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Vicia villosa ssp. villosa Roth field emergence model in a semiarid agroecosystem

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Abstract

Hairy vetch (*Vicia villosa* Roth) is a winter annual legume cultivated for pasture and hay with the capability for natural reseeding. *Vicia villosa* increases N concentrations in the soil, thus contributing to the sustainability of semiarid regions. However, under rotations of 1–2 years of pasture followed by 1 year of crop (1:1–2:1), hairy vetch could become a problematic volunteer weed in the winter cereal crop phase. This study aimed to develop a mechanistic model for hairy vetch seedling emergence in order to (i) estimate the natural reseeding of hairy vetch in the pasture phase of the field rotation, or (ii) develop control strategies considering hairy vetch as a volunteer weed in the winter cereal phase. The proposed model simulates the pattern of field emergence of hairy vetch after natural seed dispersal by integrating four submodels: (i) physical (PY) dormancy release dynamics, (ii) physiological dormancy (PD) release and germination thermal requirements, (iii) hydro-time requirements for germination, and (iv) pre-emergence growth respectively. The developed field emergence model was validated with independent field emergence data during 2013, 2014 and 2015. The model adequately predicted the timing and magnitude of field emergence flushes (RMSE < 10.1) despite the environmental variability among years. The additive effect of each submodel clearly improved the explanatory capacity of the field emergence patterns. The alleviation of PD synchronizes the timing for hairy vetch germination, while the PY determines the seedbank persistence. These outcomes suggest the potential applicability of the proposed modelling approach within management decision support systems.

KEYWORDS
agroecology, agroecosystem sustainability, combinational dormancy (PD + PY), integrated weed management, physical dormancy (PY), physiological dormancy (PD), predictive modelling, volunteer weed

1 | INTRODUCTION

The genus *Vicia* L., a member of the legume tribe *Vicieae* of the *Papilionoideae*, comprises 160–200 species, naturally distributed in Europe, Asia, America and Africa (Bryant & Hughes, 2011). *Vicia villosa* Roth (hairy vetch) is a cosmopolitan non-native invader present in several temperate regions of America, initially introduced as a

forage crop (Aarssen, Hall, & Jensen, 1986; Gunn, 1979). The inclusion of legumes in agricultural rotations has a crucial economic value in semiarid agroecosystems, where the relatively high cost of N chemical fertilization substantially affects grain crop yield and quality (Ates, Feindel, El Moneim, & Ryan, 2013; Reckling et al., 2015). The biological N fixation ability of hairy vetch, as well as its natural reseeding potential, are valuable agronomic traits that could

contribute to agroecosystem sustainability in semiarid regions (Renzi & Cantamutto, 2013).

Self-regeneration of legume species from the soil seedbank is associated with the presence of seed dormancy. Hairy vetch dormancy is controlled by a combination of physical impediments for water movement across the seed coat (PY, physical dormancy) and a physiological component of dormancy (PD, physiological dormancy; Renzi, Chantre, & Cantamutto, 2014). Embryos overcome PD and become non-PD after a short after-ripening period. The combination of a hard seed coat and a dormant embryo is considered as a "double-safety" mechanism to prevent early germination during summer when soil water content and temperature are not adequate for seedling survival (van Assche & Vandelook, 2010; Gama-Arachchige, Baskin, Geneve, & Baskin, 2013).

Under natural conditions, hairy vetch pods shatter and disperse the seeds during early summer. A healthy plant stand could generate over 1,000 seeds/m^2. However, the dispersal potential of hairy vetch is very limited due its large seed size (≈4.2 mm of length), weight (≈35 mg/seed) and absence of effective dispersal mechanisms (Jannink, Merrick, Liebman, Dyck, & Corson, 1997). Field emergence flushes occur during the following autumn when soil temperature and moisture become favourable for seedling recruitment (Renzi & Cantamutto, 2013). Temperature plays a main role in driving annual dormancy cycles, whereas rainfall influences the timing of subsequent germination (Vleeshouwers & Kropff, 2000). Nevertheless, in semiarid and arid regions characterized by a high interannual rainfall variability (e.g., south of the temperate Pampean region of Argentina) soil moisture becomes a major determinant for emergence dynamics (Holst, Rasmussen, & Bastiaans, 2007).

Although the benefits of hairy vetch can be significant, its adoption by farmers is limited due to the perception that it could become a problematic volunteer weed in winter cereals (e.g., wheat, barley) crop rotations (Crockett, Mirsky, & Curran, 2012). Hairy vetch expanded from cultivated areas to form spontaneous populations, such as in winter cereals, orchards, pastures and forestry fields (Aarssen et al., 1986). *Vicia villosa* is also present as a ruderal species along roadsides, disturbed areas and fallow fields (Renzi & Cantamutto, 2013).

When hairy vetch becomes a problematic weed, the timing of seedling emergence relative to the crop is important in planning and optimizing the time of control (Bullied, Bullock, & van Acker, 2012; Bullied, van Acker, & Bullock, 2012). Many mechanistic models based on the description of the biophysical processes have been proposed for other weed species (Colbach, Dürr, Roger-Estrade, & Caneill, 2005; Gardarin, Durr, & Colbach, 2012; Vleeshouwers & Kropff, 2000). Reductionist modelling approaches aim to provide a close description of the basic ecophysiological processes underlying weed emergence (i.e., dormancy, germination and pre-emergence growth; Forcella, Benech-Arnold, Sánchez, & Ghersa, 2000). They assume that emergence rates are proportional to the amount by which soil temperature and soil water potential exceed a given threshold value for such environmental factors (Bradford, 2002). The ability to predict both timing and amount of hairy vetch emergence patterns relative to the following crop phase is a necessary key step to make adequate control decisions within an IWM scenario (Curran, Wallace, Mirsky, & Crockett, 2015).

A mechanistic modelling approach could be useful to predict field emergence of forage legumes with natural reseeding capacity (Komatsuzaki, 2007; Taylor, Maller, & Rossiter, 1991). In the southern area of the semiarid Pampean region of Argentina, farming systems consist mainly of wheat field crops and extensive cattle ranching, with predominant mixed agricultural-cattle production. Winter cereal crops and hairy vetch rotations have proven to significantly increase both cereal grain and forage production (Assefa & Ledin, 2001; Ozpinar, 2006). In Australia, the adoption of "ley farming," where wheat and legume pastures are rotated, turned out to be a successful solution to the environmental and economic problems created by monocultures (i.e., crop-fallow systems; Carr, Poland, & Tisor, 2005; Loi, Howieson, Nutt, & Carr, 2005; Nichols et al., 2012). In the southern area of the semiarid Pampean region of Argentina, hairy vetch sowing for seed production followed by natural reseeding before winter cereals cultivation could be a very useful and profitable management strategy. In the first year, hairy vetch could be cultivated for seed production while in the second year the self-regenerating capacity could be exploited for forage, grazing or seed purposes before sowing a winter cereal crop (e.g., wheat, barley, oat or rye; Renzi, Chantre, & Cantamutto, 2017).

Despite the potential usefulness of mechanistic models based on seedling emergence subprocesses (i.e., seed dormancy, germination and pre-emergence growth), relatively few modelling approaches have been developed (Colbach, Busset, Yamada, Dürr, & Caneill, 2006; Colbach, Chauvel, Darmency, & Tricault, 2011; Colbach & Méziére, 2013; Gardarin, Guillemin, Munier-Jolain, & Colbach, 2010; Gardarin et al., 2012; Vleeshouwers & Kropff, 2000). Therefore, the objective of this work was to develop a mechanistic model for hairy vetch seedling emergence in order to (i) estimate the natural reseeding of hairy vetch in the pasture phase of the field rotation or (ii) develop control strategies considering hairy vetch as a volunteer weed in the winter cereal phase.

The model was specifically developed and calibrated for the southern area of the temperate Pampean region of Argentina, where rotations of 1–2 years of pasture followed by 1 year of crop (1:1–2:1) generally prevail.

2 | MATERIALS AND METHODS

2.1 | Field study site

Field studies were conducted from 2013 to 2015 in the experimental field of the INTA EEA Ascasubi (Buenos Aires, Argentina; 39°22′S, 62°39′W), located in the South of the semiarid temperate region of Argentina. A natural population of hairy vetch from the EEA Hilario Ascasubi (ASC) was studied during three growing seasons. This population was representative of naturalized genotypes of Argentina (see Renzi, Chantre, & Cantamutto, 2016), and it was located along the internal road margin of a winter cereal (wheat, *Triticum aestivum* and rye, *Secale cereale*) plot growing in sandy loam

soil (pH = 7.5, soil organic matter = 1.2%, available P Bray & Kurtz = 24 mg/kg). The predominate climate in this location is semi-arid-temperate with 489 mm mean annual precipitation and 14.8°C mean annual temperature (EEA H. Ascasubi, 1966–2014; http://inta.gob.ar/documentos/informes-meteorologicos).

2.2 | Seedling emergence model elements

The proposed model simulates the pattern of field emergence of hairy vetch after natural seed dispersal by integrating four submodels: (i) physical (PY) dormancy release dynamics (*submodel I*; developed by the authors, see Renzi et al., 2016), (ii) physiological dormancy (PD) release and germination thermal requirements (*submodel II*; developed by the authors, see Renzi et al., 2014), (iii) hydro-time requirements for germination (*submodel III*), and (iv) pre-emergence growth (*submodel IV*) respectively. *Submodels III* and *IV* were developed for this contribution.

The four submodels were developed and parameterized under both laboratory controlled and natural field conditions. Model testing was performed with independent data obtained under field conditions during 2013, 2014 and 2015 under no-till systems. The environmental input variables required by the model were the mean daily soil temperature and soil water potential at 10 and 0- to 50-mm depth respectively. Meteorological data were obtained either from direct measurements in the soil; or simulated using the soil temperature and moisture model (STM^2) developed by USDA-ARS (see below, "*seedling emergence experiments*"). The output variables generated by the model were (i) the proportion of non-dormant seeds (non-PY/PD seeds), (ii) germinated seeds, and (iii) emerged seedlings, on a daily scale interval.

2.2.1 | Physical dormancy release (submodel I)

Submodel I simulate physical dormancy break dynamics after seed dispersal under natural field conditions (Renzi et al., 2016). A thermal-time index was used (θ_{ATPY}) to quantify the effect of after-ripening time and temperature on the PY-breaking process in the field. The proportion of non-PY seeds as a function of thermal-time accumulation (θ_{ATPY}) was estimated as (Renzi et al., 2016):

$$\%nonPY_{seeds} = 90.52 \times \exp(-\exp(-0.001359(\theta_{ATPY} - 286.1))), \quad (1a)$$

where

$$\theta_{ATPY} = \sum_{i=1,n} \theta_n, \quad (1b)$$

$$\theta_n = \begin{cases} T_i - T_l & \text{if } T_l < T_i \\ 0 & \text{otherwise} \end{cases}, \quad (1c)$$

θ_{ATPY} is the after-ripening thermal-time accumulation for PY break at day n, T_i is the estimated mean daily soil temperature during the after-ripening time period (from 1 January to 31 August 2013, 2014 and 2015), and T_l is the base temperature below which PY break does not occur. T_l was estimated by Renzi et al. (2014) to be 9.8°C.

2.2.2 | Thermal parameters related to physiological dormancy status and seed germinability (submodel II)

Population thermal parameters were obtained by the authors (Renzi et al., 2014) following an adapted version of the mathematical approach proposed by Washitani (1987). *Submodel II* allows the estimation of two types of thermal parameters in the seed population: (i) physiological (PD) dormancy-related parameters: the lower (T_l) and upper (T_h) temperature limits for germination, which defines the amplitude of the permissive germination range, and (ii) germination-related parameters: the cardinal temperatures, base temperature (T_b), optimal temperature (T_o), maximal temperature (T_m) and the thermal-time (θ_g) requirement for germination.

Changes in PD status were described by Renzi et al. (2014) as:

$$T_{h(50)} = 12.47 + 1.3 \times 10^{-3} \times \theta_{ATPD} \quad (2a)$$

$$D_\theta = 25.52 \times \exp[(-3.4 \times 10^{-4}) \times \theta_{ATPD}] + 5.93, \quad (2b)$$

where

$$\theta_{ATPD} = \sum_{i=1,n} \theta_n, \quad (2c)$$

$$\theta_n = \begin{cases} T_i - T_{IPD} & \text{if } T_{IPD} < T_i \\ 0 & \text{otherwise} \end{cases} . \quad (2d)$$
$$T_{IPD} = 0°C$$

Cumulative germination of the seed population at a given dormancy level (i.e., according to its PY + PD status) was estimated by the authors as (adapted from Renzi et al., 2014):

$$G_{(\theta_{AT},T,t)} = [f(\theta_{ATPY})f(\theta_{ATPD})]G(T,t), \quad (3)$$

where $f(\theta_{ATPY})f(\theta_{ATPD})$ are the equations describing PY (Equation 1) and PD (Equation 2) dormancy release dynamics. Cumulative germination percentages at constant temperatures after a given incubation time ($G(T,t)$) were calculated by Renzi et al. (2014) following Washitani (1987) based on $F_l(T)$, $F_h(T)$ and $F(\theta)$ as follows:

$$F_l(T) = \phi[(T_{l(g)} - T_{l(50)})/\sigma_{T_l}], \quad (4a)$$

$$F_h(T) = 1 - [\phi(T_{h(g)} - T_{h(50)})/\sigma T_h], \quad (4b)$$

$$F(\theta_g) = 1 - [3D^{-3}(\theta_{(g)} - \theta_{50} + D_\theta)^3 + 1]^{-1/2}, \quad (4c)$$

$$G(T,t) = F_l(T)F_h(T)F_t((T - T_b)t), \quad (4d)$$

$$\text{if } T_b < T < T_o \text{ and } (T - T_b)t > \theta_{50} - D_\theta, \quad (4e)$$

$$G(T,t) = F_l(T)F_h(T)F_t([(T_m - T)(T_o - T_b)/(T_m - T_o)]t), \quad (4f)$$

$$\text{if } T_o < T < T_m \text{ and } (T - T_b)t > \theta_{50} - D_\theta, \quad (4g)$$

$$G(T,t) = 0, \quad (4h)$$

$$\text{if } T < T_b \text{ or } T > T_m \text{ or } (T - T_b)t < \theta_{50} - D_\theta, \quad (4i)$$

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where $F_l(T)$ is the proportion of germinating seeds at a given T_l of a g fraction of the seed population; $F_h(T)$ is the proportion of germinating seeds at a given T_h of a g population fraction; ϕ is the normal probability integral; $T_{l(50)}$ and $T_{h(50)}$, are the mean lower and upper limit values (°C) for germination, respectively; σ_{T_l} and σ_{T_h} are corresponding standard deviations; $F(\theta_{(g)})$ is the distribution of θ; θ_{50} is the mean thermal-time requirement (degree-days) for germination; D_θ, deviation parameter of θ; T_b, T_o and T_m are germination cardinal temperatures; T_{IPD}, basal temperature for PD release.

For modelling purposes, the following population parameters were considered constant (Renzi et al., 2014):

$$T_{l(50)} = 2.2°C; \sigma_{T_l} = 2.2°C; \sigma_{T_h} = 2.4°C; \theta_{(50)} = 30°Cd; T_b = 2.0°C;$$
$$T_o = 15°C; T_m = 30°C$$

2.2.3 | Estimation of hydro-time parameters related to physiological dormancy status and seed germinability (submodel III)

Seed material

To characterize the germination response of *V. villosa* to water potential (ψ), seeds were collected by hand (ASC population, see Section 2.1) from mature pods before natural dispersal (18th December, 2013). After harvest, seeds were cleaned by sieves, air-dried under laboratory conditions and stored in paper bags at 8%–9% (d. w. b.) of water content. Seed biomass was estimated from samples of 50 seeds each (29 ± 1.4 mg, $n = 8$).

After-ripening treatments

Vicia villosa seeds were after-ripened at 5, 20 and 30°C ($\pm 2°C$) in growth chambers. Seed germinability was assessed at 0, 20, 69, 161 and 287 days of dry storage (see Germinability tests at different water potentials). In addition, field after-ripening was assessed by placing batches of 50 clean seeds inside 100×100 mm impermeable nylon bags (Renzi et al., 2016). Seed bags were buried at 20-mm depth following a completely randomized experimental design ($n = 3$) and exhumed at different after-ripening time-periods (27, 62, 118 and 251 days of burial). Field temperature was recorded at 20-mm depth at 2-hr intervals using digital temperature data loggers (Thermochron Ibuttons, Model DS1921G-F50; Maxim Integrated Products, Inc.).

Germinability tests at different water potentials

Germination tests for seeds after-ripened in the laboratory and exhumed from the field were conducted at different water potentials (0, −0.4, −0.8, −1.2 and −1.6 MPa). Seeds were previously scarified to avoid lack of germination imposed by physical dormancy. Scarification was performed by cutting a small hole in the seed coat on the concave side of the seed with a surgical knife (van Assche & Vandelook, 2010). The solutions were prepared with polyethylene glycol (PEG 6000; Merck KGaA, Darmstadt, Germany) following

Michel (1983). Water potentials of the solutions were confirmed with a vapour pressure osmometer (VAPRO 5520; Wescor Inc., Logan, UT, USA). To keep the water potential of the incubation medium constant, PEG solutions were renewed after the first 24 hr of incubation and subsequently at weekly intervals (Ni & Bradford, 1992).

For each treatment, three replicates of 50 seeds were placed in Petri dishes on two layers of Whatman No. 1 filter paper moistened with 10 ml of solution. Hairy vetch seeds were incubated at an optimal constant temperature of 20°C ($\pm 2°C$) in the dark, as no light requirement was detected for germination in this species (Renzi et al., 2014). Petri dishes were sealed with parafilm to prevent water evaporation and wrapped in aluminium foil to provide darkness. A randomized complete-block design was used. Each replication was arranged on a different shelf in the incubator and considered as a block. Germination counting was performed at regular intervals over a 15-day incubation period, with the criterion for germination being visible protrusion of the radicle from the seed coat (≥ 1 mm). After 15 days, the total number of dead, germinated and ungerminated seeds was counted. Germination percentages were calculated for the viable fraction of the seed population. Seed viability was assessed on ungerminated seeds by slicing them longitudinally and further incubated in 0.25% tetrazolium chloride (2,3,5-triphenyltetrazolium chloride) solution for 24 hr at 35°C in the dark (International Seed Testing Association, 2011). Seeds with pink or red stained embryos were considered viable.

Modelling approach

The hydro-time model proposed by Bradford (1990, 1995) and Dahal and Bradford (1990) was implemented:

$$\theta_H = \sum_{i=1,n} \theta_n, \tag{5a}$$

$$\theta_n = \begin{cases} \psi - \psi_b & \text{if } \psi > \psi_b \\ 0 & \text{otherwise} \end{cases}, \tag{5b}$$

where θ_H is the hydro-time constant (MPa h), ψ is the water potential (MPa) of the germination medium, and ψ_b is the base (threshold) water potential value for germination. Assuming a normal distribution of ψ_b in the seed population, the median ($\psi_{b(50)}$) and standard deviation (σ_{ψ_b}) values can be derived using repeated probit regression analysis (θ_H is varied until the best fit is attained; Bradford, 1990, 1995):

$$\text{Probit}(g) = [\psi - (\theta_H/tg) - \psi_{b(50)}]/\sigma_{\psi_b}. \tag{6}$$

Germination time-course curves obtained under the different incubation water potential for seeds after-ripened in the laboratory, at each combination of storage time and temperature, were analysed by repeated probit regression to estimate the hydro-time parameters of the population ($\psi_{b(50)}$, θ_H and σ_{ψ_b}).

Changes in seed population hydro-time parameters were quantified as a function of after-ripening thermal-time accumulation for PD release (θ_{ATPD}). Model validation was performed using independent data from the field experiment.

2.2.4 | Estimation of seedling elongation rates as a function of temperature and water potential (submodel IV)

Submodel IV simulates seedling pre-emergence growth from the onset of germination. The effect of different temperatures and water potentials on hypocotyl (shoot) and radicle elongation was evaluated. Two different experiments were performed in growth chambers at (i) 5, 10, 20, 25 and 35°C (±2°C) temperatures and (ii) at 0, −0.4, −0.8, −1.2 and −1.6 MPa at 20°C (as described for *submodel II*).

For both experiments, a completely randomized block design following a factorial arrangement was implemented ($n = 8$). To obtain the necessary seedlings, 80 Petri dishes were incubated at 20°C for 3 days (30 seeds per dish). Once 1 mm radicle length seedlings were obtained, five representative seedlings were selected per dish, and they were transferred to new Petri dishes under the corresponding thermal or hydric medium for subsequent growth measurements. The five seedlings were considered as pseudo-replicates.

Seedlings hypocotyls and radicle length were measured following a non-destructive sampling method. The length of each hypocotyl and radicle was measured every 24 hr for 12 days. Petri dishes were kept in continuous darkness in growth chamber except when measurements were taken.

Sequential linear regressions of hypocotyl and radicle length versus incubation time were performed. The slopes of each linear equation represented the rate of hypocotyl and radicle elongation. Estimated elongation rates were regressed against temperature or water potential, and cubic polynomial functions were fitted to the data (Shrestha, Thomas, & Swanton, 1999).

2.3 | Seedling emergence model development

The developed model integrates the different submodels (I, II, III and IV) as detailed in Section 2.2. Model assumptions are that each fraction of the seedbank requires a certain amount of after-ripening thermal-time accumulation for PY + PD release to occur. Following, each "non-dormant" fraction of the seedbank accumulates a certain amount of hydrothermal time to achieve germination and pre-emergence growth in order to finally emergence. Thus, cumulative emergence ($E_{T,\psi}$) was represented as

$$E_{(T,\psi)} = [G_{(\theta_{AT},T,t)} K_{\psi_{b(\theta_{AT})}}] RE_{(T,\psi)}, \tag{7a}$$

$$K_{\psi_{b(\theta_{AT})}} = \begin{cases} 1 & \text{if } \psi > \psi_{b(\theta_{AT})} \\ 0 & \text{otherwise} \end{cases}, \tag{7b}$$

where $G_{(\theta_{AT},T,t)}$ is the cumulative percentage of germination of the seed population at a given dormancy level (i.e., PY + PD status) after incubation for a given time (t) and temperature (T) (Equation 3); $K_{\psi_{b(\theta_{AT})}}$ indicates whether soil water potential allows for hydrothermal-time accumulation ($K_{\psi_{b(\theta_{AT})}} = 1$) for seed germination or not ($K_{\psi_{b(\theta_{AT})}} = 0$) according to the dormancy status of the seed population (adapted from Zambrano-Navea, Bastida, & Gonzalez-Andujar, 2013). $RE_{(T,\psi)}$ is the hypocotyl elongation rate according to the soil temperature and moisture content.

January 1st was arbitrarily chosen as the onset of the after-ripening thermal-time accumulation period. In the Southern Hemisphere, seed dispersal occurs during the last months of the year (from mid-November till late December). Experimental evidence indicates that *V. villosa* seedbank replenishment by natural seed rain has already occurred by such date. Estimated required hypocotyl's elongation length for hairy vetch emergence under no-tillage systems is 30 mm.

2.4 | Seedling emergence field experiment

The experiment was conducted on an undisturbed field with a high naturalized population density of hairy vetch without crop presence during 2013, 2014 and 2015 (see Section 2.1). *Vicia villosa* seedlings with a 30 mm hypocotyl length (two expanded leaves stage) were counted at weekly intervals on five permanent quadrats (1 m² each) randomly distributed on the field. Emerged vetch individuals were controlled with glyphosate (720 g e.a./ha) after each counting (destructive method), with minimal disturbance of the soil and the vetch stubble cover. At the end of each year of experimentation, the quadrats were removed and newly distributed at random into the remaining area of the 2 ha experimental field. Thus, the seedbank of a particular year was not disturbed by seedling removal during the counting process of the previous years.

Field temperature was recorded at 10-mm depth at 2-hr intervals using digital temperature data loggers (Thermochron Ibuttons, Model DS1921G-F50; Maxim Integrated Products, Inc.). In this work, 10 mm was considered a representative seed burial depth of an undisturbed soil condition emulating a non-tillage field scenario.

The soil temperature and moisture model (STM²) developed by USDA-ARS (http://www.ars.usda.gov/services/software/software.htm; Spokas & Forcella, 2009) was used to estimate soil volumetric water content (VWC) conditions. STM² is general in purpose and calculates soil moisture and temperature based on soil composition and meteorological data. The model was calibrated using soil site-specific parameters: soil texture (sandy loam = 82% sand, 13% silt, 5% clay), organic matter content (1.2%) and bulk density (1.45 Mg/m³).

Daily minimum and maximum air temperature and precipitation (STM² input variables) were obtained from a meteorological station located less than 500 m from the experimental plot. Soil VWC values estimated with the STM² model were further validated with in situ VWC measurements registered at 0- to 50-mm soil depth on a weekly basis. VWC was calculated using the gravimetric water content and bulk soil density method (Black, 1965). A specific soil water retention curve was developed according to Richards (1949) to obtain soil water potential values between 0 and −1.5 MPa.

After natural seed dispersal, hairy vetch plants were mechanically removed and the stubble was used as soil surface coverage. Residue cover for soil VWC prediction represented by "% shade" in STM² was set as 100% (Blanco et al., 2014).

2.5 | Model evaluation

Model evaluation was performed on independent data (test set) obtained from the field experiment (Section 2.4) during 2013, 2014 and 2015. Emergence time-course curves were simulated using Equation 7, and the simulated results were compared with the experimentally obtained data. Model performance was assessed by the root-mean-square error (RMSE):

$$\text{RMSE} = \sqrt{(1/n) \sum_{i=1}^{n} (x_i - y_i)^2}. \tag{8}$$

Root-mean-square error (RMSE) is an estimator of the difference between observed (x_i) and predicted (y_i) emergence values. A small value of RMSE indicates a close agreement between observed and simulated data (Mayer & Butler, 1993). The predictive capability of the developed submodels was based on the RMSE of the test set.

3 | RESULTS

3.1 | Hydro-time parameters in relation to PD release

Hydro-time parameters $\psi_{b(50)}$, σ_{ψ_b} and θ_H showed no consistent variation when regressed as a linear function of after-ripening time

($p = .36$, $p = .91$ and $p = .13$ respectively). A mean base water potential ($\psi_{b(50)} \pm \sigma_{\psi_b}$) of -1.06 ± 0.39 MPa and θ_H of 41.4 MPa h were estimated, and no difference between laboratory and field conditions was observed (Table 1). Mean base water potential was the less variable parameter (CV < 10%), being unaffected by after-ripening time, storage temperature or field condition ($p > .05$).
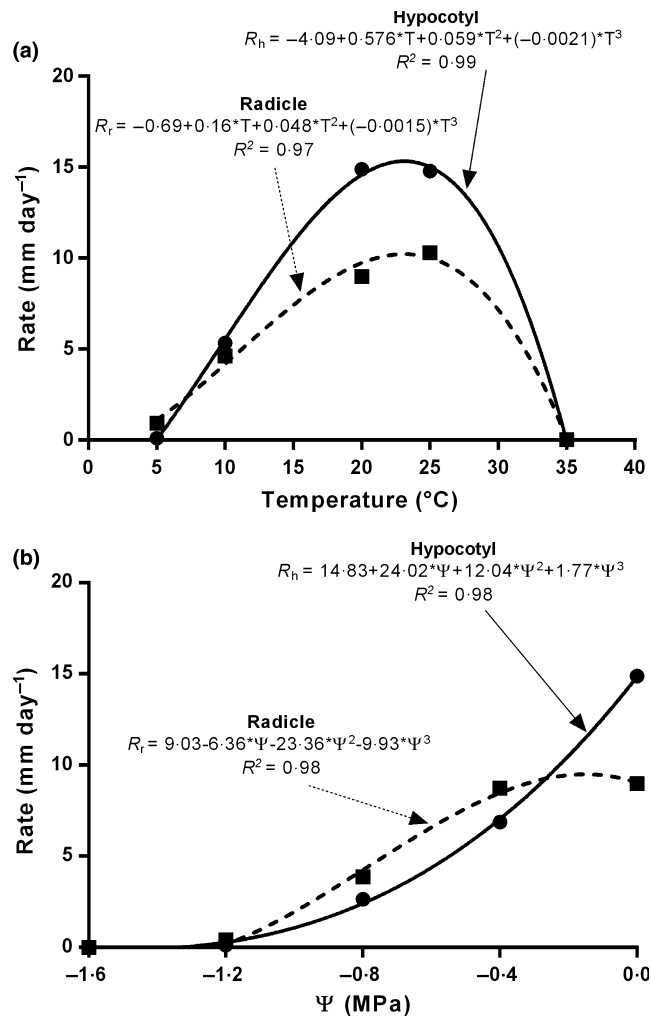
3.2 | Seedling elongation rates

The hypocotyl mean elongation rate was generally faster than for the radicle over the range of tested temperatures (Figure 1a). Temperature optima for hypocotyl elongation were between 20–25°C. No hypocotyl growth was recorded at <5°C, or >35°C. Conversely, radicle elongation rate was faster at water potentials ≤ -0.4 MPa (Figure 1b), while at −1.2 MPa, growth was nil. Hypocotyls elongation rate was adequately described as a polynomial function of the incubation temperature and water potential.

The hypocotyl elongation rate according to the soil temperature and moisture content was estimated as:

$$R_{h(T,\psi)} = -4.09 + 0.576 \times T + 0.059 \times T^2 + (-0.0021) \times T^3 \quad \text{if } R_{hT} < R_{h\psi}, \tag{9a}$$

TABLE 1 Estimated population hydro-time parameters for *V. villosa* seeds incubated in the laboratory at constant temperatures of 5, 10 and 30°C at 0, 20, 69, 161 or 287 days and buried under field conditions at 0, 27, 62, 118 or 251 days of after-ripening

Storage	Days of storage	$\psi_{b(50)}$ (MPa)	σ_{ψ_b} (MPa)	θ_H (MPa h)
Laboratory (L)	0	−1.05 ± 0.09	0.42 ± 0.09	44.0 ± 6.0
5°C	20	−1.06 ± 0.09	0.37 ± 0.09	51.2 ± 14.1
	69	−1.03 ± 0.06	0.40 ± 0.08	42.4 ± 15.2
	161	−1.10 ± 0.08	0.31 ± 0.08	41.6 ± 16.0
	287	−1.00 ± 0.06	0.40 ± 0.09	37.6 ± 11.3
20°C	20	−1.18 ± 0.24	0.46 ± 0.16	55.2 ± 8.3
	69	−1.07 ± 0.05	0.46 ± 0.07	32.8 ± 6.0
	161	−1.03 ± 0.12	0.31 ± 0.04	36.8 ± 11.8
	287	−1.08 ± 0.08	0.32 ± 0.06	37.6 ± 11.1
30°C	20	−1.15 ± 0.14	0.47 ± 0.10	64.8 ± 24.0
	69	−1.09 ± 0.09	0.33 ± 0.08	44.0 ± 18.6
	161	−1.03 ± 0.03	0.34 ± 0.06	30.4 ± 1.4
	287	−1.00 ± 0.12	0.46 ± 0.07	36.8.0 ± 18.6
Average (CV)		−1.07 (9.7)	0.39 (23.7)	42.7 (36.8)
LSD$_{0.05}$		ns	ns	ns
Field (F)	0	−0.96 ± 0.04	0.35 ± 0.02	51.2 ± 22.3
	27	−1.02 ± 0.02	0.32 ± 0.05	40.0 ± 11.1
	62	−1.06 ± 0.11	0.35 ± 0.09	29.6 ± 3.7
	118	−1.16 ± 0.17	0.44 ± 0.23	40.0 ± 6.0
	251	−1.10 ± 0.03	0.46 ± 0.05	29.6 ± 2.8
Average (CV)		−1.06 (10.0)	0.38 (29.1)	38.1 (33.8)
LSD$_{0.05}$		ns	ns	ns
L vs. F				
LSD$_{0.05}$		ns	ns	ns

(a)

Hypocotyl
$R_h = -4.09 + 0.576*T + 0.059*T^2 + (-0.0021)*T^3$
$R^2 = 0.99$

Radicle
$R_r = -0.69 + 0.16*T + 0.048*T^2 + (-0.0015)*T^3$
$R^2 = 0.97$

(b)

Hypocotyl
$R_h = 14.83 + 24.02*\Psi + 12.04*\Psi^2 + 1.77*\Psi^3$
$R^2 = 0.98$

Radicle
$R_r = 9.03 - 6.36*\Psi - 23.36*\Psi^2 - 9.93*\Psi^3$
$R^2 = 0.98$

FIGURE 1 Rate of hypocotyl and radicle elongation of *Vicia villosa* as a function of incubation temperature (at 0 MPa) (a), or incubation water potential (at 20°C) (b). R_h and R_r are the functions describing hypocotyl and radicle elongation as a function of temperature (T) and water potential (ψ)

$$R_{h(T,\psi)} = 14.83 + 24.02 \times \psi + 12.04 \times \psi^2 + 1.77 \times \psi^3 \quad \text{if } R_{hT} > R_{h\psi}. \tag{9b}$$

3.3 | Field emergence patterns

Hairy vetch seedling emergence occurred mainly from mid-summer until mid-autumn with very low emergence values (<15%) during spring (Figure 2). Seedling emergence pattern distribution was variable among years. During the emergence experiments, in summer and autumn, mean temperature at the soil was rarely below the estimated base temperature for seed PY break (9.8°C, Figure 3). Mean soil temperatures did not exceed 30°C in 2013–2015. Therefore, mean temperatures were permanently within the range in which dormancy release and germination were expected, according to results from germination tests (>2°C and <30°C).

Predicted (STM²) as a well as in situ soil moisture data for the 2013–2015 growing seasons are shown in Figure 3. Both predicted

and experimentally obtained maximum values of VWC corresponded to rainfall events. VWC estimates were generally close to in situ measurements (RMSE = 2.55 (2013), 3.96 (2014) and 6.09 (2015)).

3.4 | Physical (PY) and physiological (PD) dormancy release

From 1st January (after natural dispersal), a specific seedbank fraction loses its dormant condition on a daily basis due to after-ripening thermal-time accumulation. Accumulated dormancy release curves were depicted according the PY (Equation 1a) and PD (Equation 2a) dormancy component (Figure 4). As estimated using Equation 1a, PY-break dynamics was similar among years (Figure 4). Conversely, distinct PD-release patterns were predicted (Equation 2a) for 2013, 2014 and 2015.

## 3.5 | Observed versus predicted field emergence

Observed cumulative *V. villosa* field emergence data (Section 3.3) were compared to the outputs of the different submodels (Table 2). The additive effect of each submodel clearly improved the explanatory capacity of the field emergence patterns registered in 2013, 2014 and 2015. As observed in Table 2, a considerable reduction of RMSE values was achieved by considering the effect of the PD status on the germination-related population thermal parameters.

Cumulative field emergence predicted by the developed mechanistic model [I + II + III + IV] showed a very good correspondence and reasonable accuracy with the observed cumulative field emergence curves obtained from the independent experimental data (RMSE ≤ 10.1; Figure 5).

4 | DISCUSSION

Experimental evidence obtained from laboratory and field studies performed on different species with PD suggest that $\psi_{b(50)}$ become more negative as seeds progressively release from dormancy during the after-ripening process (Bair, Meyer, & Allen, 2006; Bauer, Meyer, & Allen, 1998; Chantre, Sabbatini, & Orioli, 2010; Gianinetti & Cohn, 2007; Hu et al., 2013). However, our results indicate that for *V. villosa* $\psi_{b(50)}$ values are not influenced by after-ripening thermal-time accumulation ($p > .05$) during the PD-release process (Table 1). Thus, a constant $\psi_{b(50)}$ value was used for modelling purposes. This $\psi_{b(50)}$ value was consistent with results recently reported by Tribouillois, Dürr, Demilly, Wagner, and Justes (2016).

The minimum threshold water potential at which germination ceases in many agricultural species ranges from −0.1 to −1.5 MPa (Bullied, Bullock, et al., 2012). Despite many species being capable of germinating at very low water potentials (i.e., *Secale cereale*, *Brassica rapa*, *Cicer arietinum*), the rate and uniformity of germination and pre-emergence growth is often compromised by suboptimal soil water potentials (Bullied, van Acker, et al., 2012; Oryokot, Murphy, Thomas, & Swanton, 1997; Tribouillois et al., 2016). As observed in
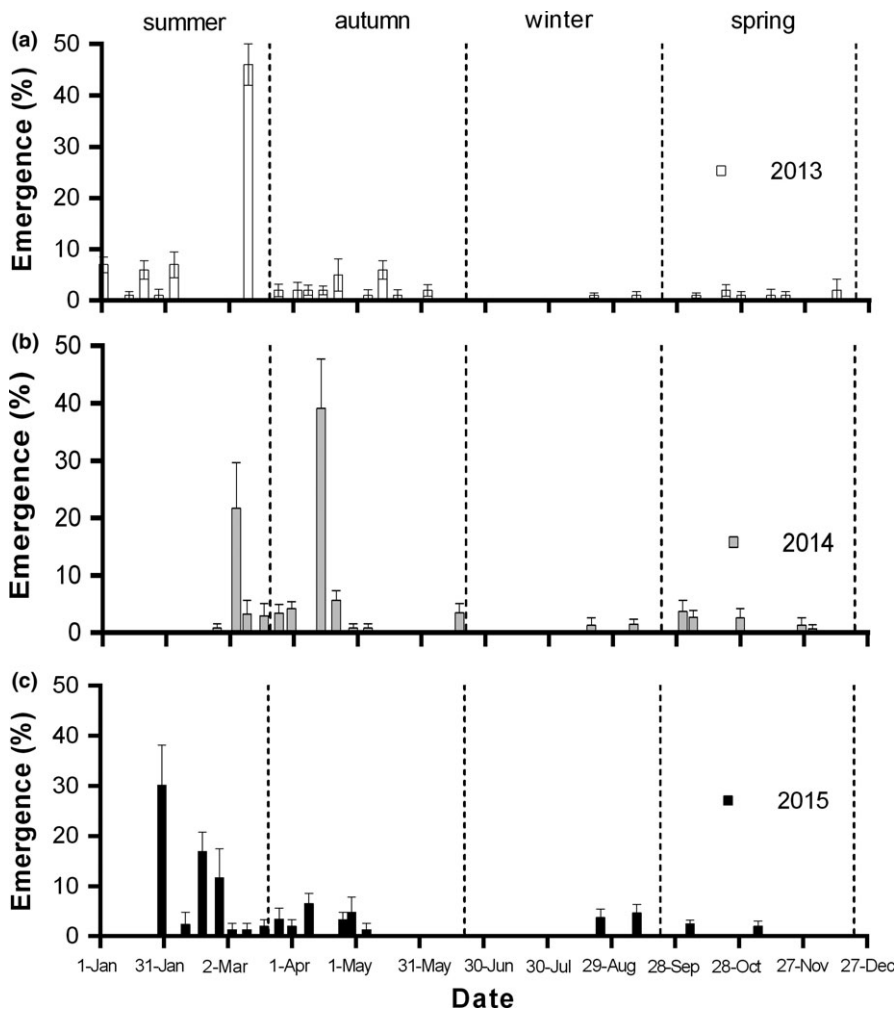
FIGURE 2 Field emergence patterns of hairy vetch during the experiments conducted in H. Ascasubi in 2013 (a), 2014 (b) and 2015 (c)
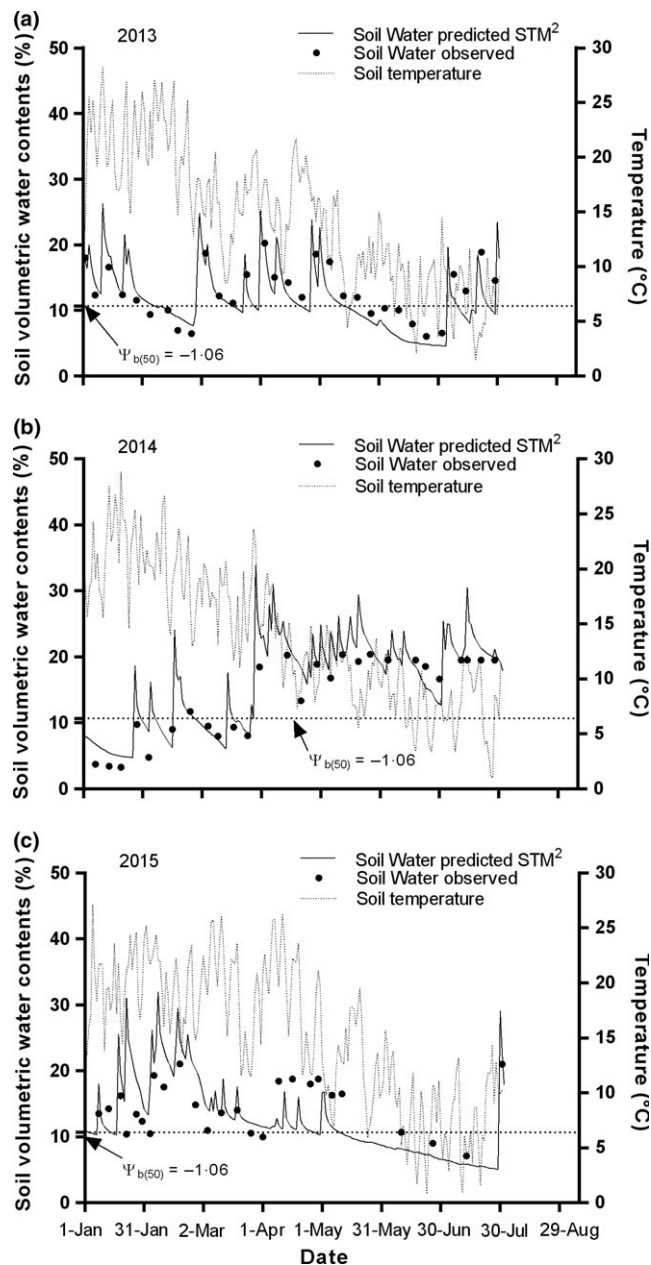
this study, although hairy vetch is able to germinate at relatively low soil water potentials ($\psi_{b(50)}$ = −1.06 MPa), the rate of hypocotyl elongation would be ≈0.8 mm/day. Therefore, theoretically the seedling would require 37 days to reach the soil surface (≈30 mm hypocotyl length). Hypocotyl growth rate decreased from 14.9 ± 0.4 to 6.9 ± 0.2 mm/day from 0 at −0.4 MPa (Figure 1b), while root growth rate remained constant (8.8 ± 0.3 mm/day). Interestingly, for water potentials below −0.4 MPa root growth rate was higher than that of the hypocotyl. This might be considered as an ecological adaptation of hairy vetch under restrictive soil moisture conditions (e.g., semi-arid environment) that would allow the root growth to be maintained until water replenishment by precipitation or artificial irrigation (Radhouane, 2007).

Both hypocotyl and radicle elongation as influenced by incubation temperature were adequately described by cubic models (Figure 1a) which accounted for 99% of data variation. Similarly, several authors have used polynomial regression equations to describe radicle and hypocotyl elongation responses to temperature (Roman, Thomas, Murphy, & Swanton, 1999; Shrestha et al., 1999). In agreement with Bullied, van Acker, et al. (2012), the minimum threshold temperature for hypocotyl elongation was higher than the base germination temperature (5 and 2°C respectively).

Estimating soil water potential under field conditions is particularly important to predict seed germination and pre-emergence growth based on the corresponding species-specific ecophysiological thresholds (Bullied, Bullock, et al., 2012). The STM² model developed by USDA-ARS (Spokas & Forcella, 2009) exhibited a good performance in the estimation of soil water content values under field experimental conditions (Figure 3). The model was previously tested for many global sites in Spokas and Forcella (2009). Specifically, for the semiarid temperate region of Argentina, STM² outcomes were validated by Damiano, López, Vigna, and Moschini (2010) showing a satisfactory agreement between predicted and observed field experimental data.
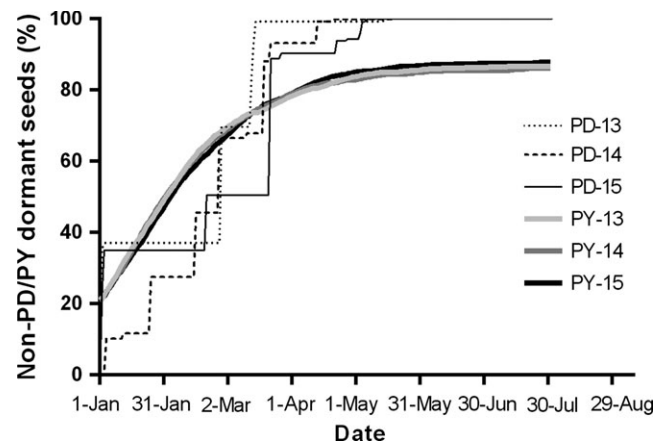
PD release of hairy vetch seeds was variable among years (Figure 4). Observed differences in dormancy release patterns suggest that the PD component is actually the dominating process during the first 3 months after dispersal, thus allowing or blocking subsequent germination according to the prevailing environmental conditions. Conversely, the PY-break process was rather stable. PY release in several legume species is associated with loss or changes of lipids composition in the seed coat. As suggested by Gama-Arachchige et al. (2013), the weakening of hydrophobic bonds increases the thermal degradation of lipids due to exposure to high summer

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FIGURE 3 Soil microclimate conditions for field emergence experiments in H. Ascasubi during 2013 (a), 2014 (b) and 2015 (c). Lines represent average daily values of soil temperature (dotter line) and volumetric water contents (VWC; solid line). The arrows show the mean lower value of soil water potential ($\psi_{b(50)} \approx 10.7\%$ VWC) for germination of *V. villosa*


FIGURE 4 Estimated physical (PY) and physiological (PD) dormancy release dynamics of hairy vetch in 2013, 2014 and 2015. PY and PD-release dynamics were calculated using Equations 1a and 2a respectively

TABLE 2 Root-mean-square error (RMSE) comparison between submodel outputs predicted and observed seedling emergence data (test set) for hairy vetch in 2013, 2014 and 2015

Submodels type	2013	2014	2015	Mean
[I] (PY release)	22.2	45.0	27.8	31.7
[I + II] (PY + PD release) + Germination Thermal parameters based on PD status	12.1	15.4	12.1	13.2
[I + II + III] (PY + PD release) + Germination Thermal + hydric parameters based on PD status	10.8	13.5	11.9	12.1
[I + II + III + IV] (PY + PD release) + Germination Thermal + hydric parameters based on PD status + Seedling (hypocotyl) elongation rate	10.1	7.1	4.9	7.4

Submodel I, physical dormancy release; Submodel II, thermal parameters related to physiological dormancy status; Submodel III, hydric parameters related to physiological dormancy and germination; Submodel IV, hypocotyl elongation rate according to the soil temperature and moisture content.

temperatures after seed dispersal. As indicated by Renzi et al. (2014), the PD component regulates the amplitude of the thermal range permissive for *V. villosa* germination. A noticeable increment in the upper limit temperature for germination was registered as after-ripening thermal time was accumulated, thus indicating an increment in the permissive thermal range for germination (Renzi et al., 2014). In addition, a more synchronous germination was observed as after-ripening thermal time for PD release progressed (Renzi et al., 2014). A widening in the thermal range permissive for germination and a

reduction in thermal-time requirements were also observed during seed after-ripening of *Buglossoides arvensis* I.M. Johnston (=*Lithospermum arvense* (L.); Chantre, Batlla, Sabbatini, & Orioli, 2009; Longas, Chantre, & Sabbatini, 2016). Similar results were also obtained for other winter annual species requiring after-ripening for physiological dormancy loss (Bair et al., 2006; Bauer et al., 1998; Foley, 1994). Thus, a double trigger mechanism could be envisioned for *V. villosa*, where PD regulates the timing of seedling emergence after PY is overcame. This is mainly due to the widening of the germination-permissive thermal range as indicated by Renzi et al. (2014). As stated by Paulsen et al. (2015), the PD mechanism does a better job than PY because it is more resilient to changes in the environmental conditions of the surrounding seed environment. In contrast to some species mentioned by Baskin and Baskin (2014), it is likely that hairy vetch PY may not act as an environmental "signal detector" for
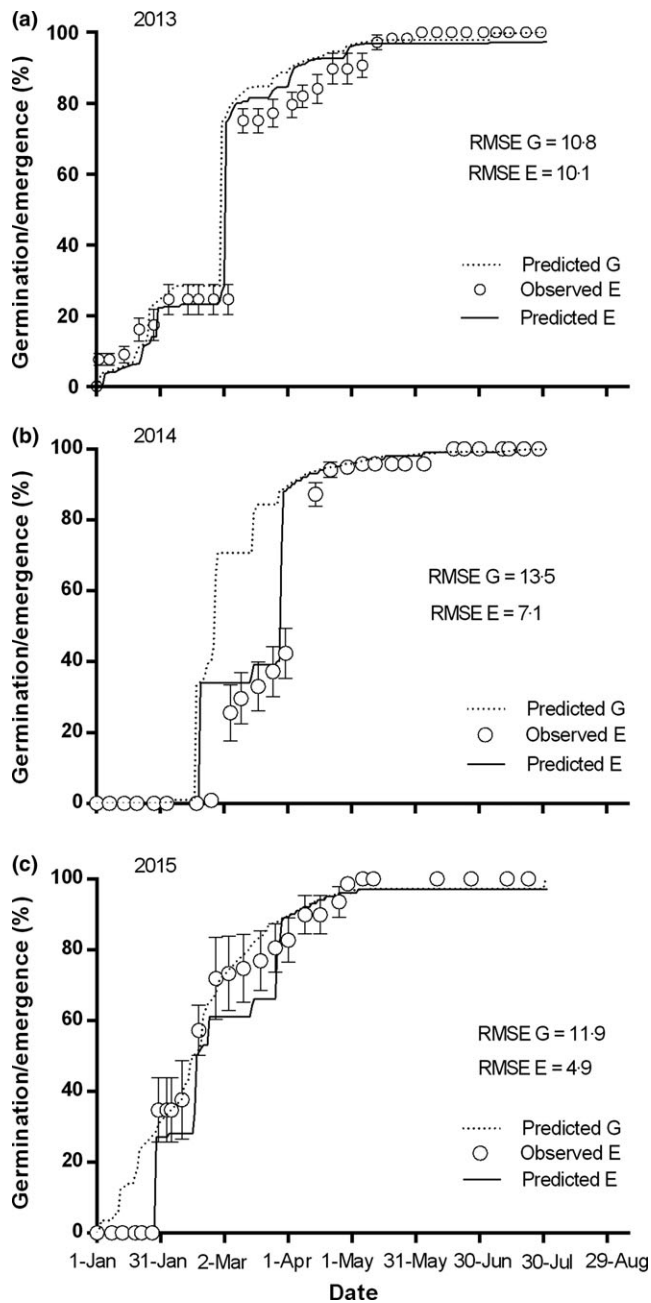
FIGURE 5 Predicted cumulative field germination (G) and seedling emergence (E) versus observed emergence data for *V. villosa* in 2013 (a), 2014 (b) and 2015 (c). The dotted and continuous lines represent field germination and emergence values predicted from simulation modelling; symbols represent observed emergence data, and vertical bars indicate *SE* (*n* = 5). RMSE, root-mean-square error

germination. However, the impermeable seed coat could act mainly as a mechanism that favours the persistence of the seed in the soil (Long et al., 2015). From a natural reseeding perspective, the alleviation of PD synchronizes the timing for hairy vetch germination, while the PY determines the seedbank persistence. According to Renzi et al. (2014), hairy vetch would correspond to a type III persistent seedbank (*sensu* Baskin & Baskin, 2014), where many seeds

germinate soon after dispersal, but a small reserve of viable seed remains ungerminated (Baskin & Baskin, 2014).

The mechanistic model developed in this work (Equation 7) corresponding to an interrupted hydrothermal-time approach (*sensu* Bullied, van Acker, et al., 2012) is able to adequately predict field germination and seedling emergence based on after-ripening thermal-time requirements for PY and PD release, thermal time and hydro-time for germination and pre-emergence growth. After PY + PD after-ripening requirements are fulfilled, each specific non-dormant seedbank fraction undergoes germination and pre-emergence growth processes by accumulating hydrothermal time (i.e., thermal time accumulates when the soil water potential (ψ_s) is greater than the base water potential ($\psi_{b(50)}$)). The simulations illustrate the large number of possible applications of the model, once it has been evaluated with independent data. An important feature of the present modelling alternative is that input variables (i.e., soil mean daily temperature and soil water potential) are easily obtained from soil microclimatic information which could be gathered from series of meteorological data available from official weather stations (Blanco et al., 2014). In addition, the modelling approach does not require the estimation of the initial seedbank which is a highly complex and time-consuming input variable (Colbach et al., 2006).

Mechanistic models may be highly sensitive to the features of each seed accession use to generate temperature-sensitive germination rates (Forcella et al., 2000). However, the population of hairy vetch used in this study largely represents most of naturalized populations of Argentina (Renzi et al., 2016).

Obtained results suggest that the development of this type of models offer an enormous potential to predict hairy vetch emergence within management decision support systems for farmers and agricultural professionals. In addition, it might help to simulate different climate change scenarios (Ooi, Auld, & Denham, 2009). Observed field emergence curves were adequately estimated (RMSE < 10.1) despite the climatic variations among years. The model correctly predicted the timing and amplitude of field emergence flushes. Fifty per cent of emergence was reached after 61 (3 March 2013), 87 (28 March 2014) and 47 (15 February 2015) calendar days respectively (Figure 5). An early emergence pattern of hairy vetch was registered during 2015, corresponding to a rainy summer (181 mm rainfall) with lower daily mean temperatures (19.6°C) compared to previous seasons (2013 = 46 mm; 21.2°C; 2014 = 36 mm, 20.6°C) respectively (Figure 3).

The proposed model would help to improve decision-making regarding sustainable management practices, either to promote or suppress seedling emergence of hairy vetch in semiarid regions. Under a crop-pasture rotation, predicting the peak of hairy vetch germination before emergence would allow the use of non-selective herbicides (e.g., glyphosate, paraquat, 2,4-D) and/or mechanical pre-emergence treatments, without affecting the hairy vetch stand. Due to the limited amount of selective herbicides, weed control is often difficult during hairy vetch post-emergence (Renzi & Cantamutto, 2013). For the cereal phase, sowing dates for wheat and barley during May–June for the semiarid conditions of Argentina would allow

a high hairy vetch control during pre-sowing, >85% of total annual emergence (Figure 5). On the other hand, hairy vetch control on cereal crops could be easily performed with several selective post-emergence herbicides (e.g., dicamba, clopyralid, prosulfuron; Curran et al., 2015).

5 | CONCLUSIONS

The information generated by this investigation could help to develop conservationist management tactics under semiarid environmental conditions. The developed model successfully predicted the emergence of hairy vetch under no-till systems. However, further testing and evaluation should be carried out in other locations to give better confidence to the model. From a climate change perspective, significant increments in temperature and rainfall variability are expected for semiarid regions (Ooi et al., 2009). In this context, the model would allow prediction of the variation in dormancy levels and hairy vetch field emergence patterns under different climate scenarios.

Considering that in Argentina hairy vetch is well adapted to anthropogenic soil disturbed areas, either as naturalized populations or voluntary weeds (Renzi et al., 2016), seedling emergence as affected by seed burial depth (e.g., shallow tillage system recommended to avoid seed predation by pigeons, Renzi et al., 2017) should be considered as an additional variable of the model. Further research is required to determine *V. villosa* field emergence patterns under different soil tillage practices over several years in winter cereal-*V. villosa* crop rotations.

CONFLICTS OF INTEREST

None.

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