Cástor Luis Zambrano Navea

TESIS DOCTORAL

Demografía y dinámica poblacional de *Conyza bonariensis* (L.) Cronq

Córdoba, 2013

TITULO: *DEMOGRAFIA Y DINÁMICA POBLACIONAL DE CONYZA BONARIENSIS (L) CROMQ.*

AUTOR: *CASTOR LUIS ZAMBRANO NAVEA*

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CONSEJO SUPERIOR DE INVESTIGACIONES CIENTÍFICAS
INSTITUTO DE AGRICULTURA SOSTENIBLE IAS

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Autor:

Cástor Luis Zambrano Navea

Dirigida por:

Dr. José Luis González Andújar

Dr. Fernando Bastida Milián

Córdoba, Mayo de 2013

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Memoria redactada para optar al grado de Doctor por la Universidad de Córdoba por el Ingeniero Agrónomo:

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Córdoba, Mayo de 2013

TÍTULO DE LA TESIS: Demografía y dinámica poblacional de *Conyza bonariensis* (L.) Cronq.

DOCTORANDO: Cástor Luis Zambrano Navea

INFORME RAZONADO DEL/DE LOS DIRECTOR/ES 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 del Instituto de Agricultura Sostenible, CSIC, y **D. Fernando Bastida Milián**, Profesor Titular del Departamento de Ciencias Agroforestales de la Universidad de Huelva, directores de la presente Tesis Doctoral

Informan:

Que el trabajo que lleva por título "**Demografía y dinámica poblacional de *Conyza bonariensis* (L.) Cronq.**" ha sido realizado bajo nuestra supervisión por el Ingeniero Agrónomo D. Cástor Luis Zambrano Navea, 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 (Artículo 25 de la Norma Reguladora de los Estudios de Doctorado, propuesta por la Comisión de Másteres y Doctorado de 14 de Diciembre de 2011 y aprobada por el Consejo de Gobierno de 21 de Diciembre de 2011). En cumplimiento con este artículo se presenta un artículo científico correspondiente al capítulo III de la presente Tesis Doctoral.

Zambrano-Navea C, Bastida F & González-Andújar JL (2013). A hidrotermal seedling emergence model for hairy fleabane (*Conyza bonariensis*). *Weed Research* (En prensa).

Weed Research, de difusión internacional cuenta con un índice de impacto de 1.924 ocupando la posición 17/80 (primer cuartil) en el descriptor "Agronomy" del ICI-JCR.

Los resultados del II capítulo, se encuentran enviados a la revista *Weed Biology and Management* bajo el título "Demography of the weed *Conyza bonariensis* (Asteraceae) in a Mediterranean climate ", y se encuentran en la fase de revisión. Esta revista de difusión internacional cuenta con un índice de impacto de 0.707 ocupando la posición 46/80 (tercer cuartil) en el descriptor "Agronomy" del ICI-JCR.

Los resultados del capítulo IV, están pendientes de ser enviados a una revista de difusión internacional del ICI-JCR.

<u>Contribuciones a Congresos</u>:

Zambrano-Navea C, Bastida F, González-Andújar JL (2012) Modelización de la emergencia de *Conyza bonariensis* en clima mediterráneo. En: Plantas Invasoras, Resistencia a Herbicidas y Detección de Malas Hierbas (Eds. JR Arévalo, S Fernández, F López, J Recasens, E Sobrino) pp. 299-302. ISBN 978-84-615-4903-0. Universidad de La Laguna. San Cristobal de La Laguna, España.

Por todo ello, se autoriza a la presentación de la Tesis Doctoral.

Córdoba, 1 Marzo de 2013

Firma de los directores

Fdo.:José Luis González Andújar

Fdo.: Fernando Bastida Milian

TÍTULO DE LA TESIS: Demografía y dinámica poblacional de *Conyza bonariensis* (L.) Cronq.

DOCTORANDO: Cástor Luis Zambrano Navea

ESCRITO RAZONADO DEL RESPONSABLE DE LA LÍNEA DE INVESTIGACIÓN (Ratificando el informe favorable del director. Sólo cuando el director no pertenezca a la Universidad de Córdoba).

D. Antonio J. Pujadas Salvà, profesor titular del Departamento de Ciencias y Recursos Agrícolas y Forestales de la Universidad de Córdoba, y coordinador responsable de la línea de investigación: Relaciones Planta-Insecto, ratifico el informe presentado por los directores de la presente Tesis Doctoral **D. José Luis González Andújar**, Investigador Científico del Departamento de Protección de Cultivos del Instituto de Agricultura Sostenible, CSIC, quien está adscrito como investigador ajeno a la Universidad de Córdoba a la línea de investigación que yo coordino, y **D. Fernando Bastida Milián**, Profesor Titular del Departamento de Ciencias Agroforestales de la Universidad de Huelva.

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 (Artículo 25 de la Norma Reguladora de los Estudios de Doctorado, propuesta por la Comisión de Másteres y Doctorado de 14 de Diciembre de 2011 y aprobada por el Consejo de Gobierno de 21 de Diciembre de 2011). En cumplimiento con este artículo se presenta un artículo científico correspondiente al capítulo III de la presente Tesis Doctoral.

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Por todo ello, se autoriza la presentación de la Tesis Doctoral.

Córdoba, 1 de Marzo de 2013

Firma del responsable de línea de investigación

Fdo.: Antonio J. Pujadas Salvà

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A mi familia,

especialmente a Cástor Andrés y Verónica

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> "Gracias a la vida que me ha dado tanto,
> me dio dos luceros que cuando los abro,
> perfecto distingo lo negro y lo blanco,
> y en el alto cielo su fondo estrellado" (Violeta Parra)

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RESUMEN

Conyza bonariensis (Asteraceae) es una mala hierba nativa de América del Sur que se comporta como una planta ruderal tanto en cultivos anuales como perennes de las regiones subtropicales y templado-cálidas del mundo, incluyendo la cuenca Mediterránea . Es una especie especialmente agresiva en los sistemas de no laboreo. El conocimiento de la ecología de las malas hierbas puede contribuir a un control más racional de las mismas. Un conocimiento más detallado de su demografía y dinámica poblacional nos permitiría desarrollar modelos predictivos para una evaluación a medio y largo plazo de la eficacia de diferentes estrategias de manejo. Bajo ese contexto y la escasez de información biológica existente sobre *C. bonariensis* se plantea este trabajo con los siguientes objetivos: 1) Estudiar la demografía (emergencia, supervivencia y fecundidad) de *C. bonariensis*; 2) Desarrollar y evaluar un modelo para predecir la emergencia de *C. bonariensis* en base a parámetros climáticos y 3) Desarrollar un modelo estocástico de dinámica de poblaciones basado en cohortes para simular la dinámica del banco de semillas bajo diferentes escenarios de manejo Los experimentos de demografía se llevaron a cabo en el campo experimental del Instituto de Investigación y Formación Agraria y Pesquera (IFAPA), Alameda del Obispo, Córdoba, durante las campañas 2010-2011 y 2011-2012. La tasa media de emergencia fue del 61 %. El patrón de emergencia se caracterizó por altas tasas iniciales de emergencia que fueron altamente dependientes de las precipitaciones. La tasa media de supervivencia de las plántulas fue del 33 %. La fecundidad alcanzó un valor medio de 86.066 aquenios planta^{-1}. En general, las cohortes más tempranas presentaron unos valores más altos de supervivencia y fecundidad, contribuyendo mas a la siguiente generación y por consiguiente serian las que deberían ser preferentemente controladas para una manejo efectivo de *C. bonariensis.* Esta especie presentó un proceso de regulación de sus poblaciones a través de un proceso dependiente de la densidad a nivel de la fecundidad. Se estimaron experimentalmente en cámaras de crecimiento la temperatura base (10.6 ºC) y el potencial osmótico base (-0.70 MPa). Los datos obtenidos se utilizaron para establecer un modelo predictivo que relacionó la emergencia acumulada con el tiempo hidrotermal acumulado (HTT). El modelo fue ajustado y adecuadamente con la función de Gompertz y validado con datos de campo independientes de los usados en la construcción del modelo. De acuerdo con este modelo la emergencia de las plántulas se inicia con 15 HTT después de la siembra, se alcanza un 50 y 95% de emergencia con 53 HTT y 105 HTT, respectivamente. Los resultados indican que este modelo puede ser usado como una herramienta predictiva que puede contribuir a un control efectivo de poblaciones de *C. bonariensis*.

Se estableció un modelo estocástico de dinámica poblacional basado en cohortes que fue parametrizado con la información obtenida en los experimentos de demografía y la existente en la literatura. Dicho modelo fue utilizado para simular diferentes estrategias de manejo basadas en sistemas de laboreo y no laboreo, la utilización de cubiertas y la aplicación de herbicidas, en cultivos perennes Mediterráneos. Los resultados obtenidos indicaron que en ausencia de control y bajo no laboreo la población del banco de semillas alcanzó una densidad de equilibrio de 378092 semillas m^{-2} (97564 plantas adultas m^{-2}). La estrategia más efectiva fue la que integró el uso de no laboreo, cubierta y la aplicación temprana y tardía de herbicidas que redujo la densidad de equilibrio del banco de semillas y de la población de plantas en un 78.7% y en un 99.5%, respectivamente. Los resultados del análisis de sensibilidad del modelo indicaron que *C. bonariensis* es particularmente sensible a pequeños cambios en los parámetros demográficos asociados a la primera cohorte y a la eficacia de los tratamientos tempranos de herbicidas. Consecuentemente, sería necesario dirigir las estrategias de control sobre la primera cohorte ya que es clave para el control de esta mala hierba.

Palabras claves: emergencia, supervivencia, fecundidad, denso-dependencia, tiempo hidrotermal, análisis de sensibilidad, simulación, modelo estocástico.

ABSTRACT

Conyza bonariensis (L.) Cronquist is an annual Asteraceae, a native of South America and widely spread over tropical and temperate-hot areas, including the Mediterranean basin. It mainly behaves like a ruderal plant, colonizing disturbed habitats like road borders, boundaries, and open ground. *C. bonariensis* has become one of those most difficult weed to control in agricultural systems, particularly in conservation ones. The knowledge of the weed ecology can contribute to a more rational control. A more detailed knowledge of their demography and population dynamics allow us the development of predictive models and the evaluation of long-term management strategies. Under these context, the aims of this work were: 1) to study the demography (emergence, survival and fecundity) of *C. bonariensis* 2) to develop and evaluate a model for predicting the emergence of *C. bonariensis*; 3) to develop a stochastic population dynamic model based on cohorts to simulate the long-term dynamics of the seed bank under different management scenarios. The seedling emergence rate was 61 %, and highly dependent on the rainfall. The mean survival rate of the plants was 33%. Fecundity reached a mean value of 86066 achenes plant^{-1}. In general, the earliest cohorts presented higher survival and fecundity values, contributing more to the following generation and, consequently, they should preferably be controlled for an effective management of *C. bonariensis.* This species showed a regulation of its populations through a density-dependence process system at a fecundity level. A hydrothermal seed germination model was fitted to time course germination data from germination tests carried out at different constant temperatures and water potentials to establish the hydrothermal parameters characterizing *C. bonariensis* seed germination. The relationship between cumulative seedling emergence and cumulative hydrothermal time under field conditions was analyzed through the Gompertz function. Base temperature and base water potential for seed germination were estimated at 10.6 ºC and -0.70MPa, respectively. The emergence model showed a very good fit to the experimental data. According to this model, seedling emergence starts at 15 accumulated hydrothermal time (HTT) after sowing, and 50 and 95% emergence is completed at 53 HTT and 105 HTT, respectively. The model was validated with independent field experiments. Results indicate that this model can be useful as a predictive tool contributing to effective control of *C. bonariensis* populations. A stochastic population dynamic model based in cohorts was developed and used to simulate different management strategies based in tillage, non-tillage systems, vegetable covers and herbicide application in Mediterranean perennials crops. Our results indicated that in the absence of any control and non-tillage the seed bank population reached an equilibrium density of 378092 of seeds m^{-2} (7121 adult plants m^{-2}). The most effective strategy was the one that integrated the use of no-till, cover and early and late application of herbicides and reduced the equilibrium density of the seed bank and plant population in 78.7% and 99.5%, respectively. The results of the sensitivity analysis indicated that *C. bonariensis* was particularly sensitive to small changes in the demographic parameters associated with the first cohort and the effectiveness of early treatment of herbicides. Consequently, the control strategies should be focused on the reduction of this first population flow.

Key words: emergence, survivorship, fecundity, density- dependence, hydrothermal time, Gompertz, sensitivity analysis, simulation, stochastic model.

INDICE GENERAL

CAPÍTULO I: Introducción General y Objetivos

CAPÍTULO II: Demography of the weed *Conyza bonariensis* (Asteraceae) in a Mediterranean climate

CAPÍTULO III: A HYDROTHERMAL SEEDLING EMERGENCE MODEL FOR HAIRY FLEABANE (*Conyza bonariensis*)

CAPÍTULO IV: STOCHASTIC MODELLING OF THE POPULATION DYNAMIC AND MANAGEMENT OF *Conyza bonariensis* IN PERENNIAL CROPS

CAPÍTULO I

Introducción general y Objetivos

CAPÍTULO I: Introducción General y Objetivos

I.1. INTRODUCCIÓN GENERAL

I.1.1. Las malas hierbas de los cultivos y sus orígenes

La adopción de la agricultura como modo de subsistencia, la llamada "Revolución Neolítica", supuso hace unos 10000 años un salto abrupto en la evolución de la humanidad que, en escasos milenios, transitó desde los pequeños grupos sociales generalmente nómadas de cazadores-recolectores a los elevados niveles de organización social asociados a la vida sedentaria y al aumento sostenido de sus poblaciones, que permitieron el nacimiento de la escritura, la arquitectura monumental y el aparato del estado (Allen, 1997). La adopción de la agricultura se produjo en diferentes culturas de forma independiente, con centros de origen reconocidos en el Creciente Fértil (Próximo Oriente), Mesoamérica y el Este de Asia (Harlan, 1992).

Desde sus centros de origen, la agricultura y las plantas domesticadas experimentaron amplia difusión geográfica a lo largo de los siglos siguientes. Los "cultivos fundadores de la agricultura", domesticados en el Creciente Fértil, incluyendo la cebada, los trigos emmer y einkorn, los guisantes, la lenteja, los yeros y el lino se difundieron por toda Europa siguiendo principalmente las vías mediterránea y danúbica (Brun, 2009). No sólo las plantas domesticadas y las técnicas agrícolas fueron exportadas desde sus centros de origen. Las plantas asociadas a estos cultivos anuales, las malas hierbas mesícolas o segetales, acompañaron en sus rutas migratorias a los cultivos. A lo largo de siglos de coevolución, estas malas hierbas fueron adquiriendo caracteres favorables para la persistencia bajo cultivo. En diferentes partes de Europa, estas especies arvenses constituyen la gran mayoría de los arqueófitos, es decir, las plantas introducidas por el hombre antiguo, entre el Neolítico y el descubrimiento de América (Brun, 2009; Pysek et al., 2005). La intensificación de la agricultura a partir de mediados del pasado siglo, especialmente el aumento del uso de fertilizantes de síntesis y herbicidas, y la mejora de las técnicas de eliminación de impurezas del grano de siembra, ha supuesto en diferentes países de Europa una drástica reducción o desaparición de muchas de estas malas hierbas altamente especializadas, que ha dado lugar a la implementación de estrategias para su conservación basadas en el mantenimiento en superficies reducidas, como los márgenes de las parcelas de cultivo (Marshall & Moonen, 2002).

A partir del descubrimiento de América, el surgimiento del comercio intercontinental a gran escala trae asociada una segunda gran oleada de introducciones de plantas. Estas plantas “recién” llegadas a Europa, o neófitos, difieren de los arqueófitos arvenses en sus centros de origen, siendo plantas principalmente americanas y, más recientemente, de origen asiático (Chytrý et al., 2008). Además, difieren en sus atributos biológicos y en su comportamiento ecológico. Los neófitos, con mayor frecuencia de plantas perennes, colonizan principalmente los entornos ruderales y los cultivos de implantación relativamente reciente, sobre todo de regadío, más que los segetales, y presentan con mayor frecuencia una elevada capacidad para la dispersión espacial de las semillas. Por el contrario, los arqueófitos arvenses son plantas anuales que dispersan las semillas en el tiempo más que en el espacio a través de la formación de bancos de semillas en el suelo, persistentes o transitorios (Lososová et al., 2006). Entre los neófitos más frecuentes en Europa y en España se encuentran varias especies del género *Conyza*.

I.1.2. El género *Conyza*: origen e introducción en Europa

El género *Conyza* Less. (Asteráceas, subfamilia Asteroideas, tribu Astereas), incluye aproximadamente 60 especies de origen americano varias de la cuales han sido introducidas ampliamente, como neófitos, en las zonas templadas y subtropicales de nuestro planeta (Fig. 1). Estas especies representan uno de los principales ejemplos de invasiones intercontinentales de plantas desde América hacia Europa (Kissmann & Groth, 1999; Thebaud & Abbot, 1995). En España se encuentran citadas como naturalizadas nueve especies de *Conyza*, cuyo tratamiento taxonómico más reciente las adscribe al género *Erigeron* L. (Anthos, 2012): *E. bilbaoanus* (J. Rémy) Cabrera (*C. bilbaoana* J. Rémy in Gay), *E. daveauanus* (Sennen) Greuter (*C. daveauana* Sennen), *E. gouanii* L. (*C. gouanii* (L.) Willd.), *E. ivifolius* (L.) Sch. Bip. (*C. ivifolia* (L.) Less.), *E. primulifolius* (Lam.) Greuter (*C. chilensis* Spreng., *C. primulifolia* (Lam.) Cuatrec. & Lourteig), *E. floribundus* (Kunth) Sch. Bip. (*C. floribunda* Kunth), *E. sumatrensis* Retz. (*C. sumatrensis* (Retz.) E. Walker, *C. albida* Willd. ex Spreng.), *E. canadensis* L. (*C. canadensis* (L.) Cronquist) y *E. bonariensis* L. (*C. bonariensis* (L.) Cronquist). Entre ellas, sólo las tres últimas son muy frecuentes y abundantes en todo el territorio peninsular así como en Europa Occidental y la Cuenca Mediterránea, donde tienen carácter invasor (Guillerm et al., 1990). *C. bonariensis* está distribuida en la totalidad de la Península Ibérica, las islas Canarias y las islas Baleares (Blanca, 2009; MAGRAMA, 2011) (Fig. 2). Debido a sus requerimientos más termófilos es más frecuente en el sur, donde se ha citado su presencia hasta los 1200 m de altitud.

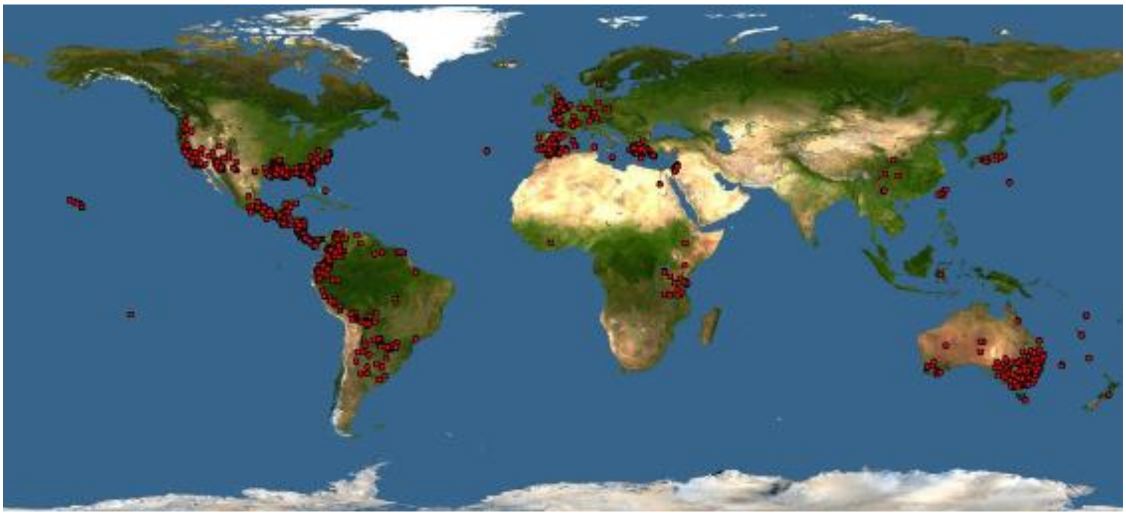

Figura 1. Distribución de *Conyza bonariensis* en el mundo (Discoverlife, 2012)

Figura 2. Distribución de *Conyza bonariensis* en la península Ibérica, Baleares y Canarias (Anthos, 2012).

En el caso de *C. canadensis* está documentada la fecha y el lugar de introducción en Europa. Esta especie fue introducida como ornamental en los jardines de Blois, cerca de París, en 1665, desde donde dispersó por todo el continente (Brun, 2009). Por ejemplo, la primera cita de esta especie en Gran Bretaña es de 1690 (Hill et al., 2002). De modo análogo, *C. sumatrensis* y *C. bonariensis* han sido introducidas en Europa dentro de los últimos 350 años (Jovet & de Vilmorin, 1975). Estudios de variación isoenzimática muestran que *C. bonariensis* y *C. sumatrensis*, de origen sudamericano, son especies estrechamente relacionadas, mientras que *C. canadensis*, de origen norteamericano, es un taxon claramente separado de los anteriores (Thebaud & Abbott, 1995). Además esta última especie es diploide (2n=18 cromosomas) y las dos especies sudamericanas son alopoliploides (2n=54) (Thebaud & Abbott, 1995). Por otro lado, se ha inferido la ocurrencia de híbridos de *C. sumatrensis* y *C. canadensis*, y de *C. sumatrensis* y *C. bonariensis* (p.e. Sennen, 1904), aunque no parecen haberse confirmado (p.e. Thebaud & Abbott, 1995).

I.1.3. *Conyza bonariensis*: caracterización biológica y ecológica

Conyza bonariensis (L.) Cronq. (*Erigeron bonariensis* L., *C. ambigua* DC.) es una especie anual, a veces perennizante (Thebaud & Abbott, 1995; Prieur-Richard et al, 2000; Wu et al., 2007). Las plantas son densamente pubescentes, hasta de 70 cm de altura. Los tallos son erectos, simples excepto en la inflorescencia. Las ramas basales superan en longitud y altura al eje principal. Las hojas, de 1.5–5 mm de anchura, son alternas, lineares o linear–lanceoladas, enteras o dentadas, aparentemente uninervadas y densamente pubescentes. Los capítulos, reunidos en panículas, son disciformes, careciendo de lígulas. El involucro del capítulo, de 5–6.5 mm de diámetro, presenta 4–5 filas de brácteas lineares y pubescentes. El receptáculo carece de escamas interseminales y es ligeramente muricado. Las flores son blanquecinas, las externas filiformes y femeninas, y las internas flosculosas y hermafroditas. Los aquenios (cipselas), de 1.2–1.6 mm de longitud, son comprimidos, oblongoideos y presentan un vilano de 3.5–4 mm, formado por pelos escábridos (Fig. 3) (Cronquist, 1943; Blanca, 2009).

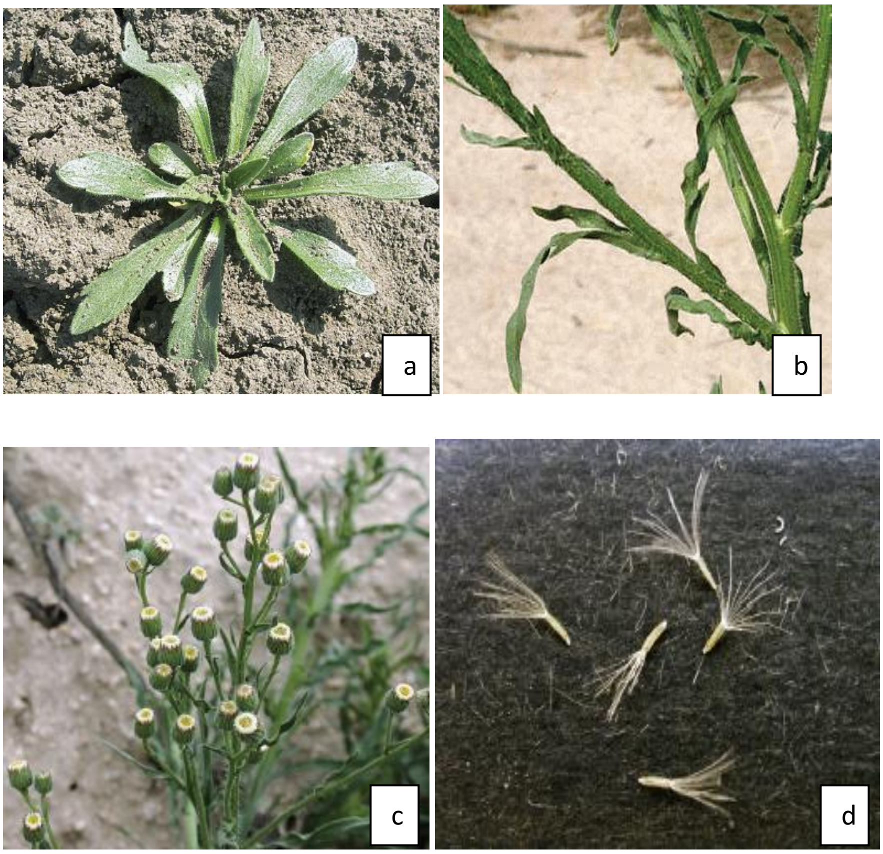

Figura 3. *Conyza bonariensis*, a) roseta, b) detalle del vástago, c) capítulos, d) aquenios (Shrestha et al. 2008)

Aunque no hay datos disponibles para *C. bonariensis*, en las especies comunes de *Conyza* se ha puesto de manifiesto la existencia de autocompatibilidad (Thebaud et al., 1996). En *C. canadensis* el polen es liberado antes de que los capítulos abran completamente lo cual sugiere la existencia de autogamia o geitonogamia, aunque los insectos visitan las flores abiertas (Smisek, 1995; Mulligan & Findlay, 1970). Utilizando plantas resistentes al herbicida paraquat como marcadoras, Smisek (1995) constató que la tasa de autogamia en las plantas de una población de *C. canadensis* varió entre el 1.2% y el 14.5%.

El ciclo vital de *C. bonariensis* es similar al de *C. canadensis* (Fig. 4), al igual que los requerimientos ambientales para su desarrollo (Shrestha et al. 2008).

Tabla 1. Valores medios de caracteres vegetativos y reproductivos medidos en plantas de *C. bonariensis*

Número de hojas	8
Longitud del tallo (cm)	41
Número de ramas	21
Edad a la floración (semanas)	14
Número de aquenios por capítulo	400
Fecundidad (número de aquenios por planta)	119100

Fuente: adaptado de Thébaud & Abbott (1995) y Wu et al. (2007)

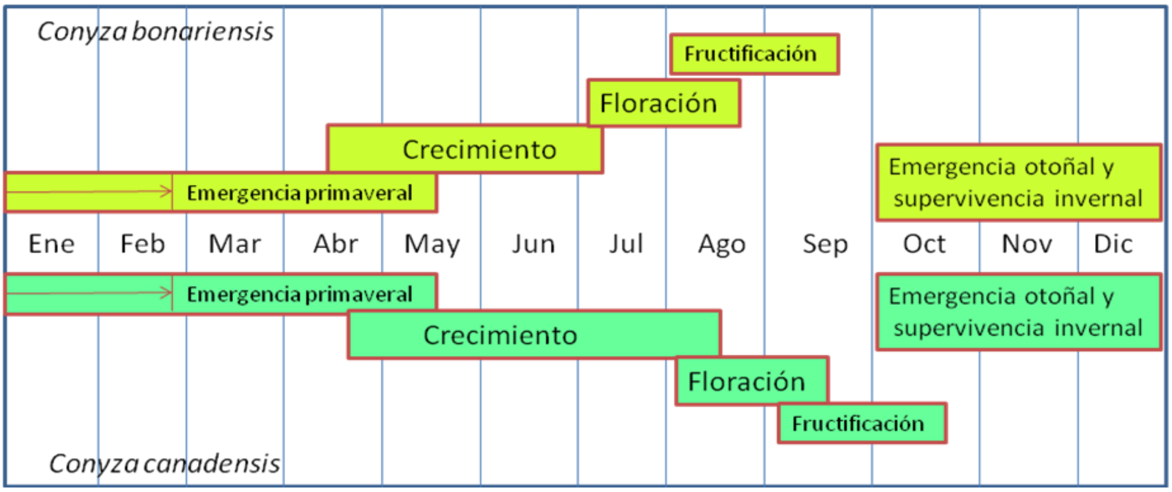

Figura 4. Fenofases del ciclo vital de *C bonariensis* y *C. canadensis* en California Adaptado de Shrestha et al. (2008).

La supervivencia invernal de rosetas de *C. canadensis* es función del momento de la emergencia y de las condiciones ambientales. En tal sentido, la supervivencia está correlacionada con el tamaño de la roseta, la cual a su vez lo está con la longitud de las raíces. Rosetas con un diámetro superior a 5cm a principios de invierno sobrevivieron en un 100% (Regehr & Bazzaz, 1979). Por otra parte, se ha observado que las plántulas de emergencia primaveral tienen una baja mortalidad pero producen muy pocas semillas (0.3 % del total de semillas producidas) en comparación con las de emergencia otoñal (Regehr & Bazzaz, 1979). La principal causa de mortalidad en el invierno es el daño por heladas, que puede suponer una mortalidad de hasta un 86 % (Regehr & Bazzaz, 1979).

El crecimiento de las plantas de *Conyza*, en forma de roseta, permite que ésta fije carbono y acumule energía a bajas temperaturas. La temperatura óptima para la fotosíntesis varía de 28 ºC en verano a 15 ºC en invierno. El punto de compensación de luz oscila entre 75 µmol m^{-2} s^{-1} a 25°C y 8 µmol m^{-2} s^{-1} a 5°C. El tiempo de respuesta fotosintética de las rosetas a la irradiancia es muy rápido, incluso a bajas temperaturas (Regehr & Bazzaz, 1979).

Por lo que se refiere a los procesos de regulación intrapoblacional, no parecen existir estudios específicos sobre *C. bonariensis*. Yoda (1963) demostró que la mortalidad dependiente de la densidad en *Conyza canadensis* se manifiesta por encima de 1000 plantas m^{-2}. Palmbland (1968) sugirió que la biomasa de las poblaciones de *C.*

canadensis está regulada por la plasticidad fenotípica más que por la mortalidad; al incrementarse la densidad, disminuye el tamaño de las plantas y consecuentemente el número de flores y el número de semillas por planta, pero la producción de semillas por unidad de área permanece relativamente constante.

Como sus congéneres *C. canadensis* y *C. sumatrensis*, *C. bonariensis* es una especie de estrategia ruderal (*sensu* Grime, 1977) que coloniza preferentemente medios ruderales, incluyendo entornos urbanos, terrenos baldíos y márgenes de cultivos, caminos y vías de ferrocarril (Thebaud & Abbott, 1995), mostrando una notable tolerancia ecológica que les permite vivir en suelos tanto oligotrofos, de textura ligera, pedregosos o arenosos (Frankton & Mulligan, 1987), como ricos en nutrientes, de textura más pesada, como los arcillosos (Wu et al., 2007). Toleran limitación hídrica una vez establecidas las plantas (Hanf, 1983), como la impuesta por el clima mediterráneo durante el verano. A esta tolerancia a condiciones de sequía estacional puede contribuir el marcado desarrollo radicular que experimentan las plantas durante la fase de roseta invernal. En *C. bonariensis* se han medido profundidades de raíces de más de 35 cm (Wu et al., 2007). Sin embargo, se ha indicado intolerancia al encharcamiento (Smith & Moss, 1998).

A diferencia de los cultivos anuales bajo laboreo, que generan perturbaciones predecibles y de gran extensión espacial, los hábitats ruderales se caracterizan por un régimen de perturbaciones poco predecible y de intensidad y extensión espacial variables (Lososová et al., 2006). En estos medios efímeros se ve favorecida una estrategia fugitiva, basada en la producción de un elevado número de semillas pequeñas, poco competitivas pero con elevada capacidad para la dispersión en el espacio y limitada persistencia en el suelo (Travis & Dytham, 1999). Estos atributos biológicos concurren en *Conyza* spp.

En tal sentido, los aquenios provistos de vilano (Fig. 5) de estas especies son dispersados eficientemente por el viento, pudiendo alcanzar distancias de dispersión superiores a 100 metros (Regehr & Bazzaz, 1979; Andersen, 1993; Dauer et al., 2006). Por otra parte, la dispersión de semillas de *Conyza* también puede ocurrir por el agua, a través de los canales de riego (Kelly & Bruns, 1975). La fecundidad de *Conyza* spp. es muy elevada. Así, *C. bonariensis* produce un promedio de 400 semillas por capítulo (Wu et al., 2007), aproximadamente ocho veces más que *C. canadensis* (Smisek, 1995;

Thebaud & Abbout, 1995), con una producción media de 119100 aquenios por planta, aunque muy variable en función del crecimiento individual (Wu et al., 2007) (Tabla 1).

Figura 5. Aquenios de *C. canadensis* (arriba) y de *C. bonariensis* (abajo) (Shrestha et al. 2008).

La longevidad de las semillas de *Conyza* spp. es bastante limitada. Así, en condiciones de laboratorio, la viabilidad de las semillas de *C. canadensis* no supera los dos o tres años (Hayashi, 1979). En experimentos de enterramiento de semillas de *C. bonariensis* se constató una brusca disminución de la viabilidad después del primer año, recuperándose únicamente un 6% de semillas viables a los tres años (Wu et al., 2007).

Las semillas maduras de *Conyza* no presentan latencia y por tanto germinan rápidamente cuando las condiciones de temperatura y humedad del suelo son favorables (Wu et al., 2007). En la literatura existen ciertas discrepancias sobre el rango de temperaturas que permite la germinación de semillas de *C. bonariensis*. Así, se ha citado un rango de 10º a 25°C (Zinzolker al., 1985) que contribuiría a explicar los patrones estacionales de emergencia de plántulas observados en las zonas templadas, con picos principales en otoño y más limitados a principios de primavera (Regehr & Bazzaz, 1979; Buhler & Owen, 1997). No obstante, otros autores estiman una temperatura mínima y máxima para la germinación de *C. bonariensis* de 4.2°C y 35°C, respectivamente (Rollin & Tan, 2006; Wu et al., 2007). La germinación de las semillas de *C. bonariensis* se ve muy reducida en la oscuridad, mostrando por tanto una respuesta fotoblástica positiva (Rollin & Tan, 2006; Wu et al,. 2007; Vivian et al., 2008; Yamashita et al., 2011). Esta respuesta y sus limitadas reservas probablemente explican la sensibilidad al enterramiento de las semillas de *C. bonariensis*. A profundidades de enterramiento mayores de 0.5 cm la probabilidad de emergencia de plántulas es muy baja (Rollin & Tan, 2006; Wu et al., 2007). Los estudios disponibles sobre respuesta de germinación al potencial hídrico del suelo indican que la germinación total y la velocidad de germinación disminuye a partir de -0,2 MPa (Yamashita & Guimãraes, 2010).

I.1.4. *Conyza bonariensis*: relevancia como mala hierba de cultivos

Conyza bonariensis se comporta como mala hierba de diferentes cultivos. Así, como consecuencia de los cambios en el manejo del suelo habidos durante los últimos años, la especie ha aumentado su frecuencia y abundancia en los sistemas de no laboreo en la península Ibérica y, junto con *Lolium* spp., está considerada una de las malas hierbas más importantes de muchos cultivos perennes (Calha et al., 2008; Urbano et al., 2007). Estos sistemas de cultivo reproducen en buena medida los patrones de perturbaciones propios de los entornos ruderales (Lososová *et al*., 2006), facilitando su colonización por *Conyza* spp. Aunque para *C. bonariensis* no hay estimaciones de su impacto en los cultivos, los datos disponibles para *C. canadensis* indican que a densidades de 150 plantas m^{-2}, puede reducir en un 83% la producción del cultivo de soja en siembra directa (Bruce & Kells, 1990). En el cultivo de la vid, esta especie disminuyó la producción en un 64%, inhibiendo el desarrollo de ramas nuevas en un 28% (Holm et al., 1997). Además de los efectos por competencia, las plantas de *Conyza* spp. parecen ejercer efectos alelopáticos, como se ha mostrado para *C. sumatrensis* (Economou et al.,

2002) y *C. canadensis* (Weaver, 2001), en este caso debidos a la presencia de poliacetilenos, exudados principalmente por las raíces. En estadios avanzados de desarrollo las plantas de *Conyza* spp. presentan una marcada tolerancia a los tratamientos herbicidas y al desbroce mecánico (Urbano, 2005). Además, la incidencia de casos de resistencia a herbicidas en *Conyza* spp. ha aumentado drásticamente en los últimos años (Heap, 2012), habiéndose detectado en España biotipos de *C. bonariensis* resistentes (Urbano et al., 2007). La elevada capacidad de dispersión en el espacio de las poblaciones de *Conyza* spp. supone una dificultad adicional en el control de los biotipos resistentes que sugiere la necesidad de respuestas proactivas, coordinadas a escala de paisaje más que de parcela individual (Dauer *et al*., 2006). Todos estos factores indican que el manejo de las poblaciones de *Conyza* spp. en los cultivos requiere una combinación de múltiples acciones, basadas en el conocimiento de su biología y de su repuesta a las prácticas culturales, como el incremento en la intensidad de manejo del suelo o la rotación de cultivos, y de control dirigido (Lizaroto et al*.*, 2008; Shrestha et al., 2008).

I.1.5. Control de *Conyza* spp. en los cultivos.

En los sistemas convencionales de cultivo, las especies de *Conyza* no suelen convertirse en problemáticas (Brown & Whitwell, 1988). El incremento en la intensidad de manejo del suelo reduce la frecuencia de presencia de *C. canadensis* en al menos un 50% (Buhler & Owen, 1997; Loux et al., 2004). Esta especie fue encontrada en un 61 % de los cultivos bajo no laboreo, mientras que su frecuencia se redujo a un 24% bajo mínimo laboreo y a solo un 8% en cultivos bajo laboreo convencional (Barnes et al., 2004). El laboreo del suelo en otoño puede reducir drásticamente las poblaciones de *Conyza* (Brown & Whitwell, 1988; Bhowmik & Bekech, 1993).

La presencia de residuos del cultivo en la superficie del suelo retrasa la emergencia de *Conyza* spp. (Buhler & Owen, 1997) e incluso llega a impedirla (Leroux et al, 1996). Así, una cobertura de 6 t ha^{-1} retrasó la germinación de semillas de *Conyza canadensis* en cuatro semanas y la emergencia total se redujo en un 80% (Bhowmik & Bekech, 1993).

En ocasiones se ha utilizado la siega mecánica (desbrozado) como método de control de *Conyza*, sin embargo la gran capacidad de rebrote de esta mala hierba hace que la eficacia de este método sea reducida, con el inconveniente adicional de que los rebrotes son más difíciles de controlar con otros métodos. No obstante, la siega puede ser la única alternativa posible cuando las plantas están demasiado desarrolladas (Urbano, 2005).

El estadio de desarrollo en el momento de aplicación de los tratamientos químicos de control de *C. bonariensis* condiciona su eficiencia. En tal sentido, Walker et al., (2012) reportaron que hubo una reducción en la eficacia de los herbicidas del 1% al aplicar el tratamiento a plantas de dos meses de edad en comparación con plantas de un mes. Cuando se aplicó sobre plantas de tres meses de edad la eficacia del tratamiento se redujo entre un 3% y un 30%. Así mismo, Papa *et al*. (2010) estudiaron la eficacia del control tardío de individuos de *C. bonariensis* que sobrevivieron a un tratamiento previo con glifosato, encontrándose que ninguno de los tratamientos probados alcanzó una eficacia superior al 90%. Todo ello indica que el momento óptimo para realizar las aplicaciones de herbicidas es el estado de plántula (Fig. 6) o roseta (Urbano, 2005).

Figura 6. Plántula de *Conyza bonariensis.*

En los cultivos leñosos bajo no laboreo del sur de España los agricultores suelen basar el control de malas hierbas en el uso de glifosato (Urbano, 2005). Sin embargo, cada vez son más frecuentes los fallos de control de *Conyza* con el uso único de este herbicida (Urbano et al. 2007; Gonzalez-Torralva et al., 2010).

Hasta la fecha se han detectado casos de resistencia a herbicidas en *C. bonariensis* en 11 países. Los herbicidas implicados pertenecen a diferentes familias químicas incluyendo glicinas, bipiridilios, inhibidores del fotosistema II e inhibidores de la ALS (International Survey of Herbicide Resistant Weeds, 2012)(Tabla 2).

Tabla 2. Casos de resistencia de *Conyza bonariensis* a herbicidas reportados en el mundo.

País	Año	Grupos de herbicidas y mecanismos de acción
Australia (New South Wales)	2010	Glicinas
Australia (Queensland)	2011	Glicinas
Australia (South Australia)	2011	Glicinas
Brasil	2005	Glicinas
Brasil	2005	Glicinas
Colombia	2006	Glicinas
Egipto	1989	Bipiridilios
Grecia	2010	Glicinas
Israel	1993	Inhibidores del fotosistema II
Israel	1993	Inhibidores de ALS
Israel	2005	Glicinas
Japón	1989	Bipiridilios
Portugal	2010	Glicinas
Suráfrica	2003	Bipiridilios
Suráfrica	2003	Glicinas
España	1987	Inhibidores del fotosistema II
España	2004	Glicinas
California	2007	Glicinas
California	2009	Bipiridilios
Resistencia múltiple		Glicinas

Fuente: Adaptado de International Survey of Herbicide Resistant Weeds

Una de las estrategias utilizadas para el manejo de la resistencia de *C. bonariensis* es el uso de mezclas de herbicidas con diferentes mecanismos de acción y degradación (Urbano, 2005; Urbano et al., 2007; Moreira et al,. 2010; Werth et al., 2010; Wu et al., 2010; Oliveira et al.,2010), a veces en combinación con estrategias culturales basadas en la siembra de trigo o avena en invierno (Paula et al., 2011). Desde el punto de vista de los métodos de control no químicos, el laboreo y el uso de cubiertas vegetales de gramíneas son eficaces en el control de *Conyza* (Urbano, 2005).

I.1.6. Contribución de los modelos matemáticos al control de las malas hierbas

Actualmente, los sistemas agrícolas son percibidos en la sociedad por valores adicionales a su eficiencia económica. Así, en relación con los métodos de control de malas hierbas, los efectos a corto y largo plazo de los herbicidas sobre la salud humana y su impacto sobre los componentes de servicios del agroecosistema y sobre los organismos con interés de conservación (p.e. malas hierbas raras), así como su acumulación y persistencia en el suelo y en los acuíferos, son aspectos que condicionan la toma de decisiones de control (Radosevich et al., 2007). Estas nuevas percepciones e intereses han llevado a la generación de una gran cantidad de información que dificulta el proceso de toma de decisiones eficientes. En tal sentido, existe la necesidad de desarrollar herramientas que faciliten el proceso de toma de decisiones, tarea compleja que requiere la integración de información sobre biología de malas hierbas, herramientas de control disponibles, riesgos ambientales, factores económicos, etc. Una vía para abordar esta situación es el uso de modelos matemáticos que ayudan a integrar la información disponible y permiten simular el impacto demográfico y económico de diferentes escenarios de manejo, constituyendo una herramienta valiosa de ayuda a la toma de decisiones eficientes (Gonzalez-Andujar et al., 2011).

Los modelos matemáticos de dinámica de poblaciones aportan conocimientos de gran valor científico brindando, desde el punto de vista teórico, la posibilidad de entender los cambios demográficos de una mala hierba e identificar los estados y procesos que son importantes para su regulación y, desde el punto de vista aplicado, permiten la exploración de los efectos a medio y largo plazo de diferentes estrategias de control (Gonzalez-Andujar, 2008).

De manera general los modelos de dinámica de poblaciones pueden clasificarse en empíricos y mecanicistas, aunque se han propuesto modelos híbridos (semiempíricos) que integran ambas aproximaciones. Los primeros establecen relaciones funcionales mediante el uso de modelos estadísticos. Los modelos mecanicistas se basan en el conocimiento de los procesos fisiológicos y biológicos subyacentes en los sistemas biológicos y establecen relaciones funcionales en base a este conocimiento (Maxwell & O`Donovan, 2007). Los modelos mecanicistas son más precisos a la hora de realizar las predicciones, pero debido a su mayor complejidad y a la gran cantidad de información requerida para su implementación han hecho que sean los modelos empíricos o semiempíricos los más utilizados en malherbología (Gonzalez-Diaz, 2012).

En el contexto de los modelos empíricos o semiempíricos, se encuentran los modelos de dinámica de poblaciones. Este tipo de modelos tiene una larga tradición en malherbologia (Holst et al., 2007) y ha mostrado su utilidad en dos ámbitos, el teórico, aportando nuevos conceptos e ideas (Gonzalez-Diaz et al., 2012) y el práctico, explorando a medio y largo plazo diferentes escenarios de manejo (Gonzalez-Andujar & Fernandez-Quintanilla, 2004).

Los modelos poblacionales se han basado en la demografía de la planta. Estos modelos establecen relaciones funcionales entre las distintas etapas del ciclo de vida de la mala hierba. Los diferentes estados funcionales (banco de semilla, plántula, planta adulta y lluvia de semillas) están conectados por tasas de transferencia: *n*, tasa de nascencia; *sp*, tasa de supervivencia de plántulas; *f*, tasa de fecundidad; *d*, tasa de dispersión; *ss*, tasa de supervivencia de semillas en el suelo (Fig. 7)(Gonzalez-Andujar, 2008).

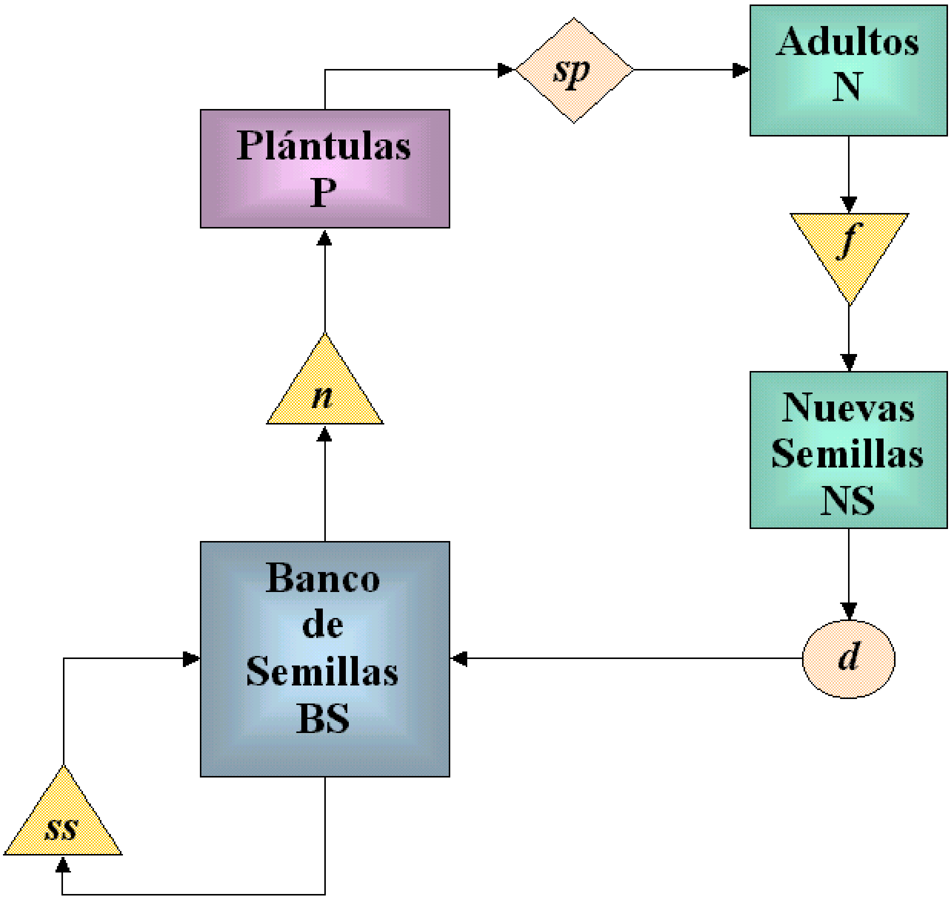

Figura 7. Modelo demográfico básico de una mala hierba anual (Gonzalez-Andujar et al., 2005)

Los modelos son parametrizados con experimentos de campo y/o invernadero (Chauhan et al., 2006; Barroso et al., 2009; Taberner, 1996; Gonzalez-Ponce, 1998) y validados con datos independientes (Gonzalez-Diaz et al., 2012). Una vez validados, los modelos están listos para su utilización como herramientas de exploración de estrategias de manejo.

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**), se siguen los **Capítulos II**, **III** y **IV** que se corresponden con los artículos publicados o pendientes de envío a diferentes revistas científicas de difusión internacional, por lo que se presentan en ingles 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.

Capítulo II: En este apartado se presentan los principales atributos demográficos de *Conyza bonariensis*. En concreto se estudian la emergencia, supervivencia y fecundidad en un entorno ruderal mediterráneo. Igualmente se explora la existencia de una regulación poblacional a través de un proceso dependiente de la densidad a nivel de la fecundidad.

Capítulo III: se desarrolla y evalúa un modelo para predecir la respuesta en la emergencia de *C. bonariensis* en base al ambiente hidrotermal del suelo. Se ajusta un modelo hidrotermal de germinación con datos obtenidos en diferentes pruebas hechas a diferentes temperaturas y potenciales hídricos para establecer los parámetros hidrotermales que caracterizan la germinación de *C. bonariensis*, obteniendo así la temperatura y potencial hídrico base para ésta especie. La relación entre la emergencia acumulada y el tiempo hidrotermal acumulado se analiza a través de la función de Gompertz, con lo cual se obtiene una herramienta para lo toma oportuna de decisiones en el manejo de ésta importante mala hierba.

Capítulo IV: se desarrolla un modelo estocástico de dinámica de poblaciones basado en cohortes para simular la dinámica del banco de semillas bajo diferentes escenarios de manejo en cultivos perennes Mediterráneos que incluyen tanto estrategias individuales como: el no laboreo, uso de coberturas, laboreo, aplicación temprana y tardía de herbicidas, así como también la combinación de las mismas. Los parámetros usados en el modelo se corresponden con los obtenidos en los estudios demográficos presentados en el capítulo II. Se realiza un análisis de sensibilidad calculando un índice de sensibilidad que proporciona información sobre la vulnerabilidad del modelo a pequeños cambios en los parámetros del mismo. La información generada con este modelo permite no solo explicar la situación actual de *C. bonariensis* en la cuenca Mediterránea, sino que también hace una aproximación a medio plazo sobre la eficacia de algunas estrategias de control utilizadas por los agricultores y la necesidad de integrarlas para el manejo sostenible de ésta mala hierba en cultivos perennes.

Capítulo V: se presentan las conclusiones finales.

I.3 OBJETIVOS DE LA TESIS

Desde la aparición de los herbicidas en los años 40, el control de las malas hierbas se ha basado en su uso indiscriminado. En los últimos años la aparición de los problemas de resistencias a los herbicidas y una mayor sensibilidad medioambiental de la sociedad ha llevado hacia la búsqueda de un manejo más racional de la flora arvense. Dicho manejo pasa por un conocimiento de su biología y ecología que permita el diseño de estrategias de manejo sostenibles. Dentro de este contexto el objetivo general de la presente Tesis Doctoral ha sido la de proveer conocimientos ecológicos a través del estudio de la demografía y la dinámica poblacional de *Conyza bonariensis*, con la finalidad de establecer estrategias de manejo de esta especie en los cultivos mediterráneos. El estudio se concretó en los siguientes objetivos específicos:

1. Estudio de la demografía de *C. bonariensis* en condiciones naturales, abordado en el capítulo II.

2. Desarrollo y evaluación de un modelo hidrotermal de la emergencia de plántulas de *C. bonariensis*, abordado en el capítulo III.

3. Desarrollo un modelo de dinámica poblacional y simulación del impacto de diferentes estrategias individuales e integradas de manejo en las poblaciones de *C. bonariensis* en cultivos perennes mediterráneos, abordado en el capítulo IV.

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CAPÍTULO II

Demography of the weed *Conyza bonariensis* (Asteraceae) in a Mediterranean climate

CAPÍTULO II: Demography of the weed *Conyza bonariensis* (Asteraceae) in a Mediterranean climate

Resumen

Conyza bonariensis es una mala hierba de creciente importancia tanto en cultivos anuales como perennes de las regiones subtropicales y templado-cálidas del mundo, sobre todo en sistemas agrícolas manejados con no laboreo. El objetivo de este trabajo fue estudiar durante dos campañas (2010-2011 y 2011-2012) la emergencia, supervivencia y fecundidad de la especie en un entorno ruderal mediterráneo. En los estudios de supervivencia y fecundidad se consideraron cuatro cohortes. La tasa media de emergencia fue del 61 %. El patrón de emergencia se caracterizó por altas tasas iniciales de emergencia que fueron altamente dependientes de las precipitaciones. La tasa media de supervivencia de las plántulas fue del 33 %. La fecundidad alcanzó un valor medio de 86066 aquenios/planta. En general, las cohortes más tempranas presentaron unos valores más altos de supervivencia y fecundidad, contribuyendo mas a la siguiente generación y por consiguiente serian las que deberían ser preferentemente controladas para un manejo efectivo de *C. bonariensis.* Esta especie presentó un proceso de regulación de sus poblaciones a través de un proceso dependiente de la densidad a nivel de la fecundidad.

Palabras clave*:* emergencia, supervivencia, fecundidad, denso-dependencia.

Abstract

Conyza bonariensis is a weed of increasing importance, both in annual and perennial crops, in subtropical and mild-hot regions worldwide, especially in agricultural systems managed with no-tillage. The aim of this work was to study during two seasons (2010-2011 and 2011-2012) the emergence, survival and fecundity of this species in a ruderal

Mediterranean environment in order to lay the foundation for its more rational control. In the survival and fecundity studies four cohorts were considered. The mean rate of emergence was 61%. The emergence pattern was characterized by high initial emergence rates, which were highly dependent on the rainfall. The mean survival rate of the plants was 33%. Fecundity reached a mean value of 86066 achenes/plant. In general, the earliest cohorts presented higher survival and fecundity values, contributing more to the following generation and, consequently, they should preferably be controlled for an effective management of *C. bonariensis.* This species showed a regulation process of its populations through a density-dependence process system at a fecundity level.

Keywords: flaxleaf fleabane, emergence, survivorship, fecundity, density- dependence.

II. 1. Introduction

*Conyza bonariens*is (L.) Cronquist is an annual Asteraceae, a native of South America and widely spread over tropical and temperate-hot areas, including the Mediterranean basin (Karlsson & Milberg 2007; Prieur-Richard *et al*. 2000). It mainly behaves like a ruderal plant, colonizing disturbed habitats like road borders, boundaries, and open ground. In addition, it is considered to be a weed in over 40 crops in 70 countries (Holm et al. 1997), and it has become one of those most difficult to control in agricultural systems, particularly in conservation ones (Wu et al. 2010). The adoption of measures to keep its populations in check is essential to prevent harvests becoming seriously reduced. Thus, for example, soybean growing may be cut back by up to 90% with densities of 100-200 plants m^{-2} (Bruce & Kells 1990). Its control is primarily based on the application of herbicides, which, currently, has become more difficult due to the appearance of populations resistant to different herbicides, among them glyphosate (Urbano et al. 2007).

It is widely accepted that a knowledge of weed biology is essential for setting up plans for the integrated management of weed populations (Cousens & Mortimer 1995). Very little information exists on the demographic aspects of *C. bonariensis* (Shrestha et al. 2008) and any information on its biology is mainly limited to studies carried out under laboratory conditions. Wu et al. (2007) reported that the emergence of *C. bonariensis* predominantly occurs on the soil's surface in the autumn and beginning of winter, and only a small fraction emerges in the spring. Karlsson & Milberg (2007) and Vivian et al. (2008) determined that *C. bonariensis* is a positive photoblastic species. with base, optimum and maximum temperatures of 4.2, 20 and 35 °C, respectively. Yamashita & Guimaraes (2010) established that the percentage and velocity of the germination of *C. bonariensis* seeds were reduced when the water potential of the soil decreased to below -0.2 Mpa.

As mentioned previously, very little is known about the demography of *C. bonariensis* and any knowledge is mostly circumscribed to greenhouse studies and it is non-existent in areas with a Mediterranean climate. So, the objective of this work was to establish the demographic attributes of *C. bonariensis* under field conditions with the aim of helping to fix the bases for a more rational control of this species.

II. 2. Materials and Methods

II. 2. 1. Study area

The study was conducted in the experimental field of the Instituto de Investigación y Formación Agraria y Pesquera (IFAPA), Cordoba, southern Spain (37° 51’ 40’’ N; 4° 47’ 56’’W; 117 m asl). It has a Mediterranean climate with a mean annual rainfall of approximately 600 mm, concentrated between the autumn and spring. The mean annual temperature of the maxima and the minima is of 27ºC and 10 ºC, respectively. The soil has a loamy texture with a pH of 8.47 and an organic matter content of 1.13%.

II. 2. 2. Experimental Design

To characterize the demography of *C. bonariensis*, three field experiments were carried out between the months of October and August during two consecutive seasons (2010-2011 and 2011-2012).

Emergence pattern and rate. To determine the temporal pattern and emergence rate of seedlings, in October six microplots of 0.3 x 0.3 m were each sown with 200 seeds of *C. bonariensis* at a depth of under 1cm. For this purpose, the soil was previously ploughed subsequently adding a fine layer of inert substrate (peat), with which the seeds were lightly mixed to prevent them from being blown away. Every three days until mid-December, counts were made and the seedlings emerging after each one were removed.

Survival and fecundity. A second experiment was performed with the aim of assessing survival and fecundity. Four cohorts, defined by their sowing date in the experimental plot (20 October. 13 December, 7 February and 4 April), were considered. At the beginning of each season, 16 plots of 1 x 1 m were established following a square arrangement of 4 x 4 plots, 1 m apart, and four plots were randomly assigned to each cohort. The soil of each plot was ploughed prior to sowing. When sowing, a large number of seeds were mixed with a fine layer of peat and then buried at a depth of under 1 cm. Watering was done daily during the month following sowing to facilitate seedling establishment. Once established, 30 seedlings were marked and the unmarked plants were periodically eliminated, thus maintaining a low density in plants (Shrestha et al. 2010). Survival counts were made weekly until the beginning of fructification. Fecundity was evaluated at the end of the plant cycle. For this purpose, at the start of flowering, three plants per plot were marked and the number of capitula produced per plant was computed. Also, 12 capitula per cohort were randomly selected at a stage immediately before the beginning of dispersion and the number of achenes in them was counted. Fecundity was estimated as the product of the number of capitula per plant and the mean number of achenes per capitulum.

Survival curves were established for each cohort and compared with the Log Rank test and the Multiple Pairwise Comparison test of Holm -Sidak ($p<0.05$) using the SIGMAPLOT v.11 programme.

The effect of the cohort on fecundity was analyzed by the non-parametric Kruskall-Wallis test and the pairwise comparison test ($p<0.05$), employing the STATISTIX v.9 programme.

Effect of density on fecundity. In order to determine the effect of density on fecundity, an in-field experiment was performed in May. 2012. Seven areas naturally infested with C. *bonariensis* plants covering a wide range of densities: 1, 55, 122, 277, 555, 777 and 1111 plants/m$^{2.}$ were selected. For each density, 3 plants were marked and the number of capitula per plant computed, and in a random sample of 10 capitula per density, the number of achenes per capitulum was counted. With the product of both variables, the number of achenes per plant (fecundity) was obtained.

The functional relationship between density and fecundity was established by means of the hyperbolic model

$$\mathbf{Y} = \frac{fo}{1 + aX} \qquad [1]$$

where Y is the number of achenes produced per plant, X is the density (plants m^{-2}) of *C. bonariensis* , *fo* represents the number of achenes produced per plant when the population density approaches zero and *a* is the area required by a plant to produce seeds. To fit the model and estimate the parameters the non linear regression module of the programme SIGMAPLOT v. 11. was used.

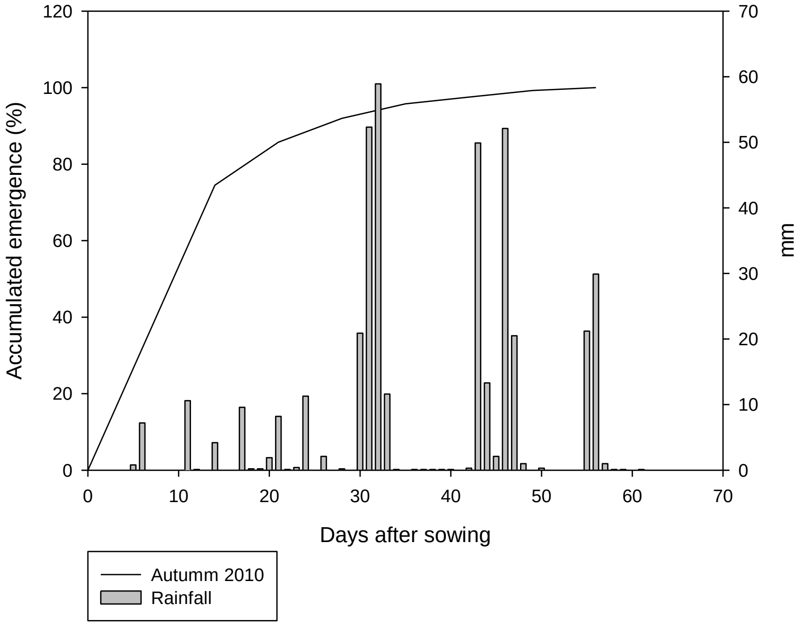
II. 3. Results

II. 3. 1. *Emergence pattern and rate*

The average emergence rate in the two study seasons was of 0.61 ± 0.16. (i.e. 0.65 ± 0.21 in the season 2010-2011 and 0.58 ± 0.14 in 2011-2012).

Figure 1 depicts the emergence pattern of *C. bonariensis* in the two years of the experiment. In autumn of 2010 (Figure 1a) there was a rapid emergence at the beginning of the experiment, which reached 90% during the 21 days after sowing (das). In contrast, in the autumn of 2011, there was a slow initial emergence (5% at 7 das), which reached 50% at 20 das and 90% at 35 das (Figure 1b). The rainfall in autumn 2010 was more abundant and more regularly distributed than in the autumn of 2011.

Autumn 2010 (a)



Autumm 2011 (b)

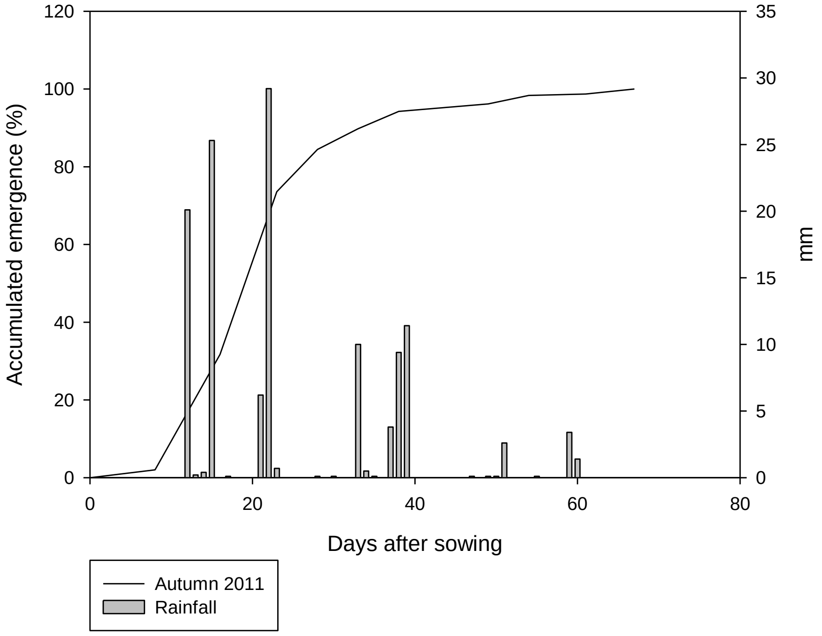
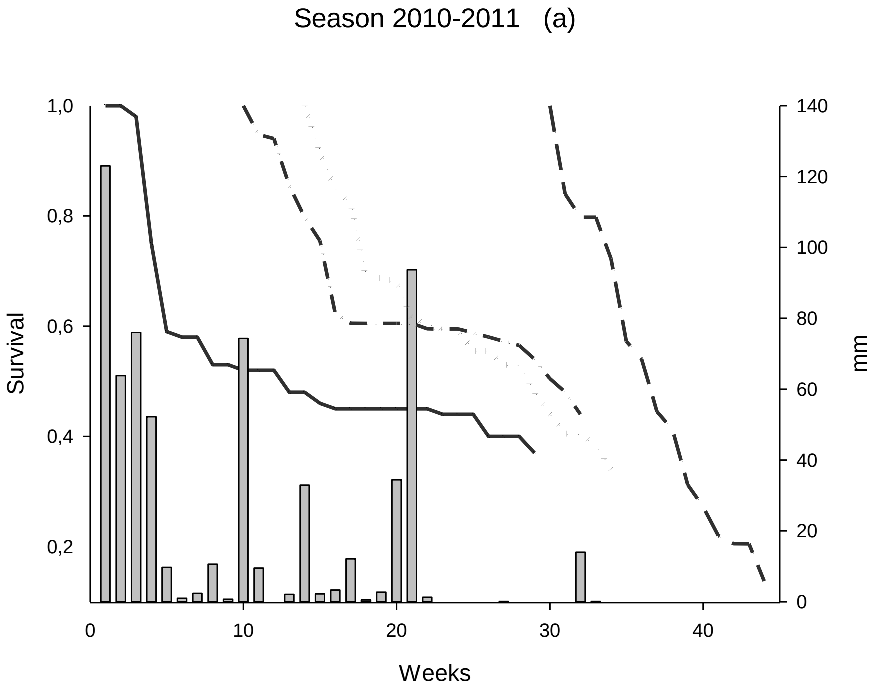


Figure 1. Accumulated emergence of *C. bonariensis* rainfall pattern (mm) during the study periods in autumn 2010 (a) and 2011 (b).

II. 3. 2. *Seedlings survival*

The mean survival rate of *C. bonariensis* seedlings in the whole of the two seasons studied was of 0.3 ± 0.2.

In the 2010-2011 season, the three earliest cohorts recorded similar survival rates, with values ranging between 0.34 and 0.44. In contrast, the latest cohort showed a substantially lower survival rate (0.13) (Table 1). In fact, the log-rank analysis confirmed the existence of significant differences between the survival curves of the cohorts ($\chi 2$= 10.157; gl=3; p=0.017; Fig. 2a). The survival curve of the latest cohort was statistically different (Holm-Sidak test, p<0.01) from the first cohort. The remaining cohorts did not present any statistical significant differences between each other (Table 2).



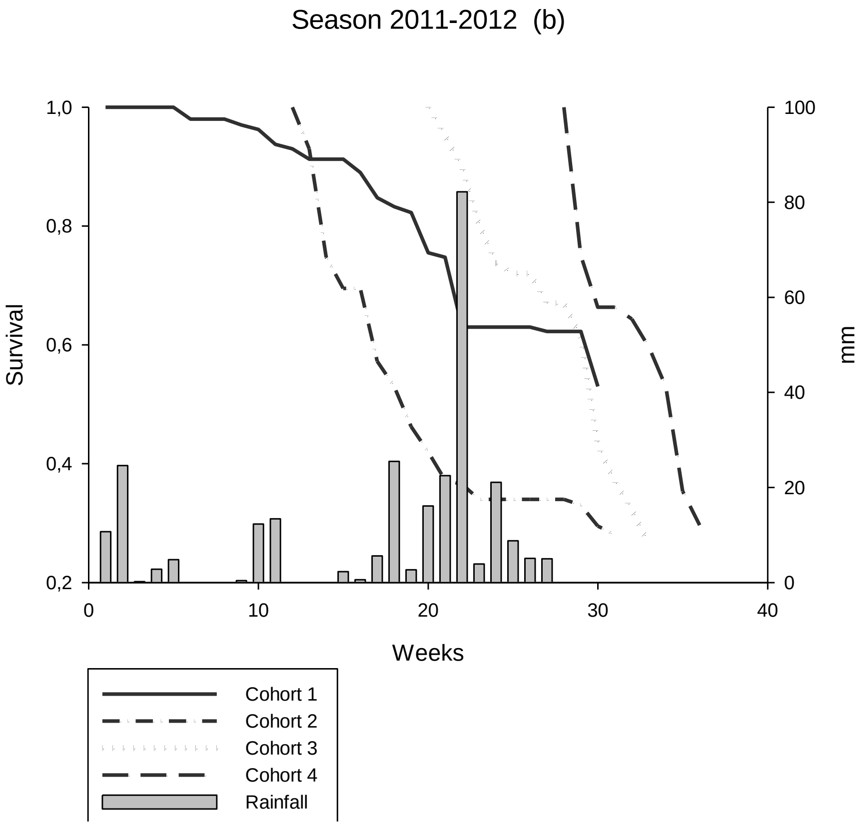


Figure 2. Survival curves up to adult stage of four cohorts (October, December, February and April) of *C. bonariensis* plants during the seasons 2010-2011 (a) and 2011-2012 (b).

Table 1. Mean survival rate up to adult stage of four cohorts of *C. bonariensis* during the two seasons being studied (2010-2011 and 2011-2012)

Season	Cohort	Survival	Standard Error
2010-2011	1	0.37	0.08
	2	0.44	0.09
	3	0.34	0.09
	4	0.13	0.01
2011-2012	1	0.53	0.02
	2	0.28	0.04
	3	0.26	0.04
	4	0.29	0.06

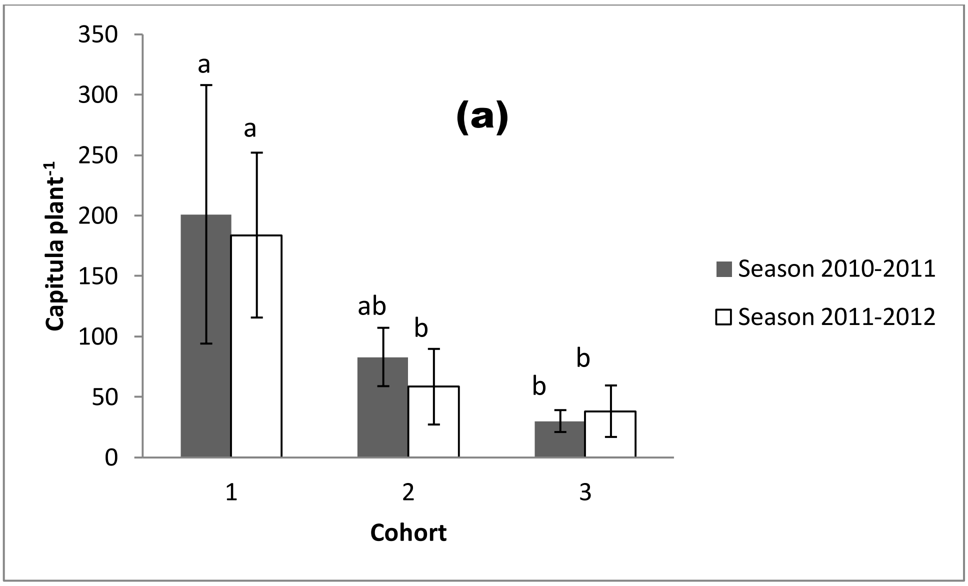
In the 2011-2012 season, the three latest cohorts recorded similar survival rates, with values ranging between 0.26 and 0.29, approximately half that of the earliest cohort (0.53, Table 1). The log-rank analysis indicated the existence of significant differences between the survival curves of the cohorts ($\chi 2= 25.261$; gl=3; $p<0.001$; Fig. 2b). On making the comparative analysis of the curves, the survival curve of the first cohort was statistically different (Holm-Sidak test. $p<0.01$) from the curves of the latest cohorts (Table 2). The rest of the cohorts did not present any significant differences between each other (Table 2).

Table 2. Result of the pairwise comparisons (Holm-Sidak test; $p<0.05$) of the survival patterns of the four cohorts of *C. bonariensis* studied in the two seasons (2010-2011 and 2011-2012).

Season	Comparisons	Statistical	P	Critical level of P
2010-2011	C_1 vs C_4	14.00	0.0001	0.008*
	C2 vs C3	2.95	0.107	0.0102
	C3 vs C4	2	0.157	0.0127
	C2 vs C4	1.5	0.221	0.017
	C1 vs C3	1.121	0.29	0.025
	C1 vs C2	0.006	0.934	0.05
2011-2012	C_1 vs C_2	15.87	0.00006	0.008*
	C_1 vs C_3	14.50	0.0001	0.01*
	C_1 vs C_4	7.26	0.007	0.01*
	C2 vs C3	1.5	0.221	0.017
	C3 vs C4	0.5	0.480	0.025
	C2 vs C4	0.081	0.775	0.05

II. 3. 3. *Fecundity*

Breaking down the variable fecundity into its components, a decreasing trend in the number of capitula produced per plant from the first to the third cohort was observed (Figure 3a). The fourth cohort did not produce any capitula and was not included in the analysis. Statistically significant differences were found both in the 2010-2011 season (χ^2=21.64; gl=29; p<0.01) and in the 2011-2012 one (χ^2=23.24; gl=35; p<0.01). In the first year, the first cohort (201±106.92 capitula/plant) was statistically different from the third one (30±9.06 capitula/plant) (Fig. 3a). The second cohort (83±24.14 capitula/plant) was not statistically different from the other two cohorts (Fig.3a). In the 2011-2012 season, the same behaviour as the previous year was followed; the first cohort (184±68.19 capitula/plant) was statistically different from the third one (38±21.31 capitula/plant) (Fig. 3a). The second cohort (58±31.27 capitula/plant) was not statistically different from the other two (Fig. 3a).



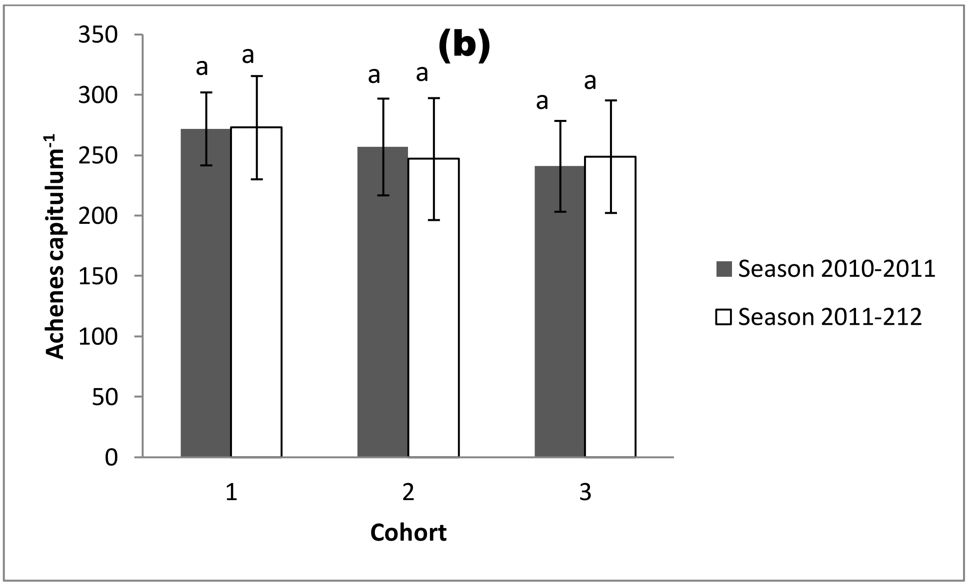


Figure 3. Number of capitula per plant (a) and achenes/capitulum (b) of *C. bonariensis* for each cohort (October, December and February) in the seasons of 2010-2011 (dark colour) amd 2011-2012 (pale colour). Bars followed by the same letter in the same season did not present any significant differences (p<0.05) in agreement with the pairwise comparisons test. The vertical lines indicate the standard error.

No significant differences were observed either in the 2010-2011 season (Kruskal-Wallis test, χ^2=1.52; gl=29; p=0.46) or in that of 2011-2012 (Kruskal-Wallis test, χ^2=2.41; gl= 35; p=0.29) in the number of achenes/capitulum (Figure 3b). In both seasons, the mean fecundity values were: for the first cohort of 272 ± 30.2 and 273 ± 42.74 achenes/capitulum, respectively; for the second cohort they were 257 ± 40.5 and 247 ± 50.48 achenes/capitulum, respectively, for the third cohort they were 241 ± 37.6 and 249 ± 46.61 achenes/capitulum, respectively.

The fecundity (achenes/plant) of the *C. bonariensis* plants was positively related to the earliness of the cohort (Fig. 4). The plants in the fourth cohort did not actually fructify. The fecundity differences between the three earliest cohorts were statistically significant both in 2010-2011 (Kruskal-Wallis test, χ^2=22.57; gl=29 p<0.01) and in 2011-2012 (Kruskal-Wallis test, χ^2=22.99; gl=35; p<0.01).

In the 2010-2011 season, the earliest cohort (70288 ± 29651.1 achenes/plant) was statistically different from the third one (8218±3794.29 achenes/plant). The second cohort (18206 ± 8747.83 achenes/plant) was not statistically different from the other two (Fig. 4). In the 2011-2012 season the first cohort (51066 ± 23893.50 achenes/plant) was statistically different from the other two. The second cohort (14930 ± 9305.45 achenes/plant) was not statistically different from the third one (9424 ± 5380.36 achenes/plant) (Fig. 4).

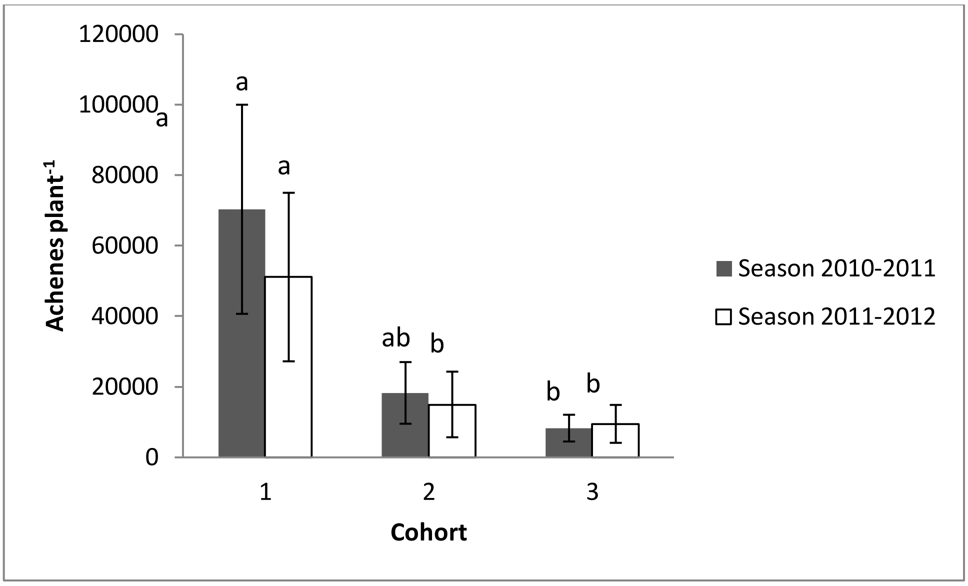


Figure 4. Mean fecundity of the different cohorts (October, December and February) of *C. bonariensis* in the 2010-2011 (dark colour) and 2011-2012 seasons (pale colour). Bars followed by the same letter in the same season do not present any statistically significant differences ($p<0.05$) in agreement with the pairwise comparisons test. The vertical lines indicate the standard error.

II. 3. 4. *Effect of density on fecundity*

The existence of a process density-dependent at a fecundity level was satisfactorily explained by the hyperbolic model (equation 1) (eqn 1) (R^2adj=0.99; RMSE=2809.67; gl=6) (Fig. 5). The values estimated for the parameters were n = 87273.96 achenes/plant (SE=3300) and a=0.06 (SE=0.01).

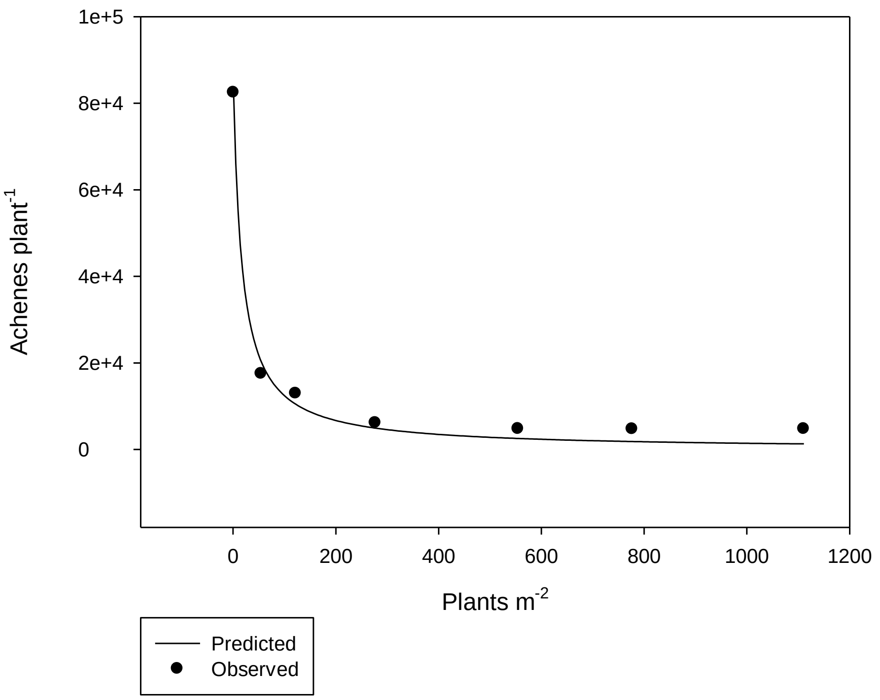


Figure 5. Relationship between fecundity and density of a *C. bonariensis* population. The line corresponds to the fit of the hyperbolic model (eqn 1). The points correspond to the values observed.

II. 4. Discussion

With the aim of understanding and predicting the population dynamics of weeds, we have to be able to relate the changes in size of the population with a series of demographic variables, such as emergence, mortality and fecundity. The spatial and temporal variations in those parameters may be large ones and must affect the dynamics of the size of the population (Forcella et al. 1992; Cousens 1995; González-Andujar & Perry 1995). In our study, although the average recruitment of plantlets was of 61%, the individual values obtained in the different experiments varied from 35 to 87%. Our result was similar to that reported by Green (2010), who, in Australia, observed an average emergence rate for *C. bonariensis* of 64%.

Both the total emergence of the seedlings and the velocity of this process was determined by the location of the seeds in the soil profile (Gramshaw & Stern 1977). In all our emergence experiments, the seeds were very superficially buried in the soil (<1 cm), as occurs with the natural seed bank of this species (Wu et al. 2007). This situation promotes a complete and rapid appearance, giving rise to high emergence rates as has been the case.

The emergence pattern of *C. bonariensis* was characterized by high initial emergence rates, which appear to be highly dependent on the amount and distribution of the precipitations (Fig. 1). The effect of the seasonal variations in rainfall and their influence on emergence patterns has been reported in other species (Stoller & Wax 1973; Mulugeta & Stoltenberg 1997; Puricelli et al. 2002). The germination of this species is particularly sensitive to scant moisture conditions, and, as no dormancy in its seeds is presented, rain and irrigation significantly stimulate emergence (Yamashita & Guimaraes 2010; Nandula et al. 2006; Wu & Walker 2004).

One of the characteristics of our study was the consideration of different cohorts which may make different contributions to the biology of the species (Mokhtassi-Bidgoli et al. 2013). The difference in survival between different cohorts has been documented by diverse authors (Fernández-Quintanilla et al. 1986; Verdú & Mas 2006; Puricelli et al. 2002; Borger et al. 2009). In general, those studies shown that the earliest cohorts have a higher survival rate than those which emerge later. Considering together the two seasons studied, our data shown a similar behaviour. The mean survival rate of the first cohort was of 0.45 and it decreases down to the last cohort, which was of 0.21. Even when taking into account the years isolatedly, those differences may not emerge clearly due to climate variations (Table 1).

The survival rates found between the different cohorts were similar to those determined by Buhler & Owen (1997) and Regehr & Bazzaz (1979) in a similar species, *C. canadensis*. These authors report that the survival of plants emerging in the autumn was of over 41%, and of 36% in those emerging in the spring.

The highest fecundity values occurred in the first cohort. Morphologically, those plants were more robust than those established in subsequent cohorts, which probably resulted in a greater capacity to produce capitula. Similar results have been found by different authors (Verdú & Mas 2006; Kiegel 1995; Gallart et al. 2010), who reported that the populations emerging earlier show a great reproductive capacity compared with those established later. For example, Green (2010) found a reduction of 29.6% in the fecundity of *C. bonariensis* plants sown in spring compared to those sown at the end of

autumn. Torra & Recasens (2008) quantified a reduction in the amount of seeds/plant in *Papaver rhoeas* from the first to the last cohorts. This reduction in seed production in the more recent cohorts is related to the smaller accumulation of biomass due to the shorter growth period (Bosnic & Swanton 1997; Knezevic & Horak 1998; Norris 1996) and probably to the inter- and intraspecific competition.
The number of achenes produced per plant varied between 96712 and 75420 with an average of 86066 achenes/plant, fairly similar to the 85074 achenes/plant found by Green (2010) in C. bonariensis in Australia. However, they were much fewer than those obtained by Wu et al. (2007) and Kempen & Graf (1981) under laboratory conditions who estimated 119100 and 266753 achenes/plant, respectively. These differences are possibly because of the optimal conditions experienced by the plants under controlled conditions in the experiments of the authors cited.

The maximum number of capitula per plant found in this work coincides with that determined for this species by Kempen & Graf (1981) and Green (2010), who obtained an average of 290 and 232 capitula/plant, respectively. However, they differ from the 400 capitula/plant found under laboratory conditions by Wu et al. (2007). Similarly, the maximum values of achenes/capitulum reported in this work are lower than the 366 achenes/capitulum found by Green (2020). In general, *C. bonariensis* has a high reproductive capacity which undoubtedly favours its expansion.

The growth of the populations can be regulated by processes depending on the density which operate in different parts of the biological cycle. In our case, the results obtained indicate that there is a regulatory effect of the population related to the diminution of fecundity at high densities of *C. bonariensis*. This type of density-dependent regulation has also been observed in different weed species like the case of *Agrostema githago* (Firbank & Watkinson 1986) or *Avena sterilis* (González-Andújar & Fernández-Quintanilla 1991, 1993). In *C. canadiensis,* Palmblad (1968) and Bhowmik & Bekech (1993), taking as a reference the amount of seeds produced per plant growing at densities of 55 plants/m^2, achieved a reduction in plant fecundity of between 50 and 68% by increasing the density to 200 plants/m^2, which coincides with the 65% reduction found in this work for that interval of densities.

With the establishment of conservation systems in agriculture, some species such as *C. bonariensis* have begun to be an important problem in crops. Woody crops (e.g olive tree) have been some of those most affected since this species has adapted itself to surviving under their canopy or between lines of trees. The best treatment for this species is in the first moments of its vegetative growth and mainly with systemic herbicides. But the continuous application of herbicides for its control has triggered the appearance of populations resistant to different herbicides (Urbano et al. 2007), so that it would be recommendable to adopt integrated strategies for their management. The results obtained in this work will help to establish those strategies, for which a knowledge of the biology of the species is determinant.

In this study it can be concluded that *C. bonariensis* is a species which presents average emergence and survival rates and a high fecundity. The earliest cohorts contributed most to the following generation, and, therefore, they would be the ones which ought preferably to be controlled. This species displays a process of regulation of its populations through a system depending on density at a fecundity level.

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CAPÍTULO III

A hydrothermal seedling emergence model for hairy fleabane (*Conyza bonariensis*)

CAPÍTULO III: A hydrothermal seedling emergence model for hairy fleabane (*Conyza bonariensis*)

Resumen

Conyza bonariensis es una especie nativa de Sur América, anual, perteneciente a la familia Asteracea e introducida en el Mediterráneo donde se comporta como una planta ruderal y es una mala hierba de difícil control en diferentes cultivos. El desarrollo de modelos predictivos pueden contribuir en la aplicación de medidas de control en tempranos estadios de crecimiento, pero actualmente no hay estudios para predecir la emergencia de las especies de *Conyza*. Los objetivos de este trabajo fueron desarrollar y evaluar un modelo para predecir la respuesta en la emergencia de *C. bonariensis* en base al ambiente hidrotermal del suelo. Un modelo hidrotermal de germinación fue ajustado con datos obtenidos en diferentes pruebas hechas a diferentes temperaturas y potenciales hídricos para establecer los parámetros hidrotermales que caracterizan la germinación de *C. bonariensis*. La relación entre la emergencia acumulada y el tiempo hidrotermal acumulado fue analizada a través de la función de Gompertz. El desarrollo de modelo se basó en dos años de experimentos de campo. La temperatura base y el potencial hídrico base para la germinación fue estimado en 10.6 ºC y -0.70 MPa, respectivamente. El modelo de emergencia mostró un buen ajuste a los datos experimentales. De acuerdo con este modelo la emergencia de plántulas se inicia con 15 HTT después de la siembra, se alcanza un 50 y 95% de emergencia con 53 HTT y 105 HTT, respectivamente. Para la evaluación del modelo, se realizaron experimentos de campo independientes de los usados en la construcción del modelo, en dos localidades. La emergencia acumulada fue predicha adecuadamente por el modelo. Los resultados indican que este modelo puede ser usado como una herramienta predictiva que puede contribuir a un control efectivo de poblaciones de *C. bonariensis*.

Palabras claves: conyza**,** modelos predictivos, tiempo hidrotermal, manejo de malas hierbas, herramienta para toma de decisiones.

Abstract

Conyza bonariensis is a South American native, annual Asteraceae introduced in the Mediterranean where it behaves as a ruderal plant and a difficult to control weed in different crops. The development of predictive models can contribute to control measures at early growth stages, but currently there are no studies to predict seedling emergence of *Conyza* species. Our objectives were to develop and evaluate a model for predicting emergence response of *C. bonariensis* to the soil hydrothermal environment. A hydrothermal seed germination model was fitted to time course germination data from germination tests carried out at different constant temperatures and water potentials to establish the hydrothermal parameters characterizing *C. bonariensis* seed germination. The relationship between cumulative seedling emergence and cumulative hydrothermal time under field conditions was analyzed through the Gompertz function. Model development was based on 2 years data from a field experiment. Base temperature and base water potential for seed germination were estimated at 10.6 ºC and -0.70±0.151 MPa, respectively. The emergence model showed a very good fit to the experimental data. According to this model, seedling emergence starts at 15 accumulated hydrothermal time (HTT) after sowing, and 50 and 95% emergence is completed at 53 HTT and 105 HTT, respectively. For model evaluation, independent field experiments were carried out in two localities. Cumulative seedling emergence was accurately predicted by the model. Results indicate that this model can be useful as a predictive tool contributing to effective control of *C. bonariensis* populations.

Keywords: flaxleaf fleabane, predictive modeling, hydrothermal time, weed management, decision tool.

III. 1. Introduction

Hairy fleabane (*Conyza bonariensis* (L.) Cronq., Asteraceae) is one of the most common introduced plant species in Spain. It is native to South America (Thebaud & Abbott, 1995) and behaves primarily as a ruderal plant, inhabiting road margins, recently abandoned fields, riverbanks, urban wasteland, etc. *Conyza* spp. occur as weeds in more than 40 crops in 70 countries (Holm et al., 1997). Recently, prevalence of hairy fleabane has increased in fruit orchards and olive groves in southern Spain, and therefore it is considered a noxious weed (Urbano et al, 2007). Prior to introduction of conservation tillage practices hairy fleabane was easily controlled with tillage (Brown & Whitwell, 1988).

The increase of hairy fleabane prevalence has been associated to the adoption of conservation cropping systems, which allows a greater water availability at the soil surface, and possibly favors seed germination (Wicks et al., 2000). Other factors were that hairy fleabane growth was favored by poor crop competition associated to sowing crops in wider rows and lower population densities, and that weed control was not specifically targeting hairy fleabane (Walker & Robinson, 2008). In addition, this species has evolved resistance to various herbicide groups, including Glycines, Bipyridiliums, ALS, and Photosystem II inhibitors (Heap, 2012).

The emergence of hairy fleabane, favored by mild conditions, occurs mainly from autumn to early winter, with few emergences in spring (Shrestha et al., 2008). Seeds have no dormancy and readily germinate at the soil surface, but germination is severely limited to very shallow soil depths (Nandula et al., 2006). Seed persistence in soil is also rather limited (Wu et al, 2007).

Emergence is possibly the most important demographic event for an annual plant as the time it occurs largely determines its survival and success (Forcella et al., 2000). Models that estimate the timing of weed seedling emergence are valuable management decision tools that can be used to optimize weed control schedules (Forcella, 1998). A number of models for predicting weed emergence patterns of some weed species have been developed (Forcella, 1998; Izquierdo et al., 2009; Royo-Esnal et al., 2010; Leguizamon et al., 2005). First-generation models for predicting weed emergence were based on the thermal time (growing degree days; GDD) concept (Roman et al., 2000; Martinson et al., 2007; Izquierdo et al., 2009). In these models, average air or soil temperature above a specific threshold is accumulated over days until weed emergence is completed. In recent years, soil water potential and soil temperature have often been integrated into hydrothermal time (HTT) models that are frequently better at predicting emergence than GDD (McGiffen et al., 2008). In these models, the GDD are accumulated when the daily average of soil water potential and temperatures are over specified threshold values below which seedlings cannot emerge (Gummerson, 1986). These models for the emergence of hairy fleabane could improve its control. That is, knowing the proportion of maximum emergence represented by each flush provides insight into the need and timing of control operations (Royo-Esnal et al., 2010).

A predictive model based on easily obtainable climatic data would provide useful information about emergence patterns, and thus could contribute to optimizing the efficacy of control measures (Izquierdo et al., 2009).

To date, there is no decision-aid tool that could be used by farmers to predict hairy fleabane emergence, for this reason the objectives of this research were to develop and evaluate a hydrothermal time seedling emergence model for hairy fleabane.

III. 2. Materials and methods

III. 2. 1. Estimation of hydrothermal parameters for seed germination

III. 2. 1. 1. *Germination tests*

Seeds of *C. bonariensis* were collected in November 2010 in a population located in Aljaraque, Huelva province, southern Spain, and incubated in germination chambers (Snijders Scientific B.V., Netherlands) at different constant temperatures (15, 20, 25 ºC) and water potentials (0, -0.3, -0.6, -1.0 MPa) under 12h photoperiod. Solutions of polyethilene glycol (PEG 8000) were prepared according to Michel (1983) to obtain the nominal water potentials which were subsequently verified using a Wescor HR-33 T osmometer and a C-52 sample chamber (Wescor Inc., USA). Lots of 50 seeds were placed on Whatman No.1 filter paper supported by a layer of 0.5 cm-diameter glass beads in 9 cm-diameter petri dishes, aimed to create a large enough solution reservoir to prevent significant changes in water potential due to water evaporation. To further limit water loss, petri dishes were sealed with Parafilm. Daily counts of newly germinated seeds were carried out from the onset up to the end of the rapid linear phase of germination and then counts were spaced 3-4 days until no germination was recorded for three consecutive observations. Tetrazolium tests were conducted to assess viability of all ungerminated seeds in treatments at $\Psi=0$. Mean seed viability, i.e. germinated plus ungerminated viable seeds, was high (96.2%) and this value was used to calculate all germination fractions. Each treatment was repeated twice. The experimental unit consisted of three petri dishes and mean values were used as data in the regression model to estimate hydrothermal parameters.

III. 2. 1. 2. *Hydrothermal seed germination model*

The hydrothermal model of seed germination initially proposed by Gummerson (1986) was fitted to time course germination data. The model states that at any constant temperature (T) not surpassing the optimum temperature and at any constant water potential (Ψ), germination time $t(g)$ of any fraction g of a seed population is a function of the extent to which T and Ψ exceed threshold or base values, T_b and Ψ_b, below which germination is prevented (Gummerson, 1986; Dahal & Bradford, 1994; Bradford, 1995):

$$\theta_{HT} = (\Psi - \Psi_b(g))\,(T - T_b)\,t(g) \qquad (1)$$

Hydrothermal time (θ_{HT}) and T_b are assumed to be constant for a seed population, whereas Ψ_b varies for different seed fractions, usually following a normal distribution (Gummerson, 1986; Bradford, 1990), but see Mesgaran et al., (2013) (The normal distribution is not necessarily the best function for base water potential in hydrothermal models and, the ´best´ distribution may vary with species), and this variation ultimately explains the distribution of germination times within a seed population. Probit transformation, which linearizes a cumulative normal distribution, allows $\Psi_b(g)$ to be expressed as a function of the mean Ψ_b, i.e. base water potential for 50% seed population ($\Psi_b(50)$) , and the standard deviation of Ψ_b ($\sigma_{\Psi b}$):

$$\Psi_b(g) = \Psi_b(50) + \text{probit}(g)\,\sigma_{\Psi b} \qquad (2)$$

Equation (2) allows the explicit introduction of germination fractions in model (1):

$$\text{probit}(g) = (\Psi - (\theta_{HT} / (T - T_b)\, t(g)) - \Psi_b(50)) / \sigma_{\Psi b} \qquad (3)$$

Equation 3 relates g to $t(g)$ at any constant T and Ψ, and thus has the advantage that data from time course germination experiments are utilized in a single regression to estimate the hydrothermal parameters (Bradford, 1990).

Model of equation 3 was fitted to time course germination data through repeated probit analysis (e.g. Bradford, 1990; Rowse & Finch-Savage, 2003) using the probit regression procedure in SPSS 17.0 (SPSS Inc., USA). The term $\Psi - (\theta_{HT} / (T - T_b)\, t(g)$ in equation 3, which is equivalent to $\Psi_b(g)$ (equation 1), was used as the explanatory variable and different values of T_b and θ_{HT} were tested for maximum fit.

III. 2. 2. Seedling emergence model

III. 2. 2. 1. *Seedling emergence experiments*

Field experiments were conducted in 2011 and 2012 in two experimental plots in southern Spain, IFAPA (37° 51’ 40’’ N; 4° 47’ 56’’ W), in Córdoba province, and La Rábida campus at Huelva University (37° 12’ 2’’ N; 6° 54’ 55’’ W), Huelva province, approximately 240 Km apart. Seeds were collected from local *C. bonariensis* populations. Soils in Córdoba and Huelva sites were a medium loam (42% sand 36% silt and 22 % clay) with 1.13 % organic matter and pH 8.4, and a sandy loam (74% sand, 21% silt and 6% clay) with 1.05% organic matter and pH 7.2, respectively.

Each seedling emergence experiment consisted of five to six microplots, 0.3 x 0.3 m (Córdoba) or 0.75 x 0.75 m (Huelva) in size, randomly arranged within a 20 m^2 plot in which existing vegetation had been previously removed using a cultivator. In Córdoba site, 200 seeds were sown per microplot in March and October 2011 and in March 2012, whereas in Huelva site 300 seeds were sown per microplot in March 2012. At sowing, seeds were spread over the soil surface and covered with a thin layer of soil to prevent wind drifting. Seedling emergence was initially monitored at 3 day intervals, and after the peak emergence periods monitoring was done at weekly intervals. Seedlings were counted as emerged and they were removed after each counting. Soil temperature (TMC6-HD, Hobo, Onset Computer Corp., USA) and electrical conductivity (Hobo EC-20, 20-cm length blade) sensors connected to a data logger (Hobo U12) set to record at hourly intervals were placed in each field at 0.5 cm depth. The relationship between soil electrical conductivity and soil water potential was established in laboratory. Soil samples from Córdoba and Huelva sites were watered to saturation every 2-3 days and variation in electrical conductivity as soil dried at ambient temperature was monitored at 15 min intervals using EC-20 sensors. Simultaneously, soil water potential was determined at intervals using the Wescor HR-33T osmometer and C-52 sample chamber. This device uses very small soil volumes (approx. 50 mm^3) and thus allows a close matching of the soil environment experienced by individual seeds. Sixty measurements were taken for each soil. For intermediate values of electrical conductivity, i.e. soil neither too wet nor too dry, large variability in water potentials was observed, thus preventing direct regression between both variables. Instead, logit regression was used to establish a soil-specific threshold value of electrical conductivity (EC_t) for which there was a high probability (95%) for the water potential to be more negative than the base water potential preventing germination of 99% of the seed population, $\Psi_b(1)$. These threshold values for Córdoba (EC_t =0.64 V) and Huelva soils (0.48 V) were implemented in the seedling emergence model.

III. 2. 2. 2. *Model development and evaluation*

The model was developed based on data from two seedling emergence experiments carried out in Córdoba site during the spring of 2011 and 2012. Model evaluation was done with independent experiments in Córdoba (Autumn-2011) and Huelva (Spring-2012).

To describe the pattern of seedling emergence, percentage cumulative emergence (Y) was related to the cumulative hydrothermal time (HTT) with the use of the Gompertz function, a commonly used model for this purpose (Haj Seyed Hadi & Gonzalez-Andujar, 2009):

$$Y = a*\exp(-\exp(-(HTT - c)/b)) \qquad [4]$$

Where Y is the cumulative percent emergence, a is the asymptote (theoretical maximum for Y normalized to 100%). Thus, this parameter was made constant to 100, c is the inflection point, and $1/b$ is the rate of increase. Accumulation of hydrothermal time, on hourly basis, was computed according to the following equation:

$$HTT = \mathbf{\Sigma}(T - T_b)K \qquad [5]$$

Where T and T_b are soil temperature and base temperature for *C. bonariensis* seed germination, respectively, and K accounts for soil water potential, taking the value 1 when soil electrical conductivity is above the soil-specific threshold value indicative of germination limiting water potentials and 0 otherwise.

Model parameters and goodness of fit were estimated by nonlinear least-squares regression using SigmaPlot v.11 (Systat Software, Inc).

Model performance was assessed by the root mean-square error (RMSE):

$$RMSE = \sqrt{(1/n)\,\sum_{i=1}^{n}(x_i - y_i)^2} \qquad [6]$$

Where x_i and y_i represent observed and predicted cumulative percentage seedling emergence, respectively, and n is the number of observations (Mayer & Butler, 1993). RMSE provides a measurement of the typical difference between predicted and actual values in units of percentage seedling emergence. Low RMSE values are indicative of overall good model performance.

III. 3. Results

III. 3. 1. *Hydrothermal parameters for C. bonariensis seed germination*

No seed germination was observed in tests carried out at -1.0 MPa, which lasted up to 48 days. Therefore, the germination model was developed based on germination responses at 0, -0.3 and -0.6 MPa. Both the intercept and the slope of the lineal model fitted through repeated probit analysis were highly significant (p<0.0001; Fig. 1). According to the model, base temperature and base water potential ($\Psi_b(50) \pm \sigma_{\Psi b}$) were estimated at 10.6 ºC and -0.70±0.151 MPa, respectively, and the hydrothermal constant

θ_{HT} at 390 MPa ° h (Figure 1). The base water potential which prevents germination of 99% of the seed population ($\Psi_b(1)$) was thus estimated at -1.06 MPa. This estimate is in accordance with experimental data as long as no seed germination was detected in tests at -1.0 MPa.

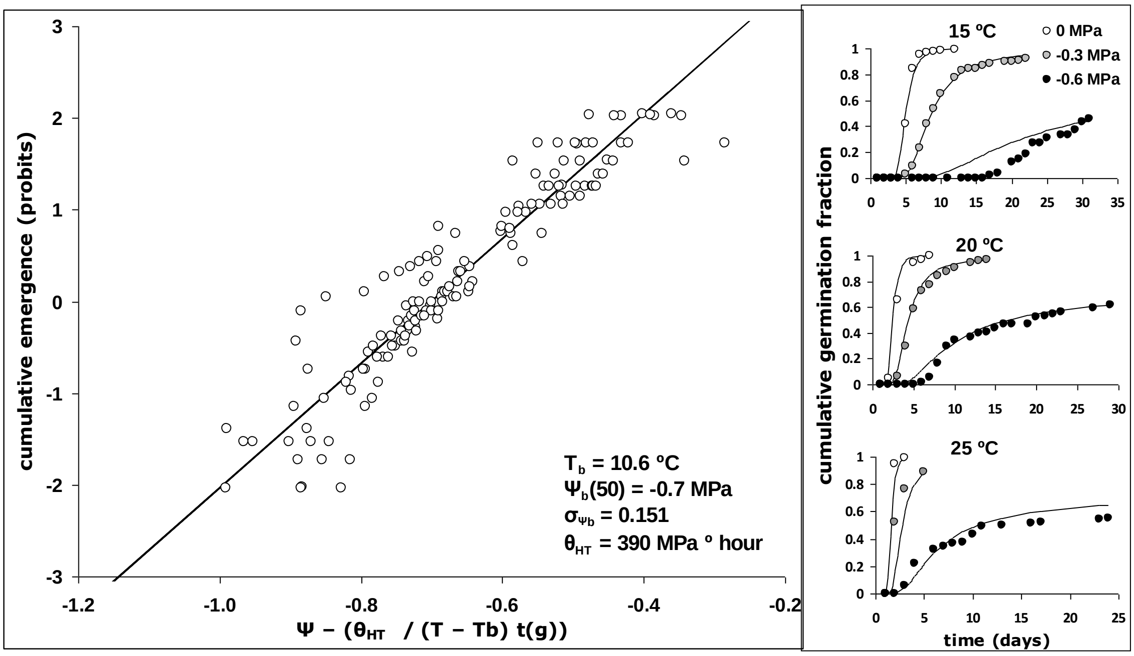
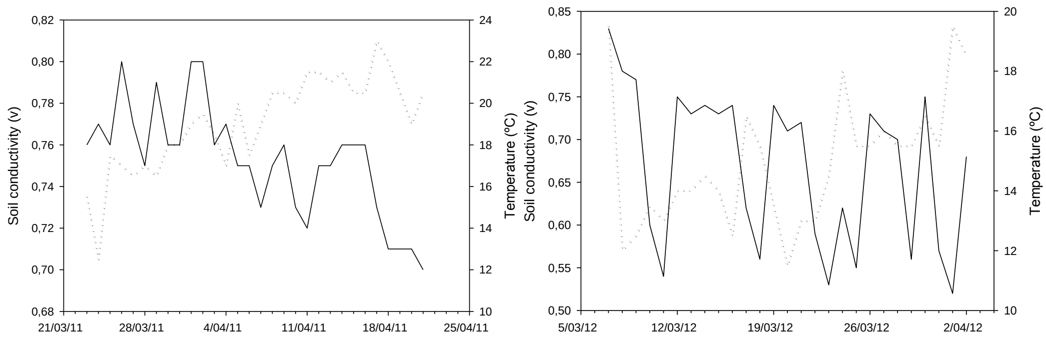


Figure 1. Estimation of hydrothermal parameters for *C. bonariensis* seed germination through repeated probit analysis (large inset), and performance of the resulting hydrothermal model in explaining germination time courses at the different temperatures and water potentials tested (small inset). The explanatory variable for probit analysis, $\Psi - (\theta_{HT} \ / \ (T - T_b) \ t(g))$, is equivalent to $\Psi_b(g)$, as can be seen from equations 2 and 3. Dots are observed values and lines represent the fitted models. Note that probits of germination fractions 0 and 1 are not defined and therefore cannot be displayed.

III. 3. 2. *Patterns of seedling emergence*

During the emergence experiments, carried out in autumn and spring, temperature at the soil surface was rarely below the estimated base temperature for seed germination, 0% and 11.1% of the time (hours) in Córdoba and Huelva sites, respectively (Figure 2). Maximum soil temperatures did not exceed 25 °C neither in Córdoba nor in Huelva sites (Figure 2). Therefore, maximum temperatures were permanently within the range in which linear variation of germination rate is expected according to results from germination tests. Under the non-limiting water availability conditions in which emergence experiments were carried out, *C. bonariensis* completed seedling emergence in a few weeks after sowing, both in autumn and spring. Fifty percent and 95% emergence was achieved, respectively, in 2-3 and 5-6 weeks in the Huelva experiment, and in 2-3 and 3-4 weeks in Córdoba experiments (Figure 3).

Córdoba 2011 (a) Córdoba 2012 (b)



Córdoba 2011 (c) Huelva 2012 (d)

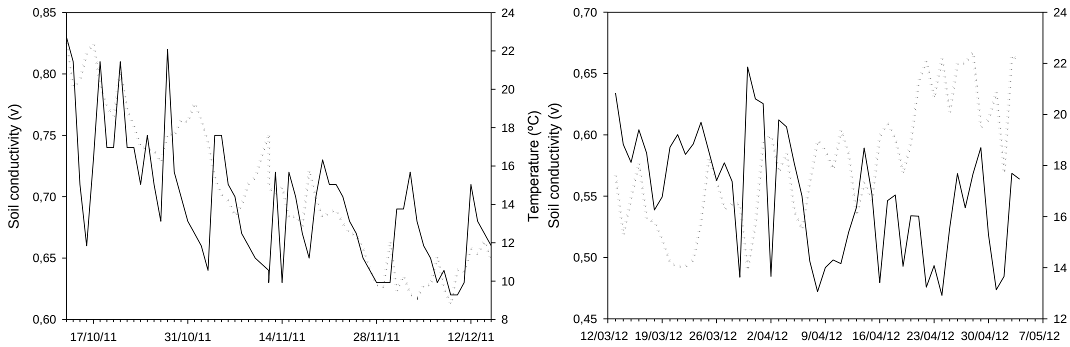


Figure 2. Soil microclimate conditions during seedling emergence experiments in Córdoba (a, b, c) and Huelva (d) sites. Lines represent average daily values of soil temperature (solid line) and electrical conductivity (dotted line), which is proportional to soil water content.

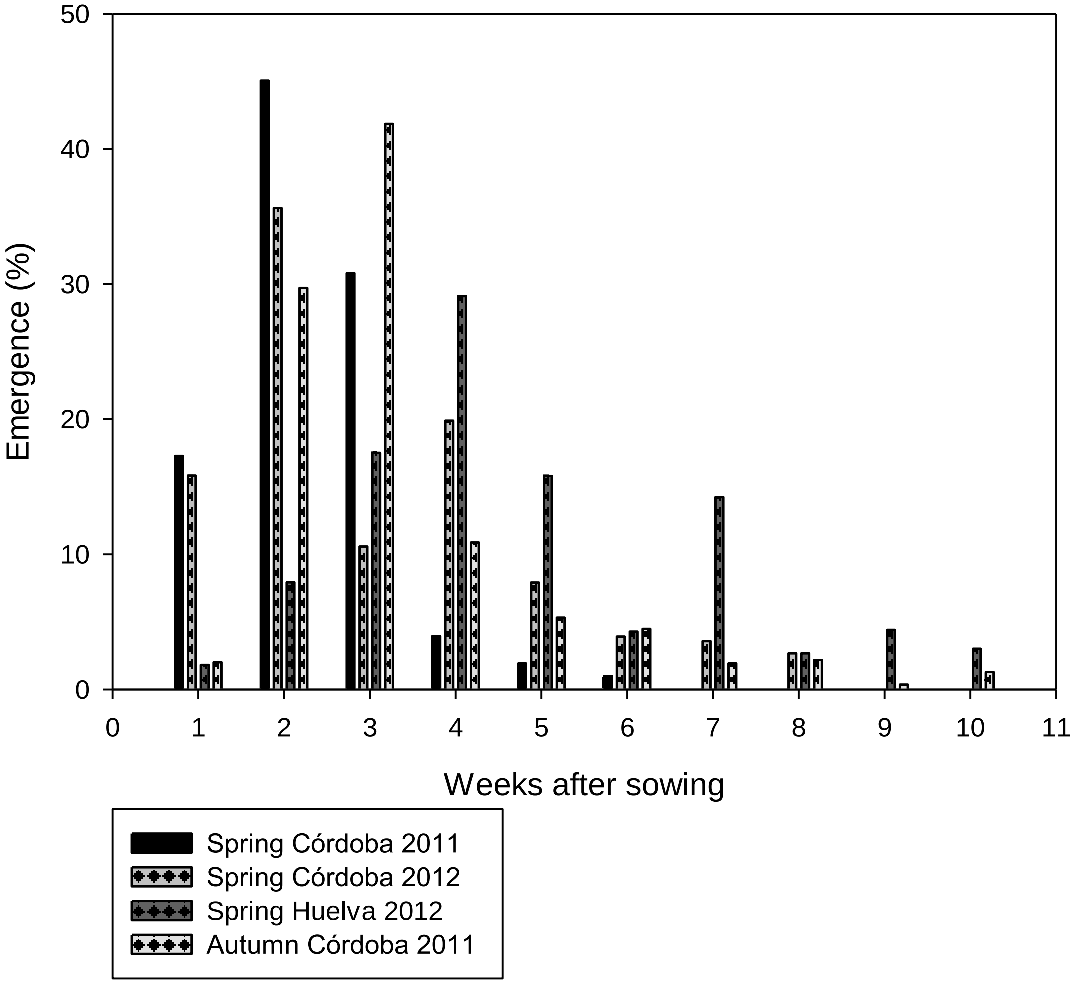


Figure 3. Seedling emergence patterns of *C. bonariensis* during the experiments conducted in Córdoba and Huelva in 2011 and 2012.

III. 3. 3. *Model development*

The model provided a good fit to the field data and was accurate enough in explaining cumulative emergence as a function of hydrothermal time (RMSE= 5.80; R^2_{adj} =0.97; n=90) (Figure 4). Parameter estimates (mean ± standard error) were c= 43.82 ± 0.72 and b= 18.99 ± 1.01.

According to model predictions, onset of hairy fleabane seedling emergence requires accumulation of 15 HTT. Afterwards, seedling emergence increases steadily and reaches 50% and 95% emergence at 53 HTT and 105 HTT, respectively.

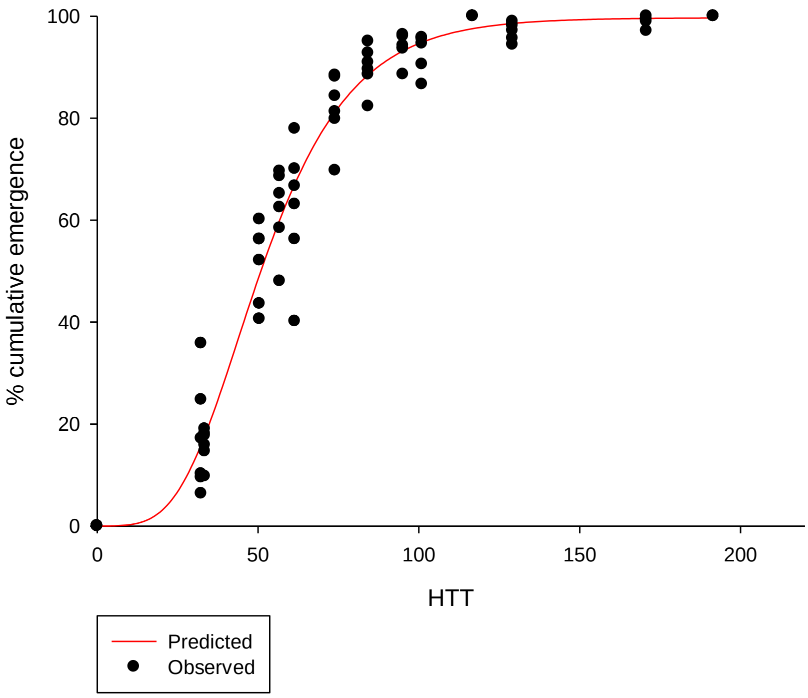
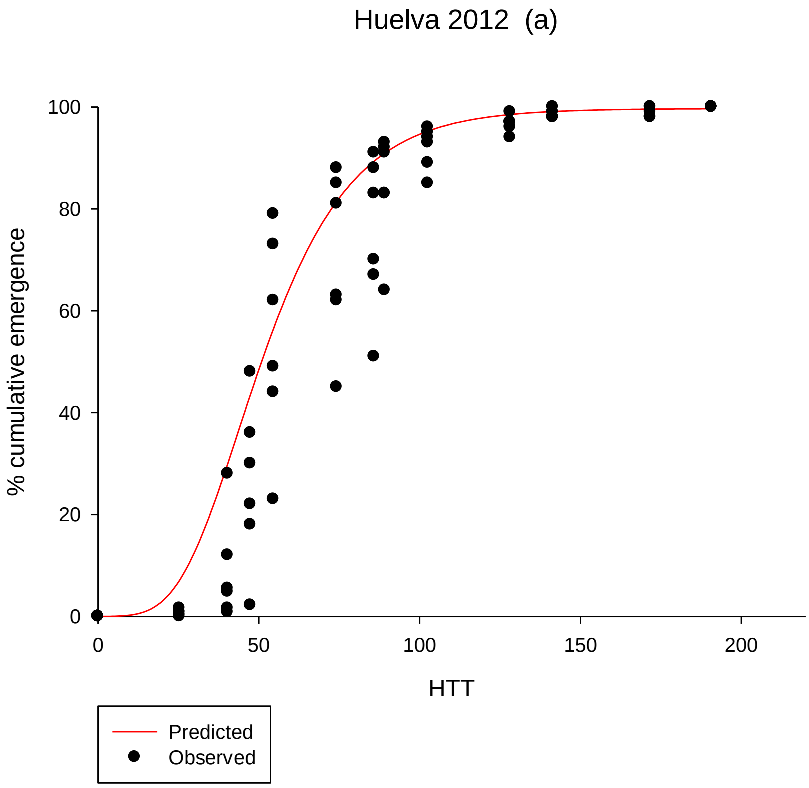


Figure 4. Observed (dots) and predicted (line) cumulative seedling emergence of hairy fleabane (*Conyza bonariensis*). Predictions are based on the Gompertz function describing emergence as a function of cumulative hydrothermal time (HTT).

III. 3. 4. *Model evaluation*

Emergence predicted by the model showed a good correspondence and reasonable accuracy with the observed emergence in the independent experiments carried out in Huelva (RMSE 13.01 %; n=54) and Córdoba (RMSE 9.13 %; n=54) (Figures 5a, 5b).



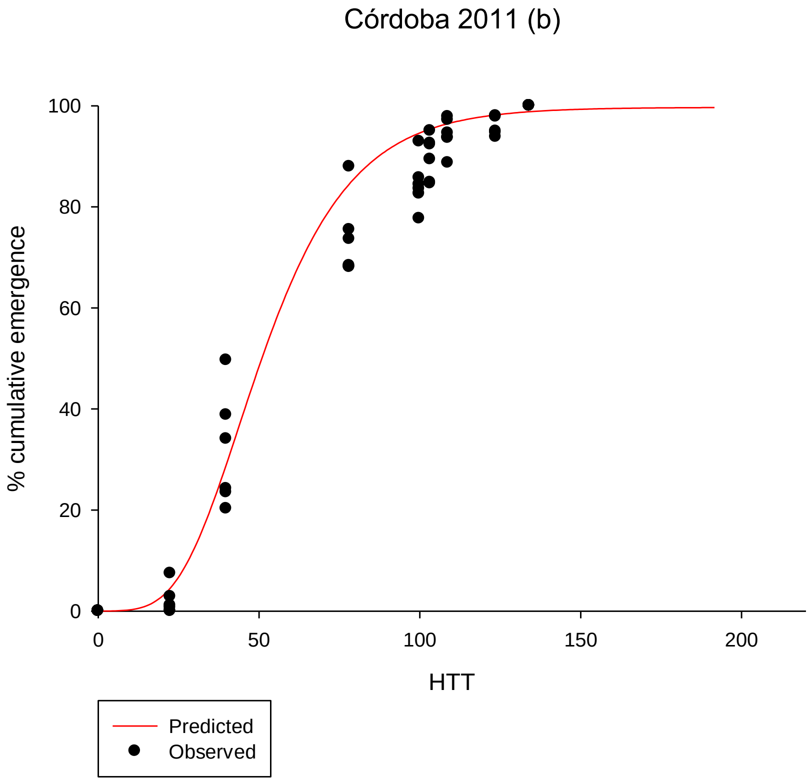


Figure 5. Evaluation of the Gompertz model (lines) for *C. bonariensis* seedling emergence with independent experiments in Huelva (a) and Córdoba (b). Dots indicate

observed values. RMSE (13.01 and 9.13 respectively) represents root mean square error values in units of percentage cumulative emergence.

III. 4. Discussion

Our estimate of the base water potential preventing germination of 99% of the seed population ($\Psi_b(1)$=-1.06 MPa), on which the resulting emergence model is based, results from the assumption of normal distribution of base water potentials. In fact, this distribution has been almost exclusively assumed so far in hydrothermal models (e.g. Gummerson, 1986; Bradford, 1990; Rowse & Finch-Savage, 2003). Nevertheless, it has been recently shown that alternative functions that allow for a right-skewed distribution of $\Psi_b(g)$, such as the log-logistic, inverse normal or lognormal distributions, can provide depending on the species a more accurate fit to germination data (Mesgaran et al., 2013). Although for *C. bonariensis* Karlsson & Milberg (2007) found good fit germination data to logistic function, this possibility remains open to further study, the traditional assumption of normal distribution of base water potentials we followed in this work has proven consistent enough regarding both experimental data, i.e. no germination response was observed at -1.0 MPa, and performance of the resulting seedling emergence model.

Specialist weeds of arable crops are adapted through seed dormancy and generally persistent soil seed banks to the temporally predictable, large-scale patterns of frequent disturbance imposed by tillage operations. For most of these species seed germination and seedling emergence takes place during a predictable, short period of time which generally follows crop sowing. In contrast, *Conyza* species conform to a fugitive strategy in which large numbers of non-dormant seeds produced in extended periods of time by individual plants are able to disseminate widely and readily germinate whereby environmental conditions are suitable for establishment and growth, making it difficult to predict the timing of seedling emergence. This strategy is most favorable in ruderal habitats, in which disturbance occurs in an unpredictable fashion at varying spatial scales (Bakker et al., 1996; Lososová et al., 2006). The large increment during recent decades of reduced tillage practices has lead to a concomitant increase in incidence of *Conyza* spp. in these more ruderal-like cropping systems (Buhler & Owen, 1997; Borger et al., 2012). Conyza plants are very difficult to control effectively after rosette stage. This situation can be managed effectively and consistently applying an integrated weed management. The joint application of non chemical control (i.e. tillage, plant residue) before the emergence of conyza and of herbicides control (amitrole+ammonium thiocyanate, glyphosate mixed with 2,4-D amine plus picloram, or three sequential application treatments of glyphosate mixtures followed by paraquat plus diquat) in the seedling stages (Walker et al., 2012; Wu et al., 2010; Bhowmik & Bekech, 1993) is an effective way to control this specie. Control could be enhaced by carefully timing weed control measures at early growth stages. Hydrothermal emergency models can be a useful tool for implementing control strategies at the optimum time.

Because of long-distance seed dispersal ability, within-season seedling emergence patterns in *Conyza* are not only determined by the environmental requirements for seed germination and early growth, but also by the ripening and after ripening seed dispersal phenology of populations established at field and at landscape scales. Due to the mild climatic conditions prevailing after summer in southern Spain, flowering and ripening of *C. bonariensis* populations span from early summer to mid autumn or early winter; therefore, seed germination can potentially occur. Therefore potential exists for seed germination to occur along the rainy season in rainfed crops, or from early summer in irrigated crops. In fact, contrasting reports of main emergence seasons for *Conyza* spp. are found in the literature. *Conyza* spp., including *C. bonariensis*, have been reported as winter annuals, germinating mainly in autumn but generally showing smaller germination fractions in spring (Regehr & Bazzaz, 1979; Wu et al., 2007) or as summer annuals with peak germinations in spring (Davis & Johnson, 2008). Our study shows that soil temperatures in autumn and spring in southern Spain are largely favorable for the seed germination of *C. bonariensis* and provided that water availability is not limiting, as is the case in most within rainy season periods seedling emergence takes place readily. The proposed emergence model, which takes into account the hydrothermal parameters characterizing *C. bonariensis* seed germination, closely predicted seedling emergence patterns as a function of soil hydrothermal time. Therefore, model predictions of seedling emergence behavior along the rainy season, from autumn to spring, together with data regarding temporal patterns of seed rain could provide useful information to properly timing control measures of *C. bonariensis* populations.

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CAPÍTULO IV

Stochastic modelling of the population dynamic and management of *Conyza bonariensis* in perennial crops

CAPÍTULO IV: Stochastic modelling of the population dynamic and management of *Conyza bonariensis* in perennial crops

Resumen

Conyza bonariensis es una mala hierba relevante en la actualidad en cultivos perennes, como los cítricos y los olivos, asociados al no laboreo, en áreas de clima Mediterráneo. En este trabajo se desarrolla un modelo estocástico de la dinámica de poblaciones de *C. bonariensis* basado en cohortes que es utilizado para simular la dinámica del banco de semillas bajo diez estrategias de manejo químico y no químico. Las estrategias consideradas se basaron en sistemas de laboreo y no laboreo, la utilización de cubiertas y la aplicación de herbicidas. El modelo fue parametrizado con información recogida de la literatura. En ausencia de control y no laboreo la población del banco de semillas alcanzó una densidad de equilibrio de 378092±10865 semillas m^{-2} (97564±7121 plantas adultas m^{-2}). La estrategia más efectiva fue la que integró el uso de no laboreo, cubiertas y la aplicación temprana y tardía de herbicidas que redujo la densidad de equilibrio del banco de semillas y de la población e plantas en un 78.7% y en un 99.5%, respectivamente. Los resultados del análisis de sensibilidad indicaron que C. bonariensis es particularmente sensible a pequeños cambios en los parámetros demográficos asociados a la primera cohorte y a la eficacia de los tratamientos tempranos de herbicidas. Consecuentemente, sería necesario dirigir las estrategias de control sobre la primera cohorte ya que es clave para el control de esta mala hierba.

Palabras claves: análisis de sensibilidad, banco de semillas, modelo estocástico de simulación, manejo integrado de malas hierbas, Conyza

Abstract

Conyza bonariensis is, currently, a relevant weed in perennial crops such as citrus fruit and olive trees associated with non-tillage in Mediterranean climate areas. In this work, a cohort-based stochastic model of *C. bonariensis* dynamics used to simulate the behaviour of the seed bank under ten chemical and non chemical management strategies has been developed. The strategies considered were based on tillage and no-till systems, the use of covers, and herbicide application. The model was parameterized with information taken from the literature. In the absence of any control and no-tillage the seed bank population reached an equilibrium density of 378092±10865 seeds m^{-2} (97564±7121 adult plants m^{-2}). The most effective method was the one which integrated the use of no-till, a cover and the early and late application of herbicides, which reduced the equilibrium density of the seed bank and of the population and plants by 78.7 and 99.5%, respectively. The results of a sensitivity analysis indicated that *C. bonariensis* was particularly sensitive to small changes in the demographic parameters associated with the first cohort and to the efficacy of the early herbicide treatments. Therefore, it would be necessary to direct the control strategies towards the first cohort since this is the key to the control of this weed.

Keywords: Sensitivity analysis, seed bank, stochastic model, hairy fleabane, integrated weed management, simulation model.

IV. 1. Introduction

Conyza bonariensis (L.) Cronquist (hairy fleabane) is an annual Asteraceae, a native of South America, which is found in mild, subtropical regions (Everett 1990; Prieur-Richard et al. 2000). The presence of *C. bonariensis* has been reported both in agricultural environments and in abandoned fields, roadsides and urban spaces (Thebaud & Abbott 1995; Prieur-Richard et al. 2000).

This species is considered to be one of the most dominant emerging weeds in agricultural systems in southern Spain, rainfed systems under direct drilling in Australia, orchards and vineyards in California and in soybean crops under direct drilling in Argentina (Urbano, 2005; Wu et al., 2007; Papa et al., 2010; Shrestha et al., 2010).

The increase in the prevalence of *C. bonariensis* in perennial crops is associated with the change from the conventional tillage system to that with zero or minimal tillage, in which there is very little disturbance of the soil, thus favoring the germination and growth of this species (Storrie, 2007; Shrestha et al., 2008). The control of this weed is based on the use of non selective herbicides, although the continuous use of the latter has triggered the appearance of resistance to several herbicide groups, including glycines, bipyridyls and inhibitors of the ALS and of photosystem II (Heap, 2012). Therefore, there is a great interest in the setting up of alternative management strategies to help in their control.

The employment of population dynamics models may be of use for the medium and long term assessment of different management strategies. Population dynamics models, based on the life cycle of weeds in crops, have been frequently used in weed research to investigate the effect of different control methods (Gonzalez-Andujar & Fernandez-Quintanilla, 2004; Zambrano-Navea et al., 2012; Mokhtassi-Bidgoli et al., 2013). Although there is information available on the demographic characteristics of *C. bonariensis* (Green, 2010; Zambrano-Navea et al., 2013a), mathematical modelling has not yet been used to explore the consequences of the application of medium and long term management strategies in the populations of this weed.

In this work, the population dynamics of *C. bonariensis* has been modelled by the setting up of a stochastic model which takes into consideration the existence of different cohorts, i.e. fractions of the population emerging at different times of the year. Later, the model has been employed to simulate the medium term effect of different management scenarios based on the use of cultural and chemical strategies. The study has been complemented with a sensitivity analysis in order to identify the most important processes influencing *Conyza* population growth.

IV. 2. Material and Methods.

C. bonariensis population dynamics were modelled with a multistate stochastic model, which considered four cohorts of seedlings defined by their sowing date in an experimental plot (20 October, 13 December, 7 February and 4 April), and two depths of the seed bank (Fig. 1).

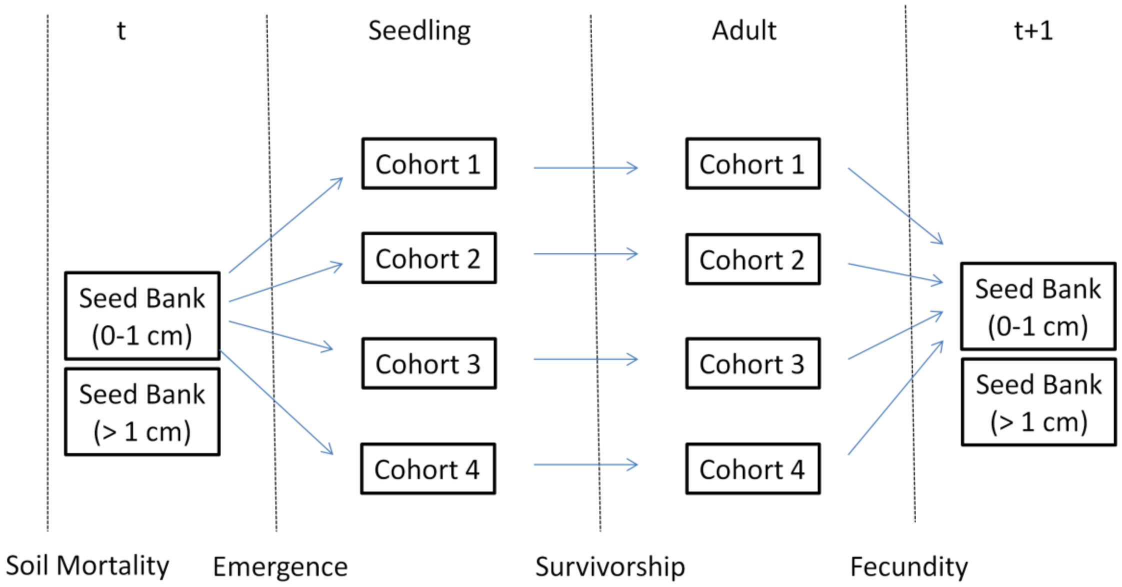

Figure 1. Life cycle diagram used to model *C. bonariensis*. *t* is time.

Bearing in mind that *C. bonariensis* seedlings cannot emerge from seeds situated at depths of over 1 cm (Wu et al., 2007), the seed bank was divided into two compartments, the surface bank (0-1 cm, Bs1) and the deep one (>1 cm, Bs2). The equation representing the seed movement between both compartments in years *t* and *t+1* is:

$$\begin{pmatrix} Bs_{1t+1} \\ Bs_{2t+1} \end{pmatrix} = \begin{pmatrix} Bs_{1t} \\ Bs_{2t} \end{pmatrix} * \begin{pmatrix} b11 & b12 \\ b21 & b22 \end{pmatrix} \qquad [1]$$

The matrix of equation 1 represents the vertical movement of the seeds due to the tillage effect between the bank's two compartments. Thus, b12 reflects the movement of the seeds from the surface bank to the deeper one; b21 depicts the opposite process, and b11 and b22 represent the seeds which remain in their compartments.

The population dynamics is described in the following way:

$$N_{t+1} = N_t\left[\sum_{i=1}^{4} e_i s_i f_i\left(\prod_{j=1}^{4}\varphi_{ij}\right) + (1-m)\right] \qquad \text{con } i = 1..4 \qquad [2]$$

Where N_t is the total number of seeds in the seed bank (Bs1 + Bs2) at time *t*, *m* is seed bank mortality, *i* is the number of cohorts. The control measures are introduced with the term φ_{ij} and refer to the proportion of individuals of each cohort which survive the control measures (e.g. Chemical and cultural treatments). The existence of a density-dependent effect on fecundity was contemplated as,

$$f_i = \frac{F(1-r_i)}{(1+aA_i)} \qquad \text{con } i = 1..4 \qquad [3]$$

Where *F* (seeds plant^{-1}) is the number of seeds produced by an isolated plant. A_i ($N_t e_i s_i$) is the number of adult plants producing seeds in each cohort (i = 1...4), r_i is the percentage of fecundity reduction in each cohort with respect to a *F* and a is the plant area required by a plant to produce *F* seeds.

IV. 2. 1. Estimation of the model's parameters:

The model was parameterized with demographic and agronomic data (Table 1). For all the simulations, an initial seed bank of 100 seeds m^{-2} (Jose-Maria & Sans, 2011) was considered.

Table 1. Demographic and agronomic parameters used in the model. Sensitivity analysis results.

Parameter		Mean	Standard desviation	Sensitivity index (SI)	References
Seed bank mortality	M	0.92	0.028	0.01	Wu et al. (2007)
Emergence cohort 1	e_1	0.06	0.016	0.13	Zambrano-Navea et al.(2013a)
Id. cohort 2	e_2	0.24	0.04	0.03	Id.
Id. cohort 3	e_3	0.18	0.04	0.07	Id.
Id. cohort 4	e_4	0.12	0.03	0.04	Id.
Seedling survivorship cohort 1	s_1	0.37	0.084	0.19	Id.
Id. cohort 2	s_2	0.44	0.09	0.01	Id.
Id. cohort 3	s_3	0.34	0.09	0.10	Id.

Id. cohort 4	s_4	0.13	0.01	0.03	Id.
Fecundity (seeds plant^{-1})	F	87273	3300	0.14	Id.
Reduction factor cohort 1	r_1	0	-	-	Id.
Id. cohort 2	r_2	0.73	-	-	Id.
Id. cohort 3	r_3	0.85	-	-	Id.
Id. cohort 4	r_4	1	-	-	
Area required to produce *F* seeds (m^2)	a	0.06	-	-	Id.
Rate control by using covers		0.71	0.12	0.02	Green (2010); Bhowmik & Bekech (1993)
Rate control by early herbicide application		0.93	0.04	0.12	Wu et al. (2010); Oliveira et al. (2010); Kruger et al. (2010); Paula et al. (2011)
Id. late herbicide application		0.85	0.07	0.0008	Papa et al. (2011); Walker et al. (2012); Kruger et al. (2010)

As the demographic and control parameters were subject to variations under field conditions as a result of different factors (climate, competition, etc), they were regarded as being stochastic and were simulated by means of the Beta and Normal statistic distributions. The parameters modelled with the Beta distribution were: seed bank mortality (m), emergence rate (e), and survival (s). Fecundity (*F*) and the efficacy of early and late herbicide treatments (Table 1) were considered to be normally distributed parameters.

The mean control percentage exerted by early application (between the seedling and rosette stages, affecting the first and second cohorts) of herbicides (ej. metsulfuronmetyl+MCPA+picloram) encompasses a range of effectiveness in the control of 90 to 97 % (mean value 93%) (Table 1). In the herbicide treatments applied late (from rosette to blooming stage, affecting all the cohorts) (e.g. glyphosate + 2,4 D Amine), a range of efficacy of 80 – 90% (mean value 85%) was considered (Table 1). The vertical movement rates of seeds between the seed bank compartments (equation 1) were taken from Spokas et al. (2007):

Tillage system:

$$\begin{pmatrix} b11 & b12 \\ b21 & b22 \end{pmatrix} = \begin{pmatrix} 0.394 & 0.091 \\ 0.606 & 0.909 \end{pmatrix}$$

Non-tillage system:

$$\begin{pmatrix} b11 & b12 \\ b21 & b22 \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}$$

IV. 2. 2. Sensitivity to variations in parameters:

A sensitivity analysis was performed on the demographic and control parameters (Table 1). On the basis of the range of values defined for each parameter, a sensitivity index was calculated (*SI*) which supplied information about the relative sensitivity of the model to variations in the parameters (Pannel, 1997; Torra et al., 2008; Mokhtassi-Bidgoli et al., 2013).

$$SI = \frac{(O_{max} - O_{min})}{O_{max}} \qquad [4]$$

where O_{max} y O_{min} are the outputs from the model when the value of the parameter is at its maximum and minimum, respectively. High values of *SI* indicate that a small variation in the parameter analyzed could result in a large variation in the model's output (Gonzalez-Andujar & Fernandez-Quintanilla, 2004).

The same as for the calculation of equation 4, it is necessary to use the maximum and minimum values of the parameters. These were established by adding or subtracting the standard deviation to their mean value (Table 1).

IV. 2. 3. Simulated control strategies:

Different individual or integrated management scenarios were simulated, using cultural (non chemical) and chemical tools. These scenarios were commonly applied in perennial crops (e.g. Olive grove, citrus fruit) in the Mediterranean basin (Table 2). The simulation covered a period of 10 years and was based on 100 replications.

Table 2. Cultural and chemical strategies considered in the management of *C. bonariensis*

A	No tillage (null strategy)
B	Tillage
C	No tillage + Covers
D	No tillage + Early herbicide application
E	No tillage + Late herbicide application
F	No tillage+ Early and late herbicide application
G	Tillage + Late herbicide application
H	No tillage + Covers + Early herbicide application
I	No tillage + Covers + Late herbicide application
J	No tillage + Covers + Early and late herbicide application

IV. 3. Results and Discussion

IV. 3. 1. *Behaviour* of *C. bonariensis in no-till and without control measures*

Strategy A has been considered as a null one (Table 2), which served as a comparison to the other strategies. Under Strategy A, the seed bank exhibited an asymptotic growth, reaching, at two years, an equilibrium density of 378092±10865 seeds m^{-2} (97564±7121 plants m^{-2}) (Figs. 2 and 3). These densities can be regarded, in ecological terms, as the carrying capacity of the environment or the maximum density of *C. bonariensis* seeds or plants which a system of these characteristics can support. The results obtained show the speed at which the problem of hairy fleabane infestation can grow, and the large populations that it can reach. These circumstances show the need for a rapid control of this species to prevent major harm in crops.

IV. 3. 2. *Behaviour of C. bonariensis under chemical and non chemical management strategies*

In woody, Mediterranean, rainfed crops, tillage is the traditional management system. According to our results, the application of this method (Strategy B) does not reduce the problem since the equilibrium density reached by the seed bank was only of 0.13% (with an equilibrium density of 377594±12328 seeds m^{-2}), which was lower than that reached in the no-till system (Fig. 2). However, there was a great difference in the adult plant population, which was reduced by 60.9% (with an equilibrium density of 38120±3065 plants m^{-2}) (Fig. 3). These differences are due to the movement of seeds in the soil produced by tillage and they are conditioned by the movement matrix of seeds (eqn 1).

Currently, the use of covers in combination with no-till is increasingly being established. However, their employment is less widespread due to the difficulty involved in installing an inert cover in wide areas, or to the limitations of live covers in agroecosytems, in which water is a production-restricting factor. This type of strategy (Strategy C) reduced the seed bank by 11.4% (335021±20772 seeds m^{-2}) (Fig. 2), and the adult plant population by 74.9% (24520±1159 plants m^{-2}) (Fig. 3).

Our results show that the deployments of non chemical methods by themselves are not sufficient for any major reduction of the seed bank in relation to the null strategy.

One of the most common ways to control *C. bonariensis* used by farmers is by herbicides. Treatments with them are applied in the autumn, when the weeds are in their initial growth stages, or in the spring in advanced growth stages. In this work, three strategies under the no-till system were simulated. These consisted of early and late herbicide application (Strategies D and E) and a combination of both (Strategy F) (Table 2). Strategies F and D reduced the seed bank by 56.2% (165682±15820 seeds m^{-2}) and 49% (192935±6283 seeds m^{-2}), respectively (Fig. 2). Conversely, Strategy E was not very effective in diminishing the seed bank (4.3 %; 361855±22830 seeds m^{-2}). With regard to the reduction of the adult plant population, Strategy F was also the most effective one (97.0%; 2949±762 plants m^{-2}), while a single early treatment (73.5%; 25825±1386 plants m^{-2}) was less favourable than a late application of the herbicide (85.6%; 14027±2403 plants m^{-2}) (Fig. 3). Although the results obtained were better than with the non chemical strategies, they were not sufficient to achieve an effective reduction of *C. bonariensis* . The results of our simulations reflect the situation observed in many fields of perennial crops in the south of the Iberian Peninsula, in which the recurrent application of non selective herbicides does not correspond to an effective control of *C. bonariensis* populations (Gonzalez-Torralva et al., 2010; Urbano et al., 2007). The least effective strategy in the control of seed banks was the one which combined tillage and a late herbicide application (Strategy G) (25,8%; 280801±43976 seeds m^{-2}), although it kept up a high efficacy in the control of the adult plant population (95.8%; 4092 plants ± 984 m^{-2}) (Figures 2 and 3).

It has been suggested that an effective control of *C. bonariensis* can be accomplished by integrating chemical and non chemical tactics (Wu et al, 2010, Mortensen et al., 2000). Our results confirm this suggestion and they are in a line with other simulation models for *Lolium rigidum* or *Phalaris brachystachys* (Gonzalez-Andujar & Fernandez-Quintanilla, 2004; Zambrano-Navea, et al., 2012), which have borne out this proposal. Among the four integrated strategies which were considered for the management of *C. bonariensis* (Table 2), the most effective one in the long term reduction of the seed bank (78.7%; 80490±8089 seeds m^{-2}) and of the adult plant population (99.5%; 467±69 plants m^{-2}) was the strategy integrating the employment of no-till with covers and early and late herbicide treatments (strategy J). In this scenario, an additional effect is probably achieved produced by the cover, affecting the light requirements (positive photoblastic) and depth (< 1 cm) necessary for the emergence of C. *bonariensis* (Wu et al., 2007), and the herbicide effect (Wu et al., 2010; Walker et al., 2012; Oliveira et al., 2010; Paula et al., 2011; Papa et al., 2011; Kruger et al., 2010). It is important to take into account that, although it would appear to be necessary to include chemical tools in integrated management strategies of *C. bonariensis* control, herbicide treatments should be designed to apply them to little-developed plants (early) to maximize effectiveness (Walker et al., 2012), and with different sites of action and degradation, in order to minimize the risk of resistance (Urbano, 2005).

The joint use of no-till and covers associated with a single herbicide treatment, early or late (strategies H and I), showed a lesser effectiveness in the control of the seed bank, 52.9% (178024±12903 seeds m^{-2}) and 45.7% (205272±12552 seeds m^{-2}), respectively, comparable to that reached in the areas with a more effective exclusively chemical control. However, these scenarios were highly effective in the control of the adult population, 91.8% (8005±830 plants m^{-2}) and 97.9% (2092±428 plants m^{-2}), respectively.

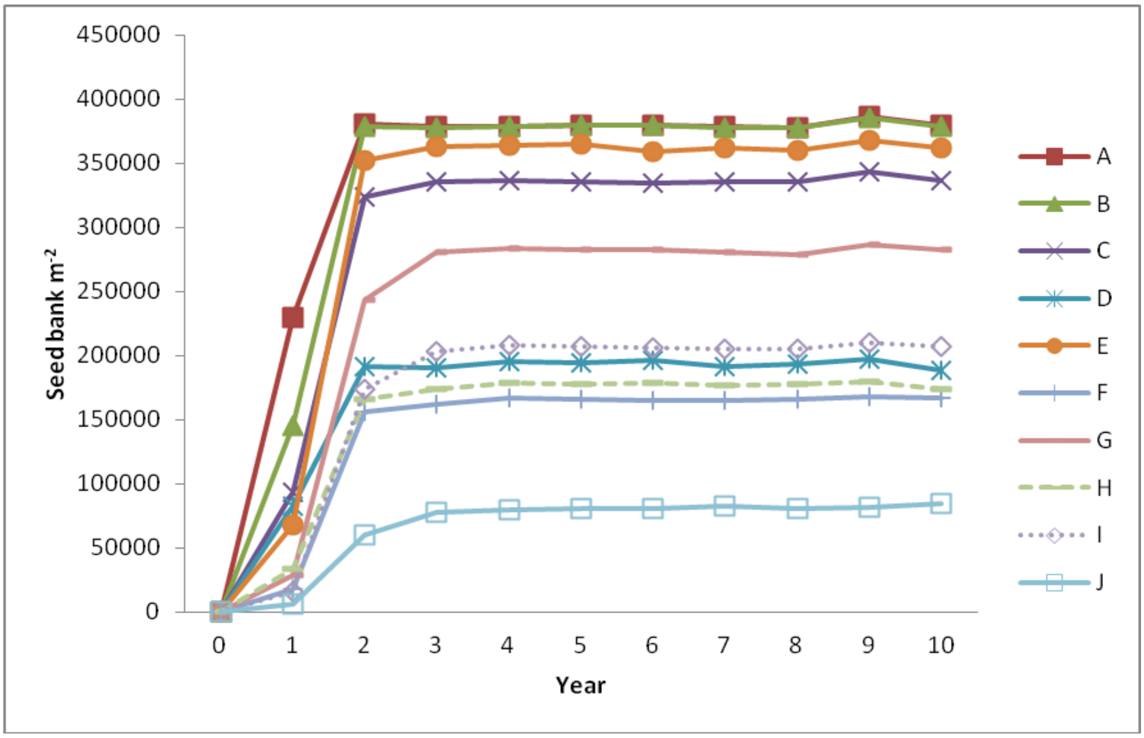

Figure 2. Evolution of the seed bank of C. bonariensis under different management scenarios: No tillage (A); tillage (B); No tillage+covers (C); no tillage+early herbicide application (D); no tillage+late herbicide application (E); no tillage+early and late herbicide application (F); tillage+late herbicide application (G);no tillage+covers+early herbicide application (H); no tillage+ covers+late herbicide application (I); no tillage+covers+early and late herbicide application (J).

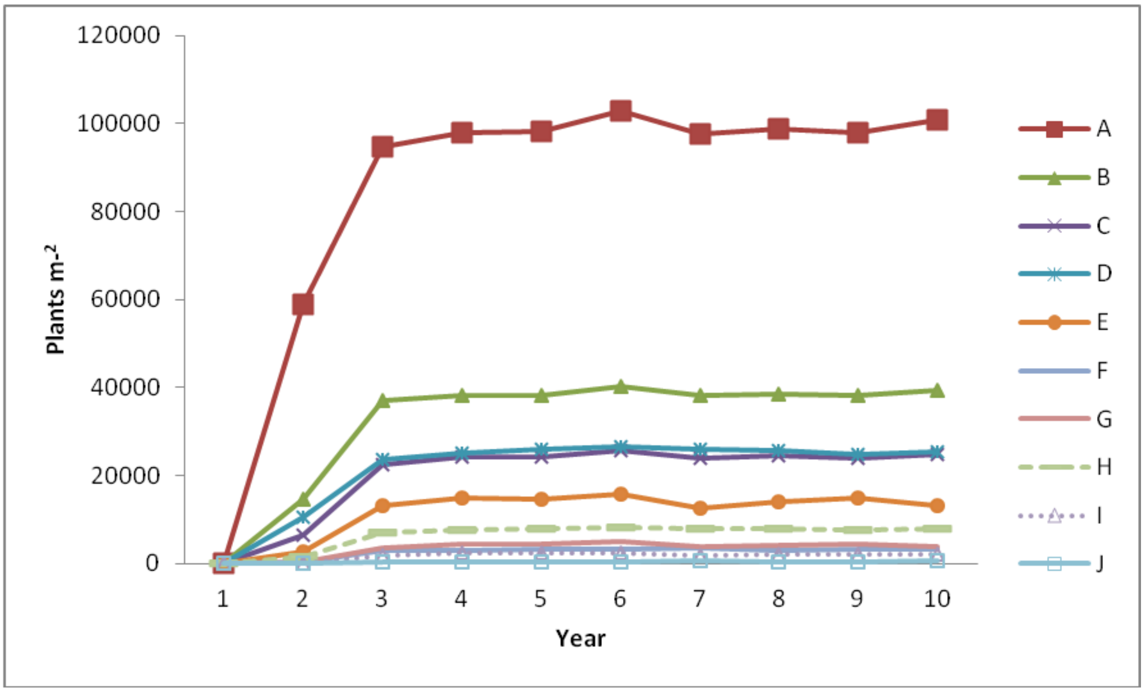

Figure 3. Evolution of adults plants populations of *C. bonariensis* under different management scenarios: No tillage (A); tillage (B); No tillage+covers (C); no tillage+early herbicide application (D); no tillage+late herbicide application (E); no tillage+early and late herbicide application (F); tillage+late herbicide application (G);no tillage+covers+early herbicide application (H); no tillage+ covers+late herbicide application (I); no tillage+covers+early and late herbicide application (J).

IV. 3. 3. *Sensitivity analysis*

The sensitivity analysis of the model permitted us to identify the most sensitive life cycle processes. Our results indicated that the size of the *C. bonariensis* populations was particularly susceptible to the demographic parameters (fecundity, emergence and survival) of the first cohort, and to the early application of herbicides (Table 1). Therefore, it would be necessary to direct the control strategies towards the first cohort since this is the key to the control of this weed.

The importance of first cohort control has been highlighted by other authors for different weed species (e.g. Torra et al., 2008; Gonzalez-Andujar & Fernandez-Quintanilla, 2004). In this sense, Mokhtassi-Bigdoli et al., (2013) found that *Bromus diandrus* in no-till systems is particularly vulnerable to changes in fecundity of the first cohort, so that it is suggested that the control strategies should be focused on the reduction of this first population flow. Although the model has considered the variability in the demographic parameters using a stochastic model, it would be desirable to explicitly incorporate the factors influencing those processes like, for example, temperature and rainfall, as a means of improving the model. In a recent work, Zambrano-Navea et al. (2013b) modelled the emergence of *C. bonariensis* in terms of climate parameters, and that model could be incorporated following the methodology established by Gonzalez-Diaz et al. (2007). Another aspect which has not been included in the model is the evolution of the resistance of this species to herbicides (Urbano et al., 2007). Finally, an experimental validation of the model would be appropriate (Gonzalez-Andujar et al., 2010) in order to provide a tool serving to help farmers and technicians in decision-making.

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CAPÍTULO V

Conclusiones Finales

CAPÍTULO V: Conclusiones finales

1. *C. bonariensis* se caracterizó por altas tasas iniciales de emergencia que fueron muy dependientes de las precipitaciones. Las cohortes poblacionales más tempranas presentaron unos valores más altos de supervivencia y fecundidad. Esta especie presentó una regulación de sus poblaciones a través de un proceso dependiente de la densidad a nivel de la fecundidad.

2. La temperatura base y el potencial hídrico base fueron 10.6 ºC y -0.70 MPa, respectivamente. La función de Gompertz permitió establecer adecuadamente la relación entre la emergencia acumulada y el tiempo hidrotermal acumulado. De acuerdo con este modelo, la emergencia de plántulas se inicia con 15 HTT después de la siembra y alcanza el 95% de las emergencias a los 105 HTT.

3. La mayor efectividad en el control de las poblaciones de *C. bonariensis* se alcanzó con un sistema integrado que aunó no laboreo, cubiertas, y la aplicación temprana y tardía de herbicidas.

4. El tamaño de las poblaciones de *C. bonariensis* en los cultivos perennes mediterráneos fue particularmente sensible a las variaciones de los parámetros demográficos (fecundidad, emergencia y supervivencia) de la primera cohorte y a la aplicación temprana de herbicidas.

5. Los resultados obtenidos en esta tesis pueden ayudar a establecer herramientas que a su vez podrían contribuir a un manejo más efectivo de las poblaciones de *C. bonariensis.*