide: full rate	1048	2015	-72
Herbicide: half rate	2218	1349	-225
Crop rotation			
- Barley	3324	560	-262
- Fallow	2448	0	
High seeding rate	1875	614	-563
***Integrated management programs*†**			
IMP1	1089	1725	-222
IMP2			
- Barley	1754	725	-305
- Fallow	1512	0	
IMP3			
- Barley	1014	2047	-49
- Fallow	962	0	
IMP4			
- Barley	492	2194	-96
- Fallow	505	0	
IMP5			
- Barley	2038	1531	-96
- Fallow	1701	0	
IMP6			
- Barley	1055	1775	-131
- Fallow	995	0	
IMP7	483	2204	-123

* Notice that the outcomes are given in hectare units instead of cell units.

† IMP1 (Herbicide at half rate + higher seeding rate, IMP2 (Barley-fallow rotation + higher seeding rate), IMP3 (Barley-fallow rotation + herbicide at full rate), IMP4 (Barley-fallow rotation + herbicide at full rate + higher seeding rate), IMP5 (Barley-fallow rotation + herbicide at half rate), IMP6 (Barley-fallow rotation + herbicide at half rate + higher seeding rate), IMP7 (Herbicide at full rate + higher seeding rate).

In general, individual management programs produced higher *L. rigidum* densities than integrated management programs. None of the individual management programs decreased the initial ryegrass density (732 seeds/cell). The best control was achieved with herbicide applications at full-rate dose, although the initial density had a large increase (1048 seeds/cell or 50 seedlings/cell) when stability was reached. These values were close to those found by Taberner (1996) in which 40 seedlings/m^2 were reached in ryegrass populations treated with herbicide at full rate. The barley-fallow rotation was the poorest strategy controlling weed density (Table 4).

Within the integrated management programs, IMP7 (higher seeding rate + full rate dose of herbicide) and IMP4 (barley-fallow rotation + higher seeding rate + full rate dose of herbicide) showed the best control of ryegrass populations (Table 4). These strategies reduced the initial weed density although those are still too high to guarantee an adequate control of *L. rigidum* in following years.

The IMP3 (full rate herbicide + barley-fallow rotation), IMP6 (half rate herbicide + barley-fallow rotation + high seeding rate) and IMP1 (half rate herbicide + high seeding rate) increased the initial weed population at the end of the long-term period (Table 4). Finally, the integrated control programs that caused the strongest increase in ryegrass density were IMP2 (barley-fallow rotation + high seeding rate) and IMP5 (full rate herbicide + barley-fallow rotation) (Table 4).

II. 3. 2. 2. Crop yield

Non control produced a strong yield reduction around 83% compared to the average barley yield in Spain of 2400 kg/ha (Table 1) as a consequence of the high ryegrass infestation (Table 4). In general, individual management strategies produced lower barley yields than integrated management programs. The application of full-rate doses of herbicide obtained better barley yield than all other individual management strategies simulated and even than some integrated management programs (Table 4).

As expected, the highest yields predicted within the integrated management programs were for IMP7 and IMP4 (Table 4). These predicted yields were, in average, 8% lower than the potential yield. The integrated management program achieving the poorest performance was IMP2, with 70% of reduction compared to the potential yield.

II. 3. 2. 3. Annualized net return

The annualized net returns were negative in all cases. Integrated management programs produced the best economic results. The highest annualized net return was obtained with strategy IMP3 (Table 4).

Again, cultural control methods (higher seeding rate, crop rotation and IMP2) appeared to be the least suitable, incurring the highest economic losses (-563 €/ha, -262 €/ha and -305 €/ha, respectively) due to low grain yields obtained with these techniques. Economic losses were reduced with herbicide application at low doses and IMP1 (half rate herbicide + higher seeding rate), although those remained being high (Table 4). Improved results were achieved when reduced doses of herbicide were associated with crop rotation and higher plant density (IMP6) reaching losses around -131 €/ha. Similar results were achieved with IMP6 and IMP7 (application of herbicide at full dose + higher plant density) because barley yields were close to the potential in such cases (Table 4). The four strategies that were economically the most efficient in decreasing order were: IMP3, full-dose herbicide, IMP5 and IMP4.

II. 3. 3. SENSITIVITY ANALYSIS

The sensitivity analysis was carried out for all parameters involved into the model, considering all management strategies and demographic and economical outputs (Table 5). The seed bank was sensitive to changes in fecundity for HRH, ROT, IMP5 and IMP7 and to the weed control exerted by FRH, HSR, IMP1-IMP4 and IMP6 programs, followed by germination or weed seedling survival in most of the cases. In general, the parameter with least influence on the model was seed dispersal (Table 5).

Annualized net returns presented different sensitivity to the changes in the model parameters depending on the management strategies analized (Table 5). ANR was especially sensitive to changes in barley price and in the weed control exerted by FRH, HRH, IMP1 and IMP3-IMP7 programs (Table 5). The demographic parameters (i.e., seedling survival and fecundity) were the most important in the remaining management strategies: ROT, HSR and IMP2. Fecundity was the most influential parameter in the scenario CON. For all strategies, the least influential parameter in ANR was dispersal (Table 5).

II. 4. DISCUSSION

We have partiality validated the model with a variety of techniques that integrated different spatial aspects of the weed population growth and with a simulated average density of weed plants per plot that were in agreement with the real ones (outputs not shown). Our spatially explicit model was able to accurately predict the observed growth rates in one (Plot_02) of the four experimental sites analyzed with all validation methods proposed. The predicted population growth rate distributions in Plot_01, Plot_03 and Plot_04 showed good agreement with the observed data. In Plot_01, the residuals showed bias leading to a general underestimation of the observed growth rates but with some overestimations in other parts of the plot. Larger underestimations of the observed growth rates were achieved in the Plot_03 and Plot_04. These underestimations might occur as the result of a decreased herbicide activity in these plots, whereby ryegrass populations may have increased instead of having decreased despite of the herbicide application. In Plot_04, the low growth rate reached in the first year

Table 5. Sensitivity analysis for model parameters using SI for both demographic (*L. rigidum* seed bank at equilibrium in barley) and economic (ANR) outputs in each management strategy.

MODEL PARAMETERS	MANAGEMENT STRATEGIES*											
	CON	**FRH**	**HRH**	**ROT**	**HSR**	**IMP1**	**IMP2**	**IMP3**	**IMP4**	**IMP5**	**IMP6**	**IMP7**
Seed bank survival, s												
- Seed bank	78	27	49	79	39	25	50	43	30	60	39	16
- ANR (€/ha)	-16	-10	-16	-17	-18	-14	-17	-7	-6	-13	-12	-7
Seed bank germination, g												
- Seed bank	-1458	-318	-821	-605	-723	-380	-313	-19	80	-301	-109	-98
- ANR (€/ha)	-131	-82	-154	-114	-162	-127	-133	-53	-41	-94	-86	-55
Seedling survival, v												
- Seed bank	30	302	151	42	30	151	34	288	259	172	-43	300
- ANR (€/ha)	-303	-132	-281	-209	-361	-216	**-219**	-64	-49	-128	-104	-86
Dispersal parameter, d												
- Seed bank	60	18	36	57	24	18	31	21	12	37	21	9
- ANR (€/ha)	-1	-1	-1	-1	-1	-1	-1	-1	0	-1	-1	-1
Fecundity, f												
- Seed bank	**5007**	1428	**2980**	**4539**	2503	1470	2441	1476	754	**2840**	1511	**673**
- ANR (€/ha)	**-546**	-130	-331	**-222**	**-509**	-223	-210	-57	-36	-124	-96	-70
Parameter i												
- ANR (€/ha)	-237	-138	-266	-180	-294	-220	-192	-70	-54	-130	-115	-90

Note: The most sensitive outputs are in bold for each management strategy.

* CON (without control), FRH (herbicide at full rate), HRH (herbicide at half rate), ROT (barley-fallow rotation), HSR (higher seeding rate), IMP1 (Herbicide at half rate + higher seeding rate, IMP2 (Barley-fallow rotation + higher seeding rate), IMP3 (Barley-fallow rotation + herbicide at full rate), IMP4 (Barley-fallow rotation + herbicide at full rate + higher seeding rate), IMP5 (Barley-fallow rotation + herbicide at half rate), IMP6 (Barley-fallow rotation + herbicide at half rate + higher seeding rate), IMP7 (Herbicide at full rate + higher seeding rate).

Table 5. Continued

MODEL PARAMETERS	MANAGEMENT STRATEGIES*											
	CON	**FRH**	**HRH**	**ROT**	**HSR**	**IMP1**	**IMP2**	**IMP3**	**IMP4**	**IMP5**	**IMP6**	**IMP7**
Parameter b												
- ANR (€/ha)	-126	-5	-32	-53	-104	-15	-47	-2	-1	-10	-6	-2
Barley price, P												
- ANR (€/ha)	175	**466**	363	151	207	415	160	**297**	**305**	257	**271**	**491**
Fixed cost, FC												
- ANR (€/ha)	-193	-193	-193	-120	-193	-193	-120	-120	-120	-120	-120	-193
Herbicide cost, $HD + HA$												
- ANR (€/ha)		-99	-52			-52		-61	-61	-32	-32	-99
Control parameter, c												
- Seed bank		**-1879**	-992	-716	**-3013**	**-1896**	**-2985**	**-2010**	**-1453**	-2137	**-2800**	-449
- ANR (€/ha)		457	**427**	120	187	**483**	191	236	205	**265**	269	244

Note: The most sensitive outputs are in bold for each management strategy.

* CON (without control), FRH (herbicide at full rate), HRH (herbicide at half rate), ROT (barley-fallow rotation), HSR (higher seeding rate), IMP1 (Herbicide at half rate + higher seeding rate, IMP2 (Barley-fallow rotation + higher seeding rate), IMP3 (Barley-fallow rotation + herbicide at full rate), IMP4 (Barley-fallow rotation + herbicide at full rate + higher seeding rate), IMP5 (Barley-fallow rotation + herbicide at half rate), IMP6 (Barley-fallow rotation + herbicide at half rate + higher seeding rate), IMP7 (Herbicide at full rate + higher seeding rate).

under real conditions and the subsequent increase in the following year under herbicide application, was contrary to the simulated results whereby the population grew up quickly in the first year.

The differences in the observed weed population behaviour between plots could be explained by the presence of other weeds as *Avena sterilis* L. (Blanco-Moreno et al., 2006) and/or the spatial heterogeneity among plots. The first could produce a reduction in the ryegrass growth rate in the first year by *L. rigidum-A. sterilis* competition and a large increase in the growth rate in the next year due to the low herbicide control. The low herbicide efficacy in *L. rigidum* control as cited by Blanco-Moreno et al. (2006) may be due to the presence of herbicide-resistant populations and adverse environmental conditions that reduced the herbicide activity. However, in Plot_02 there was a decrease in the weed population as a result of the herbicide application, so the model responded better in this location than in others. The spatial heterogeneity within each plot was not taken into account because of the small size of the plots (100 m^2), however, this heterogeneity might be significant among plots which were located at greater distances. This spatial variability might influence on the weed growth responses and explain the heterogeneity of observed results found among plots. Audsley (1993) pointed out that the herbicide effectiveness can vary spatially as consequence of non-uniform herbicide application or different soil types causing spatial heterogeneity in the outcomes. Colbach and Debaeke (1998) cited weed genotypes and phenotypes as possible causes of spatial variability that can generate a heterogeneous herbicide efficacy. These factors could explain the difference of herbicide's effect among all four plots analyzed.

In field conditions, Taberner (1996) and Izquierdo et al. (2003) reported populations of *L. rigidum* around 2000 and 4400 seeds/m^2, respectively, being close to those predicted by our model. Our attempts to reduce this potential weed density were approached through long-term management scenarios, but the residual weed populations still remained high in the field. This fact agrees with the observations noted by González-Andújar and Fernández-Quintanilla (2004) in a non-spatial modelling exercise and Cirujeda and Taberner (2009) in field experiments whereby *L. rigidum* populations were decreased in some trials but the weed densities were still high at field under individual and mixed cultural control methods. We analyzed eleven management strategies under three different sub-models to account for different aspects in the strategy behavior such as effectiveness and profitability. Strategy ranking in decreasing order of suitability for each sub-model output gave slight differences between them. For example, IMP7 was the best strategy decreasing the weed populations and the crop production losses, however, there were four strategies with better economic outputs (i.e., IMP3, IMP4, IMP5 and herbicide application at full rate) than IMP7. As cited by van den

Berg et al. (2010) the incorporation of economic analysis is crucial to test viable economic strategies and optimize the weed management programs.

In our model, the herbicide application was the only individual strategy that did not produce a severe decrease in cereal yields and got better economic returns, even better than most integrated management approaches. This fact was put into relevance by Pannell et al. (2004) who found that the cost of herbicide-based management systems was substantially lower than those based on other alternative weed control strategies. In general, the model highlights the non-profitability of the simulated strategies in the *L. rigidum* control and it was reflected in the negative economic outcomes shown in all cases. However, the control of *L. rigidum* populations is deemed more profitable than not doing so. Lacasta and Meco (2001) concluded that dryland barley monoculture in Spain presented economical negative margins and must be economically supported by the subvention from the government. The low potential yield of dry cereals mainly in the South and Central Spain and their low prices make them very sensitive to the presence of weeds and the use of control techniques that involve a high cost.

Long-term strategies that used a combination of chemical and cultural control methods reduced the ryegrass populations more than those based on only cultural methods (ROT, HSR, IMP2; Table 2). This has also been shown in the models developed by other authors (Blanco-Moreno, 2004; González-Andújar and Fernández-Quintanilla, 2004). Cultural strategies are often less effective, and even more imprecise and expensive than chemical strategies and they may not reduce the requirement of herbicide applications (Moss, 2008). This is the case for the HSR strategy which showed a significant decrease in the expected economic returns and it had a doubtful efficiency in weed control and crop yield as revealed by some authors (Izquierdo et al., 2003; Cirujeda and Taberner, 2009). The necessity of chemical control has been highlighted in our model simulations as it was pointed out by Lacasta et al. (2008) in some studies conducted in Spain in areas of cereal monoculture.

The integrated management programs using herbicide applications at full doses (IMP3, IMP4, IMP7) achieved better weed control and better crop yields than others such management strategies using low-dose herbicide applications (HRH, IMP5, IMP6). Control tactics based on herbicide applications at low rate did not produce a successful weed control resulting in significant decreases in cereal yield and generally in great economic losses. Some authors working with *L. rigidum* (Barros et al., 2008) found this control method a useful mechanism to reduce herbicide doses with a satisfactory level of weed control. In the same way, other models about *L. rigidum* propose an integrated strategy including low herbicide doses to control ryegrass populations (González-Andújar and Fernández-Quintanilla, 2004), although they had not considered an economic analysis of their outputs. Although this strategy, therefore, seems preferable to the herbicide at full doses from an environmental point of view, the associated likelihood of increasing the seed bank in the long term and the evolution of herbicide resistance in *L. rigidum* populations (Neve and Powles, 2005) should be taken into account.

L. rigidum seed bank was particularly sensitive to fecundity and the control exerted by the strategies and fecundity influenced more on the net economic returns in CON and cultural control strategies (HSR mainly) than in others. Previous modelling studies on *L. rigidum* showed similar results (González-Andújar and Fernández-Quintanilla, 2004; Blanco-Moreno, 2004). Fecundity will be one of the most important regulating the *L. rigidum* popultion and therefore, control strategies focused on reducing this factor are desirable. Besides, greater efforts are recommended to get accurate approaches of the control exerted by the strategies and their probability distributions in order to include this stochasticity in the model. The cultural control strategies also were especially sensitive to the germination fraction. Increasing rates of mortality in this parameter can achieve more successful cultural control strategies.

Other strategies including herbicide control showed annualized net returns most sensitive to the level of weed control exerted by the strategy and the cereal price. This is the case for the strategies involving herbicide applications at low doses. Adverse weather conditions during and after the herbicide application timing decrease the control rates achieved (Fernández-Quintanilla, 1999). These decreases in the herbicide efficacy will be more pronounced when low doses of herbicide are applied. When full doses of herbicide are taken into account, cereal price is the main factor influencing on ANR outputs. Cereal price will limit in many cases the amount of inputs to be applied in the crop. As cereals have a low sale price it will justify that farmers do not use control methods that increase their costs, such as herbicide applications. No herbicide application is usual in some Spanish regions with low cereal yield (Saavedra et al., 1989).

Weed seed dispersal had little effect on the outputs for all sub-models and all management strategies simulated. The importance of the dispersal process was masked by the high growth rate of each particular cell. Initial conditions are really important in the outcomes of the long-term management strategies and they should be taken into account to achieve better economic and ecological knowledge (Wang et al., 2003). In our model real initial densities of infestation were chosen as well as spatial heterogeneity in some processes (i.e., potential crop yield and weed seed production) according to nitrogen availability in field experiments. However, the model did not show a spatial variability in the results and consequently a little effect ought to seed dispersal fractions. This may be due to the initial distribution of *L. rigidum* seed bank that was spatially homogenous over the field and the lack of spatial stochasticity in other factors which are influential in the model response, e.g., potential fecundity, seedling survival and control rate exerted by the management strategies. On other hand, the temporal heterogeneity in the parameter values influences the weed cycle and it was ignored in the model simulations. Temporal heterogeneity might influence on the effectiveness of control measures implemented (Audsley, 1993) and on the weed growth rate (Auld and Coote, 1990). Both spatial and temporal heterogeneity in the parameter values should be incorporated into future modeling processes to achieve better results under more realistic situations in the context of spatially explicit models.

Given the negative economic returns coming from the developed spatial model it was evident the need for changes in the management of dry Spanish cereal (with low potential yield) which lead to increase their profitability. These tactics should involve measures with a low economic and environmental cost. Besides, the integrated management programs above do not consider other practices that can be implemented such as the possibility to use crop rotations with longer cropping sequences (González-Díaz et al., 2012) and/or cultivars more competitive against *L. rigidum* (Lemerle et al., 1995; Izquierdo et al., 2003). Lacasta and Meco (2001) proposed the cereal production under organic farming with diversified crops to achieve an increase in farmer profits.

In our simulations, herbicide applications seem to be necessary to control *L. rigidum* populations in dry cereal crops. But the integration of this control method with various cultural control techniques is more desirable from the viewpoint of weed control and evolution of herbicide-resistant populations.

II. 5. REFERENCES

Aguilar, F. J.; Agüera, F.; Aguilar, M. A.; Carvajal, F. (2005) Effects of terrain morphology, sampling density, and interpolation methods on grid DEM accuracy. Photogrammetric engineering and remote sensing 71, 805-816.

Aragon Agriculture Department (2009) Coyuntura agraria de Aragón. Secretaría general técnica. Servicio de planificación y análisis. Gobierno de Aragón, Spain.

Audsley, E. (1993) Operational research analysis of patch spraying. Crop Protection 12, 111-119.

Auld, B. A.; Coote, B. G (1990) INVADE: towards the simulation of plant spread. Agriculture, Ecosystems and Environment 30, 121-128.

Barros, J. F. C.; Basch, G.; Carvalho, M. (2008) Effect of reduced doses of a post-emergence graminicide to control *Avena sterilis* L. and *Lolium rigium* G. in no-till wheat under Mediterranean environment. Crop Protection 27, 1031-1037.

Barroso, J.; Navarrete, L.; Sanchez del Arco, M. J.; Fernández-Quintanilla, C.; Lutman, P. J. W.; Perry, N. H.; Hull, R. I. (2006) Dispersal of *Avena fatua* and *Avena sterilis* patches by natural dissemination, soil tillage and combine harvesters. Weed Research 46, 118-128.

Barroso, J.; Ruiz, D.; Escribano, C.; Barrios, L.; Fernández-Quintanilla, C. (2009) Comparison of three chemical control strategies for *Avena sterilis* ssp. *ludoviciana*. Crop Protection 28, 393-400.

Blanco-Moreno, J. M. (2004) Effects of dispersal and competition with *Avena sterilis* L. on the spatial structure and dynamics of *Lolium rigidum* Gaudin in dryland cereal fields. Ph.D. Thesis. Universitat de Barcelona, Spain.

Blanco-Moreno, J. M.; Chamorro, L.; Sans, F. X. (2006) Spatial and temporal patterns of *Lolium rigidum-Avena sterilis* mixed populations in a cereal field. Weed Research 46, 207-218.

Chauhan, B. S.; Gill G.; Preston, C. (2006) Influence of environmental factors on seed germination and seedling emergence of rigid ryegrass (*Lolium rigidum*). Weed Science 54, 1004-1012.

Cirujeda, A.; Aibar, J.; Zaragoza, C. (2011) Remarkable changes of weed species in Spanish cereal fields from 1976 to 2007. Agronomy for Sustainable Development 31, 675-688.

Cirujeda, A.; Taberner, A. (2009) Cultural control of herbicide-resistant *Lolium rigidum* Gaud. populations in winter cereal in Northeastern Spain. Spanish Journal of Agricultural Research 7, 146-154.

Colbach, N.; Debaeke, P. (1998) Integrating crop management and crop rotation effects into models of weed population dynamics: a review. Weed Science 46, 717-718.

Cousens, R. (1985) A simple model relating yield loss to weed density. Annals of Applied Biology 107, 239-252.

Cousens, R.; Dytham, C.; Law, R. (2008) Propagule dispersal and the spatial dynamics of populations and communities. In: Dispersal in plants: a population perspective, pp. 135-156. Oxford University Press, UK.

Dicke, D.; Gerhards, R.; Büchse, A.; Hurle, K. (2007) Modeling spatial and temporal dynamics of *Chenopodium album* L. under the influence of site-specific weed control. Crop Protection 26, 206-211.

Dorr, G. J.; Pannell, D. J. (1992) Economics of improved spatial distribution of herbicide for weed control in crops. Crop Protection 11, 385-391.

Doyle, C. J.; Cousens, R.; Moss, S. R. (1986) A model of the economics of controlling *Alopecurus myosuroides* Huds. in winter wheat. Crop Protection 5, 143–150.

Fernández-Quintanilla, C. (1999). Buenas prácticas agrícolas para el control de malas hierbas en cereales de invierno. In: Control integrado de las malas hierbas "Buenas prácticas agrícolas" (Eds. Fernández-Quintanilla, C.; Garrido Valero, M. and Zaragoza Larios, C.) pp. 93-102. PHYTOMA-España y Sociedad Española de Malherbología, Spain.

Fernández-Quintanilla, C.; Barroso, J.; Recasens, J.; Sans, X.; Torner, C.; Sánchez del Arco, M. J. (2000) Demography of *Lolium rigidum* in winter barley crops: analysis of recruitment, survival and reproduction. Weed Researh 40, 281-291.

Fernández-Quintanilla, C.; González-Andújar, J. L.; González-Ponce, R.; de Lucas, C.; Navarrete, L.; Recasens, J.; Sánchez del Arco, M. J.; Taberner, A.; Tiebas, M. A.; Torner, C. (1998). Using the low rate concept (LRC) for control of grassweeds in cereals under Mediterranean conditions. Proceedings of the 6th EWRS Mediterranean Symposium, 353-359. Montpellier, France.

Gerhards, R.; Wyse-Pester, D. Y.; Mortensen, D. A.; Johnson, G. A. (1997) Characterizing spatial stability of weed populations using interpolated maps. Weed Science 45, 108-119.

Ghersa, C. M.; Roush, M. L. (1993). Searching for solutions to weed problems. BioScience 43,104-109.

Gill, G. S.; Holmes, J. E. (1997) Efficacy of cultural control methods for combating herbicide-resistant *Lolium rigidum*. Pesticide Science 51, 352-358.

González-Andújar, J. L.; Fernández-Quintanilla, C. (1993) Strategies for the control of *Avena sterilis* in winter wheat production systems in central Spain. Crop Protection 12, 617-623.

González-Andújar, J. L.; Fernández-Quintanilla, C. (2004) Modelling the population dynamics of annual ryegrass (*Lolium rigidum*) under various weed management systems. Crop Protection 23, 723–729.

González-Andújar, J. L.; Fernández-Quintanilla, C.; Bastida, F.; Calvo, R.; Izquierdo, J.; Lezaun, J. A. (2011) Assessment of a decision support system for chemicals control of annual ryegrass (*Lolium rigidum*) in winter cereals. Weed Research 51, 304-309.

González-Andújar, J. L.; Perry, J. N. (1995) Models for the herbicidal control of the seed bank of *Avena sterilis*: the effects of spatial and temporal heterogeneity and of dispersal. Journal of Applied Ecology 32, 578-587.

González-Andújar, J. L.; Perry, J. N.; Moss, S. R. (1999) Modelling effects of spatial patterns on the seed bank dynamics of *Alopecurus myosuroides*. Weed Science 47, 697-705.

González-Andújar, J. L.; Saavedra, M. (2003) Spatial distribution of annual grass weed populations in winter cereals. Crop Protection 22, 629-633.

González-Díaz, L.; van den Berg, F.; van den Bosch, F.; González-Andújar, J. L. (2012) Controlling annual weeds in cereals by deploying crop rotation at the landscape scale: *Avena sterilis* as an example. Ecological Applications 22, 982-992.

Heap, I. (2012) The International Survey of herbicide resistant weeds. http://www.weeddscience.com. Accessed: 05/05/2012.

Holst, N.; Ramussen, I. A.; Bastiaans, L. (2007) Field weed population dynamics: a review of model approaches and applications. Weed Researh 47, 1-14.

Izquierdo, J.; Fernández-Quintanilla, C. (2010) Spatial variability of the competitive effect of barley (*Hordeum vulgare* L.) on *Lolium rigidum*. Agrociencia 44, 43-55.

Izquierdo, J.; Recasens, J.; Fernández-Quintanilla, C.; Gill, G. (2003) Effects of crop and weed densities on the interactions between barley and *Lolium rigidum* in several Mediterranean locations. Agronomy for Sustainable Development 23, 529-536.

Izquierdo, J.; Blanco-Moreno, J. M.; Chamorro, L.; González-Andújar, J. L.; Sans, F. X. (2009) Spatial distribution of weed diversity within a cereal field. Agronomy for Sustainable Development 29, 491-496.

Lacasta, C.; Estalrich, E.; Meco, R.; Benítez, M. (2008) Interacción de densidades de siembra de cebada y rotaciones de cultivo sobre el control de la flora arvense y el rendimiento del cultivo. Tierras de Castilla y León-Agricultura 145, 104-109.

Lacasta, C.; Meco, R. (2001) La cerealicultura ecológica es más rentable. Estudio energético y económico. La Fertilidad de la Tierra 3, 23-28.

Lacasta, C.; Meco, R. (2006) Agricultura ecológica: una alternativa económica y energética para los agrosistemas de cereal en el secano español. Tierras de Castilla y León-Agricultura 128, 86-99.

Lemerle, D.; Verbeek, B.; Coombes, N. (1995) Losses in grain yield of winter crops from *Lolium rigidum* competition depend on crop species, cultivars and season. Weed Research 35, 503-509.

MAGRAMA (2009) Ministry of Agriculture, Food and Environment, Spain. http://www.magrama.gob.es. Accessed: 10/04/2010.

Maxwell, B. D. (1992) Weed thresholds: the space components and considerations for herbicide resistance evolution. Weed Technology 6, 205-212.

Maxwell. B. D.; O'Donovan, J. T. (2007) Understanding weed-crop interactions to manage weed problems. In: Non-chemical weed management (Eds. Upadhyaya, M. K. and Blackshaw, R. E.) pp. 17-33. CAB International Cambridge, M. A., USA.

Medd, R. W.; Auld, B. A.; Kemp, D. R.; Murison, R. D. (1985) The influence of wheat density and spatial arrangement on annual ryegrass, *Lolium rigidum* Gaudin, competition. Australian Journal of Agricultural Research 36, 361-37.

Mesplé, F.; Troussellier, M.; Casellas, C.; Legender, P. (1996) Evaluation of simple statistical criteria to qualify a simulation. Ecological Modelling 88, 9-18.

Mojardino, M.; Pannell, D. J.; Powles, S. B. (2003). A multi-species bio-economic model for integrated weed management. Weed Science 51, 798-809.

Mortensen, D. A.; Bastiaans, L.; Sattin, M. (2000) The role of ecology in the development of weed management systems: an outlook. Weed Research 40, 49-62.

Moss, S. R. (2008) Weed research: is it delivering what it should? Weed Research 48, 389-393.

Neve, P.; Powles, S. (2005) High survival frequencies at low herbicide use rates in populations of *Lolium rigidum* result in rapid evolution of herbicide resistance. Heredity 95, 485-492.

Pannell, D. J. (1997) Sensitivity analysis of normative economic models: Theoretical framework and practical strategies. Agricultural Economics 16, 139-152.

Pannell, D. J.; Stewart, V.; Bennett, A.; Monjardino, M.; Schmidt, C.; Powles, S. B. (2004) RIM: a bioeconomic model for integrated weed management of *Lolium rigidum* in Western Australia. Agricultural Systems 79, 305–325.

Paruelo, J. M.; Jobbagy, E. G.; Sala, O. E.; Lauenroth, W. K.; Burke, I. C. (1998) Functional and structural convergence of temperate grassland and shrubland ecosystems. Ecological Applications 8, 194-206.

Peltzer, D. A.; Ferriss, S.; FitzJohn, R. G. (2008) Predicting weed distribution at the landscape scale: using naturalized *Brassica* as a model system. Journal of Applied Ecology 45, 567-475.

Perry, J. N; González-Andújar, J. L. (1993) Dispersal in a metapopulation neighbourhood model of an annual plant with a seedbank. Journal of Ecology 81, 453-463.

Piñeiro, G.; Perelman, S.; Guerschman, J. P.; Paruelo, J. M. (2008) How to evaluate models: observed vs. predicted or predicted vs. observed? Ecological Modelling 216, 316-322.

Rauschert, E. S. J.; Mortensen, D. A.; Bjørnstad, O. N.; Nord, A. N.; Peskin, N. (2009) Slow spread of the aggressive invader, *Microstegium vimineum* (Japanese stiltgrass). Biological Invasions 12, 563-579.

Recasens, J.; Taberner, A.; Izquierdo, J. (1997) *Lolium rigidum* Gaud. en cultivos de cerales. In: Biología de las Malas Hierbas de España (Eds. Sans, X. and Fernández-Quintanilla, C.) pp. 49-64. PHYTOMA-España y Sociedad Española de Malherbología, Spain.

Reeves, T. G. (1976) Effect of annual ryegrass (*Lolium rigidum* Gaud.) on yield of wheat. Weed Research 16, 57-63.

Romero, A.; Chamorro, L.; Sans, F. X. (2008) Weed diversity in crop edges and inner fields of organic and conventional dryland winter cereal crops in NE Spain. Agriculture, Ecosystems and Environment 124, 97-104.

Ruiz, D.; Escribano, C.; Fernández-Quintanilla, C. (2006) Assessing the opportunity for site-specific management of *Avena sterilis* in winter barley fields in Spain. Weed Research 46, 379-387.

Saavedra, M.; Cuevas, J.; Mesa-García, J.; García-Torres, L. (1989) Grassy weeds in winter cereals in southern Spain. Crop Protection 6, 181-187

Smith, E. P.; Rose, K. A. (1995) Model goodness-of-fit analysis using regression and related techniques. Ecological Modelling 77, 49-64.

Taberner, A. (1996) Biología de *Lolium rigidum* Gaud. Como planta infestante del cultivo de cebada. Aplicación al establecimiento de métodos de control. Ph.D. Thesis. Universitat de Lleida, Spain.

Thill, D. C.; Mallory-Smith, C. A. (1997) The nature and consequence of weed spread in cropping systems. Weed Science 45, 337-342.

van den Berg, F.; Gilligan, C. A.; Gerdessen, J. C.; Gregoire, L. A. H.; van den Bosch, F. (2010) Optimal weed management in crop rotations: incorporating economics is crucial. Weed Research 50, 413-424.

Vinatier, F.; Tixier, P.; Le Page, C.; Duyck, P. F.; Lescourre, F. (2009) COSMOS, a spatially explicit model to simulate the epidemiology of *Cosmopolites sordidus* in banana fields. Ecological Modelling 220, 2244-2254.

Wallach, D.; Goffinet, B. (1989) Mean squared error of prediction as a criterion for evaluating and comparing system models. Ecological Modelling 44, 299-306.

Wang, J.; Kropff, M. J.; Lammert, B.; Christensen, S.; Hansen, P. K. (2003) Using CA model to obtain insight into mechanism of plant population spread in a controllable system: annual weeds as an example. Ecological Modelling 166, 277-286.

Woolcock, J. L.; Cousens, R. (2000) A mathematical analysis of factors affecting the rate of spread of patches of annual weeds in an arable field. Weed Science 48, 27–34.

CAPÍTULO III

Controlling annual weeds in cereals by deploying crop rotation at the landscape scale: *Avena sterilis* as an example

CAPÍTULO III: CONTROLLING ANNUAL WEEDS IN CEREALS BY DEPLOYING CROP ROTATION AT THE LANDSCAPE SCALE: *Avena sterilis* AS AN EXAMPLE

RESUMEN

El control de las malas hierbas a través de la rotación de cultivos ha sido principalmente estudiado en un contexto no espacial. Sin embargo, las semillas de las malas hierbas son dispersadas más allá de los límites de la parcela por una gran variedad de vectores. Por tanto, para conseguir un control más eficaz de las malas hierbas, su manejo debería ser considerado a nivel de paisaje. En este trabajo hemos evaluado cómo la dispersión de semillas afecta a la interacción entre la rotación de cultivos y la heterogeneidad del paisaje con respecto al control de las especies arvenses. Se desarrolló un modelo espacialmente explícito a nivel de paisaje para el estudio de la dinámica de poblaciones de las malas hierbas bajo diferentes escenarios de manejo a corto y a largo plazo. Rotaciones de dos y tres cultivos y tres niveles de dispersión de las semillas de las malas hierbas entre parcelas fueron analizados en paisajes completamente homogéneos y heterogéneos. Los resultados del modelo sugieren que al igual que ocurre en las rotaciones de cultivos a nivel de parcela, la rotación de cultivos implementada a nivel de paisaje tiene un gran potencial en el control de las especies arvenses, donde tanto el número de diferentes tipos de cultivos como la secuencia de los mismos dentro de la rotación tiene un efecto significativo a corto y largo plazo en la densidad de las poblaciones de las malas hierbas. Las poblaciones de las malas hierbas llegaron a extinguirse cuando las fracciones de cada cultivo presente en el paisaje fueron aleatorizadas y la dispersión de semillas entre parcelas no fue considerada. En general, la densidad de semillas de las malas hierbas se incrementaron en los paisajes con una proporción relativa similar de cada cultivo, y en estos paisajes el nivel de dispersión de las semillas influyó en la secuencias de cultivos, dentro de las rotaciones de tres cultivos, que fueron más eficientes controlando la densidad de las malas hierbas. Ignorar la dispersión de las semillas entre parcelas podría conducir, por tanto, a la selección de estrategias subóptimas en el control de las especies arvenses, y las agregaciones de parcelas del mismo cultivo que siguen la misma secuencia de cultivos dentro de la rotación podría ser un método de control más sostenible de las malas hierbas. Un control más eficaz de las malas hierbas a través de la rotación de cultivos requiere una coordinación entre agricultores con respecto a la secuencia de los cultivos, a la disposición de los mismos en el paisaje y/o a la proporción relativa de cada cultivo en el paisaje.

Palabras clave: agregación de cultivos, *Avena sterilis*, dinámica de poblaciones, dispersión de semilla, estocasticidad regional, modelo espacialmente explícito.

ABSTRACT

Weed control through crop rotation has mainly been studied in a non-spatial context. However, weed seeds are often spread beyond the crop field by a variety of vectors. For weed control to be successful, weed management should thus be evaluated at the landscape level. In this paper we assess how seed dispersal affects the interactions between crop rotation and landscape heterogeneity schemes with regards to weed control. A spatially explicit landscape model was developed to study both short- and long-term weed population dynamics under different management scenarios. We allowed for both two and three crop species rotations and three levels of between field weed seed dispersal. All rotation scenarios and seed dispersal fractions were analyzed for both completely homogeneous landscapes and heterogeneous landscapes whereby more than one crop was present. The model results suggest that, like crop rotation at the field level, crop rotation implemented at the landscape level has great potential to control weeds, whereby both the number of crop species and the cropping sequence within the crop rotation have significant effects on both the short and long term weed population densities. In the absence of seed dispersal weed populations became extinct when the fraction of each crop in the landscape was randomized. In general weed seed densities increased in landscapes with increasing similarity in crop proportions, but in these landscapes the level of seed dispersal affected which three crop species rotation sequence was most efficient at controlling the weed densities. We show that ignoring seed dispersal between fields might lead to the selection of sub-optimal tactics and that homogeneous crop field patches that follow a specific crop rotation sequence might be the most sustainable method of weed control. Effective weed control through crop rotation thus requires coordination between farmers with regard to cropping sequences, crop allocation across the landscape and/or the fraction of each crop across the landscape.

Key words: aggregated crop patches, *Avena sterilis*, population dynamics, regional stochasticity, seed dispersal, spatially explicit model.

III. 1. INTRODUCTION

Crop rotation can be defined as the alternation of crops on the same field in a recurring sequence (Thenail et al., 2009). This is qualitatively different from crop succession which is a more flexible framework in which farmers apply a combination of sequences based on agronomic rules (Joannon et al., 2008). Crop rotation has been shown to be a successful method for weed control and has positive effects on many biotic and physical soil factors (Liebman and Dyck, 1993). This success is achieved by the heterogeneity created by the different crops and their management systems (Joannon et al., 2008) which impose different types and intensities of biotic and abiotic stresses on weeds (Liebman and Dyck, 1993). In more recent years, weed control has mainly been through herbicide use (Saavedra et al., 1989), but control methods such as crop rotation are regaining interest due to the increased pressure to develop sustainable control methods that have a limited environmental impact. An effective crop rotation deployment might thus limit, and in some cropping years even eliminate, the need of herbicide applications to control the dominant weed species.

In existing crop rotation models, the effects of the weed control established by the rotation are either introduced via individual weed life cycle parameters (González-Andújar and Fernández-Quintanilla, 1991; 1993) or through the development of more complex matrix models (Jordan et al., 1995; Mertens et al., 2002; Westerman et al., 2005; van den Berg et al., 2010). Mertens et al. (2002) studied how different crop rotation sequences, crop fractions and lengths in a two crop species rotation affect the growth rate of the weed species *Persicaria maculosa* (formerly named *Polygonum persicaria*). Although the model incorporated a lot of biological detail, it ignored the spatial aspect of seed dispersal between fields. However, Auld and Coote (1980) showed that the weed population growth rate is strongly influenced by seed dispersal which stresses the need to take seed dispersal mechanisms into account when developing weed control strategies (Ghersa and Roush, 1993). Moreover, there is a need to understand how dispersal processes and management practices interact (Thill and Mallory-Smith, 1997).

The agricultural landscape can be thought of as fields interconnected by seed dispersal driven by both agronomic factors and other human activities (Benvenuti, 2007). If weed seeds spread beyond the crop field, attempts to control the weed population through within-field crop rotation might be ineffective (Helenius, 1997). This is because meta-population theory predicts that although crop rotation deployed at the field level ensures an increased environmental stochasticity and presumably an increased weed extinction rate at the field level (Hanski, 1991), the mean regional stochasticity might be unaffected, rendering the crop rotation ineffective at the regional scale (Helenius, 1997). González-Andújar et al. (2001) studied how decisions at the field-level influence weed control at the landscape level and concluded that to achieve effective control, weed population dynamics should be integrated at different spatial scales.

The main aim of this study was to evaluate the interaction between different crop rotation sequences at the field level and the relative proportion of these crop species in the landscape in the presence of different levels of seed dispersal and the effectiveness of weed control for the dominant weed species. Both short- and long-term seed population dynamics were analyzed. The study is motivated and illustrated by the specific example of the weed species *Avena sterilis* L.

A. sterilis is the dominant cereal-infesting grass weed in the south of Spain (González-Andújar and Saavedra, 2003) and is difficult to control due to its seed dispersal (Thill and Mallory-Smith, 1997) and its dormancy strategies (Sánchez del Arco et al., 1995). Although *A. sterilis* control currently mainly focuses on control by herbicides (Saavedra et al., 1989), weed management through crop rotation has been studied both experimentally (Fernández-Quintanilla et al., 1984; Navarrete and Fernández-Quintanilla, 1996) and theoretically (González-Andújar and Fernández-Quintanilla, 1991; 1993). We will show that the omission of between-field seed dispersal from crop rotation models, such as the models developed by Mertens et al. (2002) and van den Berg et al. (2010), might lead to the selection of suboptimal weed control strategies.

III. 2. MATERIALS AND METHODS

III. 2. 1. MODEL CONSTRUCTION

The agricultural landscape was discretized into a two-dimensional square lattice with absorbing edges consisting of $V \times V$ cells with $V = 100$ cells. Each cell represented a farm field of 1 ha in which an independent weed seed population developed. Note that field sizes <2 ha are frequent in the South of Spain (Junta de Andalucía, 2010) and other European countries. For example, the mean field size in six French regions were found to be 2.1, 1.7, 1, 2.1, 3.5 and 1 ha, respectively (Colbach et al., 2009). Once the weed seed population was established in each cell, the seeds were distributed over the landscape following some specific rules.

Crops were initially allocated across the farmland in a random manner, according to the number of crop species in the rotation and their frequency in the landscape. Such a randomised crop distribution results in the aggregation of individual fields containing the same crop species. These aggregations thus can be thought of as larger fields and can therefore account for the variability in field sizes observed in the agricultural landscape. Crop distribution was subsequently changed yearly following the rotation sequence so that in each weed growing season only one of the crops in the rotation appeared in each cell. For example, in the case of the two-crop species rotation WSWS, where W and S denote different crops, cells initiated with crop W will contain crop S in year two, followed by crop W in year three and so on, whereas cells initiated with crop S followd the opposite alternation pattern.

III. 2. 1. 1. Crop species of the rotations

We studied rotations of both two and three crop species. Because the model was parameterised for *A. sterilis* we studied rotations that are commonly used in Andalusia to control this species, i.e., the two-crop species rotation of winter wheat (W) and sunflower (S) (Jurado-Expósito et al., 2005) and the three-crop species rotation that also incorporates legumes (L) (Saavedra et al., 1989).

III. 2. 1. 2. Landscape scenarios (LS)

Each cropping sequence was evaluated under different landscape scenarios based on the relative proportion of the crops across the landscape, i.e., the level of crop evenness (sensu Magurran, 2004). The resultant landscapes varied broadly from completely homogeneous in which only one crop was present each year, to heterogeneous with a maximum crop evenness, in which case all crops were simultaneously present in the landscape in equal proportions and with an initial random distribution. Percentage contributions of each crop to the landscape's spatial pattern are given in Table 1. Note that heterogeneity is introduced by two factors: (1) the number of crop species involved in the rotation and (2) crop evenness, which measures the relative proportion of crops in the landscape, and whereby an increasing value means that the relative crop proportions are increasingly equal. The process of farmers rotating their crops according to agronomic factors without applying a consistent rotation sequence was simulated by landscape scenarios 1 and 7, LS1 and LS7 respectively (Table 1), whereby the proportional distribution of the crops in the landscape was allocated at random. In all other cases, the farmers were assumed to apply a consistent rotation scheme as outlined in the next section with the proportional distribution of the crops in the landscape as a result of local decisions.

Table 1. Initial landscape-level crop distribution whereby the different landscape scenarios result in different levels of heterogeneity.

LANDSCAPE SCENARIO (LS)	Crops at the landscape level (%)		
	Wheat	**Sunflower**	**Legume**
Two-species rotations			
1	random	random	---
2	0	100	---
3	25	75	---
4	50	50	---
5	75	25	---
6	100	0	---
Thre- species rotations			
7	random	random	random
8	0	100	0
9	0	0	100
10	20	60	20
11	20	20	60
12	33	33	33
13	60	20	20
14	100	0	0

III. 2. 1. 3. Cropping sequences

Rotation lengths of more than six years are not exceeded in practise (Mertens et al., 2002) and short sequences of similar crops are recommended when trying to control other weeds or diseases associated with these crops and when trying to maintain soil properties and nutrients (Liebman and Dyck, 1993). We thus considered crop rotations of up to six years in length, whereby crops appeared in the same field for a maximum of two consecutive years.

We studied two qualitatively different types of rotations. Cyclic permutations, distinguished by letters in Table 2, are rotations with an identical cropping sequence, but are initiated with a different crop. For example, rotations WWSS and WSSW are cyclic permutations. Such rotations have identical long-term dynamics with identical growth rates or mean seed densities, but differ in some other characteristics such as the short-term population growth rate (Mertens et al., 2002). All other rotations studied were “essentially different” (Mertens et al., 2002) and are distinguished by numbers in Table 2. Essentially different rotations differ in both their short-term and long-term dynamics. Column 2 of Table 2 specifies the rotation sequence followed by cells that were initiated with a winter wheat crop. Cells initiated with an alternative crop followed the same rotation scheme, but in such a way that the landscape scenario remained constant over each rotation cycle.

Table 2. Rotation scenarios studied whereby different numbers indicate essentially different rotations and different letters indicate cyclic permutations.

ROTATION SCENARIO	**Cropping sequences for different initial crops**		
	Wheat (W)	**Sunflower (S)**	**Legume (L)**
Two-species rotations			
1	WSWS	SWSW	
2(a)	WWSS	SSWW	
2(b)	WSSW	SWWS	
Monoculture1	WWWW	SSSSS	
Three-species rotations			
3	WSLWSL	SLWSLW	LWSLWS
4	WLSWLS	SWLSWL	LSWLSW
5(a)	WWSSLL	SSLLWW	LLWWSS
5(b)	WSSLLW	SLLWWS	LWWSSL
6(a)	WWSLLS	SLLSWW	LSWWSL
6(b)	WSLLSW	SWWSLL	LLSWWS
7(a)	WWLSSL	SLWWLS	LSSLWW
7(b)	WLSSLW	SSLWWL	LWWLSS
8(a)	WWLLSS	SSWWLL	LLSSWW
8(b)	WLLSSW	SWWLLS	LSSWWL
9(a)	WSSWLL	SWLLWS	LLWSSW
9(b)	WLLWSS	SSWLLW	LWSSWL
Monoculture2	WWWWWW	SSSSSS	LLLLLL

III. 2. 1. 4. Population model

The *A. sterilis* seed bank in a given cell at the beginning of crop season t is denoted by $N_t[i,j]$ with $i \in \{1,\ldots,V\}$ and $j \in \{1,\ldots,V\}$. The seed population size at the end of crop season t, i.e., after reproduction, is given by

$$M_t[i,j] = N_t[i,j]\, f\left(N_t[i,j]\right) \qquad (1)$$

with reproduction, $f(\,)$, following Mortimer et al. (1989), i.e.,

$$f\left(N_t[i,j]\right) = \lambda g\left(1-c_x\right)\left(1+agN_t[i,j]\right)^{-b} \text{ with } x = \{\mathrm{W,S,L}\} \qquad (2)$$

and with g the proportion of seeds germinating, λ the seed production of an individual plant, a and b parameters determining self regulation, and c_x the level of weed control in crop x (Table 3). *A. sterilis* seeds start emerging in late October with around 75% of seedling production in the next two months (Aibar et al., 1991). Crops sown after this time can reduce *A. sterilis* population by means of pre-planting tillage, whereby established seedlings are destroyed (Fernández-Quintanilla et al., 1984). Moreover, weed seeds that emerge late in the growing season, i.e., after tillage operations, produce seeds at a much reduced capacity due to strong competition with the crop (Fernández-Quintanilla et al., 1984), leading to a reduced weed seed rain. Winter wheat (generally sown in October or November) does not significantly contribute to the pre-planting tillage death of *A. sterilis*, but pre-planting tillage applied to legume (generally sown in December or January) and especially sunflower crops (generally sown in March) can result in a substantial seedling death and seed production reduction of *A. sterilis*. Such crop-specific weed "control" was denoted by parameter c_x, which implicitly affected both the weed seedlings' survival and their seed production capacity at maturity (Cousens and Mortimer, 1995). The winter wheat crop was used as the reference crop, leading to $c_W = 0$, whereas the weed control exerted by the other crops relative to the control exerted by winter wheat was fixed according to the survey of Fernández-Quintanilla et al. (1984) (Table 3).

A constant crop-specific fraction, d_x, of the total number of seeds produced in a parent cell was assumed to disperse over the landscape following the von Neumann neighbourhood method, whereby seeds were equally distributed over all four directions and over a distance of a single ring of neighboring farms or cells. Due to the machinery associated with winter wheat crops, *A. sterilis* seeds spread beyond the field boundary of these crops (Shirtliffe and Entz, 2005), but this is not the case for sunflower and legume crops (i.e., $d_W \geq 0$ and $d_S = d_L = 0$). The three different fractions of seed dispersal that were studied, i.e., $d_W = 0$, $d_W = 0.014$, and $d_W = 0.12$, are based on field observations for winter wheat crops (Steinmann and Klingebiel, 2004; Shirtliffe and Entz, 2005). Because *A. sterilis* seeds are subject to dormancy (Sánchez del Arco et al., 1995) the model also incorporated a persistent seed bank, sN, with s being the fraction of seeds surviving from one generation to the next. The seed bank in the next generation was thus given by

$$N_{t+1}[i,j] = M_t[i,j] - E_t[i,j] + I_t[i,j] + sN_t[i,j] \tag{3}$$

with $E[i, j]$ and $I[i, j]$ the emigrating and immigrating weed seeds from the parent cell to its neighboring cells and vice versa.

Table 3. Parameter values for *A. sterilis* in winter wheat crops.

MODEL PARAMETERS	Symbols	Values	Units
Germination	g	0.25*	1
Potential fecundity	λ	32.15†	Seeds/plant
Parameter a	a	0.004†	1
Parameter b	b	1†	1
Survival	s	0.15*	1
Control of weeds			
- Wheat	c_{W}	0	1
- Sunflower	c_{S}	0.99‡	1
- Legume	c_{L}	0.93¶	1
Seed dispersal fractions			
- Wheat	d_{W}	0; 0.014§; 0.12**	1
- Sunflower	d_{S}	0	1
- Legume	d_{L}	0	1

* *A. sterilis* germination and seed bank survival rates under Mediterranean conditions (Sánchez del Arco et al., 1995).

† Parameters estimated according to González-Andújar and Fernández-Quintanilla (1993) for *A. sterilis* growing in winter barley.

‡ The weed control parameter can be estimated from the experiment of Fernández-Quintanilla et al. (1984). Two randomized block design field experiments were performed to evaluate effects on *A. sterilis* demography, with two and four cropping systems over four and two years, respectively. Sequences were winter wheat monoculture and fallow-spring barley rotation in the first experiment and winter barley and spring barley monocultures and fallow-winter barley and sunflower-winter barley rotations and vice versa in the second experiment. For each plot, seed bank and panicle densities were measured annually at the beginning and end of the weed life cycle. The sunflower control parameter c_{S} was estimated from $N_{t+1}=N_t\lambda g(1\text{-}c_{\mathrm{S}})(1+agN_t)^{-b}+sN_t$ with N_t, and N_{t+1} the 2-year average weed seed bank densities in sunflower at the beginning and end of the weed life cycle, respectively (from Fernández-Quintanilla et al., 1984), and all other parameters set to their default value.

¶ No literature available; estimated according to the *A. sterilis* seed bank in spring barley (Fernández-Quintanilla et al., 1984) and $N_{t+1}=N_t\lambda g(1\text{-}c_{\mathrm{L}})(1+agN_t)^{-b}+sN_t$, with N_t, and N_{t+1} the 4-year average weed seed bank densities in spring barley at the beginning and end of the weed life cycle, respectively (from Fernández-Quintanilla et al., 1984), and all other parameters set to their default value.

§ Seed fraction found 100 m away from the parent position for *Avena fatua* (Shirtliffe and Entz, 2005).

** Seed fraction found beyond the farm boundaries (each subfield was 1 ha) for *Anisantha sterilis* (formerly named *Bromus sterilis*) (Steinmann and Klingebiel, 2004), which has a seed shape similar to *A. sterilis*.

III. 2. 2. MODEL ANALYSIS

The model was implemented in Microsoft Excel, using Visual Basic macros. For all scenarios studied the initial weed seed bank density was set to the weed seed density found in cereal crops infested with *A. sterilis*, i.e., 16 seeds/m^2 (derived from 4 plants/m^2) (Saavedra et al., 1989) and each scenario was replicated 10 times. Model outputs in the form of the number of weed seeds in a given cell at the end of a crop growing season ($N_{t+1}[i, j]$) were derived at every time step, representing a complete crop growing season. To avoid equivocal results disguising the true model behavior, the method of Perry and González-Andújar (1993) was used to derive the integer equivalents of the output values, such that

$$N_{t+1}[i,j] = \mathrm{floor}(N_{t+1}[i,j]+U) = \lfloor N_{t+1}[i,j]+U \rfloor \tag{4}$$

with U being a random number between 0 and 1. The landscape-wide average seed density, $\hat{N}$, was subsequently calculated from

$$\hat{N} = \left(\sum_{i=1}^{V} \sum_{j=1}^{V} N_{t+1}[i,j] \right) V^{-2} \tag{5}$$

The long-term seed bank dynamics were restricted to the asymptotic phase, where trends have settled down to a fixed pattern and are independent of initial conditions (Caswell, 2001). Because the rotations studied have different cycle lengths, the mean seed bank density, $\overline{N}$, for a given rotation was calculated over a common cropping period, p, of 12 years:

$$\overline{N} = \frac{\sum_{k=1}^{p} \hat{N}_k}{p} \tag{6}$$

This ensured that the results for different rotation scenarios could be compared directly and that the fraction of each crop species in the total rotation sequence remained constant.

The short-term weed seed dynamics, on the other hand, do depend on the initial conditions. Therefore, for the crop rotation that resulted in the largest decrease in the long-term weed seed densities, we also studied the short-term population dynamics.

III. 3. RESULTS

III. 3. 1. CROP SUCCESSION: LANDSCAPE SCENARIOS 1 AND 7

For crop succession, whereby crop allocation across the landscape occurred at random, the weed seed densities depicted stochastic behavior in the presence of seed dispersal, whereas in the absence of dispersal, *A. sterilis* decreased markedly (Fig. 1) and eventually became extinct after a time period exceeding a 100 years (results not shown). Furthermore, increased dispersal fractions led to increased seed densities. The results were qualitatively the same for the two- and three-crop species rotations (Fig. 1a, b), although landscapes with less diversity, involving fewer crop species, resulted in higher weed seed densities (Fig. 1).

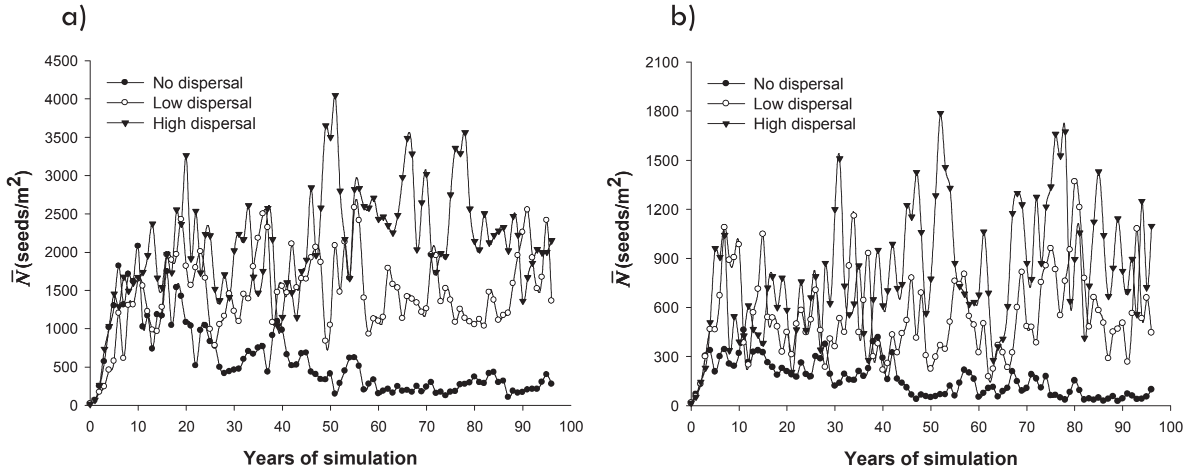

Figure 1. Mean *A. sterilis* seed population density dynamics for different seed dispersal fractions (no dispersal, $d_{\mathrm{W}} = 0$; low dispersal, $d_{\mathrm{W}} = 0.014$; high dispersal, $d_{\mathrm{W}} = 0.12$) for a) the two-crop species succession system and LS1 and b) the three-crop species succession systems and LS7.

III. 3. 2. LONG-TERM POPULATION DYNAMICS: ALL ROTATION SCENARIOS AND LANDSCAPE SCENARIOS 2-6 AND 12-14

For homogeneous landscapes (LS2, LS6, LS14), in which every year only one crop species was present, and for all monoculture scenarios, the mean long-term weed seed densities were unaffected by seed dispersal events (Tables 4 and 5). This is a direct consequence of the constant crop-specific weed seed dispersal fractions resulting in a homogeneous regional seed spread. Seed densities increased with increased crop evenness in the landscape and increased seed dispersal fractions (Tables 4 and 5). Obviously, in the absence of dispersal the mean seed population density is unaffected by the landscape scenario (Tables 4 and 5). The absence of dispersal often led to local field-level population extinction, which explains why certain results deviate from this general finding (see Rotations 2(a) and 5(a)-8(a)). Such extinction events could be avoided by increasing the initial seed bank density above the default density, in which case the mean seed densities were indeed constant across all fragmentation scenarios (results not shown).

In general, the equilibrium weed densities decreased with the number of crops involved in the rotation and winter wheat monocultures were thus least effective with respect to *A. sterilis* control (Tables 4 and 5). Note, however, that the weed populations became extinct in monocultures of sunflower (Table 4; LS2) and legume (results not shown). Overall, Rotation 1 resulted in better *A. sterilis* control than Rotation 2 and this difference in control ability was more significant for landscapes with increased crop evenness and increased seed dispersal fractions (Table 4). For three-crop rotations, it is less clear which management scenario is optimal (Table 5). In the absence of seed dispersal, Rotation 8 was the most efficient rotation. However, in heterogeneous landscapes and in the presence of either low (d_{W} = 0.014) or high (d_{W} = 0.12) seed dispersal fractions, Rotation 4 and Rotations 3, 4 and 9, respectively, all became more efficient in controlling *A. sterilis* than Rotation 8. For LS12, Fig. 2 provides a graphical representation of the changes in which rotation sequence is optimal when the seed dispersal fraction is increased. Equilibrium weed densities are only given for permutation (a), because the long-term population dynamics are identical for cyclic permutations (Tables 4 and 5).

Results for the essentially different rotation scenarios, i.e., Rotations 3 and 4, Rotations 5 and 8, and Rotations 6 and 7, show that a rotation with legume phases followed by sunflower phases performs better than rotations with sunflower phases followed by legume phases (Table 5). More generally the results reveal that the best weed control is achieved when crops are deployed within a rotation in order of increasing level of weed control, before changing back to the crop with the lowest weed control ability at the start of the next rotation cycle (Table 5).

Table 6 reveals that the *A. sterilis* population densities changed noticeably between individual phases of the rotations. Years or phases with high seed bank densities tended to coincide with years in which winter wheat was grown. This result was more pronounced for rotations with two consecutive wheat phases, in which case weed densities were much higher in the second wheat phase as compared to the other rotation phases, although these differences were less clear for Rotations 7 and 8. The results were qualitatively the same for all seed dispersal fractions and all landscape scenarios, whereby the long-term seed densities for LS8 and LS9 were similar to those for LS14, and densities for LS10 and LS11 were similar to those for LS13 (results not shown).

Table 4. Mean equilibrium *A. sterilis* seed densities (seeds/m^2) for the two-crop species rotations, different seed dispersal fractions, and landscape scenarios 2-6 (defined by relative fractions of wheat and sunflower).

ROTATION SCENARIO	Example, wheat as inicial crops	Landscape scenario (LS)														
		2			**3**			**4**			**5**			**6**		
		W(0%); S(100%)			W(25%); S(75%)			W(50%); S(50%)			W(75%); S(25%)			W(100%); S(0%)		
		Dispersal fraction (d_W)														
		0	**0.014**	**0.12**	**0**	**0.014**	**0.12**	**0**	**0.014**	**0.12**	**0**	**0.014**	**0.12**	**0**	**0.014**	**0.12**
Monoculture1	WWWW	0*	0	0	2114	2113	2099	4228	4227	4205	6341	6340	6320	8456	8454	8445
1	WSWS	1452	1452	1448	1452	1519	1955	1452	1542	2110	1452	1519	1955	1452	1452	1448
2(a)	WWSS	1246	1476	1473	1304	1646	2328	1362	1702	2569	1420	1646	2330	1477	1476	1473

* SEs are not included because of their small values (<1%).

Table 5. Mean equilibrium *A. sterilis* seed densities (seeds/m^2) for the three-crop species rotations, different seed dispersal fractions, and landscape scenarios 12-14 (defined by relative fractions of wheat, sunflower, and legume).

		Landscape scenario (LS)								
		12			**13**			**14**		
		W(33%); S(33%); L(33%)			W(60%); S(20%); L(20%)			W(100%); S(0%); L(0%)		
		Dispersal fraction (d_W)								
ROTATION SCENARIO	**Example, wheat as initial crop**	**0**	**0.014**	**0.12**	**0**	**0.014**	**0.12**	**0**	**0.014**	**0.12**
Monoculture2	WWWWWW	2818*	2834	2862	5637	5650	5661	8456	8455	8445
3	WSLWSL	258	309	740	258	296	624	258	258	257
4	WLSWLS	174	196	402	174	190	336	174	174	173
5(a)	WWSSLL	273	598	1500	306	533	1271	338	338	336
6(a)	WWSLLS	211	420	1241	236	375	998	261	261	260
7(a)	WWLSSL	156	334	1303	175	293	1030	193	193	192
8(a)	WWLLSS	123	257	1064	143	228	783	163	163	163
9(a)	WSSWLL	226	278	647	226	265	542	226	226	225

* SEs are not included because of their small values (<1%).

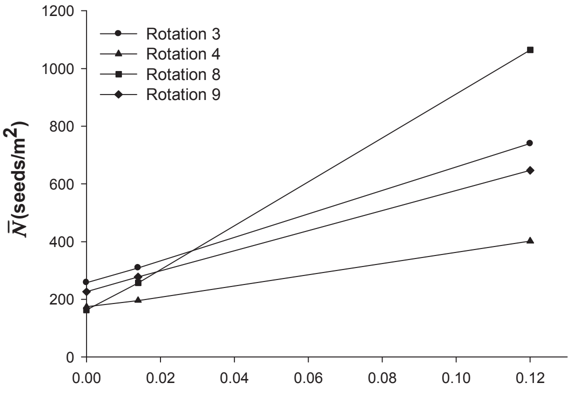

Figure 2. Equilibrium *A. sterilis* seed population densities for the four three-crop species rotations that were most efficient at controlling the long-term weed densities (i.e., Rotations 3, 4, 8, and 9 in LS12) as a function of the seed dispersal fraction, d_W.

III. 3. 3. SHORT-TERM POPULATION DYNAMICS FOR OPTIMAL LONG-TERM MANAGEMENT STRATEGIES: ROTATIONS 1, 8(a), AND 8(b) AND LANDSCAPE SCENARIOS 2, 6, AND 9

For rotations involving two crops, Rotation 1 within a homogeneous landscape (LS2 and LS6) resulted in the lowest long-term seed densities (Table 4). Analysis of the short-term population dynamics of these two scenarios revealed that for LS2, as compared to LS6, it took longer for the population dynamics to reach equilibrium because the seed population established at a lower rate (Fig. 3a). For rotations involving three crops, Rotation 8 combined with LS8, LS9, and LS14 resulted in the lowest long-term seed densities (Table 5). A comparison between these three landscape scenarios revealed that LS9 was most efficient in retarding the population dynamics (results not shown). Further analysis comparing the short-term population dynamics for the cyclic permutations of Rotation 8 in combination with LS9 showed that permutation (a) resulted in lower short-term weed seed densities than permutation (b) (Fig. 3b).

Table 6. Equilibrium *A. sterilis* seed densities for individual years within the different crop rotations, a seed dispersal fraction of $d_{\mathrm{W}} = 0.014$ and a homogeneous spatial distribution (LS14).

ROTATION SCENARIO	Example, wheat as initial crop	***A. sterilis* densities (seeds/m^2) by cropping year**											
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
1	WSWS	**2475***	**428**	2475	428	2475	428	2475	428	2475	428	2475	428
2(a)	WWSS	**975**	**4114**	**682**	**135**	975	4114	682	135	975	4114	682	135
3	WSLWSL	**579**	**116**	**76**	579	116	76	579	116	76	579	116	76
4	WLSWLS	**304**	**177**	**39**	304	177	39	304	177	39	304	177	39
5(a)	WWSSLL	**211**	**1433**	**262**	**56**	**38**	**27**	211	1433	262	56	38	27
6(a)	WWSLLS	**141**	**1017**	**193**	**120**	**78**	**18**	141	1017	193	120	78	18
7(a)	WWLSSL	**87**	**656**	**321**	**68**	**15**	**11**	87	656	321	68	15	11
8(a)	WWLLSS	**62**	**474**	**252**	**151**	**33**	**8**	62	474	252	151	33	8
9(a)	WSSWLL	**701**	**138**	**31**	**242**	**146**	**94**	701	138	31	242	146	94

Note: Densities for the shortest repeatable unit of the rotation are given in bold.

* SEs are not included because of their small values (<1%).

III. 4. DISCUSSION

Methods developed in this paper allowed for the quantification of the effect of landscape on weed dispersal and the resultant weed population dynamics for different crop rotation scenarios. Results showed that the heterogeneity introduced by the variability in the proportion of crops in the landscape facilitates weed seed exchange between fields of different crops, leading to increased weed seed populations, and that the rotation sequence that is most efficient in reducing the weed seed population strongly depends on the level of weed seed dispersal. This stresses the need to plan weed control strategies at the landscape level as opposed to planning at the field level only. The model results are discussed in detail in the next few paragraphs, where we focus on the management implications at both the field and the landscape level.

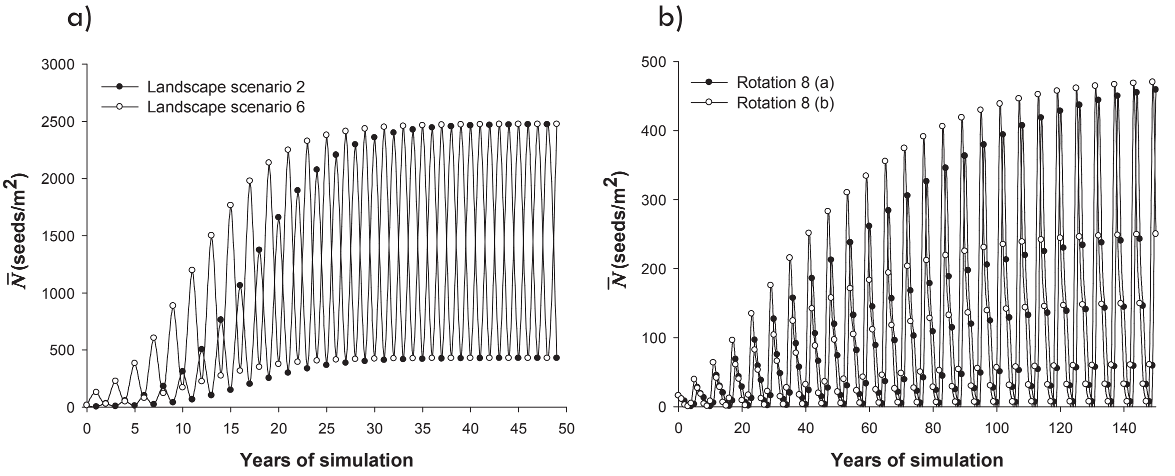

Figure 3. Short-term *A. sterilis* population dynamics for the rotation and landscape scenarios that were most efficient in controlling the long-term weed population densities. a) Rotation 1 under LS2 and LS6. b) The cyclic permutations of Rotation 8 for LS9.

III. 4. 1. MANAGEMENT IMPLICATIONS AT THE LANDSCAPE LEVEL

Model results revealed that the presence of dispersal and a randomized crop proportion in the landscape resulted in the persistence of *A. sterilis* with temporal changes in abundances and whit average abundance depending on the fraction of seeds that dispersed. However, *A. sterilis* populations became extinct in the absence of seed dispersal (Fig. 1). A survey by Saavedra et al. (1989) showed that *A. sterilis* remains associated with cereal crops and that it is the most widely distributed weed, which suggests that dispersal indeed largely contributes to the persistence of *A. sterilis*. It is thus important to increase our understanding of how weed seed dispersal can be decreased at the landscape level.

Thill and Mallory-Smith (1997) point out that tillage operations, contaminated seed stock, and combine harvesters are the main drivers for dispersal of wild oat seeds. Cleaning tillage and harvesting equipment before entering a new field, especially when the soil is wet, helps to reduce the number of adhered seeds and limits seed spread from one field to another (Thill and Mallory-Smith, 1997). Other desired tactics to avoid weed seed introduction and dispersal are the use of certified crop seeds and clean manure. Most farmers, however, conserve and grow their own crop seeds and, despite the seed cleaning procedures applied, the contamination by weed seeds was shown to be much higher than expected by the farmers (Michael et al., 2010). Furthermore, the direct weed seed dispersal through combine harvesters can be reduced by connecting a chaff collector to the back of the harvester (Shirtliffe and Entz, 2005), turning off the chaff-spreaders when the harvester is passing through weed patches (Thill and Mallory-Smith, 1997), or avoiding harvesting on windy days. Although some initial work has been done on understanding the nature of dispersal vectors (Benvenuti, 2007) and some ideas for slowing down human-related seed spread have been proposed (Thill and Mallory-Smith, 1997), more work within this area is required.

The model analysis also highlighted a significant interaction between dispersal processes and which crop rotation was optimal with respect to weed control. Although this phenomenon was not evident in rotations of two crop species it was clearly manifested in rotations of three crop species. For example, Rotation 8 (e.g., WWLLSS) was most efficient at decreasing the weed population in the absence of dispersal, but Rotation 4 (e.g., WLSWLS) obtained the best control in the presence of seed dispersal. This suggested that the omission of landscape-level dispersal processes from models developed to establish suitable weed management practices might lead to the selection of suboptimal rotation and landscape schemes.

Two practical approaches can be derived from the results of the spatial analysis. Firstly it was shown that agricultural landscapes for which the proportion of each crop present is very similar, independently of the spatial allocation of these crops, favored increased weed densities in the region. This suggests that, from a regional weed management point of view, it would be beneficial to achieve uneven crop proportions within the wider landscape. Such unequal crop proportions are of course limited by consumer demands, but are achievable as long as the market absorbs the crop production fluctuations between years. The approach will require coordination between farmers with regards to crop rotation sequences, but not their specific allocation. Although coordinated management tactics at the landscape level have been proposed previously by other authors (González-Andújar et al., 2001, Dauer et al., 2009) and would offer a suitable alternative approach to help combat the weed problem, such a coordination is a new approach and it could prove difficult for farmers to cooperate together (Colbach et al., 2001). Secondly, this study showed that homogeneous landscapes achieved the best *A. sterilis* control. This is an incongruous solution from a sustainable farmland management point of view (Benton et al., 2003), due to the need to diversify crops on a yearly basis in order to meet consumer demands and to prevent rapid spread of other pests and reduce the crop-specific risks associated with adverse environmental conditions. Other cropping patterns should thus be considered. When crops occur in aggregated patches that follow a specific rotation sequence, all crops could still be simultaneously present within the landscape. This ensures that the requirements for landscape-wide crop diversity are still met, whereas on a more local scale the homogeneous landscape within the aggregated patches helps to reduce weed populations. This approach, however, does require that farmers cooperate with regards to cropping sequences and landscape-level crop allocation. As mentioned previously, such coordination might be difficult to achieve because crop allocation has previously been shown to be affected by decisions of other farmers (Cutforth et al., 2001).

III. 4. 2. MANAGEMENT IMPLICATIONS AT THE FIELD LEVEL

The number of crop species involved in the rotation had a significant effect on the field-level equilibrium *A. sterilis* densities. Rotations of two crop species resulted in a weed population reduction of up to 83% and rotations of three crop species resulted in reductions of up to 98% as compared to the weed densities found in wheat monocultures (Tables 4 and 5). That rotations of three crops generally perform better than rotations of two crops is not surprising, considering that dispersal has such a large effect on the weed seed densities and the fact that in the three-crop species rotation, no dispersal takes place in two out of three rotation phases. However, the additional benefits that can be achieved by carefully choosing the rotation order should not be underestimated. For most landscape and dispersal scenarios, altering the crop order can lead to further weed seed bank density reductions of up to 18% and 74% for the two- and three-crop rotations, respectively. Crop diversification through rotation does, however, does not always reduce weed seed production (Westerman et al., 2005) and is in fact related to the frequency of rotation phases with crops that are successful at controlling the weed (Mertens et al., 2002). Data analysis of the national-scale farmland data sets from Great Britain revealed that crop sequences can be simplified into crop management classes to predict their effects on weed seed bank abundances, whereby the salient descriptors of the crop management classes are crop type, sowing season, and the weed group target for herbicide control (Bohan et al., 2011). Like Mertens et al. (2002) we have shown that crop order, regardless of crop frequency, is also a crucial factor in determining the asymptotic growth rate of the weed population. The very high interannual variability in the equilibrium seed bank densities resulted in annual growth rates ranging from 0.17 to 7.9, whereby the highest weed densities occurred in the wheat phases of the rotation, especially when wheat crops were sown in two consecutive years of the rotation. In phases with such increased weed densities, additional management practices such as herbicide application ought to be considered.

The highest level of weed control is achieved when the crop order within a rotation scenario is such that crops are deployed in order of increasing level of weed control before changing back to the crop with the lowest weed control ability at the start of the next rotation cycle. These results are in accordance with previous findings by Mertens et al. (2002) and van den Berg et al. (2010). Deploying the crops in order of increasing levels of weed control results in the highest possible weed seed density reduction, ensuring a much reduced seed density at the beginning of the wheat phases and, consequently, a much lower weed seed population growth rate in the wheat phases where control is limited. A sensitivity analysis for the control parameters in the sunflower and legume crops was performed for landscape scenarios LS6 and LS14 and both the two- and three-crop rotation scenarios, whereby the control parameters were varied between the minimum and maximum estimates derived from the study by Fernández-Quintanilla et al. (1984). When, in independent simulation, the control parameter values were set to their minimum values (i.e., $c_S = 0.98$ and $c_L = 0.85$), the crop rotation ranking in relation to their effectiveness in decreasing the weed seed bank density changed slightly for the three-crop species rotations. When the control values were set to their maximum values (i.e., $c_S = 1$ and $c_L = 0.99$) the weed populations became extinct for the three-crop species rotations, whereas for the two-crop species rotations a different rotation became optimal (see Appendix A).

A detailed comparison of Rotation 8 and Rotation 9 for a high seed dispersal fraction and landscape scenario 12 reveals clear consequences of the interaction between within-field and landscape-level crop deployment. In this case, Rotation 9 proves to be more efficient at controlling the weed population than Rotation 8, but it is not immediately clear why. Because in the wheat (W) phases no weed control occurs, there is a large local increase in the seed density during these phases, which will consequently result in a large seed rain into neighboring fields due to the dispersal associated with wheat crops. This is especially important in LS12, because in this case these neighboring fields are likely to be in the wheat phase during the following growing season. It is thus beneficial that the wheat phases are more frequently rotated with other crops to avoid multiple successive wheat phases (i.e., WSSWLL provides better control than WWLLSS).

The crop with which the rotation was initiated strongly affected the population dynamics of the transient phase, revealing that studies on the short-term population behavior for different cyclic permutations could complement studies of long-term population behavior when developing appropriate management strategies (see also Mertens et al., 2003). For rotation and landscape scenarios resulting in high yearly seed density variability, it can take a long time for the densities to reach equilibrium. Because farmers and advisors tend to make decisions based on short-term outcomes rather than long-term predictions, the seed densities established during the transient phase should be taken into consideration when new crop rotation schemes are designed (Mertens et al., 2002; 2003) and the crop with which the rotation is initiated should thus be chosen with care.

III. 5. REFERENCES

Aibar, J.; Ochoa, M. J.; Zaragoza C. (1991) Field emergence of *Avena fatua* L. and *A. sterilis* ssp. *ludoviciana* (dur.) Nym. in Aragon, Spain. Weed Research 31, 29-32.

Auld, B. A.; Coote, B. G. (1980) A model of a spreading plant population. Oikos 34, 287-292.

Benton, T. G.; Vickery, J. A.; Wilson, J. D. (2003) Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology and Evolution 18, 182-188.

Benvenuti, S. (2007) Weed seed movement and dispersal strategies in the agricultural environment. Weed Biology and Management 7, 141-157.

Bohan, D. A.; Powers, S. J.; Champion, G.; Haughton, A. J.; Hawes, C.; Squire, G.; Cussans, J.; Mertens, K. (2011) Modelling rotations: can crop sequences explain arable weed seedbank abundance? Weed Research 51, 422-432.

Caswell, H. (2001) Matrix population models. Construction, analysis, and interpretation. Second edition. Sinauer Associates, USA.

Colbach, N.; Clermont-Dauphin, C.; Meynard, J. M. (2001) GENESYS: a model of the influence of cropping system on gene escape from herbicide tolerant rapeseed crops to rape volunteers II. Genetic exchanges among volunteer and cropped populations in a small region. Agriculture, Ecosystems and Environment 83, 255-270.

Colbach, N.; Monok, H.; Lavigne, C. (2009) A simulaton study of the medium-term effects of field patterns on cross-pollination rates in oilseed rape (*Brassica napus* L.). Ecological Modelling 220, 662-672.

Cousens, R.; Mortimer, A. M. (1995) Extrinsic factors affecting population density. In: Dynamics of weed populations (Eds. Cousens, R. and Mortimer, A. M.) 169-216. Cambridge University Press, UK.

Cutforth, L. B.; Francis, C. A.; Lynne, G. D.; Mortensen, D. A.; Eskridge, K. M. (2001) Factors affecting farmers' crop diversity decisions: an integrated approach. American Journal of Alternative Agriculture 16, 168-176.

Dauer, J. T.; Luschei, E. C.; Mortensen, D. A. (2009) Effects of landscape composition on spread of an herbicide-resistant weed. Landscape Ecology 24, 735-747.

Fernández-Quintanilla, C.; Navarrete, L.; Torner, C. (1984) The influence of crop rotation on the population dynamics of *Avena sterilis* (L.) ssp. *ludoviciana* Dur., in Central Spain. Proceedings of the 3rd EWRS Symposium on weed problems in the Mediterranean area, 9-15. Oeiras, Portugal.

Ghersa, C. M.; Roush, M. L. (1993) Searching for solutions to weed problems: Do we study competition or dispersion? BioScience 43, 104-109.

González-Andújar, J. L.; Fernández-Quintanilla, C. (1991) Modelling the population dynamics of *Avena sterilis* under dry-land cereal cropping systems. The Journal of Applied Ecology 28, 16-27.

González-Andújar, J. L.; Fernández-Quintanilla, C. (1993) Strategies for the control of *Avena sterilis* in winter wheat production systems in central Spain. Crop Protection 12, 617-623.

González-Andújar, J. L.; Plant, R. E.; Fernández-Quintanilla, C. (2001) Modeling the effect of farmers' decisions on the population dynamics of winter wild oat in an agricultural landscape. Weed Science 49, 414–422.

González-Andújar, J. L.; Saavedra, M. (2003) Spatial distribution of annual grass weed populations in winter cereals. Crop Protection 22, 629-633.

Hanski, I. (1991) Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society 42, 17-38.

Helenius, J. (1997) Spatial scales in ecological pest management (EPM): importance of regional crop rotations. Entomological Research in Organic Agriculture 15, 163-170.

Joannon, A.; Bro, E.; Thenail, C.; Baudry, J. (2008) Crop patterns and habitat preferences of the grey partridge farmland bird. Agronomy for Sustainable Development 28, 379-387.

Jordan, N.; Mortensen, D. A.; Prenzlow, D. M.; Cox, K. C. (1995) Simulation analysis of crop rotation effects on weed seedbanks. American Journal of Botany 82, 390-398.

Jurado-Expósito, M.; López-Granados, F.; González-Andújar, J. L.; García-Torres, L. (2005) Characterizing population growth rate of *Convolvulus arvensis* in wheat-sunflower no-tillage systems. Crop Science 45, 2106-2112.

Junta de Andalucía (2010) Anuario Estadístico de Andalucía. Andalusian Autonomous Gobernment, Spain.

Liebman, M.; Dyck, E. (1993) Crop rotation and intercropping strategies for weed management. Ecological Applications 3, 92-122.

Magurran, A. E. (2004) Introduction: measurement of (biological) diversity. In: Measuring Biological Diversity (Ed. Magurran, A. E.) 1-17. Blackwell Science, UK.

Mertens, S. K.; Gilligan, C. A.; van den Bosch, F. (2003) Effects of initial conditions on weed seedbank dynamics in crop rotations. Aspects of Applied Biology 69, 223-228.

Mertens, S. K.; van den Bosch, F.; Heesterbeek, J. A. P. (2002) Weed populations and crop rotations: exploring dynamics of a structured periodic system. Ecological Applications 12, 1125-1141.

Michael, P. J.; Owen, M. J.; Powles, S. B. (2010) Herbicide-resistant weed seeds contaminate grain sown in the western Australian grainbelt. Weed Science 58, 466-472.

Mortimer, A. M.; Sutton, J. J.; Gould, P. (1989) On robust weed population models. Weed Research 29, 229-238.

Navarrete, L.; Fernández-Quintanilla, C. (1996) The influence of crop rotation and soil tillage on seed population dynamics of *Avena sterilis* ssp. *ludoviciana*. Weed Research 36, 123-131.

Perry, J. N.; González-Andújar, J. L. (1993) Dispersal in a metapopulation neighbourhood model of an annual plant with a seedbank. Journal of Ecology 81, 453-463.

Saavedra, M.; Cuevas, J.; Mesa-García, J.; García-Torres, L. (1989) Grassy weeds in winter cereals in Southern Spain. Crop Protection 8, 181-187.

Sánchez del Arco, M.; Torner, C.; Fernández-Quintanilla, C. (1995) Seed dynamics in populations of *Avena sterilis* ssp. *ludoviciana*. Weed Research 35, 477-487.

Shirtliffe, S. J.; Entz, M. H. (2005) Chaff collection reduces seed dispersal of wild oat (*Avena fatua*) by a combine harvester. Weed Science 53, 465-470.

Steinmann, H. H.; Klingebiel, L. (2004) Secondary dispersal, spatial dynamics and effects of herbicides on reproductive capacity of a recently introduced population of *Bromus sterilis* in an arable field. Weed Research 44, 388-396.

Thenail, C.; Foannon, A.; Capitaine, M.; Souchère, V.; Mignolet, C.; Schermann, N.; Di Pietro, F.; Pons, Y.; Gaucherel, C.; Viaud, V.; Baudry, J. (2009) The contribution of crop-rotation organization in farms to crop-mosaic patterning at local landscape scales. Agriculture, Ecosystems and Environment 131, 207-219.

Thill, D. C.; Mallory-Smith, C. A. (1997) The nature and consequence of weed spread in cropping systems. Weed Science 45, 337-342.

van den Berg, F.; Gilligan, C. A.; Gerdessen, J. C.; Gregoire, L. A. H.; van den Bosch, F. (2010) Optimal weed management in crop rotations: incorporating economics is crucial. Weed Research 50, 413-424.

Westerman, P. R.; Liebman, M.; Menalled, F. D.; Heggenstaller, A. H.; Hartzler, R.; Dixon, P. M. (2005) Are many little hammers effective? Velvetleaf (*Abutilon theophrasti*) population dynamics in two- and four-year crop rotation systems. Weed Science 53,389-392.

APPENDIX A. SENSITIVITY ANALYSIS FOR THE CONTROL PARAMETERS.

A sensitivity analysis was performed for the control parameters in sunflower and legume crops as they appear to be the most critical model parameters. Independent simulations were performed for the maximum and minimum values of c_S and c_L estimated from Fernández-Quintanilla et al. (1984) and the results compared with those found for default levels of control.

Table A1 shows that when the control parameter values were set to their minimum values the crop rotation ranking in relation to their effectiveness in decreasing the weed seed bank density changed slightly for the three crop species rotations, whereas the qualitative results remained unchanged for the two crop species rotations. When the control values were set to their maximum values the weed populations became extinct for the three crop species rotations whereas for the two crop species rotations Rotation 2 became more beneficial than Rotation 1.

Table A1. Mean equilibrium *A. sterilis* seed densities (seeds/m²) for different control rates in sunflower and legume crops, c_S and c_L, in both the two and three crop species rotations. All simulations are run for landscape scenarios 6 and 14 (LS6 and LS14), respectively, and a dispersal fraction of 0.014.

ROTATION SCENARIO	**Example***	**Minimum control**		**Default control**	**Maximum control**	
		c_S**=0.98‡**	c_L**=0.85¶**	c_S**=0.99‡ &** c_L**=0.93¶**	c_S**=1‡**	c_L**=0.99¶**
1	WSWS	686†		1452	885	
2(a)	WWSS	1840		1476	737	
3	WSLWSL	465	1101	258	0	0
4	WLSWLS	358	686	174	0	0
5(a)	WWSSLL	602	1317	338	0	0
6(a)	WWSLLS	507	1020	261	0	0
7(a)	WWLSSL	426	836	193	0	0
8(a)	WWLLSS	370	650	163	0	0
9(a)	WSSWLL	422	929	226	0	0

* i.e., wheat as the initial crop.

† SEs are not included because of their small values (<1%).

‡ From Fernández-Quintanilla et al.'s (1984) experiment the control parameter can be estimated. Two field experiments were performed in a randomised block design to evaluate their effects on *A. sterilis* demography. The experiments accounted for two and four cropping systems over four and two years, respectively. The cropping sequences studied were a winter wheat monoculture and a fallow-spring barley rotation in the first experiment and winter barley and spring barley monocultures and fallow-winter barley and sunflower-winter barley rotations and vice versa in the second experiment. For each plot seed bank and panicle densities were measured annually at both the beginning and the end of the weed life cycle. The sunflower control parameter c_S was estimated from $N_{t+1}=N_t\lambda g(1-c_S)(1+agN_t)^{-b}+sN_t$ with N_t and N_{t+1} the two year average weed seed bank densities in sunflower at the beginning and end of the weed life cycle, respectively, as supplied by Fernández-Quintanilla et al. (1984) and all other parameters set to their default value.

¶ No literature available. Estimated according to the *A. sterilis* seed bank in spring barley (Fernández-Quintanilla et al., 1984) and $N_{t+1}=N_t\lambda g(1-c_L)(1+agN_t)^{-b}+sN_t$, with N_t and N_{t+1} the 4 year average weed seed bank densities in spring barley at the beginning and end of the weed life cycle, respectively, as supplied by the reference and all other parameters set to their default value.

REFERENCES APPENDIX A

Fernández-Quintanilla, C.; Navarrete, L.; Torner, C. (1984) The influence of crop rotation on the population dynamics of *Avena sterilis* (L.) ssp. *ludoviciana* Dur., in Central Spain. Proceedings of the 3rd EWRS Symposium on weed problems in the Mediterranean area, 9-15. Oeiras, Portugal.

CAPÍTULO IV

Modelling the herbicide-resistance evolution in *Lolium rigidum* populations at the landscape scale

CAPÍTULO IV: MODELLING THE HERBICIDE-RESISTANCE EVOLUTION IN *Lolium rigidum* POPULATIONS AT THE LANDSCAPE SCALE

RESUMEN

El uso de herbicidas es un componente clave en las estrategias de control de las malas hierbas en los cereales de secano españoles. Sin embargo, la eficacia de esta estrategia de control está actualmente cuestionada debido al desarrollo de poblaciones resistentes a los herbicidas. En este trabajo se ha desarrollado un modelo de resistencia a los herbicidas espacialmente explícito a escala de paisaje para estudiar la evolución de la resistencia en poblaciones de *Lolium rigidum* Gaudin bajo diferentes estrategias de manejo y evaluar la importancia de las diferentes fuentes de dispersión de genes en la expansión de la resistencia. Los resultados de las simulaciones muestran un rápido desarrollo de la resistencia a los herbicidas bajo aplicaciones repetidas del mismo herbicida, influenciado principalmente por la fecundidad de la mala hierba y por la eficacia del herbicida. El desarrollo de la resistencia también se vio influenciado por la penalización en el fitness de las plantas resistentes, lo cual aumentó el número de años necesarios para alcanzar poblaciones resistentes a nivel de paisaje. Las estrategias de manejo más eficientes en retrasar el desarrollo de la resistencia en paisajes con individuos resistentes, fueron aquéllas centradas en diversificar los sistemas de cultivo (i.e., rotación de cultivo vs. monocultivo) y la aplicación de herbicidas (i.e., rotación de herbicidas con diferente modo de acción). El polen fue el principal responsable de la dispersión de la resistencia y junto con la dispersión de semillas produjeron un efecto sinérgico positivo en la expansión de las poblaciones resistentes. Estrategias de manejo basadas en reducir la dispersión de las semillas de las malas hierbas tal como el uso de semilla certificada o limpia para la siembra del cereal fueron eficientes reduciendo la dispersión de la resistencia. Sin embargo, el acoplamiento a la cosechadora de un colector de paja podría generar resultados no esperados como el enriquecimiento de la resistencia en el paisaje. El movimiento de la cosechadora también influyó en la expansión de la resistencia de tal manera que es recomendable un movimiento que minimice el desplazamiento de la cosechadora entre parcelas (i.e., cosechando las parcelas de cereal más cercanas). El modelo desarrollado es una potente herramienta que puede ser utilizado para explorar nuevas estrategias de manejo a diferentes escalas espaciales e incrementar el nivel de conocimiento sobre la dinámica de la resistencia a los herbicidas.

Palabras clave: dinámica de poblaciones, estrategias de manejo, flujo de genes, modelo espacialmente explícito, modelo explícito genotípicamente, vectores de dispersión.

ABSTRACT

Herbicide application is a key component in the weed control strategies of Spanish dry cereals. However, the efficacy of this tactic is currently threatened by the evolution of herbicide-resistant populations. In this paper, a spatially explicit herbicide-resistance model implemented at landscape scale has been developed to study the evolution of herbicide resistance in *Lolium rigidum* Gaudin populations under different management strategies and to evaluate the importance of the gene dispersal sources in the resistance spread. The simulations showed that herbicide resistance evolved rapidly under repeated herbicide applications mainly led by the weed potential fecundity and the herbicide efficacy. Fitness cost associated to resistant plants also influenced on resistance evolution increasing the time to resistance occurrence at the landscape level. The management strategies that slowed resistance evolution most efficiently when resistance is present across entire landscape, were those focused on diversifying the cropping system (i.e., crop rotation vs. monoculture) and herbicide applications (i.e., rotation of different herbicide modes of action). The pollen flow was the dispersal vector which mainly drives the herbicide-resistance spread and in conjunction with seed dispersal both had a positive synergistic effect in the resistance spread. Strategies based on limiting the seed dispersal such as the use of certified or cleaned crop seeds at sowing were efficient decreasing the resistance spread. However, the use of a seed catching device at harvest timing might generate no desirable results in the resistance evolution as it produced resistance enrichment in the area. The harvester movement around the landscape influenced on resistance spread being desirable that harvester minimizes the movement between cereals fields (i.e., choosing the nearest cereal fields). The model presented here is a potent tool that may be expanded to explore new management strategies at different spatial scales and to increase our knowledge about herbicide-resistance dynamic.

Key words: explicit genotype model, dispersal vectors, gene flow, management strategies, population dynamic, spatially explicit model.

IV. 1. INTRODUCTION

Weeds are widespread on farmland in all regions of the world. They compete with crops for space and resources and decrease yields because of their competitive capacity and abundance (Izquierdo et al., 2003). This makes them undesirable and efforts to control weeds are often based on herbicide applications (Saavedra et al., 1989) often with the same mode of action year after year (Cirujeda and Taberner, 2010). If herbicide resistant genotypes are present in populations, the high selection pressure exerted by these applications will result in the evolution of herbicide resistance (Jasieniuk et al., 1996). Currently, there are more than 300 herbicide resistant biotypes currently documented (Heap, 2011). In *Lolium rigidum* Gaudin, an important annual weed in Mediterranean cereals, resistance to as many as 11 herbicide groups has been identified (Heap, 2011) with cross-resistance and multiple resistance in many cases (Yu et al., 2007).

A study in Spain to determine the presence of resistant *L. rigidum* plants in three large cereal-growing regions identified undamaged plants following chlortoluron, chlorsulfuron, diclofop-methyl and glyphosate applications in those areas where the herbicides were tested (Loureiro et al., 2010). Catalonia, in the North of Spain, was the region with the highest rate of undamaged plants in the collected accessions at commercial doses of chlortoluron and chlorsulfuron (25% and 80%, respectively). Resistance to chlorsulfuron was particularly prevalent likely due to the wide use of this herbicide in the area (Taberner, 1996). The percentage of accessions with undamaged plants was 11.8% and 3.5% in the regions of Andalusia (in the South of Spain) and Castile and León (in the North-West of Spain) for chlortoluron and 47% and 43% for chlorsulfuron applications at single doses. In Castile and León where the glyphosate and diclofop-methyl were tested, the percentage of accessions with undamaged plants were 49% and 12.5%, respectively.

To better understand and identify the key processes affecting herbicide-resistance evolution a large number of models have been developed (see Gressel and Segel, 1978; Maxwell et al., 1990; Diggle et al., 2003). Models are useful tools to facilitate the study of weed population dynamics over a long period of time. Important factors that impact on the rate of resistance evolution include the weed biology, the genetics of the resistance genes, and herbicide and cropping system parameters (Powles and Yu, 2010). The confluence of all these factors determines the response and the rate of herbicide-resistance evolution (Jasieniuk et al., 1996). Essential components of the model are consequently based on the knowledge about these factors and their interactions and are reflected on the structure of the model. Hence, a model could include a population genetic, a weed population dynamic and a dispersal sub-model (Maxwell et al., 1990). The weed population dynamic sub-model relies on the biology of the weed such as the germination pattern, the dormancy, the seedling survival and the seed production whilst the genetic sub-model deals with the inheritance of the herbicide-resistance trait. Finally, a spatial dimension of the model cannot be omitted because of the importance of the pollen and seed flow on the evolution and spread of resistance (Busi et al., 2011).

A reduced number the models have examined spatial aspects of herbicide resistance evolution (Richter et al., 2002; Richter and Seppelt, 2004; Roux and Reboud, 2007; Roux et al., 2008; Dauer et al., 2009). Most of these models construct theoretical frameworks where management scenarios to slow resistance spread are simulated. Management strategies are studied either at the temporal scale, i.e., the management scenarios take into account diversified control methods over time (Richter et al., 2002) or at a spatio-temporal scale, i.e., the spatial organization of the control methods is also included (Roux et al., 2008; Dauer et al., 2009).

The spatial processes that result in the evolution and spread of herbicide-resistant plants are affected by diverse factors such as landscape connectivity and the distance among donor areas and areas suitable for invasion. These processes are defined by the landscape composition and biological characteristics associated with weed spread. In most previous approaches, a homogeneous landscape with equal field size, shape and distribution was considered (Roux et al., 2008). This approach is achieved using cellular automata which have a simple grid structure making models easy to implement. Another more complex approach adopts a polygonal approach to landscape composition (Dauer et al., 2009). In this case, the sizes, the shapes and the distances among polygons (i.e., fields) are not homogeneous and the distribution over space is normally that outlined from a particular landscape. We have adopted a mixed approach based on a cellular automaton grid whereby cells are aggregated to match real field size distributions for a particular study site. So, we have a heterogeneous landscape with different field sizes and distances among fields easily changeable according to the landscape structure. Taking into account these particular attributes, a spatially explicit model was developed in order to create a framework whereby the dispersal events associated with pollen and seed movement of herbicide-resistant *L. rigidum* are included according to the biology and ecology of the weed and the landscape in the South of Spain.

The objectives of this study were to explore (1) herbicide-resistance evolution under current cropping regimes, (2) the effect of diverse management strategies in slowing resistance evolution, (3) the dispersal vectors which mainly drive herbicide resistance evolution at the landscape level and (4) the key parameters which most influence model outcomes.

IV. 2. MATERIALS AND METHODS

IV. 2. 1. MODEL DESCRIPTION:

The spatially explicit model was constituted as a regular grid consisting of R x R cells with $R =$ 100. Each cell represented 1 ha. So, the simulated landscape represented an area of 10000 ha. The R cells were spatially aggregated into larger units called fields. All of the unit cells of a simulated field followed the same management program and consequently they were exposed to equal selection pressure. Eight possible size classes were considered in the model (Table 1). The number of fields in each field-size class accounted for the current field-size distribution in the Andalusian (South of Spain) landscape both in terms of the number of fields and the total area occupied by a particular field-size class (INE, 2010). Such cell aggregation followed specific rules such a rectangular shape (5:4 or the nearest possible) (Rodríguez and Wiegand, 2009), similar to those found in many European countries. Field allocation was randomized over the landscape in order of decreasing field size. An example of the simulated landscape is depicted in the Fig. 1. As this routine makes the model stochastic each simulation scenario was replicated 100 times.

Table 1. Field-size classes and the major crop distribution according to the Andalusian landscape (INE, 2010).

FIELD-SIZE CLASS	Unit field size (ha/field)	Field dimension	Number of fields	Total field size (ha)	Cereal crops (%)	Sunflower crops (%)
Class 1	1	1 x 1	26	26	89	11
Class 2	2	1 x 2	74	148	88	12
Class 3	4	2 x 2	77	308	69	31
Class 4	6	2 x 3	108	648	79	21
Class 5	10	2 x 5	59	590	81	19
Class 6	15	3 x 5	57	855	77	23
Class 7	27	3 x 9	56	1512	78	22
Class 8	81	9 x 9	73	5913	77	23

The crops included in the model were those most abundant in the Andalusia farmland (INE, 2010): cereal and sunflower. Cereal crops are sown in monoculture or in cereal-sunflower two-year rotations. Sunflower crops are always sown in rotation with cereals. Around 58% of the whole landscape was under cereal monoculture and the remaining 42% was under cereal-sunflower rotation. The initial assignment of both crops over the simulated landscape was randomized according to the current area distribution (Table 1).

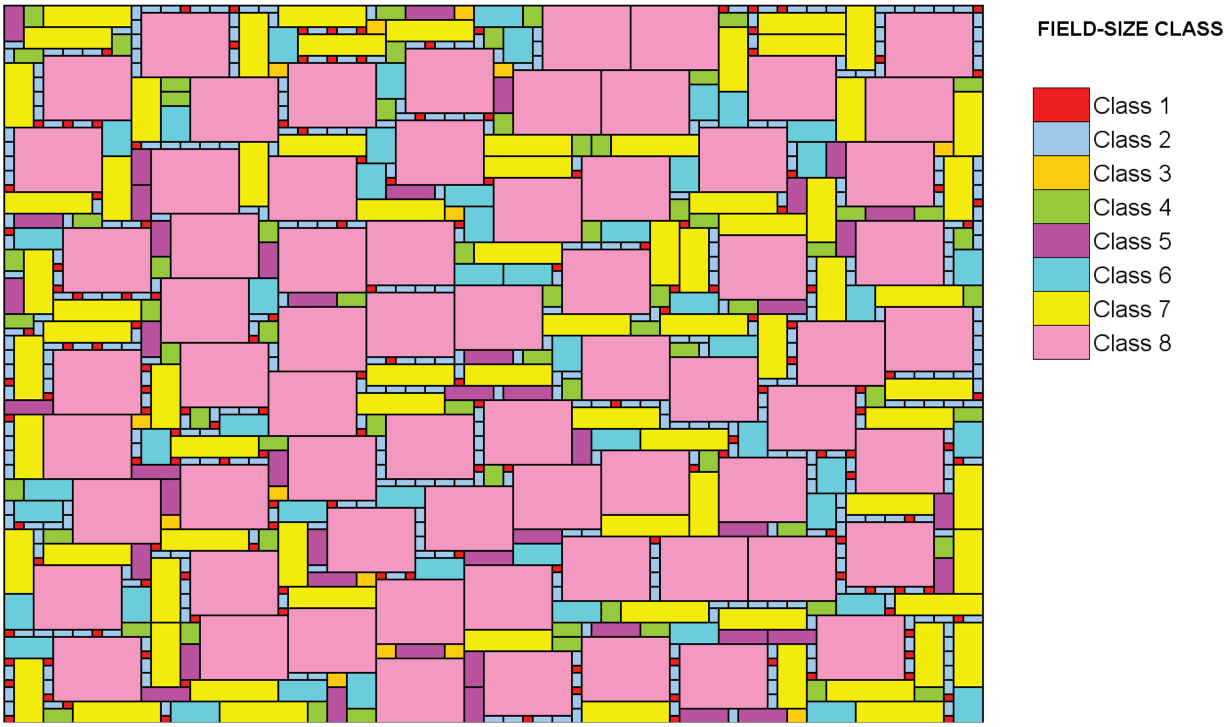

Figure 1. An example of the randomized field-size classes distribution over the landscape.

In all cells, a population dynamics sub-model was implemented. Processes of interchange of *L. rigidum* pollen and seeds between cells allow gene flow over the landscape and these processes are included as another sub-model. Both sub-models are addressed in depth later and are schematized in Fig. 2.

IV. 2. 1. 1. Population dynamic sub-model

The population dynamic sub-model combines a weed population dynamic and a single-gene explicit genotype model. The first describes the weed life cycle and the second is a population genetic model whereby the frequency of individual herbicide susceptible and herbicide resistant genotypes is accounted. The herbicide-resistance gene is a major nuclear dominant gene with two alleles denoted by A and a, i.e., A codes for resistance and a for susceptibility to herbicides. Then, we would have three possible genotypes: homozygous susceptible (aa), heterozygous resistant (aA) and homozygous resistant (AA).

The weed population dynamic sub-model was parameterized for *L. rigidum* and accounts for the main states of the weed life cycle. Such states are interconnected by fluxes derived from the weed biology itself and operational events in the crop (Fig. 2).

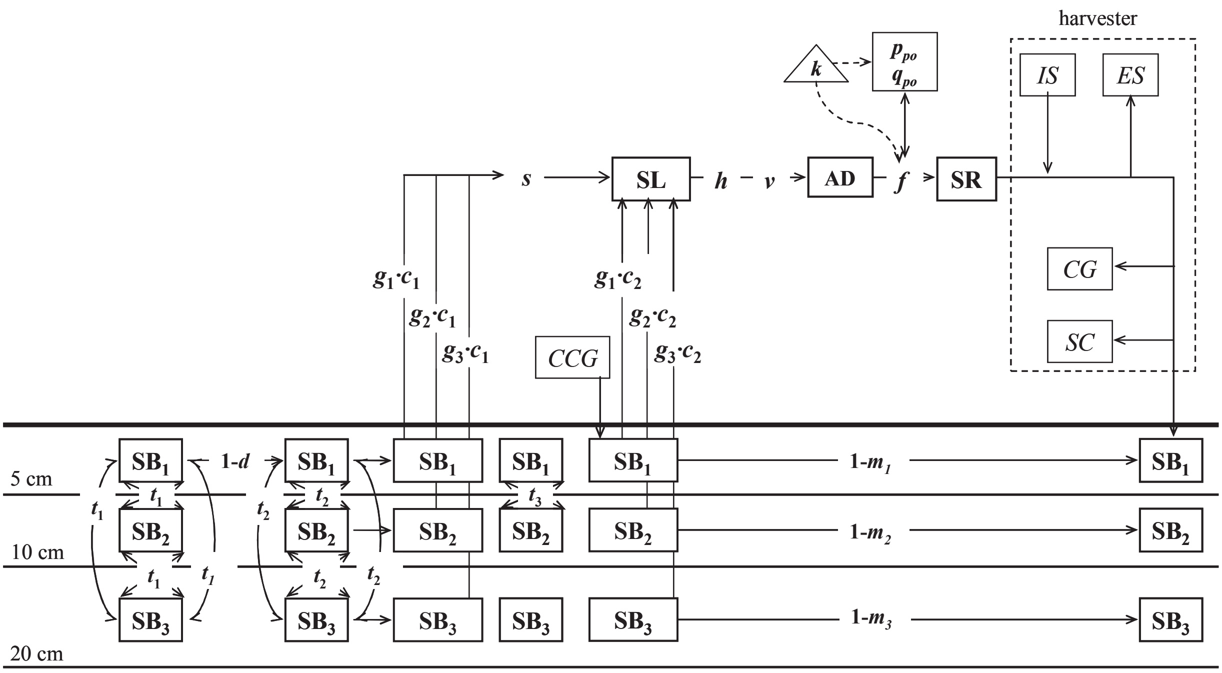

Figure 2. Model diagram of the weed life cycle and the gene flow sub-models for a depth-structured seed bank in a cereal cropping season. The state variables for the weed life cycle sub-model are the seed bank, **SB**, the seedlings, **SL**, the adult plants, **AD** and the seed rain, **SR**. Other variables which take part in the gene flow sub-model are the weed seeds that are imported and exported by the harvester, *IS* and *ES*, the weed seeds contaminating the crop grain at the harvest timing, *CG*, the weed seeds contaminating the cereal seeds at the crop seeding timing, *CCG,* the weed seeds caught by seed catcher, *SC*, and the frequency of the resistance alleles in the pollen cloud, p_{po} and q_{po}. The constant of the model are the seed interchange fraction between the three soil layers for each tillage plough, t, the structured germination fraction, g, of each cohort, c, the natural seed bank mortality fraction, m, the seedling survival fraction following the tillage operation, s, the seed bank predation fraction, d, the survival fraction following the control exerted by the herbicide application, h, the natural seedling survival fraction, v, the mutation rate, k, and the potential fecundity of an isolated plant, f.

IV. 2. 1. 1. 1. Seed bank dynamic and seedling survival

The model has a depth-structured seed bank in three different soil layers. The first layer constitutes the surface to 5 cm depth, the second layer from 5 cm to 10 cm depth and the final layer deeper than 10 cm. At the beginning of the simulations, the total initial weed seed density (SB_{ini}) in the soil was concentrated in the first soil layer with the genotype frequencies based on Hardy-Weinberg equilibrium (Jasieniuk et al., 1996) calculated according to an initial frequency of the herbicide resistance allele, p_{ini}.

A model simulation year starts in August with a new cropping season and finishes with the crop harvest in July of the following year. As the weed seed bank is a depth-structured variable the model was organized in terms of matrices with a structure similar to that used in the model developed by Richter et al. (2002). Then, the weed life cycle main stages for each genotype can be represented as a state vector whereby its components are the seed bank in each soil layer (SB_1, SB_2, SB_3), the seedlings (SL), the adult plants (AD) and the seed rain (SR). The state vector in each cell position $[i, j]$,

$\mathbf{Z}^{t}_{y,xx}[i,j] = \left(SR[i,j], AD[i,j], SL[i,j], SB_1[i,j], SB_2[i,j], SB_3[i,j]\right)^{t}_{y,xx}$, is indexed by the time step in the life cycle evolution (subscript y, with values from 1 at the beginning of the weed life cycle to 9 at the end of the weed life cycle) within every model simulation year (superscript t) and genotype (subscript xx, with values aa, aA and AA).

The initial weed population structure at the beginning of the cropping season $\mathbf{Z}^{t}_{1,xx}$ is that at the end of the previous cropping season $\mathbf{Z}^{t-1}_{9,xx}$.

$$\mathbf{Z}^{t}_{1,xx}[i,j] = \mathbf{Z}^{t-1}_{9,xx}[i,j] \tag{1}$$

The exchange of seeds between soil layers and the death of established seedlings result from the tillage operations related to the crop grown during each year. The matrix which accounts for these processes is denoted by $\mathbf{T}l_{,n}$ with l being 1, 2 or 3 with regard to the order of the tillage event during the cropping season. The elements of the matrix $\mathbf{T}$ are indexed by the subscript n which means the crop to be grown in the current cropping season with values 1 and 2 for cereal and sunflower crops, respectively.

A primary soil cultivation to incorporate the stubble from the previous crop harvest is a common crop-related operation in Andalusia that facilitates the weed seed movement into the soil. A disc and a paraplow are the tillage tools usually used for cereal and sunflower crops respectively (Perea-Torres and Gil-Ribes, 2006)

$$\mathbf{Z}^{t}_{2,xx}[i,j] = \mathbf{T}1_{n} \cdot \mathbf{Z}^{t}_{1,xx}[i,j] \tag{2}$$

$$\text{with } \mathbf{T}1_{n} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & t1_{11,n} & t1_{21,n} & t1_{31,n} \\ 0 & 0 & 0 & t1_{12,n} & t1_{22,n} & t1_{32,n} \\ 0 & 0 & 0 & t1_{13,n} & t1_{33,n} & t1_{33,n} \end{pmatrix}$$

The matrix elements $t1$ are indexed by the source and recipient soil layer in the seed movement, e.g., $t1_{32}$ is the fraction of seeds coming from the soil layer 3 to the soil layer 2 as a consequence of the first soil cultivation.

Seed removal from the shallow soil layer by harvester ants may have a large impact in decreasing the weed seed bank size in dryland cereals (Baraibar et al., 2009). The weed seed removal rate by the predation activity is included in the model as element d of the projection matrix $\mathbf{D}$.

$$\mathbf{Z}^{t}_{3,xx}[i,j] = \mathbf{D} \cdot \mathbf{Z}^{t}_{2,xx}[i,j] \tag{3}$$

$$\text{with } \mathbf{D} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1-d & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

L. rigidum has a germination period focused on the winter season and mainly associated with cereal crop germination time with some weed plants already established at crop seeding time (Taberner, 1996). Hence, we distinguish two cohorts in relation to crop seeding event. Seedlings of cohort 1 are those that germinate prior to crop seeding and are affected by a second tillage event with a field cultivator or a deeper tillage with a scarifier in fields where cereal or sunflower crops are expected to be grown (Perea-Torres and Gil-Ribes, 2006). The seed bank and the established seedlings are affected as follows

$$\mathbf{Z}^{t}_{4,xx}[i,j] = \mathbf{T}2_{n} \cdot \left(\mathbf{G}_{1} \cdot \mathbf{Z}^{t}_{3,xx}[i,j]\right) \tag{4}$$

$$\text{with } \mathbf{T}2_{n} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s2_{n} & 0 & 0 & 0 \\ 0 & 0 & 0 & t2_{11,n} & t2_{21,n} & t2_{31,n} \\ 0 & 0 & 0 & t2_{12,n} & t2_{22,n} & t2_{32,n} \\ 0 & 0 & 0 & t2_{13,n} & t2_{33,n} & t2_{33,n} \end{pmatrix}$$

$$\text{and } \mathbf{G}_1 = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & g_1c_1 & g_2c_1 & g_3c_1 \\ 0 & 0 & 0 & 1-g_1c_1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1-g_2c_1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1-g_3c_1 \end{pmatrix}$$

The fraction of the seed bank that remains in the soil or germinates in each soil layer is given in the germination matrix $\mathbf{G}_1$ (indexed by the cohort) by the expressions (1- gc_1) and (gc_1). The proportion of overall germination, g (indexed by the soil layer position), contributed by cohort 1 is denoted by the constant c_1 with $s2$ the fraction of seedlings surviving the second mechanical control.

A common practice for farmers is to sow a fraction of cereal seeds from the previous harvested crop (Michael et al., 2010; José-María and Sans, 2011). This crop seed may have been contaminated with weed seeds that increase the weed seed bank in the first soil layer. The weed seeds contaminating the crop seeds to be sown in a field are denoted by CCG and it corresponds with a fraction of weed seeds contaminating the cereal seeds from the previous harvested cereal crop in such field. The matrix which accounts for this process is denoted by $\mathbf{CCG}^{t-1}_{n,xx}[i,j] = (0,0,0,CCG_{n,xx}[i,j],0,0)^{t-1}_{n,xx}$

$$\mathbf{Z}^{t}_{5,xx}[i,j] = \mathbf{Z}^{t}_{4,xx}[i,j] + \mathbf{CCG}^{t-1}_{n,xx}[i,j] \qquad (5)$$

Once the weed cohort 2 has germinated the established weed seedlings of both cohorts are controlled according to the crop sown in the field; mechanical control in sunflower crops and chemical control by post-emergence herbicide application in cereal crops. The fraction of the seedlings that survives to the post-emergence herbicide application is given in the matrix $\mathbf{H}_n$ (indexed by the crop). The seed bank and seedlings surviving these control methods are

$$\mathbf{Z}^{t}_{6,xx}[i,j] = \mathbf{T3}_n \cdot \mathbf{H}_n \cdot \left(\mathbf{G}_2 \cdot \mathbf{Z}^{t}_{5,xx}[i,j]\right) \qquad (6)$$

$$\text{with } \mathbf{T3}_n = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s3_n & 0 & 0 & 0 \\ 0 & 0 & 0 & t3_{11,n} & t3_{21,n} & t3_{31,n} \\ 0 & 0 & 0 & t3_{12,n} & t3_{22,n} & t3_{32,n} \\ 0 & 0 & 0 & t3_{13,n} & t3_{33,n} & t3_{33,n} \end{pmatrix}$$

$$\text{and } \mathbf{H}_n = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & (1-h_{n,xx}) & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

$$\text{and } \mathbf{G}_2 = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & g_1c_2 & g_2c_2 & g_3c_2 \\ 0 & 0 & 0 & 1-g_1c_2 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1-g_2c_2 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1-g_3c_2 \end{pmatrix}$$

With c_2 being the proportion of overall germination contributed by the cohort 2 and $s3_n$ the survival fraction following mechanical control. The control exerted by the herbicide on each of the three weed genotypes, $h_{n,xx}$, can be different and reflects dominance and fitness in the presence of the herbicide.

As no density-dependent mortality has been observed for *L. rigidum* seedlings (González-Andújar and Fernández-Quintanilla, 2004) a fixed proportion v of total established seedlings reaches maturity. The projection matrix $\mathbf{V}$ accounts for natural seedling survival.

$$\mathbf{Z}_{7,xx}^{t}[i,j] = \mathbf{V} \cdot \mathbf{Z}_{6,xx}^{t}[i,j] \tag{7}$$

$$\text{with } \mathbf{V} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & v & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

IV. 2. 1. 1. 2. Seed production

The established mature individuals produce haploid ova (unfertilized seeds) and pollen in relation to their own genotype. Ova are produced by adult plants in direct proportion to predicted seed production (see below) and pollen is produced by individual plants in excess. The pollen produced in each cell and the pollen that is dispersed into the cell by pollen flow from neighboring cells fertilize the ova present to produce seeds of the three resistance genotypes.

We denoted the amount of ovules (seeds) produced by the adult plants as $OV_{xx}[i, j]$ with genotype xx according to a density-dependent hyperbolic model fitted to *L. rigidum* by González-Andújar and Fernández-Quintanilla (2004).

$$OV_{xx}[i,j] = \frac{AD_{xx} \cdot f_n}{1 + b \cdot AD_{total}[i,j]} \tag{8}$$

with $AD_{total}[i,j] = AD_{aa}[i,j] + AD_{aA}[i,j] + AD_{AA}[i,j]$

The total seed rain, $SR_{total}[i, j]$, is

$$SR_{total}[i,j] = OV_{aa}[i,j] + OV_{aA}[i,j] + OV_{AA}[i,j] \tag{9}$$

The frequency of the herbicide-resistant and herbicide-susceptible allele, p and q respectively, of the produced ova is estimated as

$$p[i,j] = \frac{OV_{AA}[i,j] + \frac{1}{2} OV_{aA}[i,j]}{SR_{total}[i,j]} \tag{10}$$

$$q[i,j] = \frac{OV_{aa}[i,j] + \frac{1}{2} OV_{aA}[i,j]}{SR_{total}[i,j]} \tag{11}$$

These frequencies can be modified by spontaneous mutation at the locus coding for herbicide resistance. The mutation rate is k and the new frequencies of the resistance alleles, p_m and q_m, are

$$p_m[i,j] = p[i,j] - k \cdot p[i,j] + k \cdot q[i,j] \tag{13}$$

$$q_m[i,j] = q[i,j] - k \cdot q[i,j] + k \cdot p[i,j] \tag{14}$$

If we denote $p_{po}[i, j]$ and $q_{po}[i, j]$ as the frequency for each allele in the pollen cloud of a particular cell, which takes into account pollen movement (see later), and assuming that *L. rigidum* is an obligated outcrossing species, the genotype frequency of the seed rain, GF_{xx}, after the mating is calculated as follows

$$GF_{aa}[i,j] = q_{po}[i,j] \cdot q_m[i,j] \tag{15}$$

$$GF_{aA}[i,j] = p_{po}[i,j] \cdot q_m[i,j] + q_{po}[i,j] \cdot p_m[i,j] \tag{16}$$

$$GF_{aa}[i,j] = p_{po}[i,j] \cdot p_m[i,j] \tag{17}$$

After mating, the already produced seed rain is incorporated into the system, matrix $\mathbf{F}_{xx}$. The mortality of the seed bank during the cropping season is denoted by the matrix $\mathbf{M}$.The state vector at this point is

$$\mathbf{Z}^t_{8,xx}[i,j] = \mathbf{M} \cdot \mathbf{Z}^t_{7,xx}[i,j] + \mathbf{F}_{xx}[i,j] \tag{18}$$

with $\mathbf{M} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1-m_1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1-m_2 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1-m_3 \end{pmatrix}$

and $\mathbf{F}_{xx}[i,j] = \begin{pmatrix} SR_{total}[i,j] \cdot GF_{xx}[i,j] & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$

The natural mortality of ungerminated seeds is denoted by m_1, m_2 and m_3, i.e., the fraction of seed removal in the first, second and third soil layer.

Finally, the new produced seeds are incorporated to the soil surface finishing the weed life cycle in the detailed cropping season.

$$\mathbf{Z}^t_{9,xx}[i,j] = \mathbf{S} \cdot \mathbf{Z}^t_{8,xx}[i,j] \tag{19}$$

with $\mathbf{S} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$

As described above, movement of seeds between cells by the harvester is avoided and every weed seed is dispersed in the cell where it was produced. Weed seed movement over the landscape by the harvester is further detailed in the gene flow sub-model.

IV. 2. 1. 2. Gene flow sub-model

Gene flow and consequently herbicide resistance dispersal over the landscape can be driven by two long-distance dispersal sources: pollen and seeds. The maximum distance and the shape of the dispersal distribution for pollen and seeds depends on the dispersal agent i.e., wind and agricultural machinery for *L. rigidum* pollen and seeds, respectively.

IV. 2. 1. 2. 1. Pollen dispersal

The pollen is dispersed around a focal cell following the von Moore method (Richter et al., 2002), i.e., a central cell spreads pollen grains to its eight neighboring cells. The Moore radius, denoted by r in Eq. (20) takes values from 1 to z, a value of 1 indicating that pollen is spread to directly neighboring cells only and where z is the maximum of rings of cells that the pollen cloud disperses to. Therefore, the pollen quantity received by a cell in the landscape, PO, is weighted by its distance from all pollen-donating cells with this pollen cloud being mainly composed of pollen grains from the closest cells. The pollen is spread isotropically to the cells belonging to the same ring,

$$PO[i,j] = SR[i,j] \cdot pol_0 + \sum_{r=1}^{z} \frac{\sum_{v=j-r}^{j+r} \sum_{u=i-r}^{i+r} SR[u,v] - \sum_{v=j-r-1}^{j+r-1} \sum_{u=i-r-1}^{i+r-1} SR[u,v]}{r \cdot 8} \cdot pol_r \tag{20}$$

with $pol_0, pol_1, \ldots, pol_z$ the weighting factor of the pollen coming from cells belonging to a particular ring in the pollen cloud.

We supposed that the proportion of resistant alleles in the produced ova and pollen was equal and based on the proportions of mature plant genotype in a given cell. Hence, the p_m and q_m values are equal for the produced ova and pollen. The frequency of the resistance alleles in the pollen for a cell, p_{po} and q_{po}, is a weighted sum of the frequency of the resistance alleles in the pollen cloud for such cell,

$$p_{po}[i,j] = \frac{SR[i,j] \cdot pol_0 \cdot p_m[i,j] + \sum_{r=1}^{z} \frac{\sum_{v=j-r}^{j+r} \sum_{u=i-r}^{i+r} SR[u,v] \cdot p_m[u,v] - \sum_{v=j-r-1}^{j+r-1} \sum_{u=i-r-1}^{i+r-1} SR[u,v] \cdot p_m[u,v]}{r \cdot 8} \cdot pol_r}{PO[i,j]} \tag{21}$$

$$q_{po}[i,j] = 1 - p_{po}[i,j] \quad (22)$$

IV. 2. 1. 2. 2. Seed movement

Weed seed movement over the landscape may occur via two mechanisms, both originating from the crop harvest. These are seed dispersal as a result of harvester movement between cereal cells and seed dispersal between cells of the same field as a result of sowing weed-contaminated cereal grain obtained from the harvested cereal crop in the previous cropping season.

Harvesting cereal crops

The fate of newly produced seeds depends on the timing of seed maturation. Seeds dropping earlier from the mother plant will be immediately incorporated into the shallow layer of the seed bank (SB_1) of the current cell while later-ripening seeds may be harvested with the cereal crop and dispersed by the harvester or as contaminants of cereal grain. We denoted the fraction of produced seeds entering the harvester as gat. A fraction of these seeds will become mixed with the cereal grain (con), while the remainder will be returned to the soil surface following dispersal by the harvester. Dispersal by the harvester will result in seed being returned to the soil surface in cells distant from where they were produced. In our model the fraction of produced seeds exported from a cell are denoted by ES and CG, for seed dispersal vectored by movement of the harvester or seed contamination, respectively. The variable IS represents the seeds imported into the current cell coming from the previous harvested cell and it is equivalent to the ES fraction exported from such previous harvested cell. The state vector $\mathbf{Z}_9$ is rewritten to include the weed seed dispersal at the harvest timing,

$$\mathbf{Z}^{t}_{9,xx}[i,j] = \mathbf{S} \cdot \mathbf{Z}^{t}_{8,xx}[i,j] + \mathbf{IS}_{xx}[i,j] \quad (23)$$

$$\text{with } \mathbf{S} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 1 - CG - ES & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

and $$\mathbf{IS}_{xx}[i,j]=\begin{pmatrix}0\\0\\0\\IS_{xx}[i,j]\\0\\0\end{pmatrix}$$

$$CG = gat_n \cdot con_n \tag{24}$$

$$ES = gat_n \cdot (1-con_n) \cdot ext_n \tag{25}$$

$$IS_{xx}[i,j] = SR_{xx}[i_{har-1}, j_{har-1}] \cdot ES \tag{26}$$

with ext the fraction of seed exported from one cell to the next by the harvester. The position of the previous harvested cell according to the harvester movement is denoted by the coordinates $[i_{har\text{-}1}, j_{har\text{-}1}]$. In the model, the harvester movement is similar to the LOCAL harvesting procedure from Rodríguez and Wiegand's (2009). The harvester driver knows the harvesting area and minimizes the movement between cereals fields (i.e., choosing the nearest cereal fields).

Sowing weed-contaminated grain

The extent of crop grain contamination with weed seed is calculated on a per field basis as the average of contamination in all cells harvested in that cereal field. A fraction of this cereal crop seed may then be sown in the following cereal cropping season in the same field where it was harvested. The potential weed seeds to contaminate the cereal cells at the following seeding timing, CCG_1, would be described as follows

$$CCG_{1,xx}[i,j] = \frac{sr}{yield} \cdot \frac{\sum_{e=1}^{size} SR_{xx}[i,j]_e \cdot CG}{size} \tag{27}$$

with sr the seeding density and $yield$ the expected cereal yield. Denoted by $size$ is the field size or cell number of the field under consideration. The coordinate $[i, j]_e$ refers to the position of the cells into the field. In sunflower cells Eq. (27) takes the value of zero, CCG_2 = 0.

IV. 2. 1. 3. Stochastic routines

To avoid overestimates of herbicide resistance evolution resulting from the inclusion of fractional seeds and plants in the weed life cycle (see Neve 2008) values were rounded to an integer according to the methods of Perry and González-Andújar (1993), such that

$$X = \text{floor}(X + U) = \lfloor X + U \rfloor \qquad (28)$$

with U a random number between 0 and 1 and X the outputs, i.e., adult plants, $AD[i, j]$, and seed rain, $SR[i, j]$.

IV. 2. 1. 4. Parameters of the model and initial conditions

The parameters used in the model are listed in the Table 2 according to the data coming from the literature. As far as possible, the parameter values were taken from Spanish data sets to get a more accurate description of the environment where the model was developed.

IV. 2. 2. SIMULATION SCENARIOS

The model was used to study a variety of management scenarios to predict evolution of herbicide-resistance in *L. rigidum* populations in the current Andalusian landscape. The influence of biological, ecological and genetic factors was also investigated in order to best understand the herbicide resistance behavior at the farmland scale. The outputs were analyzed based on the dynamics of herbicide resistance evolution, i.e., the total weed seed bank and the phenotypic frequency of herbicide resistance over the landscape. The spatial spread of herbicide resistance was studied based on the area occupied by weed populations with evolved resistance (i.e., more than 20% of the seed bank is herbicide resistant Neve et al., 2003). The relative importance of each dispersal vector in herbicide resistance spread was studied in a sequence of separate simulations and dispersal patterns were compared.

IV. 2. 2. 1. Section 1: Evolution of the herbicide-resistant *L. rigidum* populations

Predictions for herbicide resistance evolution were simulated with the parameters and initial conditions fixed to the default values and the management system given in the model procedure (scenario = EST0). Cereal crop seed sown in all fields was a portion of that which was harvested in the previous year in that field (certified seed was not sown). Parameter values in all subsequent simulations were those discussed in the preceding section and included in Table 2 unless otherwise stated.

Table 2. Initial conditions and parameter values and their sources for *L. rigidum* growing in cereal and sunflower crops.

PARAMETERS	Symbol			Cereal crop			Sunflower crop			References
Initial conditions										
Initial seed bank	SB_{ini}			$2.7 \cdot 10^6$ seeds/ha*			$2.7 \cdot 10^6$ seeds/ha*			Saavedra et al. (1989)
Initial frequency of herbicide-resistant allele	p_{ini}			$2.16 \cdot 10^{-5}$†			$2.16 \cdot 10^{-5}$†			Preston and Powles (2002)
Initial weed seeds in the crop seeding density for each genotype	CCS^0_{aa}			0‡			0‡			
	CCS^0_{aA}			0			0			
	CCS^0_{AA}			0			0			
Model parameters										
First tillage operation, $t1$	$t1_{11}$	$t1_{21}$	$t1_{31}$	0.59¶	0.41	0.06	0.70¶	0.15	0.01	Spokas et al. (2007)
	$t1_{12}$	$t1_{22}$	$t1_{32}$	0.34	0.50	0.06	0.20	0.53	0.03	
	$t1_{13}$	$t1_{23}$	$t1_{33}$	0.07	0.09	0.88	0.10	0.32	0.96	
Second tillage operation, $t2$	$t2_{11}$	$t2_{21}$	$t2_{31}$	0.80¶	0.13	0.01	0.85§	0.31	0	Spokas et al. (2007)
	$t2_{12}$	$t2_{22}$	$t2_{32}$	0.13	0.74	0.01	0.15	0.69	0.04	
	$t2_{13}$	$t2_{23}$	$t2_{33}$	0.07	0.13	0.98	0	0	0.96	
Third tillage operation, $t3$	$t3_{11}$	$t3_{21}$	$t3_{31}$	1**	0	0	0.80¶	0.13	0.01	Spokas et al. (2007)
	$t3_{12}$	$t3_{22}$	$t3_{32}$	0	1	0	0.13	0.74	0.01	
	$t3_{13}$	$t3_{23}$	$t3_{33}$	0	0	1	0.07	0.13	0.98	

* Calculated from the average L. rigidum adult plants in cereal fields of Andalusia landscape.

† Averaged from the frequency of L. rigidum survivors under herbicide selection in the laboratory experiments and assuming the populations are in Hardy-Weinberg equilibrium.

‡ A crop seeding density free of weed seeds was initially considered in both crops.

¶ The one-centimeter soil layers of Spokas et al.'s (2007) study were aggregated according to the soil layer depths in the model.

§ No literature available. The plowing matrix for the scarifier was taken from the data of chisel plow.

** The tillage operation was not implemented.

Table 2. Continued

PARAMETERS	**Symbol**	**Cereal crop**	**Sunflower crop**	**References**
Removal fraction by predation activity	d	0.5 ††	0.5 ††	Baraibar et al. (2009)
Germination fraction				
- Soil layer 1	g_1	0.53‡‡	0.53‡‡	Jiménez-Hidalgo et al. (1991)
- Soil layer 2	g_2	0.27	0.27	
- Soil layer 3	g_3	0.02	0.02	
Contribution of each weed cohort to the total germination fraction				
- Cohort 1	c_1	0.65¶¶	0.65¶¶	Owen et al. (2011)
- Cohort 2	c_2	0.35	0.35	
Survival fraction following mechanical control				
- Second mechanical operation	$s1$	0§§	0§§	
- Third mechanical operation	$s2$	1**	0§§	
Herbicide control for each genotype	h_{aa}	0.95[a]	0[b]	
	h_{aA}	0	0	
	h_{AA}	0	0	
Natural seedling survival fraction	v	0.76	0.76	Fernández-Quintanilla et al. (2000)
Potential seed production	f	935 seeds/plant	935 seeds/plant	González-Andújar and Fernández-Quintanilla (2004)

†† Taken from data of *Lolium multiflorum* and *Vicia villosa* seeds removed by invertebrate predators from dryland cereal fields.

‡‡ The data from the soil layer depths in the reference were aggregated according to the soil layer depths in the model.

¶¶ Averaged from the herbicide-susceptible individuals.

§§ The tillage operation was supposed to eliminate all established seedlings.

[a] Herbicide resistance was a dominant trait. Data estimated according to the L. rigidum control exerted by commercial doses of herbicides (Fernández-Quintanilla et al., 1998).

[b] Herbicide was not applied in the sunflower crops.

Table 2. Continued

PARAMETERS	**Symbol**	**Cereal crop**	**Sunflower crop**	**References**
Parameter of the hyperbolic model	b	0.000034 ha[c]	0.000034 ha[c]	González-Andújar and Fernández-Quintanilla (2004)
Mortality of the seed bank				
- Soil layer 1, 2 and 3	$m_1 = m_2 = m_3$	0.30	0.30	Gramshaw and Stern (1977)
Mutation rate for herbicide resistance	k	$2.7 \cdot 10^{-8}$ [d]	$2.7 \cdot 10^{-8}$ [d]	Harms and DiMaio (1991)
Maximum ring around focus cell which is achieved by pollen dispersal	z	1[e]	1[e]	Giddings et al. (1997)
Spread and weighted pollen at distance				
- Focus cell	pol_0	1[e]	1[e]	Giddings et al. (1997)
- Ring 1	pol_1	0.029	0.029	
Harvester parameters	gat	0.91[f]	0[h]	Shirtliffe and Entz (2005)
	con	0.08[f]	0	
	ext	0.02[g]	0	

[c] Value fitted to ha from m^2 unit in the reference for *L. rigidum.*

[d] Taken from the mutation rate for the primisulfuron herbicide in tobacco plants.

[e] Calculated as the probability of a *Lolium perenne* pollen grain to be spread further than 80 meters.

[f] Calculated according to the fraction of *L. rigidum* seeds taken from the cereal fields and the fraction of such which are incorporated to the crop grain (Matthews et al., 1996).

[g] Calculate as the probability of the weed seeds getting into the harvester in a 100-meters trajectory would spread in the next cell (Shirtliffe and Entz, 2005).

[h] No literature availability. There is a low probability that *L. rigidum* seeds spread long distances from the source during sunflower harvester or contaminate the sunflower seeds due to the enormous differences in the morphology of both sunflower and *L. rigidum* seeds.

[i] Calculated according to the fraction of *L. rigidum* seeds eliminated from the cereal grain in the cleaning process.

IV. 2. 2. 2. Section 2: Resistance management strategies

Management strategies to delay the evolution and dispersal of herbicide resistance can be thought as strategies carried by farmers individually at the field level but with landscape effects. These strategies arise from two general groups of measures: decreasing selection for resistance by diversifying weed control methods and/or slowing herbicide resistance spread. In the first group of measures we consider both an increasing farming area with crop rotation and the rotation of different herbicide modes of action among years. The fraction of fields over the whole landscape with a crop rotation program (EST1), i.e., cereal-sunflower rotation, was implemented in the 100% of the landscape. Cereal crop was grown as the starting crop in year 1 in half of the simulated fields and sunflower crop was grown as the starting crop in year 1 in the remainder fields. Herbicide rotation in cereal crops through the use of alternative modes of action were implemented at random in 50 and 100% of the landscape (EST2 and EST3, respectively). Both herbicides were equally efficient at controlling the weed but one of them selected for the target herbicide resistance.

The second group of measures depends on the sowing of certified crop seed in the cereal cropping season for all fields in the landscape (EST4) and the collection of the chaff ejected by the harvester (EST5). The use of certified crop seeds is supposed to reduce in 100% the weed seeds incorporated by sowing. In EST5, when a seed catcher was connected to the harvester, the amount of seed returned to the soil surface was reduced by 66% (Matthews et al., 1996). Combinations of the single measures implemented in EST1 to EST5 (except EST2) were simulated in groups of two (EST6 to EST11), three (EST12 to EST15) and four (EST16) individual strategies as detailed in the Table 3.

IV. 2. 2. 3. Section 3: Importance of the dispersal vector in the evolution of herbicide resistance

Individual simulations were conducted to establish the importance of each dispersal vector in determining the pattern and quantity of herbicide-resistance spread over the landscape. To avoid equivocal results the mutation rate was set to zero in the simulations and just one herbicide-resistant weed-infested cell (with the frequency of the herbicide-resistant allele equal to unity) was allocated in the middle of the area with equal weed density as the remainder of cells in the landscape. The dispersal vectors were: pollen flow, seed movement by sowing contaminated crop seeds and by the harvest process and all possible combinations.

Strategies based on the use of a seed catcher and cleaned crop seeds for seeding were also included in an attempt to slow resistance spread. The seed cleaning operations by farmers or any external cleaning contractor can reduce the *L. rigidum* seed presence in the crop seeds for sowing in around 98% (Michael et al., 2010).

Table 3. Single and multiple management strategies (i.e., combination of single control strategies) simulated.

MANAGEMENT STRATEGIES	**Description**
EST0	Crop rotation in the 42% of the landscape
EST1	Crop rotation in the 100% of the landscape
EST2	Rotation of herbicide modes of action in the 50% of the landscape
EST3	Rotation of herbicide modes of action in the 100% of the landscape
EST4	Sowing of certified cereal crop seed in the 100% of the landscape
EST5	Seed catcher connected to the cereal harvester
EST6	EST1 + EST3
EST7	EST3 + EST4
EST8	EST3 + EST5
EST9	EST1 + EST4
EST10	EST4 + EST5
EST11	EST1 + EST5
EST12	EST1 + EST3 + EST4
EST13	EST1 + EST3 + EST5
EST14	EST3 + EST4 + EST5
EST15	EST1 + EST4 + EST5
EST16	EST1 + EST3 + EST4 + EST5

IV. 2. 2. 4. Section 4: Sensitivity analysis

Sensitivity analyses were performed on demographic, genetic and dispersal parameters and spatial patterns. The parameter values and the spatial patterns (i.e., model modules) evaluated were those with higher variability, difficult to estimate or with a known influence on the model outputs (González-Andújar and Fernández-Quintanilla, 2004; Rodríguez and Wiegand, 2009; Neve et al., 2010).

The uncertain demographic and genetic parameters were the potential fecundity, herbicide control efficacy, the mutation rate, the fitness penalty and the spatial variability of the initial conditions, i.e., the initial weed density and the initial frequency of the resistant allele. These parameters were evaluated under the conditions specified in Section 1. The effects of the fitness penalty were included as decreased potential fecundity of resistant plants.

The uncertain dispersal parameters and spatial patterns to be evaluated in sensitivity analyses were the length of the tail of the pollen flow distribution and the pattern of harvester movement over the landscape. Both were analyzed in the context of the conditions specified in the simulations of section 3. The harvester movement over the landscape during the harvest process was changed as described by Rodríguez and Wiegand (2009) to represent FOREIGN movement whereby the harvester driver did not know the working area and consequently the relative position of the cereal fields to each other.

The domain of each parameter is detailed in the Appendix A. Each parameter was evaluated independently using the default value for all others parameters in the model.

IV. 3. RESULTS

IV. 3. 1. Section 1: Evolution Of Herbicide-Resistant *L. rigidum*

The evolution of herbicide resistance in *L. rigidum* populations was first observed during the third year of simulations (Fig. 3) and during the next four generations the weed population became constituted completely by herbicide-resistant adult plants. The evolution pattern was similar if we focus on weed seed bank (Fig. 3) but its buffer effect provoked a delayed and smoothed growth rate of the herbicide-resistant *L. rigidum* seed bank. This pattern is similar in others simulations although in some cases the buffer effect of the seed bank is much more evident. Because the seed bank is more stable over time than the adult plants, the seed bank dynamic was chosen to explain the outcomes of the model in future simulations.

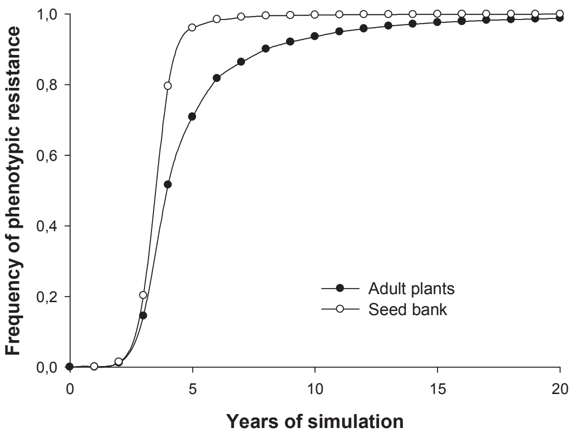

Figure 3. Temporal evolution of the frequency of the herbicide-resistant *L. rigidum* population over the landscape.

The frequency of the herbicide-resistant weed seed bank in cereal monoculture increased faster than it did in crop rotations (Fig. 4) where the increase in resistance frequency oscillated and there was more than a three-year delay in reaching the maximum value.

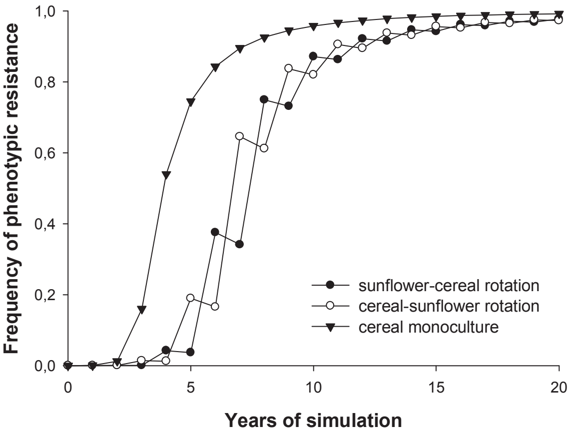

Figure 4. Temporal evolution of the frequency of the herbicide-resistant *L. rigidum* seed bank over the landscape and for different cropping systems.

After four years of simulations the weed population became herbicide-resistant in more than the half landscape (Figs 5 and 6). A weed population was considered to be herbicide-resistant when more than 20% of its total seed bank is heterozygote or homozygote herbicide-resistant (Neve et al., 2003). After eight generations all the fields in the landscape showed herbicide-resistant weed populations (Figs 5 and 6).

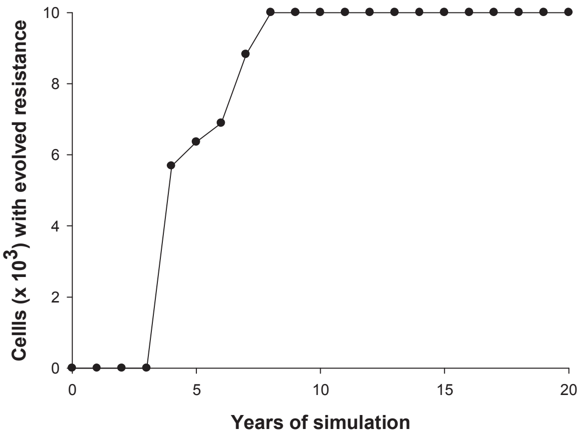

Figure 5. Temporal evolution of the cells (ha) occupied by herbicide-resistant *L. rigidum* seed bank over the landscape. The seed bank is deemed to be resistant when 20% of seeds are phenotypically resistant (AA or aA genotype).

IV. 3. 2. SECTION 2: RESISTANCE MANAGEMENT STRATEGIES

IV. 3. 2. 1. Weed population

The weed seed bank increased over the landscape in all individual strategies simulated (Fig. 7a). The individual strategies EST1 (crop rotation in the entire landscape) and EST5 (seed catcher connected to the harvester) achieved the greatest reduction in weed density over the landscape. No effect was seen in the total seed bank for EST4 (sowing of certified seed) compared to the baseline strategy EST0. The application of a herbicide with different mode of action in rotation over time in the half (EST2) or the entire landscape (EST3) showed an oscillatory behaviour in the seed bank evolution, and weed infestation levels halfway between strategies previously cited (Fig. 7a).

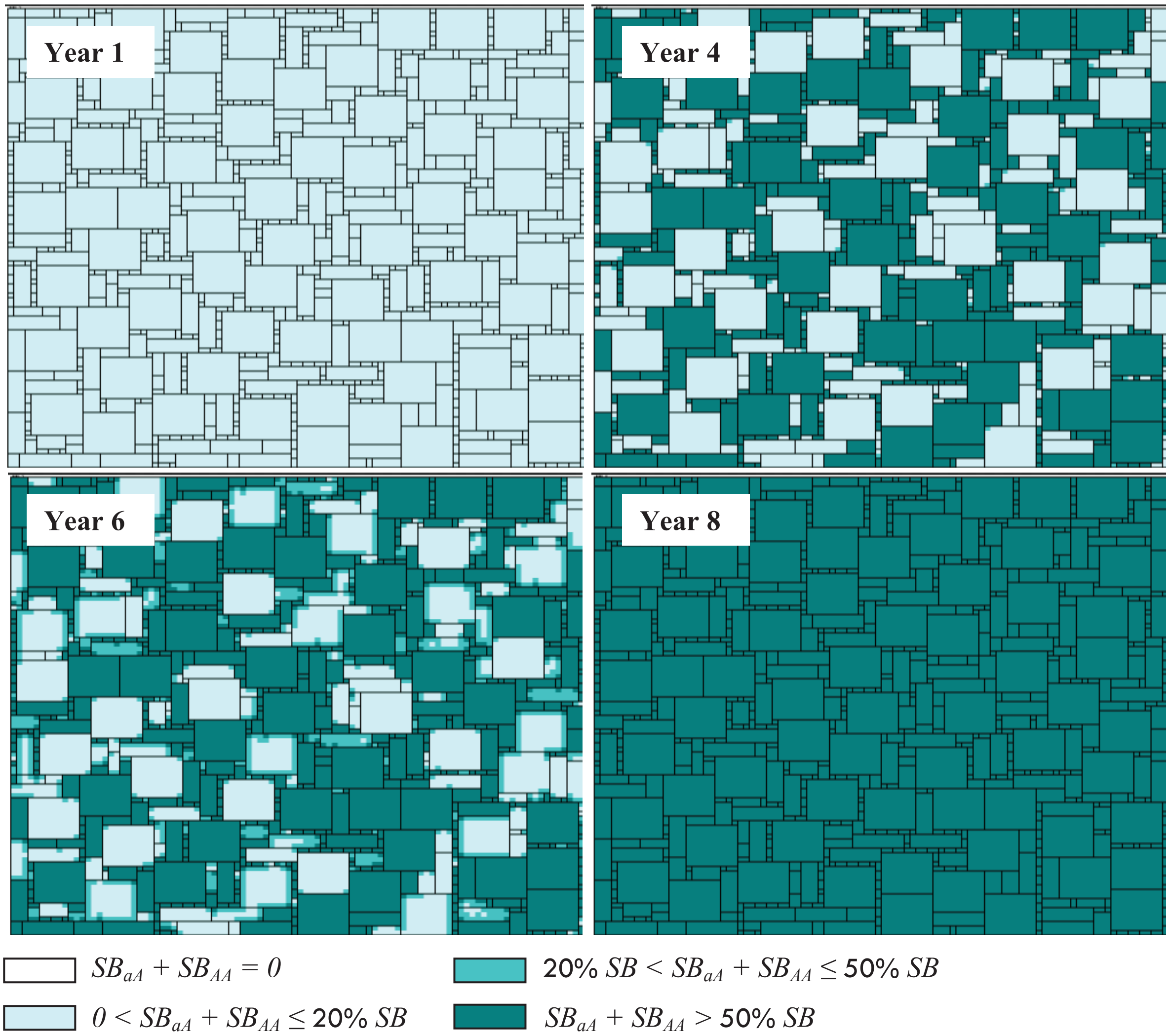

Figure 6. Resistance spread over the landscape after 1, 4, 6 and 8 years of simulation. Where SB_{AA}, SB_{aA} and SB are the homozygous resistant, the heterozygous resistant and the total seed bank ($SB = SB_{AA} + SB_{aA} + SB_{aa}$) respectively. The percentages correspond with the level of resistance in the total seed bank of each cell.

Combinations of individual strategies produced an extra control in the weed seed bank in many cases (Fig. 7b). EST13 and EST16 resulted in the lowest seed banks (Fig. 7b) even lower than initial seed bank over the 20 years of simulations. Similar pattern showed the EST11 and EST15 during the first eight years of simulations, after that, the seed bank increased more than the initial seed bank. All other strategies different to EST13 and EST16 did not reduce the initial seed bank over the simulated period of time.

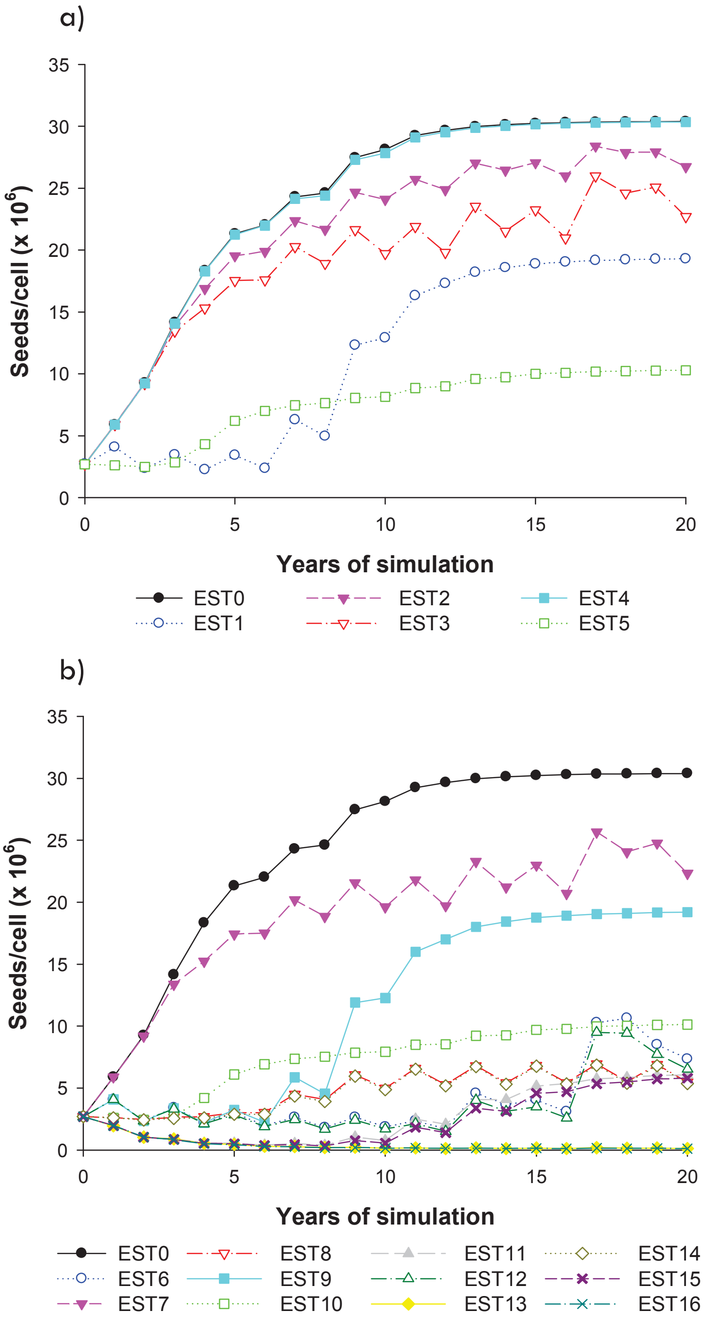

Figure 7. *L. rigidum* seed bank dynamics over the landscape a) for the individual strategies EST1 to EST5 and b) for the multiple strategies EST6 to EST16 compared to the baseline strategy EST0. EST14 underlies EST8. EST15 underlies EST11 and EST16 underlies EST13 in the graphic b. (Meaning of the abbreviations in Table 3).

IV. 3. 2. 2. Resistance frequency

The frequency of herbicide resistance increased quickly in all individual strategies (EST1 to EST5) simulated (Fig. 8a). EST4 and EST5 resulted in very similar increases in herbicide resistance over time and were similar to EST0. However, EST1, EST2 and EST3 slowed resistance evolution. The time taken for 50% of the weed population to become herbicide resistant was delayed by two years for EST2, by more than two years for EST1 and by more than four years for EST3. The time to reach a completely herbicide-resistant population was greater for EST3 than for EST1 and EST2.

The resistance evolution was slowed in some cases when individual strategies were in combination (Fig. 8b). As EST4 and EST5 did not show a significant reduction in resistance evolution, the double strategies which included one of these strategies (EST7 to EST11) and the triple strategies which included both of these strategies (EST14 to EST15) did not significantly improve resistance management (Fig. 8b). EST6 and EST12 were the multiple management strategies which most decreased resistance evolution over the landscape (Fig. 8b). Intermediate levels of control were achieved in the remainder strategies (EST13 and EST16).

IV. 3. 2. 3. Resistance spread

With regards to the spread of the resistance, EST4 and EST5 resulted in herbicide resistance spreading over the half of the described landscape in four year time. This was observed after six-seven years for EST1, EST2 and EST3. EST2 and EST3 predicted a five- and six-year delay in the time taken to reach the asymptote relative to EST1 (Fig. 9a).

Some multiple strategies increased the control exerted in the resistance spread over the landscape (Fig. 9b). As cited previously for resistance evolution, EST4 and EST5 did not show a significant reduction in resistance spread and consequently EST7 to EST11 and EST13 to EST14 did not significantly improve resistance management (Fig. 9b). EST6, EST12 to EST13 and EST16 predicted six-year delay in the time taken to spread the observed herbicide resistance over the half of the landscape compared to the most efficient individual strategies (EST1 and EST3). EST16 which involves all individual strategies slowed the dispersal rate of the resistance over the landscape more efficiently than all strategies over the 20 years of simulation (Fig. 9b).

IV. 3. 3. SECTION 3: IMPORTANCE OF THE DISPERSAL VECTOR IN THE EVOLUTION OF HERBICIDE RESISTANCE

The influence of different dispersal vectors on resistance spread over the landscape can be analyzed over two time intervals: the short and the long term. In the short term, sowing contaminated crop seed increased the area infested by herbicide-resistant populations faster than the other vectors (Fig. 10a) and consenquently the resistance travelled further distances in a short period of time (Fig. 10b). However, spread by this vector was truncated in the long term by the impossibility of infesting new fields (Fig. 10a, b). In the long term, resistance spread a greater distance from the focal cell as a result of pollen flow than it did as a result of harvester movement (Fig. 10b), although there were some large ranges of variation in the data. Harvester movement resulted in a linear increase in herbicide resistance spread with lower rates of spread than the other dispersal vectors (Fig. 10a).

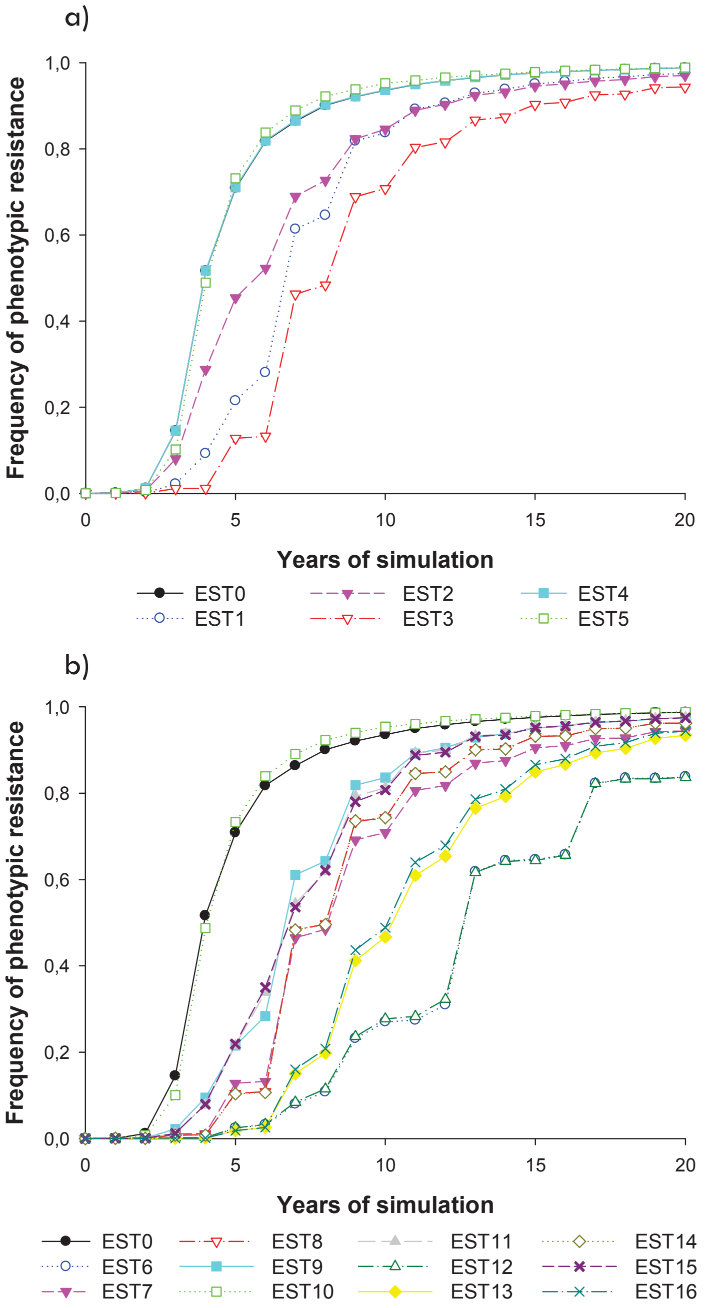

Figure 8. Temporal evolution of the frequency of the herbicide-resistant *L. rigidum* seed bank over the landscape a) for the individual strategies EST1 to EST5 and b) for the multiple strategies EST6 to EST16 compared to the baseline strategy EST0. EST4 underlines EST0 in the graphic a and EST12 underlies EST6, EST15 underlies EST11 and EST14 underlies EST8 in the graphic b. (Meaning of the abbreviations in Table 3).

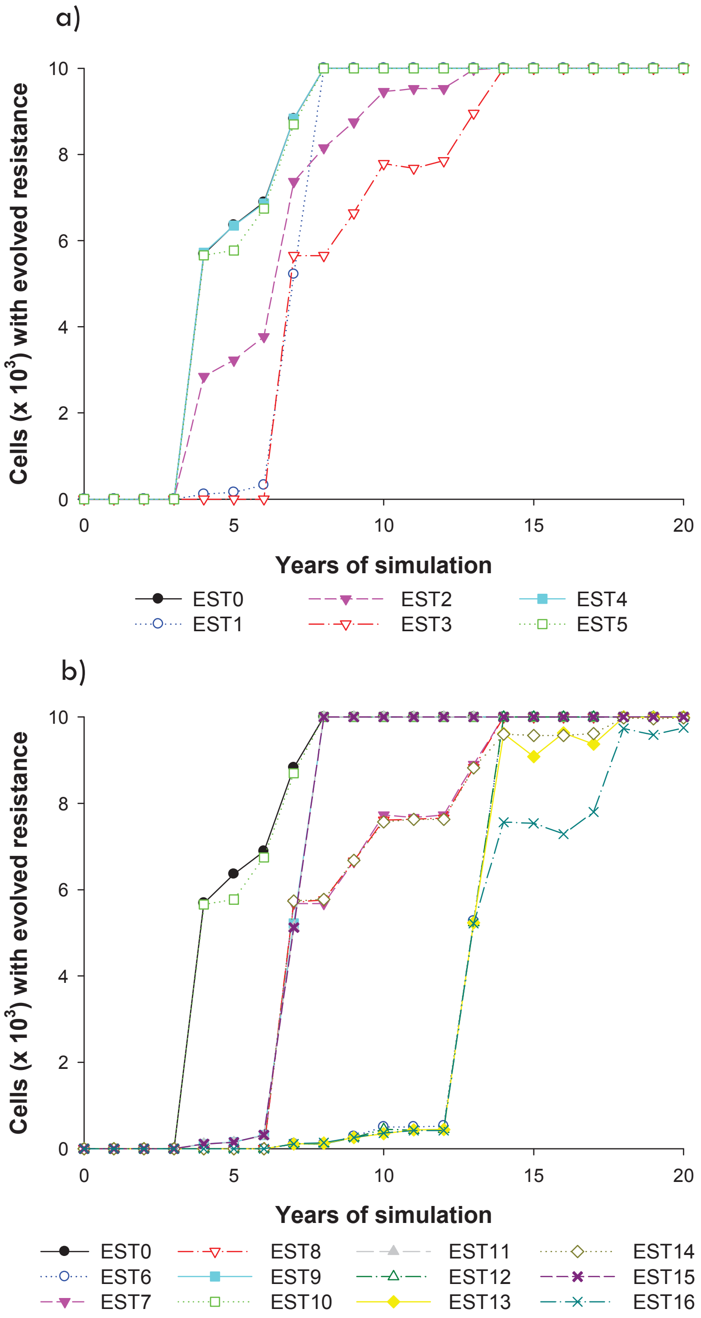

Figure 9. Temporal evolution of the cells (ha) occupied by herbicide-resistant *L. rigidum* seed bank over the landscape a) for the individual strategies EST1 to EST5 and b) for the multiple strategies EST6 to EST16 compared to the baseline strategy EST0. EST4 underlines EST0 in the graphic a and EST8 underlies EST7, EST12 underlies EST10 and EST15 underlies EST9 and EST11 in the graphic b. (Meaning of the abbreviations in Table 3). The seed bank is deemed to be resistant when 20% of seeds are phenotypically resistant (AA or aA genotype).

A positive synergistic effect was found when including all dispersal vectors together (results not shown). This synergy was greatest when pollen flow and weed contaminated-crop seed seeding were considered together. The area occupied by a herbicide resistance weed population rose by 6.8 times in this case and by 9 times when all dispersal factors were considered together with respect to simulations where pollen flow alone was considered.

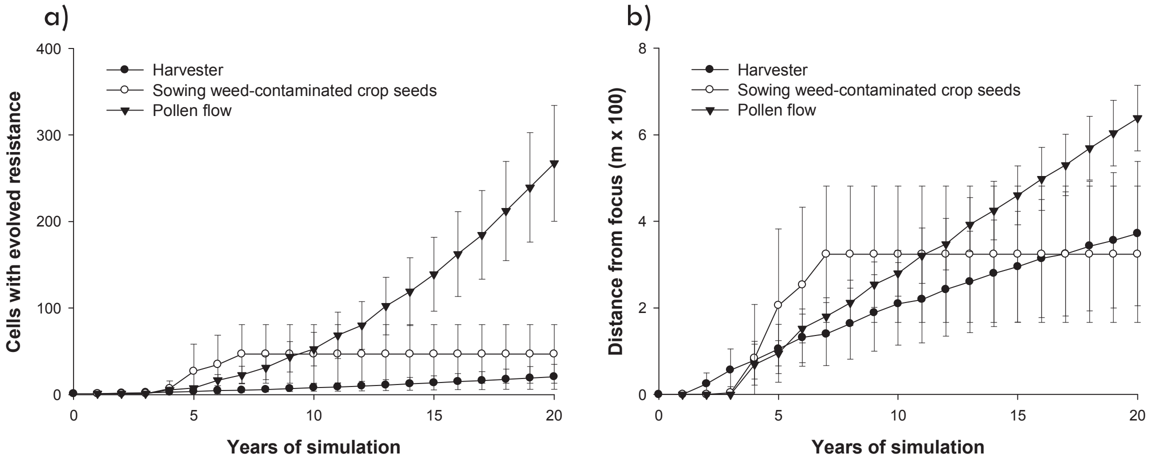

Figure 10. a) Temporal evolution of the cells (ha) occupied by herbicide-resistant *L. rigidum* seed bank over the landscape and b) the distance from the cells occupied by herbicide-resistant *L. rigidum* seed bank to the initial herbicide-resistant focus for the dispersal vectors of gene flow (harvester, sowing weed-contaminated crop seeds and pollen flow). The seed bank is deemed to be resistant when 20% of seeds are phenotypically resistant (AA or aA genotype). Vertical bars indicate the ranges of variation.

IV. 3. 4. SECTION 4: SENSITIVITY ANALYSIS

The model was sensitive to the potential weed fecundity, herbicide efficacy and fitness cost (Fig. 11). Variations in potential fecundity had the greatest impact on the model, significantly impacting the years to resistance evolution across the entire landscape (i.e., more than 20% of the total seed bank in the landscape is herbicide resistant) (Fig. 11a) and over half of the landscape (i. e., more than 50% of the cells in the landscape have a herbicide-resistant weed population) (Fig. 11b) and both responses were not linear. The time to resistance evolution and spread was much greater as the potential fecundity decreased. The seed bank density also highly decreased its potential value under a decreased potential fecundity (results not shown). The fitness cost and herbicide efficacy showed a linear pattern over their uncertain domains on the time to resistance evolution, although this effect was almost non-significant for the fitness cost with just a one-year delay on resistance evolution. The herbicide control did not influence the potential weed seed bank (results not shown) but it delayed the time until resistance was observed over half of the landscape by up to four years (Fig. 11b). On the other hand, the fitness cost decreased the potential growth of the seed bank by up to 60% (results not shown) but it did not influence the herbicide-resistance expansion rate (Fig. 11b). The model was not sensitive to the distributions of the initial weed density and the initial frequency of the resistant allele for either output analyzed (results not shown).

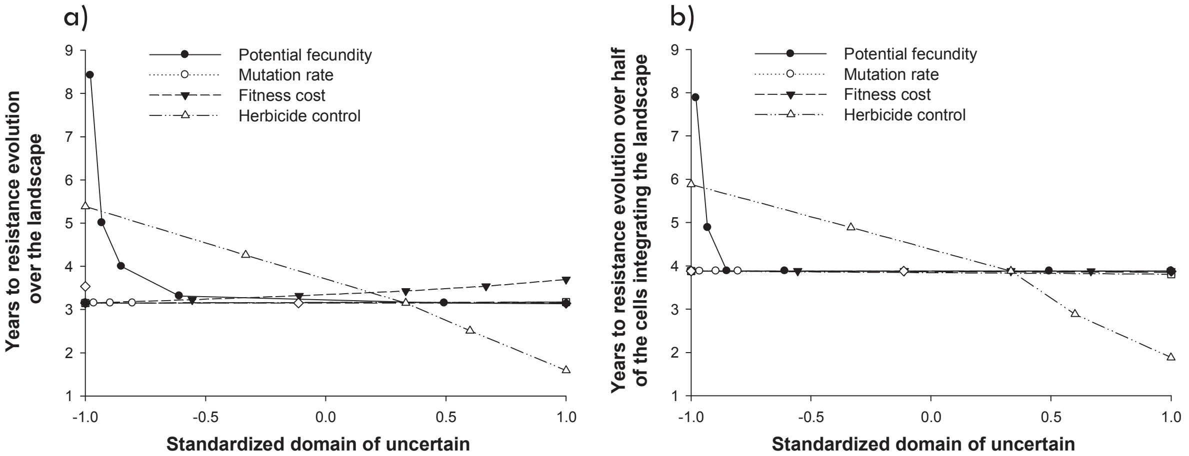

Figure 11. Sensitivity analysis of the model for the demographic and genetic parameters as a function of a) the time to resistance evolution over the landscape and b) the time to resistance evolution over half of the cells integrating the landscape. The minimum value of the potential fecundity is not shown because the herbicide resistance did not evolve over the landscape in the weed population after 20 years of simulation. The resistance is deemed to be evolved when 20% of the weed seed bank is phenotypically resistant (AA or aA genotype).

The distance travelled by the pollen flow had a very significant effect on the total area occupied by herbicide-resistant weed populations (Fig. 12a) and consequently on the distance which resistance was spread (results not shown). As the length travelled by the pollen cloud increased, the area with resistance at year 20 increased. The module of the model which described the harvester movement over the landscape also showed a significant effect in the model outputs (Fig. 12b). The FOREIGN movement spread the resistance over 3220 ha more and to a greater distance (results not shown) than the LOCAL movement. Longer pollen distribution tails and an unknown landscape for the harvester driver increased the herbicide resistance spread.

IV. 4. DISCUSSION

Our simulations suggest that target-site herbicide resistance will evolve rapidly in weed populations with repeated annual applications of the same herbicide mode of action. In only three years, resistance was predicted over 20% of the landscape. This is in agreement with experimental results whereby herbicide-resistant *L. rigidum* populations became evident in the field after three consecutive years of selection with the herbicide sethoxydim (Tardif et al., 1993). Sethoxydim belongs to the cyclohexanedione (CHD) herbicides which inhibit the plastidic enzyme acetylcoenzyme A carboxylase (ACCase). The resistance evolved by repeated application of sethoxydim was endowed by a less sensitive form of ACCase (Tardif et al., 1993) and therefore it was resistance attributed to target enzyme modifications. In other studies (Menchari et al., 2006) frequencies up to 99% of resistant ACCase alleles were observed at field after 12 years of herbicide application in agreement with our outcomes. However, although resistance evolved very rapidly over the landscape, a farmer may not detect this problem because the number of adult plants was still low at the simulation year four (20 plants/m^2).

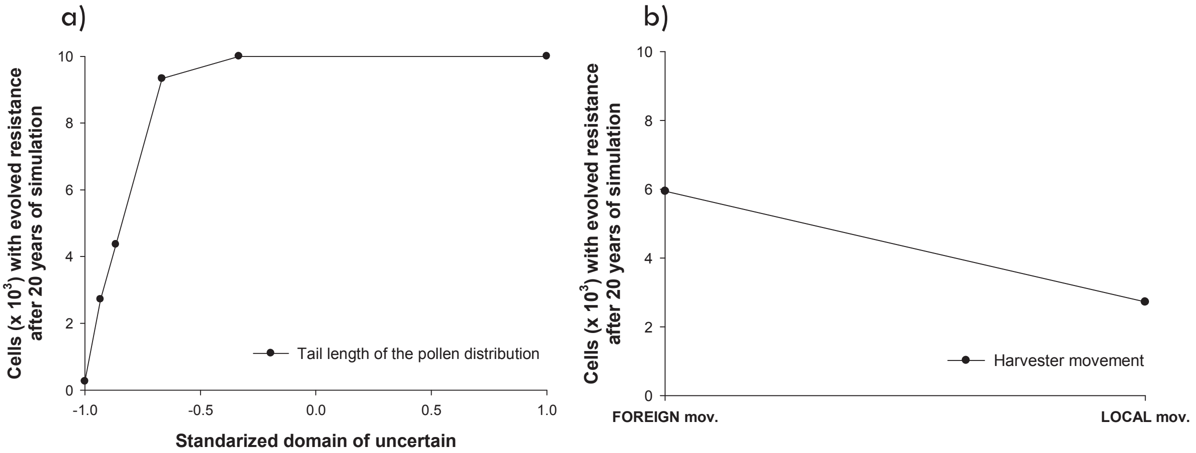

Figure 12. Sensitivity analysis of the model for a) the dispersal parameter and b) the spatial pattern of harvester movement (i.e., FOREIGN movement or LOCAL movement). Y-exe corresponds to the cells (ha) occupied by herbicide-resistant *L. rigidum* seed bank over the landscape after 20 years of simulation. The seed bank is deemed to be resistant when 20% of seeds are phenotypically resistant (AA or aA genotype).

In Spain, and particularly in Andalusia, there are reports of herbicide-resistant *L. rigidum* populations (Heap, 2011), although the evolution of resistance may have been much slower than predicted by the model. According to the sensitivity analysis, the parameters with the greatest influence on resistance evolution were the potential fecundity and herbicide efficacy. As the profits associated to cereal crops are low in some parts of the Andalusia region, this may mean that herbicides are not applied every year and there may even be rotation with fallow (Saavedra et al., 1989) decreasing the herbicide pressure and consequently resistance evolution. Default parameter values for fecundity were from a study in central Spain (González-Andújar and Fernández-Quintanilla, 2004) where fecundity was high (935 seeds/plant). Fecundity in this region may be higher than it is in Andalusia where environmental conditions are different. This could explain in part the rapid evolution of the resistance under the conditions detailed in the model. It could be interesting to include a randomized pattern of these parameters, i.e., potential fecundity and the herbicide control rate in further models to predict the resistance appearance in *L. rigidum* populations in order to increase the variability in the resistance evolution over the landscape.

The rapid evolution of resistance evident in the weed adult plants was however buffered in the weed seed bank. Other models have obtained similar results (Maxwell et al., 1990) predicting a slower response to selection in the weed seed bank than in growing weed populations. *L. rigidum* is an annual weed with a seed bank living in the soil no more than two cropping seasons (Taberner, 1996), the buffering effect of the seed bank may be increased in weeds with greater seed bank persistence whereby the time to evolve resistance could be delayed as has been shown in other modelling exercises (Richter et al., 2002).

The rate of spread of resistance was very pronounced such that after four years of simulations over half of the simulated landscape had a seed bank containing over 20% of resistant phenotypes. This value was coincident with the proportion of fields under cereal monoculture. In fields with crop rotation resistance evolved later due to a lower intensity of herbicide application. Some fields under crop rotation achieved higher levels of resistance due to stochastic dispersal events. The randomised mutation events did not show any effect (results not shown), though. However, the dispersal events were not an important impact in the model outputs as can be seen in the sensitivity analysis and the management scenarios (EST4 and EST5). The source of the resistance and its rapid expansion over the landscape was probably due to the large size of the individual cells explored and consequently the high initial weed density at this scale compared to the initial frequency of the resistant allele. The initial frequency of resistance and large population sizes, both resulted in resistance appearing during the first year of simulations in the seed bank of every field. Although Menchari et al. (2006) proposed multiple independent appearances of mutant ACCase alleles in a region as the origin of the herbicide-resistant *Alopecurus myosuroides* populations rather than resistance dispersal, other studies show a more important role of the gene flow in resistance expansion (Busi et al., 2011). In our model, the weed infestation was homogeneously distributed within the 1 ha field but it is known that weeds are commonly grouped into patches although *L. rigidum* populations do not usually show persistent patches over time (Blanco-Moreno et al., 2006). In reality, this may decrease the initial weed density at the beginning of simulations and consequently the resistance appearance and its rapid evolution within the field. Further work increasing the spatial variability of such parameters and decreasing the initial density and the initial frequency of resistance in order to reduce the probability of resistance appearance over the landscape are also recommended to create a stochastic mosaic of resistance which is more realistic. Peck et al. (1999) and Richter et al. (2002) showed two different approaches to get a variance in the initial starting frequency of resistance among fields.

The magnitude and existence of fitness costs associated with herbicide resistance in *L. rigidum* populations remain unclear and may vary depending on the type of resistance mechanism (Vila-Aiub et al., 2005a). In the model, a fitness cost had a significant influence on the model outcomes. It was included in the model as a reduction in the fecundity of the homozygous herbicide-resistant weeds, however, fitness costs and trade-offs could affect many processes in the weed life cycle (Vila-Aiub et al., 2009). Vila-Aiub et al. (2005b) found a different seed dormancy and germination dynamics in the fraction of *L. rigidum* weed seeds with the Ile-1781–Leu ACCase mutation. Although this is not a fitness cost per se this behavior may be important in the management of resistance evolution (Vila-Aiub et al., 2009). A relationship between dormancy and herbicide resistance has been observed by other authors (Owen et al., 2011). We ran an extra simulation with a modified pattern in the germination of the herbicide-resistant weed seeds (a reduction of 40% and 20% in the germination for the first and the second soil layer, respectively) in order to find changes in the resistance evolution. The model, however, did not show any effect in the resistance evolution but increased the carrying capacity of the system to store *L. rigidum* seeds (results not shown).

IV. 4. 1. HOW TO DELAY THE HERBICIDE RESISTANCE DEVELOPMENT AT THE LANDSCAPE LEVEL

The model simulations suggest that the strategies focused on diversifying the cropping sequence and herbicide applications, either individually or in conjunction, were the most effective at slowing herbicide resistance evolution at the landscape scale. These strategies together with incorporation of seed catching at harvest represented the management program that most successfully decreased the weed seed bank at the landscape level. The management strategies focused on decreasing the movement of seeds over the landscape, i.e., the use of certified crop seeds at sowing and a seed catcher at harvest timing did not have any import impact on the resistance evolution and spread.

The annual rotation of post-emergence herbicides with a different mode of action to control the target weed is an effective strategy evaluated and proposed widely by advisors and model simulations (Cavan et al., 2000). This was the individual strategy that most effectively slowed the herbicide resistance evolution and spread over the landscape. It is important to notice that this strategy is useful if the resistance occurs through target-site insensitivity as it was supposed in the model. Resistance by nontarget-site based mechanisms can endow resistance to herbicides with a different mode of action, and then, to rotate herbicides mode of action could not be a solution. The implementation of a cropping system which involves more than one crop obtained better control of the seed bank at the landscape level. The success of crop rotation will depend on one of the crops preventing the successful completion of the weed life cycle without herbicide application and this is achieved here with the sunflower crop.

Special care should be taken in the interpretation of seed bank densities at different scales. If the seed bank density at the landscape scale is lower in some strategies than in others, it does not necessarily mean that the strategy with the lowest seed bank had the lowest seed bank and/or adult density at the field scale. It is because the high weed seed or adult densities in cereal fields are offset by the low weed densities in sunflower fields when the landscape scale is considered. In our simulations the number of adult plants at cereal fields is lower in the herbicide rotation strategy than in the crop rotation strategy. This is because the first is not as effective controlling the weed seedlings as the latter in the fields under cereal crops. To compare strategies more accurately, a model of weed-crop competition and an economic analysis could be very useful (van den Berg et al., 2010) but it was not the objective of our study.

Other possible tactics such as herbicide mixtures (Beckie and Reboud, 2009) or the application of pre-emergence herbicides (Beckie, 2007) could be studied by the model as these have been proposed as optimal strategies to mitigate resistance evolution. A study (Cirujeda and Taberner, 2010) developed in Spain to investigate the possible chemical control of herbicide-resistant *L. rigidum* populations showed that the most sequential applications of pre-emergence and post-emergence herbicides tested did not significant increase the efficacy of control and a pre-emergence applications might be enough depending on the annual rainfall pattern as alternatives to post-emergence selective herbicides.

High initial frequency of resistance in all fields simulated in the model provoked a rapid resistance evolution everywhere. It did not give chance to dispersal vectors to act actively in the resistance evolution and spread. Despite the fact that strategies based on slowing the spread of resistance were masked by the presence of a high initial frequency of herbicide-resistant alleles in all fields, it is known these strategies play an important role in herbicide resistance spread (Délye et al., 2010). The contribution of each dispersal vector and its management will be discussed in the next section.

IV. 4. 2. HOW TO SLOW THE HERBICIDE RESISTANCE EXPANSION

Individually, the pollen flow was the dispersal vector which mainly drives the herbicide-resistance spread over the landscape. The combination of the all three dispersal vectors, i.e., the harvester, the pollen flow and the sowing of the weed-contaminated crop seeds had a positive synergistic effect in the total area infested with herbicide-resistant weed populations and the dispersal distance achieved by the resistance. The association of both the pollen flow and the sowing of the weed-contaminated crop seeds, however, accounted for the main effect in the resistance spread.

Experimental studies (Balfourier et al., 2000) have cited that the pollen flow showed more impact than the seed flow in the resistance dispersal. And the statement that the resistance can be moved in the pollen grain (Richter and Powles, 1993) evidence the importance of this dispersal vector in the resistance spread. The pollen cloud movement and an effective pollination are known to depend on the biological, environment and crop management factors and their interactions as the synchrony of flowering and pollen production (Beckie and Hall, 2008). Some of these factors have been taken into consideration in many modelling studies (e.g., Richter and Seppelt, 2004; Colbach et al., 2001). However, in our study no differences were considered between pollen flow according to differences in the date of flowering because of the short duration of this phase in *L. rigidum* populations (Taberner, 1996) and more accurate pollen cloud movement in relation to environment factors escapes from the objective of this work. As the distance to be travelled by the pollen cloud might be of thousands of meters (Busi et al., 2008) and it resulted to be very influent in the model (Fig. 7) a necessity of more carefully studies on such dispersal vector is evident. However, although the practical application of measures focused on the pollen cloud control is doubtful (Jasieniuk et al., 1996), some modelling and experimental approaches have been studied (Maxwell et al., 2002; Ghersa et al., 1994).

Practical applications focused on limiting the seed movement might be more successful and easier to apply. Some extra simulations to test the efficacy of the use of certified crop seeds and the seed catching in the resistance spread showed unexpected results. The sowing of weed-free crop seeds highly decreased the risk of resistance over the landscape in around 75% (results not shown). Many farmers use their own cleaned crop seeds instead of certified crop seeds for sowing with a reduction around 98% in the crop seed- contaminating *L. rigidum* seeds (Michael et al., 2010). Even if farmers use cleaned crop seeds, a reduction around 40% in the resistance spread may be achieved (results not shown). Those practices are therefore advisable to reduce the spread of resistance. However, the use of a seed catching device at harvest accelerated the resistance enrichment over the landscape in around 17% (result no shown) although it significantly decreased the weed seed bulk in around 77%. As previously cited, the seed catching is a useful tool to reduce the weed seed bank but it might generate no desirable results in the resistance evolution. It would be recommended to study the effect of the seed catching on the resistance evolution through field experiments in order to test and to understand the given results and to advise farmers in consequence.

Regards to the effect of the harvester movement in the resistance spread, the model showed sensitivity to the variation of this module. A harvester driver who knows the working area spread the resistance over the landscape much less than a foreign harvester driver because of the latter moves around the landscape in a more randomized pattern. A harvest planning whereby the nearest cereal fields are harvested one after another might reduce the resistance spread at the landscape level. Obviously a harvester cleaning process when the harvester moves from one field to another as it is suggested in many studies (Thill and Mallory-Smith, 1997; Légère et al., 2000) may slow the resistance spread between fields independently to the harvester movement.

Despite the strategies simulated to control the resistance spread, the resistance was always increasing on the landscape. To diversify the management strategies and prevent the appearance of new resistance focus are useful tools to delay the resistance spread and enlarge the useful life of herbicides. On other hand, the knowledge of the biological processes responsible of the herbicide resistance in a specific weed is crucial in the design of control management programs (Cirujeda and Taberner, 2010; Powles and Yu, 2010). In our study, a nuclear gene mutation was the origin of the herbicide resistance. Many *L. rigidum* plants are resistant to ACCasa and ALS-inhibiting herbicides ought to gene mutations (Tranel and Wright, 2002; Délye, 2005). In these cases and under the specifications made in the model many of the recommendations given in this study might be useful to slow the herbicide-resistance evolution. The model also may contribute to the knowledge on the resistance dynamic over the landscape and could be used in the search of new management strategies at different scales.

IV. 5. REFERENCES

Balfourier, F.; Imbert, C.; Charmet, G. (2000) Evidence of phlogeographic structure in Lolium species related to he spread of agriculture in Europe. A cpDNA study. Theoretical Applied Genetic 101, 131-138.

Baraibar, B.; Westerman, P. R.; Carrión, E.; Recasens, J. (2009) Effects of tillage and irrigation in cereal fields on weed seed removal by seed predators. Journal of Applied Ecology 46, 380-387.

Beckie, H. J. (2007) Beneficial management practices to combat herbicide-resistant grass weeds in the Northern Great Plains. Weed Technology 21, 290-299.

Beckie, H. J.; Hall, L. M. (2008) Simple to complex: modeling crop pollen-mediated gene flow. Plant Science 175, 615-628.

Beckie, H. J.; Reboud, X. (2009) Selecting for weed resistance: herbicide rotation and mixture. Weed Technology 23, 363-370.

Blanco-Moreno, J. M.; Chamorro, L.; Sanx, F. X. (2006) Spatial and temporal patterns of *Lolium rigidum-Avena sterilis* mixed populations in a cereal field. Weed Research 46, 207-218.

Busi, R.; Michel, S.; Powles, S. B.; Délye, C. (2011) Gene flow increases the initial frequency of herbicide resistance alleles in unselected *Lolium rigidum* populations. Agriculture, Ecosystems and Environment 142, 403-409.

Busi, R.; Yu, Q.; Barrett-Lennard, R.; Powles, S. (2008) Long distance pollen-mediated flow of herbicide resistance genes in *Lolium rigidum*. Theoretical and Applied Genetics 117, 1281-1290.

Cavan, G.; Cussans, J.; Moss, S. R. (2000) Modelling different cultivation and herbicide strategies for their effect on herbicide resistance in *Alopecurus myosuroides*. Weed Research 40, 561-568.

Cirujeda, A.; Taberner, A. (2010) Chemical control of herbicide-resistant *Lolium rigidum* Gaud. in north-eastern Spain. Pest Management Science 66, 1380-1388.

Colbach, N.; Clermont-Dauphin, C.; Meynard, J. M. (2001) GENESYS: a model of the influence of cropping system on gene escape from herbicide tolerant rapeseed crops to rape volunteers II. Genetic exchanges among volunteer and cropped populations in a small region. Agriculture, Ecosystems and Environment 83, 255-270.

Dauer, J. T.; Luschei, E. C.; Mortensen, D. A. (2009) Effects of landscape composition on spread of an herbicide-resistant weed. Landscape Ecology 24, 735-747.

Délye, C. (2005) Weed resistance to acetyl coenzyme A carboxylase inhibitors: and update. Weed Science 53, 728-746.

Délye, C.; Clèment, J. A. J.; Pernin, F.; Chauvel, B.; Le Corre, V. (2010) High gene flow promotes the genetic homogeneity of arable weed populations at the landscape level. Basic and Applied Ecology 11, 504-512.

Diggle, A. J.; Neve, P. B.; Smith, F. P. (2003) Herbicides used in combination can reduce the probability of herbicide resistance in finite weed populations. Weed Research 43, 371-382.

Fernández-Quintanilla, C.; Barroso, J.; Recansens, J.; Sans, X.; Torner, C.; Sánchez del Arco, M. J. (2000) Demography of *Lolium rigidum* in winter barley crops: analysis of recruitment, survival and reproduction. Weed Research 40, 281-291.

Fernández-Quintanilla, C.; González-Andújar, J. L.; González-Ponce, R.; de Lucas, C.; Navarrete, L.; Recasens, M. J.; Sánchez del Arco, A.; Taberner, A.; Tiebas, M. A.; Torner, C. (1998) Using the low rate concept (LRC) for control of grassweeds in cereals under Mediterranean conditions. Proceedings of the 6th EWRS Mediterranean Symposium, 353-359. Montpellier, France.

Ghersa, C. M.; Martínez-Ghersa, M. A.; Brewer, T. G.; Roush, M. L. (1994) Use of gene flow to control diclofop-methyl resistance in italian ryegrass (*Lolium multiflorum*). Weed Technology 8, 139-147.

Giddings, G. D.; Sackville-Hamilton, N. R.; Hayward, M. D. (1997) The release of genetically modified grasses. Part 1: pollen dispersal to traps in *Lolium perenne*. Theoretical Applied Genetics 94, 1000-1006.

González-Andújar, J. L.; Fernández-Quintanilla, C. (2004) Modelling the population dynamics of annual ryegrass (*Lolium rigidum*) under various weed management systems. Crop Protection 23, 723-729.

Gramshaw, D.; Stern, W. R. (1977) Survival of annual ryegrass (*Lolium rigidum* Gaud) seed in a Mediterranean type environment. II. Effects of short-term burial on persistence of viable seed. Australian Journal of Agricultural Research 28, 93-101.

Gressel, J.; Segel, L. A. (1987) The paucity of plants evolving genetic resistance to herbicides: possible reasons and implications. Journal of Theoretical Biology 75, 349-371.

Harms, C. T.; DiMaio, J. J. (1991) Pirimisulfuron herbicide-resistant tobacco cell lines. Application of fluctuation test design to *in vitro* mutant selection with plant cells. Journal of Plant Physiology 137, 513-519.

Heap, I. (2011) The International Survey of herbicide resistant weeds. http://www.weeddscience.com. Accessed: 11/11/11.

INE (2010) National Statistics Institute, Spain. http://www.ine.es. Accessed: 09/05/11.

Jasieniuk M.; Brûlé-Babel, A.; Morrison, I. N. (1996) The evolution and genetics of herbicide resistance in weeds. Weed Science 44, 176-193.

Jiménez-Hidalgo, M. J.; Palma, V.; Saavedra, M.; Pastor, M. (1991) La emergencia de *Lolium rigidum* Gaudin en Andalucía. In: Actas Reunión de la Sociedad Española de Malherbología (Ed. García-Torres, L.) pp. 128-132. Sociedad Española de Malherbología, Spain.

José-María, L.; Sans, F. X. (2011) Weed seedbanks in arable fields: effects of management practices and surrounding landscape. Weed Research 51, 631-640.

Légère, A.; Beckie, H. J.; Stevenson, C.; Thomas, G. (2000) Survey of management practices affecting the occurrence of wild oat (*Avena fatua*) resistance to Acetyl-CoA carboxylase inhibitors. Weed Technology 14, 366-376.

Loureiro, I.; Rodríguez-García, E.; Escorial, C.; García-Baudín, J. M.; González-Andújar, J. L.; Chueca, M. C. (2010) Distribution and frequency of resistance to four herbicide modes of action in *Lolium rigidum* Gaud. Accessions randomly collected in winter cereal fields in Spain. Crop Protection 29, 1248-1256.

Maxwell, B. D.; Roush, M. L.; Radosevich, S. R. (1990) Predicting the evolution and dynamics of herbicide resistance in weed populations. Weed Technology 4, 2-13.

Matthews, J.; Llewellyn, R.; Jaeschke, R.; Powles, S. (1996) Catching weed seeds at harvest: a method to reduce annual weed populations. Proceedings of the 8th Australian Agronomy Conference, 684-685. Toowoomba, Australia.

Menchari, Y.; Camilleri, C.; Miche, S.; Brune, D.; Dessaint, F.; Le Corre, V.; Délye, C. (2006) Weed response to herbicides: regional-scale distribution of herbicide resistance alleles in the grass weed *Alopecurus myosuroides*. New Phytologist 171, 861-874.

Michael, P. J.; Owen, M. J.; Powles, S. B. (2010) Herbicide-resistant weed seeds contaminate grain sown in the western Australian Grainbelt. Weed Science 58, 466-472.

Neve, P. (2008) Simulation modeling to understand the evolution and management of glyphosate resistance in weeds. Pest Management Science 64, 392-401.

Neve, P.; Diggle, A. J.; Smith, F. P.; Powles, S. B. (2003) Simulating evolution of glyphosate resistance in *Lolium rigidum* I: population biology of a rare resistance trait. Weed Research 43, 404-417.

Neve, P.; Norsworthy, J. K.; Smith, K. L.; Zelaya, I. A. (2010) Modelling evolution and management of glyphosate resistance in *Amaranthus palmeri*. Weed Research 51, 99–112.

Owen, M. J.; Michael, P. J.; Renton, M.; Steadman, K. J.; Powles, S. B. (2011) Towards large-scale prediction of *Lolium rigidum* emergence. II: Correlation between dormancy and herbicide resistance levels suggests and impact of cropping systems. Weed Research 51, 133-141.

Peck, S. L.; Gould, F.; Ellner, S. P. (1999) Spread of resistance in spatially extended regions of transgenic cotton: implication for management of *Heliothis virescens* (Lepidoptera: Noctuidae). Journal of Economic Entomology 92, 1-16.

Perea-Torres, F.; Gil-Ribes, J. (2006) Consumo de gasoil y tiempos de trabajo de la maquinaria agrícola. Agricultura de Conservación 3, 23-27.

Perry, J. N.; González-Andújar, J. L. (1993) Dispersal in a metapopulation neighbourhood model of an annual plant with a seedbank. Journal of Ecology 81, 453-463.

Powles, S. B.; Yu, Q. (2010) Evolution in action: plants resistant to herbicides. Annual Review of Plant biology 61, 317-347.

Preston, C.; Powles, S. B. (2002) Evolution of herbicide resistance in weeds: initial frequency of target site-based resistance to acetolactate synthase-inhibiting herbicides in *Lolium rigidum*. Heredity 88, 8-13.

Rodríguez, C.; Wiegand, K. (2009) Evaluating the trade-off between machinery efficiency and loss of biodiversity-friendly habitats in arable landscapes: the role of field size. Agriculture, Ecosystems and Environment 129, 361-366.

Richter, O.; Powles, S. B. (1993) Pollen expression of herbicide target site resistance genes in annual ryegrass *(Lolium rigidum)*. Journal of Plant Physiology 102, 1037-1041.

Richter, O.; Seppelt, R. (2004) Flow of genetic information through agricultural ecosystems: a generic modeling framework with application to pesticide-resistance weeds and genetically modified crops. Ecological Modelling 174, 55-66.

Richter, O.; Zwerger, P.; Böttcher, U. (2002) Modelling spatio-temporal dynamics of herbicide resistance. Weed research 42, 52-64.

Roux, F.; Paris, M.; Reboud, X. (2008) Delaying weed adaptation to herbicide by environmental heterogeneity: a simulation approach. Pest Management Science 64, 16-29.

Roux, F.; Reboud, X. (2007) Herbicide resistance dynamics in a spatially heterogeneous environment. Crop Protection 26, 335-341.

Saavedra, M.; Cuevas, J.; Mesa-García, J.; García-Torres, L. (1989) Grassy weeds in winter cereals in southern Spain. Crop Protection 6, 181-187.

Shirtliffe, S. J.; Entz, M. H. (2005) Chaff collection reduces seed dispersal of wild oat (Avena fatua) by a combine harvester. Weed Science 53, 465-470.

Spokas, K.; Forcella, F.; Archer, D.; Reicosky, D. (2007) SeedChaser: vertical soil tillage distribution model. Computers and Electronics in Agriculture 57, 62-73.

Taberner, A. (1996) Biología de *Lolium rigidum* Gaud. como planta infestante del cultivo de cebada. Aplicación al establecimiento de métodos de control. Ph.D. Thesis. Universitat de Lleida, Spain.

Tardif, C. J.; Holtum, J. A. M.; Powles, S. B. (1993) Occurrence of a herbicide-resistant acetyl-coenzyme A carboxylase mutant in annual ryegrass *(Lolium rigidum)* selected by sethoxydim. Planta 190, 176-181.

Thill, D. C.; Mallory-Smith, C. A. (1997) The nature and consequence of weed spread in cropping systems. Weed Science 45, 337-342.

Tranel, P. J.; Wright, T. R. (2002) Resistance of weeds to ALS-inhibiting herbicides: What have we learned? Weed Science 50, 700-712.

van den Berg, F.; Gilliagan, C. A.; Gerdenssen, J. C.; Gregoire, L. A. H.; van den Bosch, F. (2010) Optimal weed management in crop rotations: incorporating economics is crucial. Weed Research 50, 413-424.

Vila-Aiub, M. M.; Neve, P.; Powles, S. B. (2005a) Resistance cost of a cytochrome P450 herbicide metabolism mechanism but not an ACCase target site mutation in a multiple resistant *Lolium rigidum* population. New Phytologist 167, 787-796.

Vila-Aiub, M. M.; Neve, P.; Powles, S. B. (2009) Fitness costs associated with evolved herbicide resistance alleles in plants. New Phytologist 184, 751-767.

Vila-Aiub, M. M.; Neve, P.; Steadman, K. J.; Powles, S. B. (2005b) Ecological fitness of a multiple herbicide-resistant *Lolium rigidum* population: dynamics of seed germination and seedling emergence of resistant and susceptible phenotypes. Journal of Applied Ecology 42, 288-298.

Yu, Q.; Cairns, A.; Powles, S. (2007) Glyphosate, paraquat and ACCase multiple herbicide resistance evolved in a *Lolium rigidum* biotype. Planta 225, 499-513.

APPENDIX A: SENSITIVITY ANALISIS FOR THE MODEL PARAMETERS

The sensitivity analysis was performed in the uncertain following parameters: potential fecundity, herbicide control, mutation rate, fitness penalty and asymptote tail length of the pollen dispersal distribution. The evaluated parameter ranges varied from their minimum to their maximum known value given in the literature. Fitness penalty was included as a decreased potential fecundity of the homozygous resistant plants according to the work of Menchari et al. (2008). And the length of the tail of the pollen flow distribution was increased or decreased in order to vary the distance travelled by the pollen cloud. It was introduced into the model through the weighting factors of the added or removed rings around the pollen-donating cell. The distance whereby pollen grains lay ranged from 0 m (ring 0) to 3000 m (ring 30) (Busi et al., 2008). The weighted factor of the pollen in each cell of a ring different to the pollen-donating cell was equal to the default value for ring 1 since it belongs to the asymptotic tail of a leptokurtic distribution (see Beckie and Hall, 2008). All other parameter values and the sources they come from are detailed in the Table A1.

Some uncertain modules of the model were also evaluated to show the variability in the behavior of some model steps according to the literature. The modules were the spatial distribution of initial conditions, i.e., the initial weed density and the initial frequency of the resistant allele, and the harvester movement over the landscape. The initial conditions were randomized over each cell of the landscape following the normal distribution according to the data given by Saavedra et al. (1989) of ($2.7 \cdot 10^6$, $5.4 \cdot 10^6$) for the initial weed density and by Preston and Powles (2002) of ($2.16 \cdot 10^{-5}$, $1.84 \cdot 10^{-5}$) for the initial frequency of the resistant allele. The harvester movement over the landscape in the harvest process was changed by that detailed by Rodríguez and Wiegand (2009) called FOREIGN movement whereby the harvester driver did not know the working area and consequently the relative position of the cereals fields each other.

The outputs to analyze the sensitivity of the model (according to the conditions specified on the Section 1) to the parameter variation were the years to resistance evolution over the landscape, the years in which resistance evolved over half of the cells integrating the landscape and the seed bank density evolution and its value in the asymptote. Those outputs are complementary in the study of resistance evolution at the landscape scale (Peck et al., 1999). The average area in which resistance evolved and the average distance travelled by the resistance were the outputs analyzed in the sensitivity analysis carried out over the model and the conditions specified on the Section 3. The domain of the quantitative parameters was standardized to the interval [-1, 1] to make easier comparisons between them.

Table A1. Parameter domain and the sources they come from.

MODEL PARAMETERS	Values	References
Potential fecundity, f	Max.*: 1250 seeds/plant Min.†: 7 seeds/plant	González-Andújar and Fernández-Quintanilla (2004)
Herbicide control, h_{aa}	Max.: 1 Min.: 0.85	Fernández-Quintanilla et al. (1998)
Mutation rate, k	Max.: $5 \cdot 10^{-7}$ Min.: 10^{-9}	Rajasekaran et al. (1996) Cited in Preston and Powles (2002)
Fitness cost, s	Max.: 0.36 Min.: 0	Menchari et al. (2008) Vila-Aiub et al. (2005)

* Max.: maximum value of the parameter

† Min.: minimum value of the parameter

REFERENCES APPENDIX A

Beckie, H. J.; Hall, L. M. (2008) Simple to complex: modeling crop pollen-mediated gene flow. Plant Science 175, 615-628.

Busi, R.; Yu, Q.; Barrett-Lennard, R.; Powles, S. (2008) Long distance pollen-mediated flow of herbicide resistance genes in *Lolium rigidum*. Theoretical and Applied Genetics 117, 1281-1290.

Fernández-Quintanilla, C.; González-Andújar, J. L.; González-Ponce, R.; de Lucas, D.; Navarrete, L.; Recasens, J.; Sánchez del Arco, M. J.; Taberner, A.; Tiebas, M. A.; Torner, C. (1998) Using the low rate concept (LRC) for control of grassweeds in cereals under Mediterranean conditions. Proceedings of the 6th EWRS Mediterranean Symposium, 353-359. Montpellier, France.

González-Andújar, J. L.; Fernández-Quintanilla, C. (2004) Modelling the population dynamics of annual ryegrass (*Lolium rigidum*) under various weed management systems. Crop Protection 23, 723-729.

Menchari, Y.; Chauvel, B.; Darmency, H.; Délye, C. (2008) Fitness costs associated with three mutant acetyl-coenzyme A carboxylase alleles endowing herbicide resistance in black-grass *Alopecurus myosuroides*. Journal of Applied Ecology 45, 939-947.

Peck, S. L.; Gould, F.; Ellner, S. P. (1999) Spread of resistance in spatially extended regions of transgenic cotton: implication for management of *Heliothis virescens* (Lepidoptera: Noctuidae). Journal of Economic Entomology 92, 1-16.

Preston, C.; Powles, S. B. (2002) Evolution of herbicide resistance in weeds: initial frequency of target site-based resistance to acetolactate synthase-inhibiting herbicides in *Lolium rigidum*. Heredity 88, 8-13.

Rajasekaran, K.; Grula, J. W.; Anderson, M. (1996) Selection and characterization of mutant cotton (*Gossypium hirsutum* L.) cell lines resistant to sulfonylurea and imidazolinone herbicides. Plant Science 119, 115-124.

Rodríguez, C.; Wiegand, K. (2009) Evaluating the trade-off between machinery efficiency and loss of biodiversity-friendly habitats in arable landscapes: the role of field size. Agriculture, Ecosystems and Environment 129, 361-366.

Saavedra, M.; Cuevas, J.; Mesa-García, J.; García-Torres, L. (1989) Grassy weeds in winter cereals in southern Spain. Crop Protection 6, 181-187.

Vila-Aiub, M. M.; Neve, P.; Steadman, K. J.; Powles, S. B. (2005) Ecological fitness of a multiple herbicide-resistant *Lolium rigidum* population: dynamics of seed germination and seedling emergence of resistant and susceptible phenotypes. Journal of Applied Ecology 42, 288-289.

CAPÍTULO V

Conclusiones finales

CAPÍTULO V: CONCLUSIONES FINALES

1. Un control más eficiente de las malas hierbas se podría conseguir a través de estrategias de manejo integrado a diferentes escalas espaciales, de parcela y de paisaje. Ya que ignorar la dinámica espacial de las poblaciones de especies arvenses puede conducir a la selección de estrategias subóptimas.

2. Un análisis económico se plantea como una etapa necesaria y complementaria en la selección de estrategias de manejo de las malas hierbas. Las estrategias que mayor control ejercieron sobre las poblaciones de *L. rigidum* no siempre fueron las más adecuadas desde el punto de vista económico. Es necesario el establecimiento de estrategias de bajos inputs y altos niveles de control para conseguir mayor rentabilidad en los cereales de secano españoles.

3. La aplicación de herbicida a dosis completa en combinación con métodos de control culturales son las estrategias a escala de parcela más eficaces y rentables en el control de las poblaciones de *L. rigidum* bajo las condiciones especificadas en el modelo.

4. La rotación de cultivos implementada tanto a nivel de parcela como de paisaje tiene un gran potencial en el control de *A. sterilis* a corto y a largo plazo. El nivel de control alcanzado depende del número de diferentes tipos de cultivos y de la secuencia de los mismos en la rotación. A nivel de paisaje es también necesaria una coordinación entre agricultores con respecto a la secuencia de los cultivos en la rotación, a la disposición de los mismos y/o a la proporción relativa de cada cultivo en el paisaje para conseguir mayores niveles de control de las poblaciones de la mala hierba.

5. Las estrategias de manejo centradas en diversificar los sistemas de cultivo (i.e., rotación de cultivo vs. monocultivo) y la rotación de herbicidas (i.e., herbicidas con diferente modo de acción) mostraron ser las más eficaces en retrasar el desarrollo de la resistencia a los herbicidas a escala de paisaje en las poblaciones de *L. rigidum* que inicialmente presentaron individuos resistentes. La aplicación anual del mismo herbicida produjo un rápido desarrollo de la resistencia en dichas poblaciones.

6. El polen fue el principal responsable de la dispersión de la resistencia a los herbicidas en las poblaciones de *L. rigidum* y junto con la dispersión de semillas provocaron un efecto sinérgico positivo en la expansión de las poblaciones resistentes en el paisaje.

7. El uso de semilla certificada o limpiada en la siembra del cereal y un movimiento de la cosechadora que minimice su desplazamiento entre las parcelas del paisaje durante la cosecha frenaron de manera eficaz la expansión de las poblaciones resistentes de *L. rigidum*. Por el contrario, el acoplamiento a la cosechadora de cereal de un remolque colector de paja que recoja las semillas de *L. rigidum* tras la cosecha incrementó el nivel de resistencia en el paisaje.

8. Los parámetros más influyentes en el modelo de *L. rigidum* a escala de parcela variaron con las estrategias de manejo y con el output analizado. El precio de venta del cereal y el porcentaje de control fueron los parámetros más influyentes en los retornos económicos de aquéllas estrategias que incluyeron la aplicación de herbicidas, y la fecundidad y la supervivencia de las plántulas en las estrategias de control basadas en métodos culturales. El banco de semilla de *L. rigidum* fue especialmente sensible a la fecundidad y al porcentaje de control.

9. Los parámetros más influyentes en los resultados del modelo de resistencia de *L. rigidum* a escala de paisaje fueron la fecundidad, la eficacia del herbicida y la penalización en el fitness.

UNIVERSIDAD DE CÓRDOBA

CSIC
CONSEJO SUPERIOR DE INVESTIGACIONES CIENTÍFICAS

INSTITUTO DE AGRICULTURA SOSTENIBLE IAS