

Trait-based prioritization of native herbaceous species for restoring biodiversity in Mediterranean olive orchards



Stephanie Frischie, 2017

PhD Thesis dissertation

**University of Pavia, Department of Earth & Environmental
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Semillas Silvestres, S. L.

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Context of research

The research presented herein was conducted as part of the NAtive Seed Science TEchnology and Conservation (NASSTEC) project, a European Union Framework 7 Marie Curie Initial Training Network. The primary goal of NASSTEC is to advance the native seed sector in Europe by connecting applied research to industrial partners. In my research, I characterized underutilized native herbaceous species for their suitability 1) as cover crops for olive orchards and 2) to cultivation for purposes of multiplying and producing commercial quantities of seeds. The industrial partner was Semillas Silvestres, S. L. a native seed company in Córdoba, Spain with over two decades of experience in native plant materials.



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**Trait-based prioritization of native herbaceous species for restoring biodiversity
in Mediterranean olive orchards**

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Author's declaration

I, Stephanie Lynn Frischie, declare that this thesis, submitted in partial fulfilment of the requirements for the award of Doctor of Philosophy, in the School of Earth and Environmental Sciences, University of Pavia, is wholly my own work unless otherwise referenced or acknowledged. This work has not been submitted for any other degree or professional qualification at any other academic institution. I confirm that the work submitted is my own, except work which was part of jointly-authored publications as follows. The work presented in Chapter 1, "Germination response of winter annuals in old-field Mediterranean landscapes of southern Spain" was submitted to *Plant Biology* in October 2017. The authors are Stephanie Frischie (self, PhD student), Eduardo Fernández-Pascual, Cándido Gálvez Ramirez (co-tutor) Peter Toorop, Matías Hernández González, and Borja Jiménez-Alfaro (tutor). The work presented in Chapter 2, "Seed farming potential of 27 native Mediterranean forbs" was submitted to *Restoration Ecology* in October 2017. The authors are Stephanie Frischie (self, PhD student), Cándido Gálvez Ramirez (co-tutor), and Borja Jiménez-Alfaro (tutor). The work presented in Chapter 3, "Traits-based decision making tool for promoting native cover crops in olive orchards" is in preparation to be submitted to *Agriculture, Ecosystem and Environment*. The authors are Stephanie Frischie (self, PhD student), Cándido Gálvez Ramirez (co-tutor), Geoff Squire and Borja Jiménez-Alfaro (tutor).

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Statement of style

The chapters in this thesis have been prepared as articles for scientific publications. Because of this, there may be some overlap or repetition of content. The formatting follows the guidelines for each journal.

Introduction

Seed-based restoration

Ecological restoration uses many techniques and practices (Clewell et al., 2005; Falk et al., 2006; Society for Ecological Restoration, 2004) to reset the trajectory of a site or habitat to achieve specific goals. When a site is particularly degraded or altered from target conditions, plants must be added or reintroduced (Bakker et al., 1996; Hobbs and Cramer, 2008). Seeds are an effective way to establish the desired plant species, particularly for herbaceous species. Seeds are plants too but compared to seedlings, seeds are relatively durable, compact and low maintenance which makes them more economical to use. Seeds can be stored, transported and sown across large areas. Another benefit of using seeds for restoration is the ability to deploy many species in one operation through seed mixes of multiple species. Establishing plants via seeding can serve as a filter to screen for adaptedness to the site conditions (Temperton et al., 2004). If seeds cannot successfully germinate and establish, this indicates an issue with site conditions or a mismatch between the seed source and the site (Calvino-Cancela, 2011). Restoration practitioners can use this as a test to adjust the site conditions or seed source accordingly. Varying degrees of dormancy within a seed lot stagger establishment over time which may or may not be advantageous, depending on the restoration condition and goals.

There are two parts to working with seeds in restoration. One part is getting the seeds - the supply. Seeds for use in restoration are usually acquired either by collection from wild populations or by harvesting seeds from plants which are cultivated for that purpose, a practice referred to herein as seed farming. Successfully obtaining seeds for restoration depends upon understanding the phenology of flowering, seed set and

dispersal. Subsequently, fruits and/or seeds often require cleaning to remove inert matter or appendages which would interfere with seed deployment. The other part of working with seeds in restoration is using the seeds. Sowing, seeding, planting or deployment are terms which all refer to the same action of putting the seeds out on the restoration site so that they germinate, establish and develop the desired plant community. Understanding seed biology and seed ecology is important for successful seed-based restoration (Jiménez-Alfaro et al., 2016). Aspects of seed biology such as dormancy and germination response affect the timing of germination for a seed and the likelihood of establishment in the field.

Seed-based restoration is practical and effective, but there are some inherent challenges that must be addressed (Hölzel et al., 2012). Once the need for plant introductions via seeds has been determined, the next step is deciding which species to add. All restoration activities need to address species selection, the process of deciding which species are desired at the site and of those, which ones should be actively added. Restoration projects need to create a restoration species pool (Ladouceur et al., 2017) for specific habitats and related environmental conditions (Kiehl, 2010). Species selection for any given restoration project should consider historic reference community, target species, performance, social or functional traits overlain with the unique combination of site conditions, restoration goals and budget (Graff and McIntyre, 2014; Meli et al., 2014; Waller et al., 2015). Next the appropriate ecotype and origin of plant material for sourcing the seeds (Vander Mijnsbrugge et al., 2010) must be determined and cross checked for availability. Possible sources for getting or generating seeds are through purchase, wild collection or in-house seed farming (Borders et al., 2011; Havens et al., 2015). Seed farming, the cultivation of plants for their production of seeds, is an effective way to generate

volumes of seed more economically than wild collecting (Broadhurst et al., 2016; Merritt and Dixon, 2011; Nevill et al., 2016), but seed multiplication should be done with attention to maintaining the spectrum of diversity and the resilience it provides to restorations (Basey et al., 2015). Between production and use, proper storage conditions are required to maintain seed quality (Bissett, 2006). In the final stages of seed use, proper site preparation, sowing methods and subsequent management methods are required for successful establishment and maintenance of the desired plant community (Kiehl et al., 2010).

Study system: Mediterranean olive agroecosystems

The Mediterranean Basin (MB) is one of the global biodiversity hotspots (Myers et al., 2000). Within the MB, southern Spain has a particularly rich native flora due to the Iberian Peninsula's relative ecological isolation from rest of the European continent combined with Mediterranean-type climate and proximity to Africa (Matesanz and Valladares, 2014; Nardini et al., 2014; Rey Benayas and Scheiner, 2002). However, due to the long history of inhabitation and use by humans, landscapes in southern Spain are semi-natural and further degraded by intensive agricultural use and urban development (Myers et al., 2000; Underwood et al., 2009). The target conditions for restoration are usually semi-natural habitats which have been heavily modified and are subject to semi-arid conditions (Bonet, 2004; Nunes et al., 2016). These include agroecosystems, especially where the crops are woody species such as in the dehesa systems of *Quercus ilex* and *Q. suber* (Bergmeier et al., 2010; Linares, 2007; Moreno et al., 2007; Vallejo et al., 2009), vineyards and in fruit, nut or olive orchards (Fleskens and Graaff, 2010; Gonzalez-Sanchez et al., 2015).

The cultivated olive (*Olea europaea* subsp. *europaea*) was domesticated in the Mediterranean Basin (Connor, 2005) and today, this region is still the primary global production area for olive orchards. Spain produces eighty percent of global olive production (“Agriculture Database,” 2014) and 80% of Spain’s production comes from the autonomous community of Andalusia, where 30% of land cover is under olive production (“Agriculture Database,” 2014). Hundreds of varieties exist, each suitable for a given use (table olives, olive oil or dual purpose) and a particular combination of microclimate and soil type (Barranco and Rallo, 2000). The choice of variety also depends upon the plantation type which olive farmers use. The least intensive plantation types have 1-4 trunks per canopy which are pruned for optimum hand harvest (de Graaff et al., 2008; Sánchez et al., 2011). Spacing between trees may be as much as 10 meters in a grid layout. Intensive plantations have one trunk per canopy and the grid spacing between trees is closer to 7 meters. The fruits are harvested with mechanical vibrating shakers. In super-intensive plantations, the trees are planted close together in distinct rows. They are pruned to form hedges and are harvested by machines which mount the row and using rotating brushes to remove the fruits. Irrigation follows the intensive continuum, with the less-intensive plantations being rain fed while underground drip irrigation is used for intensive production. Of specific interest to our research, another practice under intensive and super-intensive models is to keep the soil free of non-crop vegetation since this vegetation competes for water with the trees during the critical summer months when precipitation is minimal and when trees are filling the fruits (Gómez-Limón et al., 2012).

The need for native cover crops and native seed supply

Spain’s high olive productivity has been achieved primarily by converting production to the intensive and super-intensive plantation models (Fernandez Escobar et al.,

2013; Gómez et al., 2014). The costs for intensive production are the simplification of the agroecosystem resulting in the loss of soil through erosion and the loss of ecosystem services provided by understory plants. The value and benefits of cover crops to protect the soil have been shown (Gómez et al., 2011, 2009; Gómez and Giráldez, 2010; Metzidakis et al., 2008). However, there is low adoption by farmers because most available cover crop species are forage grasses and legumes from temperate climates (Ward et al., 2012; Wayman et al., 2016) which are mismatched to the Mediterranean climate and the management and ecology of olive orchards. The available cover crop species are perennials which persist into the summer and farmers must manage against them to avoid competition with the olives for water (Juárez-Escario et al., 2013). The ideal herbaceous cover in the understory would be native, have a short life cycle and naturally senesce and disperse seeds at the onset of summer in May (Rodríguez-Entrena and Arriaza, 2013). As seeds, the cover crops persist through the difficult environmental period of summer without competing for water during that critical season. Then, the seeds germinate in autumn and the plants protect the soil during the rainy season while providing resources for beneficial insects. Due to their suitability and potential as cover crops, there is a growing interest in developing and managing native species for this purpose (Palese et al., 2015; Rodrigues et al., 2015; Siles et al., 2016).

The native seed sector is nascent and in development in Spain. Forestry species have been produced and used for decades, but the available herbaceous species are collected from the wild (Nunes et al., 2016). Large-scale, commercial production is needed for an affordable and sufficient supply of native seeds (Broadhurst et al., 2015; Nevill et al., 2016). The Mediterranean herbaceous flora is rich and offers many

possible species (Vogiatzakis et al., 2006) for inclusion in native plant materials and seed production.

Aims of the work

The primary aim of this PhD was to characterize a subset of native herbaceous species for their suitability to 2 purposes. The characterizations are applicable to develop both native seed production and cover crops in Spain. The first purpose is the value and utility as cover crops sown between rows of trees to increase the sustainability and biodiversity in olive orchards. The second purpose is the amenability to cultivation as seed crops under seed farming for commercial scale seed production to provide a source of affordable plant materials for establishing the under story in olive orchards.

Chapter 1 focuses on the application of seed biology and ecology to seed use. We characterized degree of dormancy and germination response to temperature, storage and water stress for 10 ruderal winter annual dicot species with the potential for use in restoration. Using seeds from wild populations, we measured final germination and calculated germination rate and the cardinal temperatures. Our results contribute to the body of general knowledge about the germination ecology of these understudied wildflowers. Specifically, the results provide information about the range of responses to environmental conditions and the corresponding ideal times or seasons for sowing and can be applied for successful seed use in restoration.

Chapter 2 addresses the supply of seeds for restoration. We studied native forb species from Mediterranean semi-dry habitats for characteristics of interest to seed farming and to establish cultural guidelines for seed producers to produce commercial quantities of seeds. We measured (1) establishment for a given seeding rate, (2) plant growth form and how this architecture should be considered in row spacing, (3)

phenology of key stages in crop development, and (4) seed yield and the effect of maturity on seed quality. Overall, our results are expected to provide useful recommendations to seed producers interested in the restoration of Mediterranean habitats.

Chapter 3 covers our species selection methodology. We evaluated the suitability of 30 native herbaceous taxa for native cover crops using the combined attribute values for function in the restored habitat (olive farming) with attribute values for generating seed supply (seed farming). The use of DEXi as a selection tool was practical and convenient. The flexibility of DEXi allows it to be adapted for use in selecting species for other purposes, such as cover crops in almond orchards or vineyards. Additional data can be added by users (seed companies and farmers) in future years to continue to improve the power of the selection tool.

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**Chapter 1. Hydrothermal thresholds for seed germination in
winter annual forbs from old-field Mediterranean
landscapes**

Full title: Hydrothermal thresholds for seed germination in winter annual forbs from old-field Mediterranean landscapes

Short running title: Germination response of annual forbs

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Abstract

The seeds of winter annuals are generally dormant upon dispersal, lose dormancy in summer through after-ripening, and germinate in early winter. Under semi-dry Mediterranean climate with dry-hot summers and cool-wet winters, many forbs with potential for habitat restoration are winter annuals, but there is very little information about their germination. We calculated hydrothermal thresholds from germination responses to temperature, after-ripening and water stress of 13 ruderal dicots native to Andalusia (southern Spain), measuring the germination of fresh seeds from natural populations across nine temperature treatments, from 5°C to 35 °C, constant and alternate, and the effect of after-ripening and water stress. Final germination ranged from 0-100% and results were mixed in response to temperature. Base temperature was below 6 °C, optimal temperature was around 14 °C and the ceiling temperature around 23 °C. For five species, 10 months of after-ripening improved total germination, indicating a dormancy-breaking effect, but the other species did not respond or had their germination reduced. All species were tolerant to water stress, with base water potential ranging from -0.8 MPa to -1.8 MPa. Our results suggest that hydrothermal germination thresholds, rather than physiological dormancy, are the main drivers of germination phenology in annual forbs from Mediterranean semi-dry environments. Given known temperature and water conditions, it is possible to predict the germination of these forb species. The higher variability of germination response compared to annual grasses is a possible consequence of the natural and anthropogenic disturbances in ruderal habitats.

1.1 Introduction

Mediterranean-type ecosystems (MTEs) are characterized by a wet/cool winter and a dry/hot summer, reflecting an extreme version of temperate seasonal climates (Aschmann 1973). The Mediterranean climate has favoured plant strategies adapted to match the growing season with the cool months when water is available, and a dormant stage or water-conserving traits to endure the hot, dry season (Bell *et al.* 1993; Keeley 1995; Connor 2005; David *et al.* 2007; Nardini *et al.* 2014). Herbaceous winter annuals are a significant part of the MTEs' flora in terms of taxa, biomass and range; and interest is growing to study their regeneration (Bell *et al.* 1993; Bretzel *et al.* 2009; Saatkamp *et al.* 2011; Sánchez *et al.* 2014; Benvenuti 2016). However, despite a number of studies addressing the germination timing of winter annuals from temperate climates, much less information exists from MTEs (Köchy & Tielbörger 2007; Sánchez *et al.* 2014).

Winter annuals are defined as plants with a life cycle in which they flower, disperse seeds and senesce by early summer; persisting in the soil seed bank through the warmest and driest months. The strategy of winter annuals is thus a short life cycle, with resources intensively invested toward reproduction, that is, seed production. Seeds are generally dormant at dispersal, undergo dormancy loss through exposure to warm summer temperatures, or dry after-ripening, and germinate during autumn or winter (Baskin & Baskin 2014). Those which strictly germinate early in the wet season are *obligate* winter annuals, while those that can germinate over a range of dates and into early spring are *facultative* winter annuals (Cici & Van Acker 2009). Physiologically, this phenology is usually achieved through type 1 non-deep physiological dormancy, meaning that at dispersal seeds are only able to germinate at

cool temperatures associated with the winter season (Baskin & Baskin 1983), but their ceiling temperature for germination increases as they lose dormancy (Soltani et al 2017).

In mid-latitudes, winter annuals use this reproductive strategy to match their growth season with autumn and/or winter, when temperatures are cooler and precipitation more reliable (Baskin *et al.* 1993). Nevertheless, studies on germination of winter annuals have been mainly focused on grasses, given that many of them behave as weeds in crop systems (Cheplick 1998; Scherner et al. 2017). Understanding the seed germination traits of the understudied winter annual forbs in MTEs is important to predict their response to environmental conditions, with implications in community assembly, climate change and ecological restoration (Jiménez-Alfaro *et al.* 2016).

Winter annual forbs are potentially important for the regeneration of degraded habitats in semi-dry ecosystems, supporting nutrient cycling, pollination and related ecosystem services (Valladares & Gianoli 2007; Jaunatre et al. 2014). The use of these and other native herbaceous species for ecological restoration is however limited by the lack of proper scientific information about seed germination (Ladouceur et al. 2017).

Here, we focus on the germination strategy of ruderal forbs in old-field Mediterranean landscapes of Andalusia, southern Spain. Our study system is characterized by old agricultural landscapes in semi-arid conditions, most of them cultivated with large extensions of olive orchards and vineyards. Our main aim was to assess the germination response of 13 understudied ruderal herbaceous dicot species under varying environmental treatments. We tested whether these species from ruderal and semi-arid habitats with similar ecological requirements had a common germination response to temperature and water stress. Additionally, we evaluated the primary

dormancy state(s) of seeds soon after dispersal and the dormancy state after 10 months of storage, reflecting the scenario for seeds stored for later use in ecological restoration. We expected the germination of both post-dispersal and after-ripened seeds to be higher under cooler temperatures representative of autumn. We also expected lower germination rates in fresh seeds, given a requirement for dry after-ripening (physiological dormancy) or softening of the seed coat (physical dormancy). Finally, we expected a relatively high ability of the seeds to germinate under water stress, as an adaptation to germinate with intermittent precipitation, which is characteristic of the beginning of autumn, the natural germination season for Mediterranean winter annuals.

1.2 Materials and methods

1.2.1 Species selection; seed collection, cleaning and storage

From a list of 979 taxa recorded in a plant inventory of cultivated and ruderal habitats in the Córdoba Province (Pujadas Salvá 1986), we identified a subset of 284 native, annual angiosperm taxa observed in habitats related to olive orchards and vineyards. From those, we chose 13 understudied herbaceous dicot species (Table 1) from a range of plant families which are representative of the extensive old-field habitats and which have mature seeds in early summer. Two of the study species, *Anthyllis vulneraria* and *Scabiosa atropurpurea*, can also grow as biennial or perennials, but in the study system they are mostly found as annuals.

In June 2015, we collected seeds by hand from wild populations along ruderal right-of-ways and field margins in the Spanish provinces of Córdoba and Jaén. All the collection sites fell within the “Mediterranean South” environmental zone of Europe

(Metzger *et al.* 2005). Sampled populations had a minimum of 500 individuals and seeds were collected from at least 100 haphazardly selected individuals, following the European Native Seed Conservation Network protocol (ENSCONET 2009). The harvested plant material was stored under ambient conditions (~22 °C, ~20 % RH) for an average of 9 weeks before being cleaned (Table 1). Accompanying herbarium vouchers were deposited at the Jardín Botánico Atlántico, Gijón (JBAG). Hereafter, “seed population” refers to the sample of seeds used in the experiments, from and representing a single wild population for each species.

Small quantities and/or small-seeded species were cleaned by hand, roughing up the seed heads against metal sieves and then sifting to remove the inert material. Large quantities were cleaned using a stationary threshing machine (Wintersteiger LD 350) at 500 rpm with a 3x9 mm metal basket concave followed by separation with a winnower (Seed Processing Holland type 4111.10.00.2). Care was taken to avoid excessive cleaning and separation in order to maintain a more complete range of seed sizes and densities (Basey *et al.* 2015).

As the focus of this study was to address the natural response of the seeds, for the 4 species with supposed physical dormancy, we did not apply any additional scarification or nicking beyond what the seeds received through the mechanical cleaning process described above. Additionally with *Anthyllis vulneraria*, we included 4 diaspore types to evaluate any differences in dormancy due to scarification: the natural dispersal unit (single seeded legume inside of calyx), partially processed dispersal unit (single seeded legume with calyx removed), fully cleaned seed with scarification (seeds with light scarification from mechanical cleaning with calyx and fruit covering removed), and fully cleaned seed without scarification (cleaned by hand to mimic seed in nature without scarification and with

covering structures removed to reduce infection and improve imbibition). The seed populations were stored in opaque breathable packages within a seed warehouse where fluctuations of temperature and relative humidity conditions (Fig. SI 1) were comparable to those in the original collection sites.

1.2.2 Germination Tests

Three laboratory germination experiments were done to determine the effect of temperature, after-ripening and water potential. In the first experiment (temperature), we tested the effect of temperature on the germination of recently dispersed (2-5 weeks since collection) seed populations. A range of four constant and four alternating temperature treatments was chosen to represent field temperatures in autumn, winter, spring and summer (Table 2). Additionally, an extreme treatment of 35/5 °C was included to test if extreme diurnal temperature fluctuation released dormancy in the physically dormant species (McKeon & Mott 1982; Santana et al. 2013; Santana et al. 2010; Vázquez-Yanes & Orozco-Segovia 1982). In the second experiment (after-ripening), we tested the effect of 10 months of dry after-ripening (Fig. SI 1) on the subsequent germination of the same seed populations. After-ripened seeds were germinated at a single temperature of 20/10 °C, representing spring (Table 2). In the third experiment (water potential), we tested the ability of seeds to germinate under drought stress. For this experiment, we germinated after-ripened seeds at 20/10 °C, as described above. We prepared eight treatments of water stress: 0 MPa (control), -0.1 MPa, -0.2 MPa, -0.3 MPa, -0.4MPa, -0.6MPa, -0.8 MPa, -1.0MPa. These were chosen based on similar studies (Bradford 1990; Bochet *et al.* 2007; Cubera & Moreno 2007; Santo *et al.* 2014; Ahmadian *et al.* 2015; Luna & Chamorro 2016). We used solutions of polyethylene glycol (PEG) 8000 (Panreac AppliChem brand) to achieve the water potential treatments. Since our experiments

were carried out under an alternating temperature regime, we used the average PEG concentration that corresponded to the two temperatures (Michel 1983; Money 1989).

For the temperature experiment, the constant temperature treatments were programmed in walk-in rooms (Trident Refrigeration, United Kingdom) and the alternating temperature treatments in upright chambers (LMS Ltd., United Kingdom). The after-ripening and water potential experiments were conducted in an upright chamber (JP Selecta, Spain). For every experimental treatment of each species, four replicates of 25 seeds each were placed inside 9 cm polyethylene petri dishes with 2 layers of filter paper (Whatman Grade #1 85mm) and moistened with 4 mL distilled water. Throughout the experiments, distilled water was added as needed to maintain availability of free water. Light conditions in the chambers cycled through 12 hours of 30-35W cool white fluorescent light and 12 hours of darkness. Dark periods coincided with the cooler temperature in the alternating temperature regimes.

Germination was defined as visible radicle emergence. The tests were ended once the germination rate had slowed to 0 (4-10 weeks depending upon the species).

Ungerminated seeds were cut and examined to determine viability. The germination proportion was calculated on the basis of the total number of viable seeds.

1.2.3 Data analysis

To compare the final germination proportions across treatments we fitted Generalized Linear Models (binomial error, logit link). We started by fitting fully factorial models and removed non-informative interactions and model parameters until achieving the minimal adequate model for each experiment and species (Crawley 2013). We also estimated the time needed to reach successive deciles of final germination at each experimental treatment (GR) by fitting cumulative germination curves. We calculated

the germination rates as the inverse of the times until 50% of the sown seeds had germinated. We used R (version 3.2.3 (2015-12-10)) (R Core Team 2015) to fit the Generalized Linear Models and cumulative germination curves. Using the germination rates, we calculated the thermal and water potential thresholds for seed germination.

For the thermal thresholds or cardinal temperatures (Garcia-Huidobro *et al.* 1986; Hardegee 2006; Orrù *et al.* 2012), we plotted the germination rates against temperature, and then divided the temperatures in suboptimal and supraoptimal temperature ranges. We fitted a linear regression to each range, and calculated the base temperature (T_b) as the x-intercept of the suboptimal regression, the ceiling temperature (T_c) as the x-intercept of the supraoptimal regression; and the optimal temperature (T_o) as the intercept of the two regression lines. For the water potential threshold we plotted the germination rates against PEG concentration and calculated the base water potential (ψ_b) as the x-intercept of a fitted linear regression (Gummerson 1986; Bradford 2002). We repeated these calculations for each available germination decile, and averaged the results to obtain the final hydrothermal thresholds for germination.

1.3. Results

1.3.1 Effect of temperature

The final germination of 6 unscarified seed populations with physical dormancy (*Helianthemum ledifolium*, *Tuberaria guttata*, *Medicago orbicularis*, and three diaspore types of *Anthyllis vulneraria*) was very low (< 5%) and we did not include these populations in further analyses. In the extreme alternating temperature treatment

of 35/5 °C, all seeds were ungerminated and infected at the end of the experiment, and those results are not presented either.

For most seed populations, we found that in the cooler treatments of 10°C and 15°C, there was higher final germination in the constant treatments compared to the corresponding diurnally alternating treatments of 15/5°C and 20/10°C (Fig. 1). The opposite was true for the warmer temperature treatments of 20°C and 25°C. In this case, final germination was higher in the diurnally alternating treatments (25/10°C and 30/20°C) and lower in the constant treatments (Fig. 1). Some exceptions to this pattern were *T. barbata* and *A. vulneraria* which germinated at high proportions across most treatments while for *A. cotula*, germination was low and there was no effect of temperature on germination (Fig. 1). *Scabiosa atropurpurea* had the highest final germination at higher temperatures, while *Stachys arvensis* had the highest final germination in alternating regimes, except for the coolest treatment of 10°C (Fig. 1). With the germination rates we were able to calculate the cardinal germination temperatures of *A. vulneraria*, *C. lusitanica*, *S. atropurpurea*, and *T. barbata* (Table 3a). T_b ranged between 3.6°C and 6°C, T_o were around 14°C, and T_c were around 23°C.

1.3.2 Effect of storage

Ten months of after-ripening increased the final germination of five species: *M. moricandioides*, *S. atropurpurea*, *C. lusitanica*, *A. cotula* and *T. maximum* (Fig. 2). Two seed populations, *T. barbata* and *A. vulneraria*, which reached high final germination regardless of temperature treatment likewise germinated at high final germination regardless of storage treatment (Fig. 2). Three seed populations, *S. arvensis*, *N. damascena*, *E. plantagineum* had higher final germination when fresh

than following storage (Fig. 2).

1.3.3 Effect of water potential

Five species (*S. atropurpurea*, *T. maximum*, *C. lusitanica*, *T. barbata* and *A. vulneraria*) had high final germination in the control and a decrease in final germination with increased water stress (Fig. 3). *Echium plantagineum*, *M. moricandioides* and *S. arvensis* had overall low final germination even in the control and additional water stress lowered final germination further (Fig. 3). Of note, increased water stress did not affect the final germination of *N. damascena* and *A. cotula*, even under the highest treatment (-1.0 MPa) of water stress (Fig 3). We were able to calculate ψ_b for *A. vulneraria*, *C. lusitanica*, *N. damascena*, *S. atropurpurea*, *T. barbata* and *T. maximum* (Table 3b). All of them had a relatively low base water potential, from -0.8 MPa to -1.8 MPa, thus indicating their ability to germinate under low moisture conditions.

1.4. Discussion

1.4.1 Influence of temperature

Our results indicate that the studied species have the potential to function as facultative winter annuals since they germinated within the range of 6°C to 22°C. This strategy agrees with a recent survey of field germination of Mediterranean herbs, which found that most of them are facultative annuals with similar germination whether sown in early winter (November) or in late winter (February) (Benvenuti & Pardossi 2016). Despite a range of responses across temperatures, the values for the cardinal temperatures were similar across species: T_b were between 3°C to 6°C, T_o around 14°C, and T_c around 23°C. These values indicate that the species would not

germinate when field temperatures remain above 23 °C, i.e. from June to September, whereas the maximum germination rates would be reached in November. Given the general lack of frost or temperatures close to 0 °C in the studied sites, field temperatures are expected to remain above T_b during almost all the year. Thus T_b , which incidentally showed more variation across species, does not seem to have the adaptive importance of T_o or T_c in these habitats. Another noticeable pattern was the contrasting effect of alternating temperatures, which improved germination under the higher temperature treatments (20°C and 25°C), but reduced it at the lower temperatures (10°C and 15°C). The germination response seems to be conservative towards the low end of the temperature scale because of the risk of frost near the base temperature, even though the populations must have been in the area for a long time. In contrast, the higher temperatures close to or above the ceiling temperature may not pose a threat for the future seedling if sufficient growth is achieved prior to the dry hot summer, presumably providing sufficient protective mechanisms that must be present in adult plants. Therefore, the risky temperature range for germination is perceived better through alternating rather than constant temperatures.

In general, the studied species germinated across a wide range of temperatures with at least 50% final germination in all species except *A. cotula*. The lower final germination under some temperature treatments can be explained by the higher degree of dormancy expected in these relatively fresh, post-dispersal seed populations. In a study of *A. cotula* as a non-native weed, achenes which had been stored for about 6 months and were germinated in darkness reached final germination of 20% to 45% under constant temperatures of 10°C, 15°C, 20°C and 25°C but germination was 12% or less in the extreme temperatures of 5°C, 30°C and 35°C (Gealy *et al.* 1985). In our study, there was no effect of temperature or oscillation and

final germination was low (less than 3%) for *A. cotula*. A partial explanation for the low final germination could be explained by the effect of the pericarp on lowering germination when compared to seeds (Gealy *et al.* 1985).

1.4.2 After-ripening and dormancy

Winter annuals are typically dormant at the time of dispersal (Hilhorst & Toorop 1997; Thompson 2001; Baskin & Baskin 2014). Contrary to the expectation that there would be overall lower germination in the post-dispersal seed populations and higher germination in the stored treatments, instead there were three types of response. Two species, *A. vulneraria* and *T. barbata*, had the same final germination post-dispersal and after storage. For three species (*S. arvensis*, *N. damascena* and *E. plantagineum*) the effect of 10 months of after-ripening was the opposite of our expectation, with higher final germination in the post-dispersal treatments compared to the stored treatments. Five species (*T. maximum*, *A. cotula*, *M. moricandioides*, *C. lusitanica* and *S. atropurpurea*) responded as expected, with higher final germination following several months of after-ripening.

We found less dormancy than expected in the post-dispersal seeds, and reduced germination in 10-months after-ripened seeds that can be explained by dormancy. Warmer maternal environments can lower the primary dormancy of fresh seeds (Gutterman 2000; Donohue 2005) and May 2015 was unseasonably warm which may have affected the studied seed populations (Dwyer & Erickson 2016) which were ripening on the mother plants in that period. Another possible explanation for the levels of dormancy that we observed is the lack of distinct post-dispersal and storage/after-ripening treatments. Even the post-dispersal seeds had been stored 2 to 7 weeks when the experiments began and could have undergone some after-ripening

during that period and therefore were less dormant than would be expected otherwise.

While there was a range to the degree of dormancy among the dicotyledonous species in our study, seed populations of 6 ruderal annual grass species from the same habitats and collection sites used in this study were all non-dormant when fresh and after-ripened and additionally there was little effect of temperature or water potential on final germination (Hernández-González et al. pers.comm.). Moreover, since the field temperatures during summer are well above the T_c of germination, seed dormancy may not be needed to prevent germination until autumn. After-ripening of more than one year increased germination in *A. cotula* from the cold Himalayan deserts (Rashid *et al.* 2007). Similarly, after-ripening of 10 months increased germination in the Mediterranean population of *A. cotula* in our experiment. Seeds of *M. moricandioides* collected from wild Spanish populations and stored at 5°C for 4-8 months germinated to nearly 90% under the alternating temperatures of 20/7°C (Herranz *et al.* 2006) although that experiment did not assess baseline germination of fresh seeds.

Although we were not explicitly testing scarification treatments on the physically dormant species, we can conclude that the passive scarification that the physically dormant seeds received via the mechanical cleaning process was not sufficient to alleviate dormancy and allow for imbibition in these experiments. In our separate field studies (Frischie et al., unpublished data) of the same species, the two Fabaceae (*M. orbicularis* and *A. vulneraria*) germinated and established well, despite low germination response in the lab tests. Additional abrasion from soil particles or wider contrasts in temperature fluctuation at the soil surface may explain this difference (Baskin, Baskin, Aguinagalde, *et al.* 2000; Santana *et al.* 2010) between lab and field results. In contrast, the two Cistaceae (*H. ledifolium* and *T. guttata*) did not imbibe

and germinate in the lab nor did they emerge and establish in the field trials. This could be due to field planting depth, which was too much for the small-seeded species. It is also possible that different conditions such as heat treatments akin to fire exposure (Keeley 1995; Luna & Chamorro 2016) or additional scarification beyond the mechanical cleaning we used may be required to alleviate dormancy in these Cistaceae species.

1.4.3 Water potential

As expected, there was a general tolerance to water stress in the seed populations we studied with a decrease in germination as water potential decreased (Bradford 1990). All ten species germinated well under moderate levels of water stress and the base water potential ranged from -0.8 MPa to -1.8 MPa. This exceeds the soil water potential which has been measured in ruderal Mediterranean habitats (Bochet *et al.* 2007; Ben-Gal *et al.* 2009; Gómez-del-Campo 2013). Two seed populations (*A. cotula* and *N. damascena*) were not limited by the lowest water potential (-1.0 MPa) in this experiment, indicating they would germinate well under the dry conditions between rainfall events in Mediterranean climates. The base water potential for *N. damascena* was very low, at -1.8 MPa. Interestingly, *N. damascena* also had its germination strongly inhibited by the warmer temperature treatments, so it may rely only on cold temperatures as a germination cue, and attempt to germinate even in the driest conditions. Water potential from -0.4 to -1.0 MPa reduced germination in *A. cotula* achenes (Gealy *et al.* 1985) from Oregon (USA) populations, where the plants were observed as weeds and limited to moister parts of fields. The other eight species responded as expected with a decrease in final germination as water potential decreased. These results are similar to those for 22 ruderal species that colonize road cuts in Spain. In that study, there was a notable reduction in germination when water

potential decreased from -0.05 MPa to -0.35 MPa and no species germinated at the lowest water potential of -1.5 MPa (Bochet *et al.* 2007). Ability to germinate under water stress was correlated with colonizing ability in these disturbed habitats.

1.4.4 Conclusions

The hydrothermal thresholds for germination among our species seem to be in accord with the general traits of Mediterranean annuals. Our values are comparable to those of the perennial grass from semi-arid Mediterranean grasslands, *Stipa tenacissima*, (Krichen *et al.* 2014) which germinated most between 10-20°C and was limited by water potentials lower than -0.8 MPa. However, even if the species are all native winter annuals from ruderal habitats, this study suggest that there was no single, general response of winter annual forbs to environmental cues. The variation in germination responses can be understood in the context of the high diversity of ruderal and semi-arid habitats due to both anthropogenic and natural disturbances (Fernández-Alés *et al.* 1993; Rey Benayas & Scheiner 2002; Bonet 2004). In our study area, a mosaic of micro-habitats is formed by the interplay of disturbances, stresses, topography, aspect, soil type and precipitation (Gallego Fernández *et al.* 2004). Other studies have discussed the disturbances and stresses of Mediterranean habitats, mainly heat and drought, which lead to diverse floras and often local adaptations (McIntyre *et al.* 1999; Pausas 1999; Millington *et al.* 2009; McIntyre & Grigulis 2013; Matesanz & Valladares 2014; Nardini *et al.* 2014). For example, among four annuals from gypsum soils, germination response fell within the winter annual strategy, yet plasticity allowed for bet hedging and micro-adaptation to the mosaic of Mediterranean habitats (Sánchez *et al.* 2014). This suggests that, in these systems, hydrothermal germination thresholds, rather than physiological seed dormancy, seem to be the main drivers of germination phenology. In our study

species, sowing in October-November (i.e., when field temperatures fall below 23 °C) should ensure a rapid and successful establishment in Mediterranean semi-arid habitats subject to ecological restoration. Species from Fabaceae and Cistaceae will need mechanical external factors to break physical dormancy. Despite a range of germination responses in other families, winter annual forbs follow a common pattern in germination timing that generally matches the harsh but predictable Mediterranean environments.

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Conflicts of Interest

None.

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Tables and Figures

Table 1. Study species, main habitat requirements and number of days between seed collection and germination experiments.

Taxonomy follows theplantlist.org, dormancy class is from Baskin & Baskin (2014), and habitat is from Castroviejo (1986-2012).

managed as an annual. * dormancy class for the genus. † dormancy class for the family. In the cases where plants and/or fruits were entirely senescent and brittle, no herbarium voucher was made.

Scientific name	Family	Dormancy class	Herbarium number	Soil	Habitat	Days between collection and onset of experiment for “post-dispersal” seed populations
<i>Anthemis cotula</i> L.	Asteraceae	PD	SF - 0304		fields and disturbed areas	36

<i>Anthyllis vulneraria</i> L. #	Fabaceae	PY	--	indifferent	seaside sand and cliffs, rocky clefts and plains, pastures, openings, matorral	27
<i>Cleonia lusitanica</i> (L.) L.	Lamiaceae	PD†	SF - 0320	limestone, clay, gypsum, sandy or gravelly and generally poor soils	dry pastures and matorral scrublands, openings in oak woodlands (encinar, quejigar) and juniper woodlands (sabinar)	11
<i>Echium plantagineum</i> L.	Boraginaceae	PD†	SF - 0278	basic or acidic	fields, disturbed sites, right of ways	48
<i>Helianthemum</i> <i>ledifolium</i> (L.) Mill.	Cistaceae	PY*	--	limestone, silica, gypsum, marl	dry annual grasslands	23
<i>Medicago orbicularis</i> (L.) Bartal.	Fabaceae	PY	--	indifferent, nitrophile	grasslands and fields	51

<i>Moricandia moricandioides</i> (Boiss.) Heywood	Brassicaceae	PD*	SF - 0307	limestone	marl slopes, clay or sandy hills, rock clefts	34
<i>Nigella damascena</i> L.	Ranunculaceae	MPD*	SF - 0305		crop fields, untilled areas, rocky or sandy pastures	36
<i>Scabiosa atropurpurea</i> L. #	Caprifoliaceae	PD*	--	indifferent, nitrophile	pastures, fallow areas, right of ways, slopes	19
<i>Stachys arvensis</i> (L.) L.	Lamiaceae	PD*	SF - 0287	silica, sand, clay or rarely basic	annual grasslands, openings in woodlands and matorral, fallow and cultivated fields	41
<i>Tolpis barbata</i> (L.) Gaertn.	Asteraceae	PD*	SF - 0318	sand	understorey of woodlands and shaded fields	48

<i>Tordylium maximum</i> L.	Apiaceae	PD†	SF - 0310		right of ways, crop fields and fallow areas	34
<i>Tuberaria guttata</i> (L.) Fourr.	Cistaceae	PY	SF - 0275	sand, acidic	annual grasslands, ditches, slopes, plains, openings in matorral	40

Table 2. Average daily maximum and minimum air temperature for the region of Córdoba for January, April, July and October and corresponding temperature treatments (Instituto de Investigación y Formación Agraria y Pesquera).

	Average day/night T in Córdoba	Constant Treatment	Alternating Treatment
Autumn (October)	25/13°C	20°C	25/15°C
Winter (January)	15/4°C	10°C	15/5°C
Spring (April)	23/10°C	15°C	20/10°C
Summer (July)	37/19°C	25°C	30/20°C
Experimental extremes	n/a	5°C	35/5°C

Table 3. Cardinal temperatures (a) and base water potential (b) for germination. Missing values are due lack of three or more temperatures in the corresponding suboptimal or supraoptimal ranges.

a. Seed population	T _b	SD	T _o	SD	T _c	SD
<i>A. vulneraria</i> T alternating	--	--	--	--	23.9	± 0.4
<i>A. vulneraria</i> T constant	6.1	± 0.8	13.4	± 3.4	23.7	± 0.6
<i>C. lusitanica</i> T constant	3.6	± 2.0	14.0	± 1.4	23.7	± 0.3
<i>S. atropurpurea</i> T constant	6.5	± 3.4	--	--	--	--

<i>T. barbata</i> T alternating	--	--	14.6	± 0.1	24.2	± 0.3
<i>T. barbata</i> T constant	4.1	± 3.8	--	--	--	--

b. Seed population	ψ_b	SD
<i>A. vulneraria</i>	-0.84	± 0.04
<i>C. lusitanica</i>	-1.03	± 0.06
<i>N. damascena</i>	-1.82	± 0.13
<i>S. atropurpurea</i>	-0.81	± 0.20
<i>T. barbata</i>	-0.86	± 0.20
<i>T. maximum</i>	-0.85	± 0.07

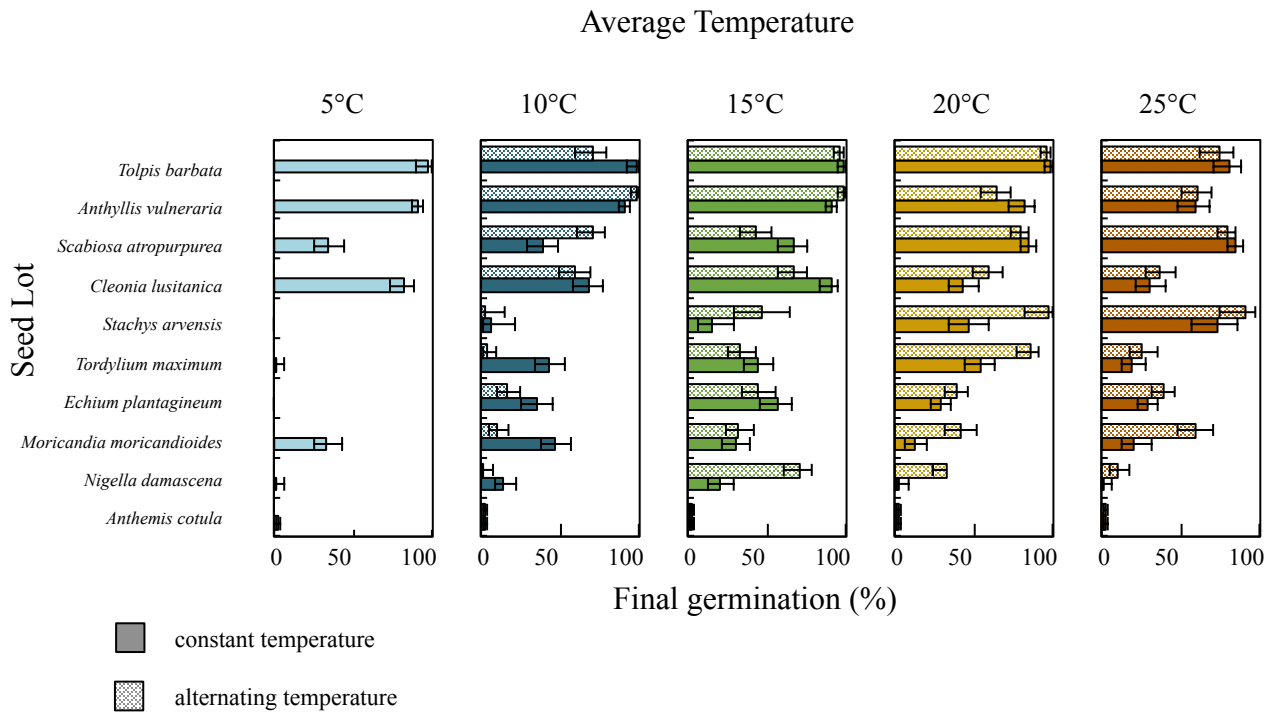


Figure 1. Final germination proportions of post-dispersal seeds modelled for each species across all temperature treatments. Species are generally ordered from higher to lower final germination. Darker bars are constant temperatures and lighter bars are alternating temperatures; e.g. 10°C constant is displayed with 15°C/5°C alternating. See Table SI 1 for model parameters.

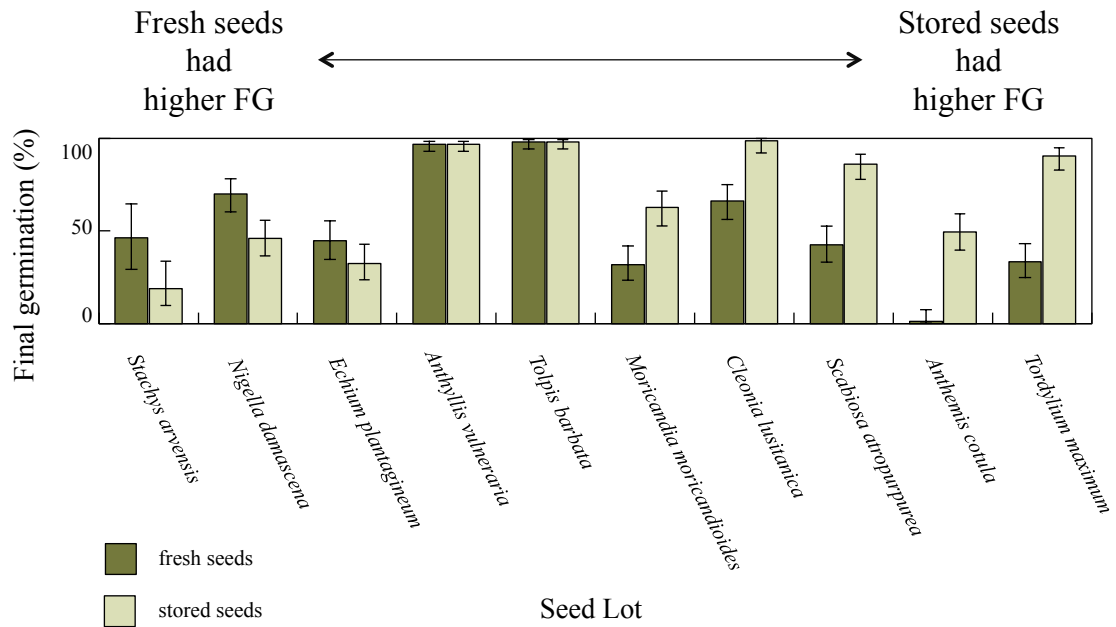


Figure 2. Modelled effect of storage (10 months) on final germination proportion. FG was higher for fresh seeds of species to the left of centre and lower for species to the right of centre. See Table SI 2 for model parameters.

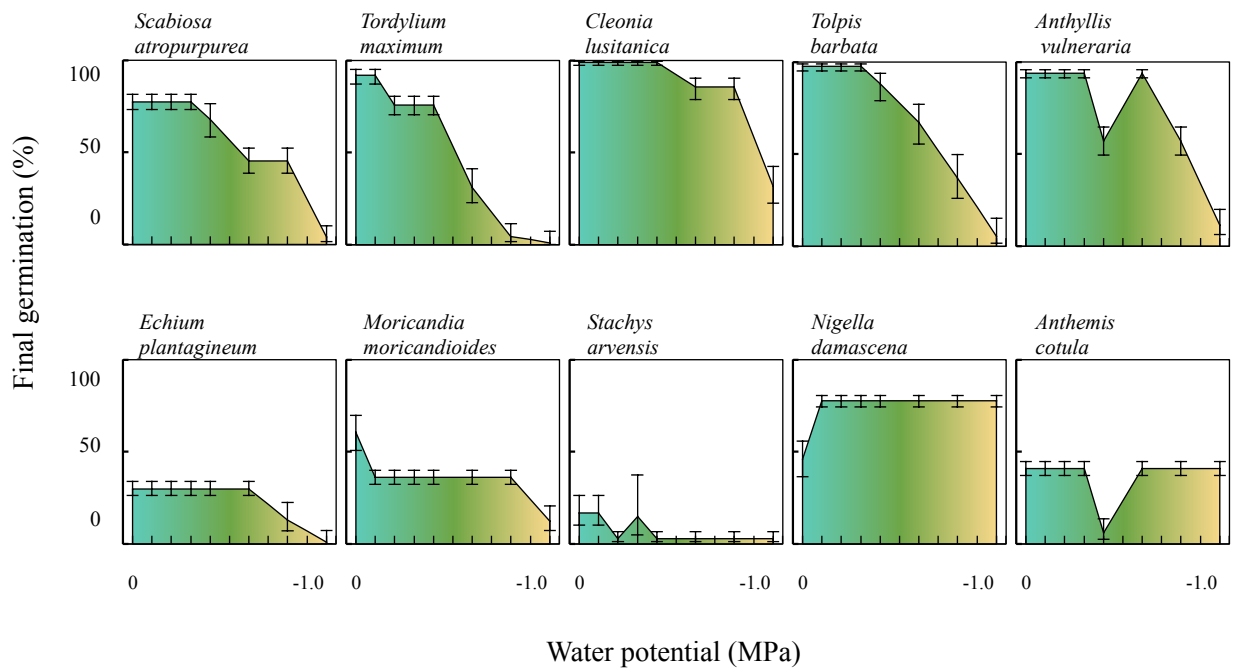


Figure 3. Effect of water stress on final germination proportion. Modelled results. See Table SI 3 for model parameters.

Supporting Information

Table SI 1. Generalized linear model parameters and output of effect of temperature on final germination proportion.

Species	Parameter	Effect	S.E.	t	p
<i>Anthemis cotula</i>	Intercept	-3.571	0.216	-16.520	<0.001
<i>Anthyllis vulneraria</i>	Intercept	3.807	0.506	7.530	<0.001
	ANVA5.10.15Temperature20C	-3.226	0.550	-5.862	<0.001
	ANVA5.10.15Temperature25C	-3.383	0.549	-6.161	<0.001
	Oscillationconstant	-1.496	0.547	-2.734	0.006
	ANVA5.10.15Temperature20C:Oscillationconstant	2.399	0.647	3.707	<0.001
	ANVA5.10.15Temperature25C:Oscillationconstant	1.424	0.625	2.279	0.023
<i>Cleonia lusitanica</i>	Intercept	0.388	0.210	1.845	0.065
	Oscillationconstant	0.385	0.305	1.265	0.206
	Temperature15C	0.290	0.302	0.959	0.338
	Temperature20C	-0.026	0.296	-0.088	0.930
	Temperature25C	-0.927	0.299	-3.099	0.002
	Temperature5C	0.750	0.347	2.163	0.031
	Oscillationconstant:Temperature15C	1.183	0.513	2.306	0.021
	Oscillationconstant:Temperature20C	-1.023	0.423	-2.415	0.016
	Oscillationconstant:Temperature25C	-0.669	0.433	-1.543	0.123
<i>Echium plantagineum</i>	Intercept	-1.646	0.273	-6.029	<0.001
	ECPL20.25CTemperature15C	1.434	0.350	4.102	<0.001
	ECPL20.25CTemperature20and25C	1.196	0.312	3.833	<0.001
	Oscillationconstant	1.020	0.352	2.895	0.004
	ECPL20.25CTemperature15C:Oscillationconstant	-0.559	0.466	-1.199	0.231
	ECPL20.25CTemperature20and25C:Oscillationconstant	-1.470	0.417	-3.525	<0.001
<i>Moricandia moricandioides</i>	Intercept	-2.208	0.333	-6.628	<0.001
	Oscillationconstant	2.088	0.389	5.371	<0.001
	Temperature15C	1.453	0.398	3.650	<0.001
	Temperature20C	1.872	0.392	4.772	<0.001
	Temperature25C	2.590	0.414	6.261	<0.001
	Temperature5C	-0.573	0.293	-1.958	0.050
	Oscillationconstant:Temperature15C	-2.189	0.495	-4.427	<0.001
	Oscillationconstant:Temperature20C	-3.721	0.538	-6.922	<0.001
	Oscillationconstant:Temperature25C	-3.805	0.544	-6.999	<0.001
<i>Nigella damascena</i>	Intercept	-3.882	0.714	-5.434	<0.001
	Oscillationconstant	2.066	0.770	2.682	0.007
	Temperature15C	4.729	0.747	6.331	<0.001
	Temperature20C	3.143	0.746	4.213	<0.001
	Temperature25C	1.684	0.788	2.137	0.033
	Temperature5C	-2.770	1.046	-2.649	0.008

	Oscillationconstant:Temperature15C	-4.300	0.839	-5.127	<0.001
	Oscillationconstant:Temperature20C	-4.803	0.992	-4.844	<0.001
	Oscillationconstant:Temperature25C	-4.464	1.309	-3.409	<0.001
<i>Scabiosa atropurpurea</i>	Intercept	0.867	0.221	3.917	<0.001
	SCAT20.25Temperature15C	-1.161	0.303	-3.836	<0.001
	SCAT20.25Temperature20and25C	0.494	0.285	1.732	0.083
	SCAT20.25Temperature5C	-0.180	0.300	-0.600	0.549
	Oscillationconstant	-1.333	0.305	-4.374	<0.001
	SCAT20.25Temperature15C:Oscillationconstant	2.320	0.425	5.454	<0.001
	SCAT20.25Temperature20and25C:Oscillationconstant	1.687	0.407	4.143	<0.001
<i>Stachys arvensis</i>	Intercept	-3.714	1.012	-3.669	<0.001
	Oscillationconstant	1.006	1.248	0.806	0.420
	Temperature15C	3.570	1.081	3.304	<0.001
	Temperature20C	7.240	1.433	5.052	<0.001
	Temperature25C	5.947	1.180	5.038	<0.001
	Oscillationconstant:Temperature15C	-2.597	1.377	-1.885	0.059
	Oscillationconstant:Temperature20C	-4.680	1.631	-2.869	0.004
	Oscillationconstant:Temperature25C	-2.217	1.441	-1.538	0.124
<i>Tolpis barbata</i>	Intercept	0.847	0.244	3.473	<0.001
	TOBA15.20Temperature15and20C	2.358	0.483	4.886	<0.001
	TOBA15.20Temperature25C	0.191	0.373	0.511	0.609
	TOBA15.20Temperature5C	-0.759	1.236	-0.615	0.539
	Oscillationconstant	3.509	1.036	3.389	<0.001
	TOBA15.20Temperature15and20C:Oscillationconstant	-2.391	1.324	-1.806	0.071
	TOBA15.20Temperature25C:Oscillationconstant	-3.128	1.111	-2.815	0.005
<i>Tordylium maximum</i>	Intercept	-3.229	0.510	-6.333	<0.001
	Oscillationconstant	2.958	0.547	5.409	<0.001
	Temperature15C	2.536	0.553	4.589	<0.001
	Temperature20C	4.998	0.581	8.598	<0.001
	Temperature25C	2.171	0.560	3.876	<0.001
	Temperature5C	-4.374	1.024	-4.271	<0.001
	Oscillationconstant:Temperature15C	-2.501	0.620	-4.035	<0.001
	Oscillationconstant:Temperature20C	-4.573	0.645	-7.092	<0.001
	Oscillationconstant:Temperature25C	-3.325	0.647	-5.142	<0.001

Table SI 2. Generalized linear model parameters and output of effect of storage (after-ripening) on final germination proportion.

Species	Parameter	Effect	S.E.	t	p
<i>Anthemis cotula</i>	Intercept	-4.477	1.006	-4.452	<0.001
	DARYES	4.456	1.026	4.342	<0.001
<i>Anthyllis vulneraria</i>	Intercept	3.390	0.587	5.775	<0.001
	DARYES	0.022	0.830	0.027	0.979
<i>Cleonia lusitanica</i>	Intercept	0.677	0.217	3.121	0.002
	DARYES	3.753	1.029	3.647	<0.001
<i>Echium plantagineum</i>	Intercept	-0.213	0.218	-0.974	0.330
	DARYES	-0.515	0.314	-1.637	0.102
<i>Moricandia moricandioides</i>	Intercept	-0.756	0.218	-3.471	<0.001
	DARYES	1.272	0.301	4.226	<0.001
<i>Nigella damascena</i>	Intercept	0.847	0.218	3.883	<0.001
	DARYES	-1.008	0.296	-3.399	<0.001
<i>Scabiosa atropurpurea</i>	Intercept	-0.294	0.206	-1.424	0.155
	DARYES	2.109	0.354	5.950	<0.001
<i>Stachys arvensis</i>	Intercept	-0.143	0.379	-0.378	0.706
	DARYES	-1.304	0.546	-2.388	0.017
<i>Tolpis barbata</i>	Intercept	3.651	0.716	5.097	<0.001
	DARYES	0.653	1.236	0.529	0.597
<i>Tordylium maximum</i>	Intercept	-0.693	0.213	-3.251	0.001
	DARYES	2.950	0.410	7.194	<0.001

Table SI 3. Generalized linear model parameters and output of effect of water stress on final germination proportion.

Species	Parameter	Effect	S.E.	t	p
<i>Anthemis cotula</i>	Intercept	-0.369	0.080	-4.631	<0.001
	ANCO0.1.2.3.6.81newMPaMPa-0.4	-2.391	0.468	-5.110	<0.001
<i>Anthyllis vulneraria</i>	Intercept	2.758	0.202	13.638	<0.001
	ANVA0.1.2.3.6and.4.8newMPa.4.8	-2.467	0.258	-9.559	<0.001
	ANVA0.1.2.3.6and.4.8newMPaMPa-1	-4.799	0.392	-12.234	<0.001
<i>Cleonia lusitanica</i>	Intercept	4.475	0.450	9.950	<0.001
	CLLU0.1.2.3.4and.6.8newMPa.6.8	-2.699	0.508	-5.315	<0.001
	CLLU0.1.2.3.4and.6.8newMPaMPa-1	-5.242	0.509	-10.309	<0.001
<i>Echium plantagineum</i>	Intercept	-0.848	0.094	-9.006	<0.001
	ECPL0.1.2.3.4.6newMPaMPa-0.8	-1.054	0.352	-2.995	0.003
	ECPL0.1.2.3.4.6newMPaMPa-1	-3.640	1.010	-3.604	<0.001
<i>Moricandia moricandioides</i>	Intercept	0.431	0.206	2.094	0.036
	MOMO.1.2.3.4.6.8newMPa.1.2.3.4.6.8	-1.002	0.223	-4.495	<0.001
	MOMO.1.2.3.4.6.8newMPaMPa-1	-2.377	0.371	-6.408	<0.001
<i>Nigella damascena</i>	Intercept	-0.160	0.201	-0.799	0.424
	NIDA.1.2.3.4.6.81newMPa.1.2.3.4.6.81	1.403	0.220	6.373	<0.001
<i>Scabiosa atropurpurea</i>	Intercept	1.240	0.120	10.360	<0.001
	SCAT0.1.2.3and.4and.6.8newMPaMPa-0.4	-0.486	0.246	-1.980	0.048
	SCAT0.1.2.3and.4and.6.8newMPa.6.8	-1.421	0.186	-7.649	<0.001
	SCAT0.1.2.3and.4and.6.8newMPaMPa-1	-4.418	0.524	-8.429	<0.001
<i>Stachys arvensis</i>	Intercept	-1.595	0.293	-5.442	<0.001
	STAR0.1and.2.4.6.81MPa.2.4.6.81	-1.937	0.540	-3.586	<0.001
	STAR0.1and.2.4.6.81MPaMPa-0.3	-0.140	0.691	-0.202	0.840
<i>Tolpis barbata</i>	Intercept	3.788	0.413	9.175	<0.001
	TOBA0.1.2.3newMPaMPa-0.4	-1.766	0.544	-3.244	0.001
	TOBA0.1.2.3newMPaMPa-0.6	-3.073	0.485	-6.337	<0.001
	TOBA0.1.2.3newMPaMPa-0.8	-4.316	0.489	-8.818	<0.001
	TOBA0.1.2.3newMPaMPa-1	-6.678	0.723	-9.241	<0.001
<i>Tordylium maximum</i>	Intercept	2.439	0.269	9.061	<0.001
	TOMA0.1and2.3.4newMPa.2.3.4	-1.293	0.303	-4.266	<0.001
	TOMA0.1and2.3.4newMPaMPa-0.6	-3.228	0.348	-9.281	<0.001
	TOMA0.1and2.3.4newMPaMPa-0.8	-5.484	0.578	-9.484	<0.001
	TOMA0.1and2.3.4newMPaMPa-1	-6.928	1.041	-6.655	<0.001

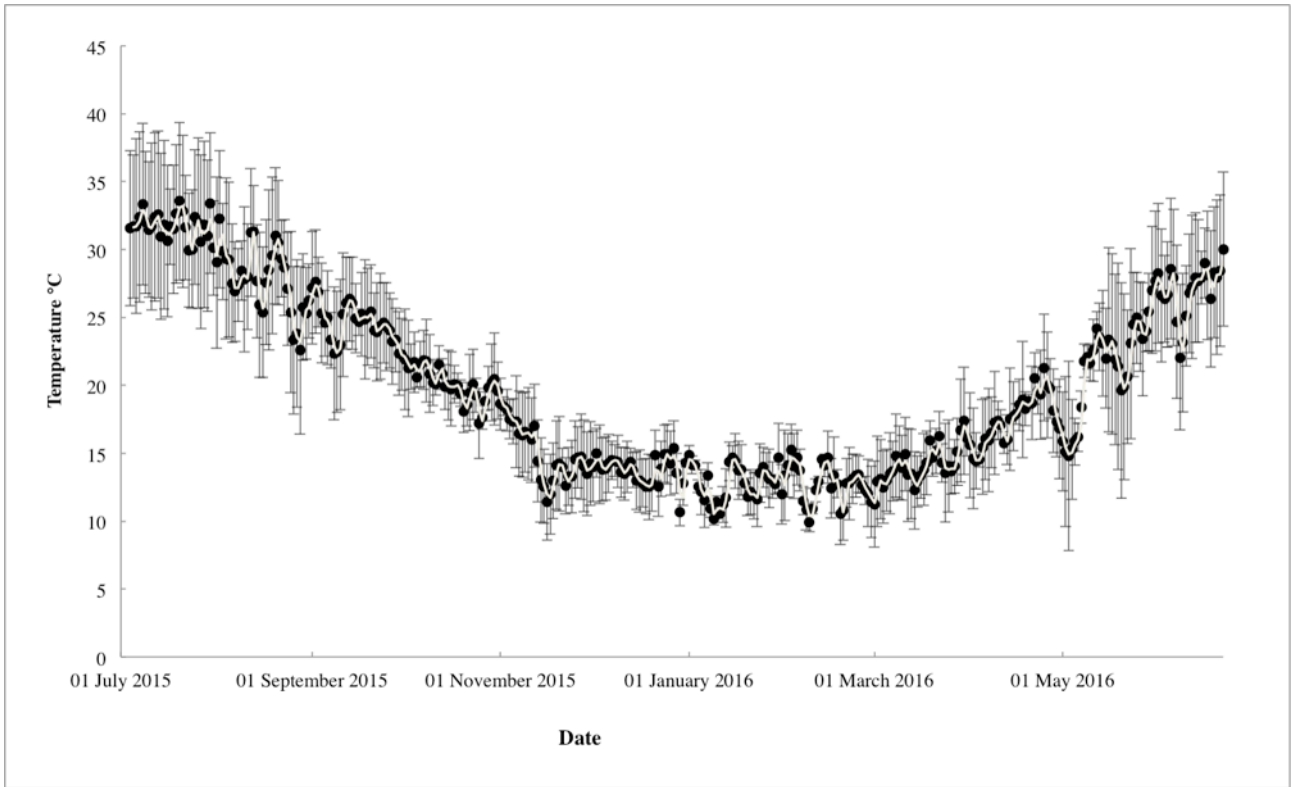


Figure SI 1. Temperature conditions in the warehouse during the seed storage period. Black circles show the daily average and error bars indicate the daily minimum and maximum. The white trend line is added for clarity.

Additional Supporting Information

The following are available at <https://github.com/Cleonia/GerminationNiche>

1. R Script glm FG T
2. R Script glm FG storage
3. R Script glm FG water potential
4. R Script germination rate (t_{50})
5. Raw data files

**Chapter 2. Seed farming potential of 27 native
Mediterranean forbs**

Title: Seed farming potential of 27 native Mediterranean forbs

Running head: Seed farming of Mediterranean forbs

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Abstract

Seed farming, the large-scale mechanized cultivation and harvest of wild species for seed production, is necessary to generate native seed mixes that are appropriate, affordable and consistently available for use in ecological restoration. Due to the diversity of wild species and their non-domesticated status, trial evaluations can help determine which species and which cultural practices are most suitable for seed farming. In Mediterranean habitats, forbs have the potential to enhance biodiversity and provide ecosystem services yet remain understudied and underutilized for ecological restoration. We evaluated 27 Mediterranean dicots for four main characteristics important to seed farming: establishment, growth form, phenology and yield. Row spacing was adequate for 19 species but could be improved for eight. Twenty-four species have fruit height suitable for mechanized harvest while fruits are too low in three species. The time from sowing to seed maturity varied among species and harvest windows were one to six weeks long. Seed yield ranged from 2 g/m² to 55 g/m². The results provide seed producers with useful recommendations for sowing rate, row spacing and harvest time for each species. Characterization of seed farming traits for these native forbs provides a starting point to stimulate the native seed production sector. Seed supplies of native species are needed for applications such as restoring biodiversity, ecological restoration, native landscaping, or enhancing ecosystem services in Mediterranean agroecosystems. This is the first study to describe and evaluate characteristics of native Mediterranean herbaceous species for seed farming and to provide recommendations for cultivation to seed producers.

Keywords: cultural practices, native seed, restoration, seed increase, seed multiplication, seed production

Implications for Practice

- We characterized 27 Mediterranean forbs for seed farming. Four species require further study and trials of alternative cultivation methods due to low establishment and delayed crop development.
- For higher seed lot viability, native seed producers should harvest later rather than earlier in the ripening period rather than earlier.
- The traits described in this study contribute to a dataset that is useful for species selection and prioritization of native plants in Mediterranean restoration projects.
- This baseline study provides a foundation for additional crop years, production sites, and species.

2.1 Introduction

Globally, ecological restoration is increasingly important to rehabilitate degraded ecosystems and restore ecological functions and ecosystem services which life depends upon (Hobbs & Harris 2001; Society for Ecological Restoration 2004). To restore severely altered terrestrial systems, seeds are an effective and efficient means of adding missing plant species (Hobbs & Cramer 2008; Miller *et al.* 2016).

Historically, seeds for use in restoration have been sourced from nearby wild populations. Using wild populations as a source of seeds may be a good practice where local ecotypes are desired and populations are abundant and accessible (Vander Mijnsbrugge *et al.* 2010). However, wild seed collection has its limits both because it

may be time consuming and costly to arrive at a population to manually collect seeds plant by plant, and because excessive removal of seeds from a population can negatively impact the demography, genetics and future conservation of the donor population and the restored population(s) (Broadhurst *et al.* 2008). A practical solution to generate seeds from wild species is through *seed farming*, the cultivation of wild plants to produce seed crops and seed supplies for use in restoration (Kiehl *et al.* 2014; Broadhurst *et al.* 2016; Nevill *et al.* 2016).

To scale up seed production, an evaluation of wild species' behavior under cultivation identifies species that readily lend themselves to seed farming. Primary characteristics of interest are germination and establishment in production plots, manageability of weeds, yield and amenability to mechanized sowing, harvest and seed cleaning (Houseal 2007; Bartow 2015; Scotton 2016). Mechanization allows for large-scale seed production, which provides a sufficient supply of seeds at accessible cost. The ability to mechanize depends upon characteristics inherent to species biology such as location of the fruits on the plant, length of the harvest window, and the nature of fruit and seed shatter and dispersal (McDonald & Copeland 1997). Evaluating species for their adaptability to seed farming identifies the low-hanging fruit, those species with characteristics that can readily be managed and farmed. It also identifies issues or challenges to address through further evaluation and trials, particularly for more difficult species that are of interest and value in restoration so that there is a supply of appropriate and affordable seeds (Mortlock 2000; Nevill *et al.* 2016)

In southern Europe, native plant materials and seed production protocols have been mainly developed for forestry species. The use of seeds to restore herbaceous communities has increased in recent decades (Ballesteros *et al.* 2015; Scotton 2016). The interest and demand for native plant materials and seeds in the Mediterranean

Basin is growing (Nunes *et al.* 2016) and shifting from the use of non-natives or cultivars to species with more wild-type and native characteristics (Medrano *et al.* 2014; Rodrigues *et al.* 2015). Demand for forbs is driven by their value as pollinator resources, biodiversity enhancement and low-maintenance landscaping. However, while there is a huge diversity of native plants in Mediterranean countries (Rey Benayas & Scheiner 2002) seed-based restoration is nascent, and there is a need to develop a commercial and affordable source of wild seeds. Within the unique climate and floristic region of the Mediterranean Basin, there have been some initiatives to evaluate native species for use in revegetation (Navarro Cerrillo & Gálvez-Ramírez 2001; Saavedra *et al.* 2006; Ballesteros *et al.* 2015) but these did not address seed farming.

The aims of this study were to evaluate native forb species from Mediterranean semi-dry habitats for characteristics of interest to seed farming and to establish cultural guidelines for seed producers to produce commercial quantities of seeds. We measured (1) establishment for a given seeding rate, (2) plant growth form and how this architecture should be considered in row spacing, (3) phenology of key stages in crop development, and (4) seed yield and the effect of maturity stage on seed quality. Our results will provide useful recommendations for seed producers supplying seeds for the restoration of Mediterranean habitats.

2.2 Methods

Field Trials

We conducted experimental field trials with 30 native herbaceous species (Table S1). Species selection began with a species pool inventoried from ruderal habitats in the

province of Córdoba (Pujadas Salvá 1986). We focused on ruderal species because they form the main pool of native species thriving in semi-dry agricultural areas (e.g. olive groves, degraded areas), which are a major target for ecological restoration in Southern Spain. From the inventory, we filtered for native, therophyte (annual), angiosperm taxa. Three taxa (*A. vulneraria*, *S. verbenaca*, and *S. atropurpurea*), which can function as annuals, biennials or short-lived perennials were included in the evaluation because they had previously been identified as hosts for beneficial insects (Aguado Martín *et al.* 2015). Plant height and flowering season (Castroviejo 1986-2012) were used to further limit the taxa to those with short to medium (less than 1m) stature. Species with a winter annual life cycle were chosen because that fits with the herbaceous growing season. These are all pre-defined characteristics to facilitate seed production and seed harvest for the target climate and applications.

In early summer 2015 we collected seeds from wild populations under European protocols (ENSCONET 2009) for sowing the trial plots. Herbarium vouchers were deposited at the Jardín Botánico Atlántico, Gijón, Spain. Field trials were conducted in the growing period of November 2015 to June 2016 at the “El Naranjal” farm, near the Guadalquivir River in Villarrubia, Córdoba, Spain (37.829741, -4.905091). The site was formerly an orange orchard and in recent years has been in row crops. The soil is sandy loam with pH of 7.43, 0.7% nitrogen, and 1.24% organic matter. Overhead irrigation was used when rainfall was insufficient for normal crop development.

The field was 25 m x 155 m with buffer lanes of 3 m between the surrounding crops (*Citrus spp.*, *Melilotus officinalis*, *Brachypodium phoenicoides*, and grass field trials). Within the field, each species was sown in a 3m x 3m plot, randomly assigned to plots across 3 replicate blocks. The spacing between blocks was 5 m and the spacing

between plots was 1.75 m. Within each plot, seeds were sown in seven rows with 50 cm between rows. Seeds were sown by hand at a depth of 1 to 5 cm and covered by lightly raking lengthwise along the row. Field prep was done with tillage to a depth of about 10 cm when the soil was wet and the resulting large clods likely affected the accuracy of planting depth. Sowing dates were November 30 and December 1-2, 2015.

With a target sowing rate of 400 seeds per m², calculated on the average 1000 seed weight (Royal Botanic Gardens Kew 2017), we prepared a fixed amount of seeds (g) to sow in the plot rows (Table S2). Seeds from multiple populations for each species were combined to increase the within-species diversity of the produced seed crop (Basey *et al.* 2015). Each population contributed equally by mass to the composite seed lot. We used a laboratory balance (COBOS CB Complet Model M-220, Barcelona, Spain) and a stainless steel riffle divider style (HGG-I) to subdivide the composite seed lots into the correct quantity for sowing each row. A subsample of each composite seed lot was tested for purity and viability (germination + cut test) to determine pure live seed (PLS) and the realized sowing rate.

2.2.1 Establishment density and row spacing (within plot)

When most plots had reached full development, (26 weeks), establishment density was recorded in order to evaluate the 1) success of plants developing from seed to maturity the 2) adequateness of the seeding rate. Evaluating establishment informs adjustments of the sowing rate for future crops and identifies species that may need other treatments or techniques to promote emergence from seed in the field.

Establishment was evaluated on an ordinal scale of zero (no plants) to five (overly dense) (Fig. 1).

The measure of row spacing considers the space filled or unfilled between sown rows when plants are mature. Proper row spacing is important because too much space between rows leaves an open niche for weeds to grow and it can reduce seed yield per area. Too little space between rows can cause diseased or weak plants through intraspecific competition resulting from crowding, poor airflow, and shading. Adequate space between rows can be adjusted based on each species' growth habit of upright to spreading and mature size. We evaluated row spacing when the plants in the plots were fully developed (26 weeks after sowing) using five categories of coverage (Fig. 1)

2.2.2 Height (max and min) of fruits from ground level and growth habit

The range of height of fruits in part determines a species' suitability for mechanized harvest. Fruits that are very near to the ground (<10 cm) are typically too low for mechanized harvest and require hand harvest. To measure fruit height, a pole marked with decimeter increments was placed perpendicular to the ground at three haphazardly selected points within each plot. At each point, maximum and minimum fruit heights of the plants next to the pole were measured by rounding down to the nearest decimeter. The average maximum and average minimum for each species was calculated from the 9 (3 per plot x 3 plots per species) measurements and the absolute minimum and absolute maximum height were also determined. We classified species according to growth habit. Growth habit refers to the plant architecture and is innate to the species biology. We included growth habit as part of the characterization of these species, in order to plan adequate row spacing and to classify their utility for ground covers or landscaping. We defined four categories: erect, round (spherical), rosette, and creeping.

2.2.3 Phenology

Plant development is an important trait to include as part of characterizing these species under cultivation so that growers have an idea of what timeline to expect for key crop stages of emergence, flowering, dispersal window and senescence. Of critical interest for seed harvest is the period from fruit and seed maturity to dispersal or shattering. To track phenology, plots were visited at 2 week intervals and the dominant phenological stage was noted. As these are wild species and development is relatively non-uniform, other stages present the plot were recorded as secondary stages. The phenology scale followed the single digit principal stages of the extended BBCH (**B**iologische **B**undesanstalt, **B**undessortenamt and **C**hemical Industry) (Meier 2001) but modified to accommodate our species (Table S2).

2.2.4 Maturity index at harvest and seed quality and yield

A universal challenge to cultivating and managing wild species with indeterminate ripening is to optimize the harvest date. A harvest that is made too early could have low seed quantity and/or quantity of seeds because there was not enough time for the seeds to fully mature. Postponing harvest too long may decrease yield due to seeds lost to natural dehiscence and dispersal. To measure the effect of crop maturity (phenological stage) on seed lot quality, we harvested each plot at 2 dates. The phenological stage was recorded at the harvest date. Even though each plot for the same species was sown on the same date, months later at harvest time, there was sometimes variation in dominant phenological stage between plot replicates. For this reason, phenological stage and not harvest date was used as the explanatory variable for a test of seed quality. The harvested seeds for each species were dried and cleaned using the same equipment and settings for both harvest dates. The seed quality was

measured as the proportion of viable seeds as determined by germination and subsequent cut tests of ungerminated seeds.

The combination of asynchronous ripening, type of dehiscence, and length of dispersal period limit the precise measurements of seed yield per plant or area. We used the final weight (g) of cleaned seeds from the plots per area as a measurement of yield, recognizing it is the achieved yield of the seed farmer, but does not capture the true potential of a species.

2.3 Results

Eleven species had establishment scores of 2.5 or lower, 8 species had scores from 2.6 to 3.5 and 11 species had establishment scores above 3.6 (Table 1). For row spacing, 11 species had scores of 2.5 or lower and 19 species had scores above 2.5 (Table 1). Here we present scores for 30 species, but for three of these (*A. bellidifolium*, *H. ledifolium*, and *T. guttata*), establishment was insufficient to collect further data in these trials.

Fruit height at maturity ranged from 0 to 150 cm (Fig. 2). Eight species were described as erect, 15 as round, 4 as rosette, and 3 as creeping (Fig. 2, Table S1).

Roughly half of the species developed and ripened along the same timescale for each key phenology stage (Fig. 3). *Calendula arvensis* had the shortest cropping period (Mean \pm SD; 18.6 ± 0 weeks) from sowing to onset of ripening seeds. Three species had maturing fruit by 23 weeks after sowing: *C. bursa-pastoris* (21.1 ± 0 weeks), *S. colorata* (22.0 ± 0 weeks), and *S. verbenaca* (22.8 ± 1.3 weeks). Another seven species had maturing fruit by 26 weeks. The remaining 16 species were the latest to have ripening fruit begin after 29 weeks after sowing.

At seed harvest, all plots were at phenology stage 7, 8 or 9 (Table 2). For the 23 species that were evaluated, viability of seed was the same at any phenology for 17 species (Table 2). For six species (*A. cotula*, *B. auriculata*, *C. capillaris*, *G. segetum*, *S. verbenaca*, *S. arvensis*), phenology stage at harvest had a significant effect on viability. Of note is that in all six of these cases, viability was higher in the later phenology stage(s). The mean seed yield of all species was 12.2 g/m² and the median yield was 5.5 g/m² (Fig. 4). The highest-yielding species was *V. hispanica*, which produced 54.7 g/m² ± 14.3. The lowest yield was 1.9 g/m² ± 1.7 for *Misopates orontium*.

2.4 Discussion

This study is the first to describe and evaluate the characteristics relative to seed farming potential of native Mediterranean herbaceous species and to provide recommendations for their cultivation to seed producers. Our results offer practical information for seed farming of 27 species with potential for use in the ecological restoration of semi-dry habitats. We also discuss the main recommendations for seed production according to the four main variables investigated in order to support and advance the development of the native seed multiplication sector in Spain. In addition to applying the results of cultivation methods, plant traits and phenology to determine best-practices for seed production, the characterization of these species is also useful for selecting their use as novel native cover crops, native landscaping (Bretzel *et al.* 2009) or revegetation following wildfires.

2.4.1 Establishment density and row spacing

Of the 30 species in our study, general establishment was good, with 27 species growing from germination to maturity and seed harvest. Species with an average establishment score of 2.6 to 3.5 were considered optimal and the same seeding rate is recommended. Species with an average establishment score of 0 to 2.5 were considered too low, and the recommendation is to use higher seeding rates in future trials. Species with an average establishment score of 3.6 to 5.0 were considered too dense and lower seeding rates are recommended. This may take trial and error over several growing seasons until an optimal range for seeding rate is known. The measurement of row spacing was on a scale of 0 – 4. We considered scores of 0 – 2.5 (Table 1) indicative of wasted space between rows and suggest to use a future row spacing that is less than the 50 cm which was used in these trials. Optimum row spacing will help with weed management.

Both of the Cistaceae, *T. guttata* and *H. ledifolium* established poorly. Laboratory germination test results were low for both species. Seeds in this family exhibit physical dormancy (Baskin, Baskin, & Li 2000) and we suggest the use of physical scarification to release dormancy and improve germination and establishment in the field. Another possible reason that *T. guttata* did not establish is that even the shallow sowing depth of 0-2 cm or the formation of soil crust following rain may have prevented germination by covering the very small seeds too deeply. Similarly this could explain the low establishment of *A. bellidifolium*. In addition to sowing depth, the surface of the prepared field may have been too uneven for these small-seeded species covered by soil crust following rainfall or irrigation. For future trials, we recommend preparing seedbeds with fine and even soil and to sow small-seed species on the surface (Houck 2009).

2.4.2 Height (max and min) of fruits from ground level and growth habit

A plot combine harvester with a cutting head cannot cut plants off at ground level. Plants and fruits must be at a minimum height above the ground for the combine to cut and harvest them without catching soil or stones that would damage the machine and contaminate the seed lot (Wintersteiger 2017). Over the relatively flat fields of the trials, our plot combine (Wintersteiger Nursery Master Elite) was able to harvest seeds held above 10 cm. Three species (*T. lappaceum*, *M. orbicularis*, *M. polymorpha*) had fruits too close to the ground to allow for mechanical harvest, which means other harvest methods should be evaluated for their feasibility. Since the fruits disperse intact from the plant, a vacuum or sweeper could be used to harvest fruits from the ground following senescence (Houseal 2007; Kiehl *et al.* 2014).

2.4.3 Phenology

There was a range among species in the time from sowing to key crop periods of onset of fruit ripening, seed dispersal and harvest date. Half of the species required the same length of time (29 weeks) to reach the stages of fruit maturation and seed dispersal, with the remaining species reaching those stages earlier. This varied range is desirable for a seed producer because the harvest period runs for several weeks or months and this longer period makes the workload manageable (Pfaff *et al.* 2002; Tucson Plant Materials Center & Coronado Resource Conservation and Development Area 2004; Houseal 2007; Bartow 2015). Nevertheless, a drawback to this study is that the experimental design included harvesting the seeds/plants/plots before maximum dispersal. To better understand phenology, dispersal and the harvest window, leaving part of the plots unharvested would have served that. Also for species that mature rapidly, the interval of 2 weeks between harvests was too long.

2.4.4 Maturity index at harvest and seed quality and yield

For six species where phenology stage at harvest had a significant effect on viability, the higher viability was always obtained by harvesting at the later phenology stage(s). This suggests that seed producers should target the harvest for a date when the crop is more mature rather than less mature, unless loss due to shattering is a concern.

For 16 species (n=24), the phenology stage at harvest did not affect viability. There may be no difference, or it is possible that the process of seed cleaning, which was the same for all phenology stages, removed nonviable seeds. Our plots were not large enough to sample for seed yield at different phenology stages. As a next step in this line of research, we recommend evaluation of seed quantity relative to harvest phenology in larger-scale field trials. The yield data provide a baseline, which can be built upon with data from subsequent crop years and field site/regions. This information will help farmers learn about the potential yield of each species and to know if a particular crop has been successful or could have produced more.

Increasingly, the need for sufficient and appropriate native plant materials and seed supply has been highlighted (Broadhurst et al. 2015; Tischew et al. 2011). This study supports that aim by describing and evaluating native Mediterranean forbs for characteristics important to seed farming. Overall, we have characterized twenty-seven native forb species that are immediately compatible with seed farming and large-scale production for the developing native seed sector in Spain and the Mediterranean region.

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Tables and Figures

Table 1. Establishment and row spacing scores and weeks to key phenology stages of thirty native Mediterranean forbs characterized for agronomic seed production. For species indicated with #, low establishment precluded further data collection during the experiment. For species indicated with *, data was collected from one replicate only. For species indicated with §, the phenology stage was not observed.

Scientific Name	Establishment score (0 - 5)	Row spacing score (0 - 4)	Number of weeks from sowing to onset of phenology stage #8 (mature fruits/seeds)	Number of weeks from sowing to onset of phenology stage #9 (seed dispersal)	Number of weeks from sowing to harvest
<i>Anarrhinum bellidifolium</i> #	1.0 ± 0.0	1.0 ± 0.0			

<i>Anthemis cotula</i>	4.0 ± 0.0	4.0 ± 0.0	26.3 ± 0.0	29.0 ± 0.7	29.4 ± 0.0
<i>Anthyllis vulneraria</i>	3.7 ± 0.6	1.7 ± 0.6	28.1 ± 0.0	28.1 *	29.4 *
<i>Biscutella auriculata</i>	4.7 ± 0.6	4.0 ± 0.0	25.1 ± 1.0	26.3 ± 0.0	28.9 ± 2.0
<i>Calendula arvensis</i>	5.0 ± 0.0	4.0 ± 0.0	18.9 ± 0.0	18.9 ± 0.0	24.5 ± 0.2
<i>Capsella bursa-pastoris</i>	2.0 ± 0.0	1.0 ± 0.0	21.1 ± 0.0	21.1 ± 0.0	22.1 ± 0.2
<i>Cleonia lusitanica</i>	3.0 ± 0.0	4.0 ± 0.0	28.1 ± 0.0	30.0 ± 0.0	29.8 ± 0.2
<i>Crepis capillaris</i>	3.3 ± 0.6	4.0 ± 0.0	26.5 ± 1.1	27.7 ± 0.0	29.1 ± 0.2
<i>Echium plantagineum</i>	3.3 ± 0.6	4.0 ± 0.0	25.4 ± 1.0	26.0 ± 0.0	29.6 ± 0.1
<i>Glebionis segetum</i>	4.0 ± 0.0	4.0 ± 0.0	27.2 ± 1.1	27.9 ± 0.0	29.3 ± 0.1
<i>Helianthemum ledifolium</i> #	0.7 ± 0.6	0.7 ± 0.6			
<i>Medicago orbicularis</i>	3.3 ± 0.6	4.0 ± 0.0	25.7 ± 1.0	25.7 ± 1.0	28.2 ± 0.2

<i>Medicago polymorpha</i>	4.0 ± 0.0	4.0 ± 0.0	24.6 ± 0.0	26.3 ± 0.0	26.6 ± 0.0
<i>Misopates orontium</i>	2.3 ± 0.6	1.3 ± 0.6	27.9 ± 0.0	27.9 ± 0.0	30.0 ± 0.0
<i>Moricandia moricandioides</i>	3.7 ± 0.6	3.0 ± 1.7	27.0 ± 2.1	§ 0.0	29.1 ± 0.0
<i>Nigella damascena</i>	3.7 ± 0.6	1.3 ± 0.6	28.0 ± 0.2	28.0 ± 0.2	29.3 ± 0.0
<i>Papaver dubium</i>	2.0 ± 0.0	1.0 ± 0.0	24.9 ± 1.0	24.9 ± 1.0	26.2 ± 0.2
<i>Salvia verbenaca</i>	2.7 ± 0.6	1.7 ± 1.2	22.8 ± 1.3	22.8 ± 1.3	24.3 ± 0.0
<i>Scabiosa atropurpurea</i>	3.0 ± 1.0	3.3 ± 1.2	27.9 ± 0.0	27.9 ± 0.0	30.3 ± 0.0
<i>Silene colorata</i>	4.0 ± 0.0	4.0 ± 0.0	22.0 ± 0.0	22.0 ± 0.0	28.1 ± 1.6
<i>Silene gallica</i>	3.3 ± 0.6	3.3 ± 1.2	23.7 ± 2.6	24.9 ± 1.0	28.2 ± 1.6
<i>Stachys arvensis</i>	2.3 ± 0.6	3.3 ± 0.6	26.6 ± 1.1	27.2 ± 1.1	29.7 ± 0.0
<i>Tolpis barbata</i>	2.3 ± 0.6	3.0 ± 0.0	27.9 ± 0.0	27.9 *	29.7 *

<i>Tordylium maximum</i>	3.3 ± 0.6	2.3 ± 1.5	27.9 ± 0.0	29.1 ± 1.1	29.7 ± 0.0
<i>Trifolium angustifolium</i>	2.3 ± 0.6	1.0 ± 0.0	27.7 ± 0.0	28.6 ± 0.7	29.0 ± 0.1
<i>Trifolium hirtum</i>	2.3 ± 0.6	3.3 ± 0.6	27.1 ± 1.1	28.0 ± 1.8	29.0 ± 0.0
<i>Trifolium lappaceum</i>	2.3 ± 0.6	3.0 ± 0.0	27.7 ± 0.0	29.0 ± 0.0	29.0 ± 0.0
<i>Trifolium stellatum</i>	3.7 ± 0.6	4.0 ± 0.0	26.5 ± 1.1	26.5 ± 1.1	29.0 ± 0.0
<i>Tuberaria guttata</i> #	0.0 ± 0.0	0.0 ± 0.0			
<i>Vaccaria hispanica</i>	4.7 ± 0.6	4.0 ± 0.0	24.3 ± 0.0	27.9 ± 0.0	28.0 ± 1.6

Table 2. Seed quality (viability) relative to phenology stage at harvest was compared with generalized linear models. When there was no difference in viability between phenology stages, the model results are on the same line. The phenology stages in bold text were significantly different from the other stages for that species.

Scientific name	Phenology stage at harvest	Estimate for viability	lower	upper	Intercept estimate	Std. Error	z value	Pr(> z)
			CI	CI				
<i>Anthemis cotula</i>	7	19%	12%	28%	-1.45	0.25	-5.69	<0.001
	8 and 9	26%	20%	33%	0.40	0.30	1.34	0.180
<i>Biscutella auriculata</i>	7	80%	71%	87%	1.39	0.25	5.55	<0.001
	8	89%	81%	94%	0.70	0.41	1.74	0.083

<i>Cleonia lusitanica</i>	7 and 8	93%	89%	96%	2.66	0.29	9.26	<0.001
<i>Crepis capillaris</i>	7	89%	81%	94%	2.09	0.32	6.54	<0.001
	8.5	93%	86%	97%	0.50	0.51	0.98	0.327
<i>Echium plantagineum</i>	7, 8 and 9	97%	95%	99%	3.59	0.36	10.03	<0.001
<i>Glebionis segetum</i>	7	51%	41%	61%	0.04	0.20	0.20	0.842
	8	36%	27%	46%	-0.62	0.29	-2.13	0.033
	9	65%	55%	74%	0.58	0.29	2.00	0.046
<i>Medicago orbicularis</i>	7 and 8	98%	94%	99%	3.66	0.45	8.09	<0.001
<i>Medicago polymorpha</i>	7 and 8	100%	98%	100%	27.94	50638.17	0.00	1.000

<i>Misopates orontium</i>	7, 8 and 9	96%	93%	98%	3.12	0.28	10.99	<0.001
<i>Moricandia moricandioides</i>	7 and 8	94%	90%	97%	2.75	0.30	9.22	<0.001
<i>Nigella damascena</i>	7 and 8	99%	96%	100%	4.60	0.71	6.47	<0.001
<i>Papaver dubium</i>	7 and 9	93%	88%	95%	2.51	0.27	9.36	<0.001
<i>Salvia verbenaca</i>	7	48%	38%	58%	-0.08	0.20	-0.40	0.689
	8	92%	85%	96%	2.52	0.42	6.01	<0.001
	8 (from stems that resprouted after first harvest)	33%	25%	43%	-0.63	0.29	-2.15	0.032

<i>Silene colorata</i>	7 and 9	98%	94%	99%	3.66	0.45	8.09	<0.001
<i>Silene gallica</i>	7 and 8	100%	98%	100%	27.96	50621.53	0.00	1.000
<i>Stachys arvensis</i>	7	36%	27%	46%	-0.58	0.21	-2.76	0.006
	8	58%	48%	67%	0.88	0.29	3.03	0.002
<i>Tolpis barbata</i>	7 and 8	94%	89%	96%	2.67	0.29	9.30	<0.001
<i>Tordylium maximum</i>	7, 8 and 9	95%	92%	97%	3.02	0.27	11.05	<0.001
<i>Trifolium angustifolium</i>	7 and 9	100%	97%	100%	5.29	1.00	5.28	<0.001
<i>Trifolium hirtum</i>	7 and 8	98%	95%	99%	3.89	0.51	7.71	<0.001

<i>Trifolium lappaceum</i>	8 and 9	99%	96%	100%	4.60	0.71	6.47	<0.001
<i>Trifolium stellatum</i>	7 and 9	99%	95%	100%	4.18	0.58	7.19	<0.001
<i>Vaccaria hispanica</i>	7 and 8	86%	80%	90%	1.77	0.20	8.84	<0.001

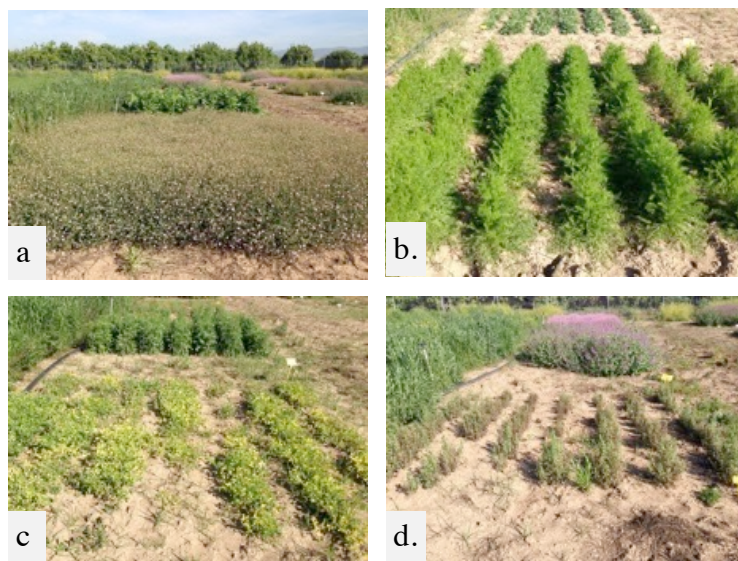


Figure 1. Examples of establishment scores and row spacing scores. a.

Establishment score = 5, row spacing score = 4; b. Establishment score = 4, row

spacing score = 2; c. Establishment score = 3, row spacing score = 3; d.

Establishment score = 2, row spacing score = 1.We defined establishment scores

as: 0=no establishment, 1=sparse establishment (less than 50 plants per plot),

2=light establishment (more than 50 plants per plot, but with unfilled space

within plot), 3=complete establishment (plant density covered the plot completely

and excluded weeds from the plot, but seeds were not wasted by planting too

many per area), 4=thick establishment (plant density covered the plot completely

and excluded weeds from the plot but there was slight crowding among plants,

indicating that the seeding rate was excessive, 5=dense establishment (plant

density covered the plot completely and excluded weeds from the plot but plants

crowded or shaded themselves, evidenced by mildew and/or chlorosis of lower

leaves). Establishment scores 5, 4, 3, and 2 are shown. Scores 1 and 0 are not

shown because so few established crop plants are not distinguishable from

spontaneous weeds in photos. For row spacing categories were defined as: 0=no

establishment, 1=some space between rows with gaps between plants within a row, 2=some space between rows with no gaps between plants within a row, 3=no space between rows with some gaps between plants within a row, 4=no space between rows with no gaps between plants within a row. Row spacing scores of 4, 3, 2, 1 are shown. Score 0 (no plants) is not shown.

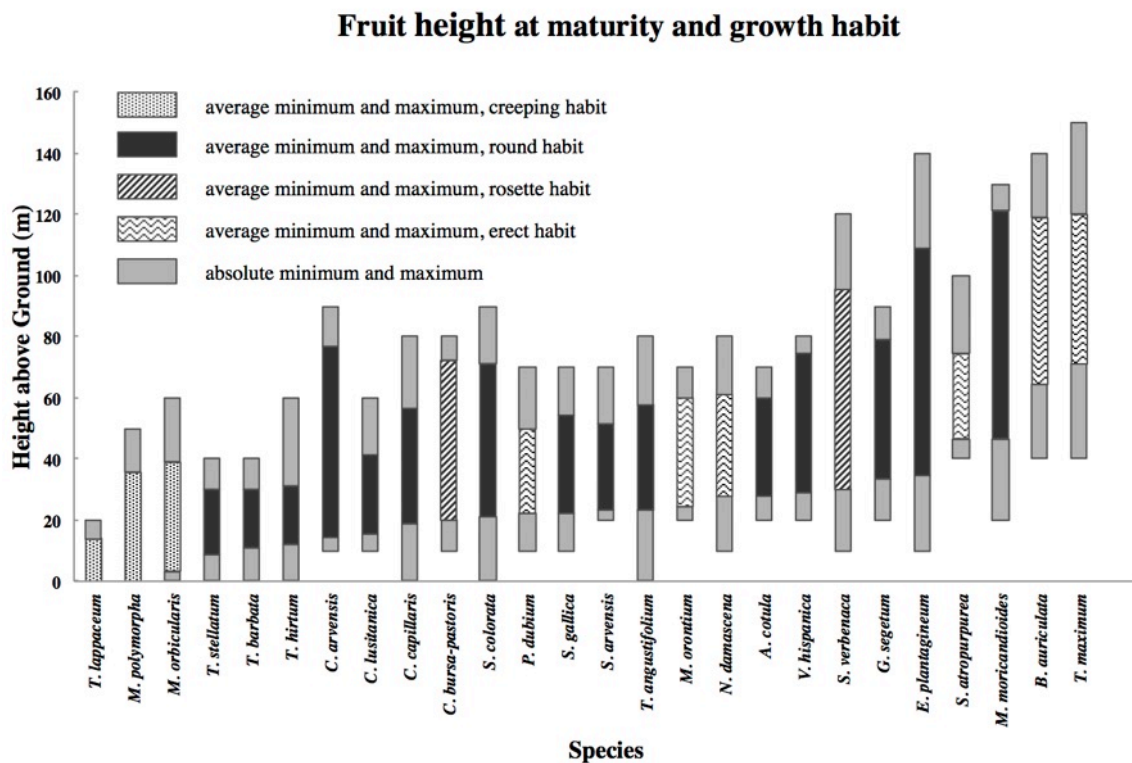


Figure 2. Range of fruit heights at maturity, organized from shortest to tallest minimum height and the growth habits (creeping, round, rosette, erect) for 26 species that established and reached maturity.

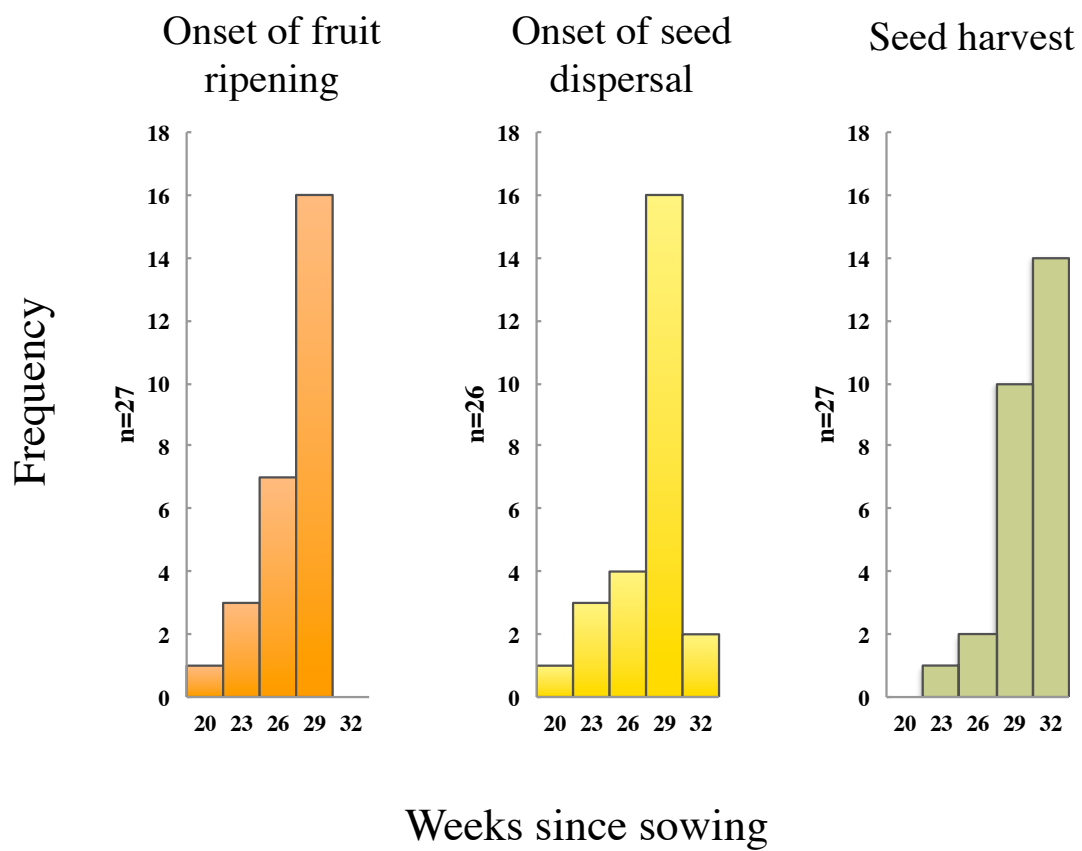


Figure 3. The number of weeks to reach key phenological stages for crop development and the frequency of species that had reached each stage.

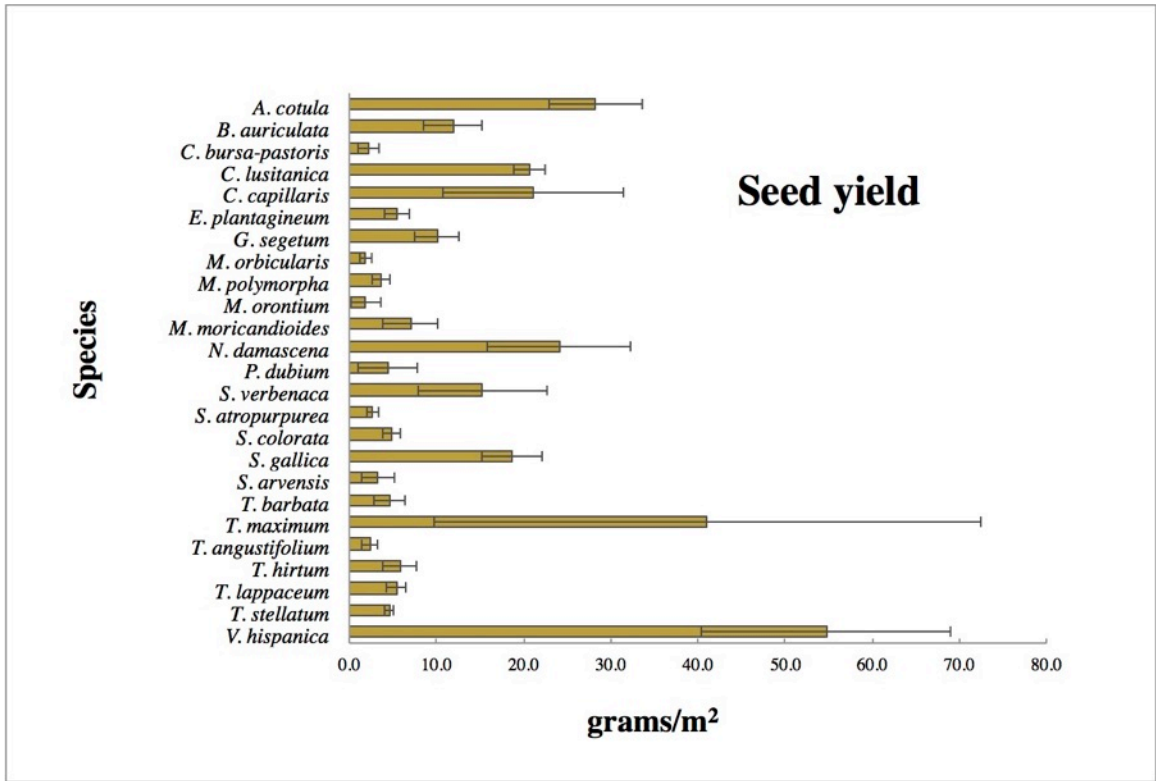


Figure 4. Average seed yield per species. Error bars show standard deviation.

Supporting Information

Table S1. Taxonomy, fruit type, growth habit and distribution of the 30 studied species.

Scientific Name	Family	Fruit type	Growth habit	Distribution (Pujadas 1986)
<i>Anarrhinum bellidifolium</i> (L.) Willd.	Plantaginaceae	dehiscent capsule	rosette	adjacent to Mediterranean Basin
<i>Anthemis cotula</i> L.	Asteraceae	achene (2 forms)	round	adjacent to Mediterranean Basin
<i>Anthyllis vulneraria</i> L.	Fabaceae	legume (single seeded, dispersal unit retains corolla)	rosette	western Mediterranean Basin
<i>Biscutella auriculata</i> L.	Brassicaceae	non-dehiscent silicle	erect	western Mediterranean Basin
<i>Calendula arvensis</i> M.Bieb.	Asteraceae	achene (3 forms)	round	adjacent to Mediterranean Basin

<i>Cleonia lusitanica</i> (L.) L.	Lamiaceae	nutlet	round	Iberian Peninsula and near-Africa
<i>Crepis capillaris</i> (L.) Wallr.	Asteraceae	achene (2 forms)	round	Mediterranean Basin-Eurasia
<i>Echium plantagineum</i> L.	Boraginaceae	nutlet	round	adjacent to Mediterranean Basin
<i>Glebionis segetum</i> (L.) Fourr.	Asteraceae	achene (2 forms)	round	eastern Mediterranean Basin
<i>Helianthemum ledifolium</i> (L.) Mill.	Cistaceae	dehiscent capsule	erect	Mediterranean Basin
<i>Medicago orbicularis</i> (L.) Bartal.	Fabaceae	legume (non-dehiscent)	creeping	adjacent to Mediterranean Basin
<i>Medicago polymorpha</i> L.	Fabaceae	legume (non-dehiscent)	creeping	adjacent to Mediterranean Basin
<i>Misopates orontium</i> (L.) Raf.	Plantaginaceae	dehiscent capsule	erect	adjacent to Mediterranean Basin
<i>Moricandia moricandioides</i> (Boiss.) Heywood	Brassicaceae	non-dehiscent silique	round	Iberian Peninsula
<i>Nigella damascena</i> L.	Ranunculaceae	dehiscent capsule	erect	adjacent to Mediterranean Basin
<i>Papaver dubium</i> L.	Papaveraceae	poricidal capsule	erect	eastern Mediterranean Basin
<i>Salvia verbenaca</i> L.	Lamiaceae	nutlet	rosette	Mediterranean Basin-Eurasia
<i>Scabiosa atropurpurea</i> L.	Caprifoliaceae	achene (2 forms)	erect	Mediterranean Basin

<i>Silene colorata</i> Poir.	Caryophyllaceae	dehiscent capsule	round	adjacent to Mediterranean Basin
<i>Silene gallica</i> L.	Caryophyllaceae	dehiscent capsule	round	adjacent to Mediterranean Basin
<i>Stachys arvensis</i> (L.) L.	Lamiaceae	nutlet	round	Mediterranean Basin-Eurasia
<i>Tolpis barbata</i> (L.) Gaertn.	Asteraceae	achene (2 forms)	round	Mediterranean Basin
<i>Tordylium maximum</i> L.	Apiaceae	schizocarp	erect	adjacent to Mediterranean Basin
<i>Trifolium angustifolium</i> L.	Fabaceae	legume	round	adjacent to Mediterranean Basin
<i>Trifolium hirtum</i> All.	Fabaceae	legume	round	adjacent to Mediterranean Basin
<i>Trifolium lappaceum</i> L.	Fabaceae	legume	creeping	adjacent to Mediterranean Basin
<i>Trifolium stellatum</i> L.	Fabaceae	legume	round	adjacent to Mediterranean Basin
<i>Tuberaria guttata</i> (L.) Fourr.	Cistaceae	dehiscent capsule	erect	Mediterranean Basin-Eurasia
<i>Vaccaria hispanica</i> (Mill.) Rauschert	Caryophyllaceae	dehiscent capsule	round	eastern Mediterranean Basin

Table S2. Realized sowing rates (based on PLS and 1000 seed weight calculations) and the measured establishment scores.

Scientific Name	seeds / m ²	g / m ²	g / linear m	Establishment	
				score	and standard deviation
<i>Anarrhinum bellidifolium</i>	1,386	0.04	0.01	1.0	± 0.0
<i>Anthemis cotula</i>	328	0.13	0.02	4.0	± 0.0
<i>Anthyllis vulneraria</i>	868	2.70	0.39	3.7	± 0.6
<i>Biscutella auriculata</i>	886	2.84	0.41	4.7	± 0.6
<i>Calendula arvensis</i>	126	0.77	0.11	5.0	± 0.0
<i>Capsella bursa-pastoris</i>	963	0.10	0.01	2.0	± 0.0
<i>Cleonia lusitanica</i>	789	0.71	0.10	3.0	± 0.0

<i>Crepis capillaris</i>	2,368	0.62	0.09	3.3	± 0.6
<i>Echium plantagineum</i>	939	4.13	0.59	3.3	± 0.6
<i>Glebionis segetum</i>	682	1.24	0.18	4.0	± 0.0
<i>Helianthemum ledifolium</i>	1,085	0.54	0.08	0.7	± 0.6
<i>Medicago orbicularis</i>	1,011	9.71	1.40	3.3	± 0.6
<i>Medicago polymorpha</i>	1,088	6.53	0.93	4.0	± 0.0
<i>Misopates orontium</i>	1,148	0.15	0.02	2.3	± 0.6
<i>Moricandia</i>					
<i> moriciandoides</i>	613	0.18	0.03	3.7	± 0.6
<i>Nigella damascena</i>	981	2.06	0.29	3.7	± 0.6
<i>Papaver dubium</i>	455	0.09	0.01	2.0	± 0.0
<i>Salvia verbenaca</i>	213	0.55	0.08	2.7	± 0.6
<i>Scabiosa atropurpurea</i>	1,060	4.24	0.61	3.0	± 1.0

<i>Silene colorata</i>	2,279	0.58	0.08	4.0	± 0.0
<i>Silene gallica</i>	1,037	0.34	0.05	3.3	± 0.6
<i>Stachys arvensis</i>	600	0.42	0.06	2.3	± 0.6
<i>Tolpis barbata</i>	2,433	0.29	0.04	2.3	± 0.6
<i>Tordylium maximum</i>	945	3.20	0.46	3.3	± 0.6
<i>Trifolium angustifolium</i>	658	1.19	0.17	2.3	± 0.6
<i>Trifolium hirtum</i>	400	1.28	0.18	2.3	± 0.6
<i>Trifolium lappaceum</i>	1,296	1.17	0.17	2.3	± 0.6
<i>Trifolium stellatum</i>	1,088	3.26	0.47	3.7	± 0.6
<i>Tuberaria guttata</i>	903	0.05	0.01	0.0	± 0.0
<i>Vaccaria hispanica</i>	972	4.81	0.69	4.7	± 0.6

Table S3. Phenology scale based on Meier 2000 and modified for wild species and to include seed dispersal.

Stage	Description	Notes on
(*modified)		modifications
0	Pre-Germination: Dry seed	
1	Leaf development (main shoot): Cotyledons completely unfolded	
2	Formation of side shoots / tillering: Side shoots develop	
3*	Stem elongation /shoot development (main shoot): Beginning of stem elongation	Did not use; not applicable to dicots.
4*	Vegetative propagation and/or booting: Vegetative reproductive organs begin to develop	Did not use; not applicable to dicots.
5	Inflorescence emergence (main shoot) / heading: Inflorescence or	

flower buds visible

6 Flowering (main shoot): Anthesis

7 Development of fruit

8 Ripening or maturity of fruit and seed

9* Fruits and/or seeds disperse

Added dispersal as a critical stage for species with indeterminate ripening and as part of evaluating suitability for cultivation for seed increase.

10* Senescence

Shifted senescence from stage 9 to stage 10 to accommodate

dispersal as stage 9



**Chapter 3. Trait-based species selection tool for promoting
native cover crops in olive orchards**

Trait-based species selection tool for promoting native cover crops in olive orchards

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Abstract

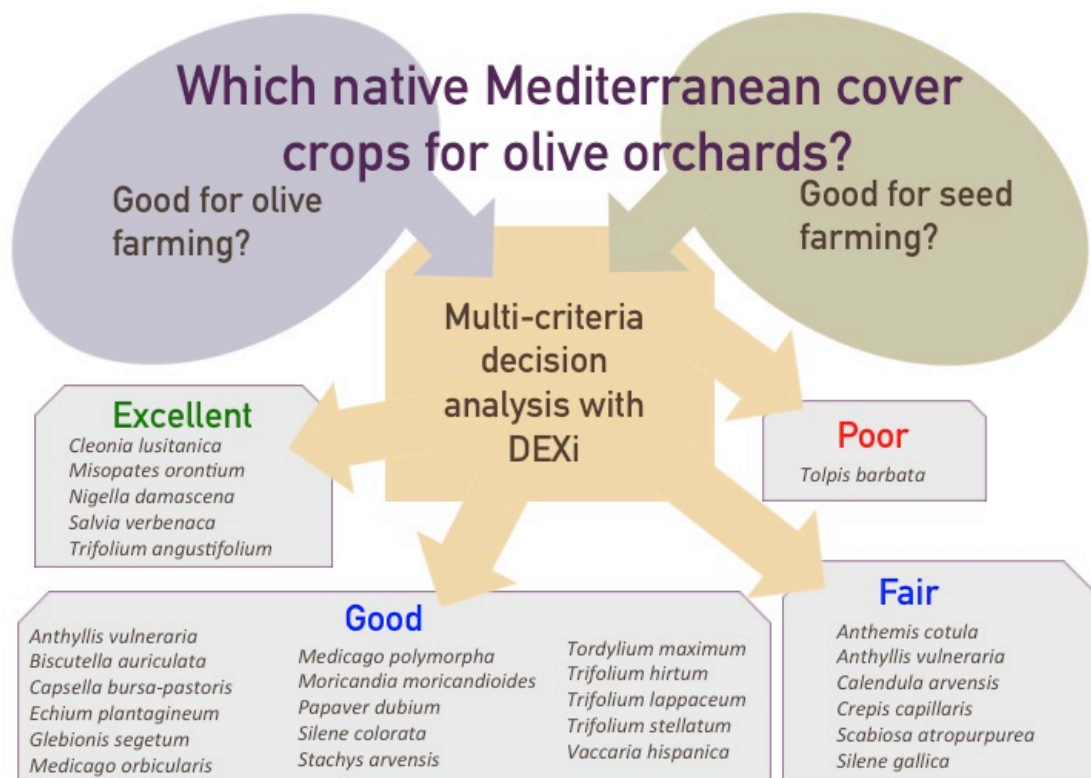
A key step in seed-based restoration is determining which species to sow. Primary considerations for species selection are historical communities of reference, restoration objectives (habitat, conservation, function, ecosystem services), site conditions, disturbance regimes and cost or availability of seeds. The availability of quality seeds in sufficient quantities and at accessible prices is crucial for the success of landscape-scale restoration, yet the feasibility of seed farming for target species is often overlooked when planning restoration projects.

There is an emerging need and demand for native seeds in the Mediterranean Basin to establish native forb species as cover crops and restore biodiversity and increase sustainable production in perennial agroecosystems of olive, citrus, almond, vineyard and other woody crops. With over 2.4 million hectares of land under olive production in southern Spain, there is great potential for native cover crops to integrate conservation and agricultural production within the Mediterranean Basin.

A Suitability Index for 30 native Mediterranean forbs was calculated to identify, prioritize and develop native species as cover crops using DEXi multi-attribute decision-making software. The criteria were from 2 main categories: 1) compatibility with olive production, including ecosystems services, and 2) feasibility for seed farming so that a commercial supply of seeds is available to establish the cover crops. There were 5 species considered “Excellent”, 15 “Good”, 5 “Fair” and 1 was “Poor”. We provide a detailed example of a species selection process for increasing the biodiversity and sustainability of olive orchards and the growing native seed sector in Spain. The method can be adapted to choose taxa that will meet both ecological restoration goals and the realities of plant materials programs. The DEXi software

was a practical and effective method for species selection. Twenty native forbs are suitable cover crops for Mediterranean olive orchards. Just as critical, these 20 species can be cultivated for seed farming to produce the seeds needed to establish the native cover crops in the agroecosystems.

Graphic Abstract



Keywords: species selection, sustainable agriculture, ecological restoration, DEXi, native seed production, Mediterranean Basin

3.1 Introduction

Species selection in ecological restoration

A fundamental question in planning and managing a restoration is to choose which plant species to actively add to the site through sowing or transplanting (Society for Ecological Restoration 2004; Clewell *et al.* 2005). Typically, the list of chosen species is shaped by the current environmental conditions and species assemblages at the site, the future goals for the function or ecological trajectory of the site/system, and also practical factors of budget and availability of suitable plant material (Ladouceur *et al.* 2017). While each restoration project must consider these factors, the unique combinations of factors for any given restoration result in a customized species list. There is an overall generalized process common to all restoration projects, which at a detailed level is tailored to and unique for each project. The question of species selection is not addressed in a review of restoration practices (Rowe 2010) and guidelines for restoration list general steps, but don't provide methodologies (Society for Ecological Restoration 2004; Clewell *et al.* 2005). To date, only a few standardized methodologies (Graff & McIntyre 2014; Meli *et al.* 2014) exist as templates which restoration planners can use to weigh and prioritize their particular set of factors.

At its beginnings, the field of restoration ecology focused on restoring natural communities which were degraded, fragmented or destroyed (Court 2012). This continues to be a focus, but as the discipline grows and develops, it has expanded to include ecosystem function, novel systems, reclamation and revegetation following mining (Rey Benayas *et al.* 2009; Hobbs *et al.* 2014). Restoration of former or active agricultural lands is another application. These restorations aim towards re-

establishing biodiversity in places that were intensively farmed (Walker *et al.* 2004; Arriaza *et al.* 2005) or towards creating agriculture production systems that are diverse and echo the assembly and function of natural systems (Tschardt *et al.* 2005; Moonen & Bàrberi 2008). Many agroecosystems are primarily focused on productivity and inherently reduce biodiversity by favoring short-term production over long-term sustainability and ecological integrity (Giller *et al.* 1996; Matson *et al.* 1997; Altieri 1999). This simplification reduces the ecological complexity and diversity of the systems. The benefits of higher levels of biodiversity compared to lower levels are a suite of ecosystem services which are the foundation for productivity over time (Hooper *et al.* 2005; Moonen & Bàrberi 2008).

The agro ecosystems of olive orchards are especially important in Spain, accounting for 2.47 million of the 2.9 hectares of land in woody crops in the country (EuroStat, 2014), followed by 1.8 million hectares of land under wine-grape vineyards. Spain produces eighty percent of global olive production (EuroStat, 2014) and 80% of Spain's production comes from the autonomous community of Andalusia, where 30% of land cover is under olive production (EuroStat, 2014).

Cover crops are a viable solution to long-term management of agricultural landscapes (Pardini *et al.* 2002; Rodrigues *et al.* 2015) to provide ecosystem services. Interest in cover crops by farm managers is increasing (Pardini *et al.* 2002; Rodríguez-Entrena & Arriaza 2013; Gonzalez-Sanchez *et al.* 2015), but adoption is limited by a lack of suitable cover crop choices (Siles *et al.* 2016). Forage grasses and legumes are available, but these types of cover crops of temperate origin are not specifically adapted to Mediterranean conditions and fail to meet the needs of farmers and of their crops (Ramirez-Garcia *et al.* 2012; Hernández González *et al.* 2015). Native species are adapted to Mediterranean climate and with so much diversity to choose from,

there are species that show potential for use as cover crops in olive orchards (Conejo 2012; Rodrigues *et al.* 2015; Siles *et al.* 2016). Among the rich flora of the Mediterranean Basin, annual or short-lived perennial native species have many characteristics which make them potentially suitable as cover crops to restore long-term sustainability in olive orchards (Cowling *et al.* 1996; Rey Benayas & Scheiner 2002; Matesanz & Valladares 2014). However, decades of intensive practices have depleted the soil seed banks of desirable native plants. Seeds must be sown in order to establish appropriate cover crops as understory vegetation.

Seed supply for native cover crops

The native seed sector is nascent and in development in Spain. Forestry species have been produced and used for decades, but the available herbaceous species are collected from the wild (Nunes *et al.* 2016). Large-scale, commercial production is needed for an affordable and sufficient supply of native seeds (Broadhurst *et al.* 2015; Nevill *et al.* 2016).

Seed supply is fundamental to using seeds in restoration and we developed a species selection approach that with this critical aspect in mind. We evaluated the suitability of 30 native herbaceous taxa for native cover crops using the combined attribute values for function in the restored habitat (olive farming) with attribute values for generating seed supply (seed farming).

3.2 Methods

3.2.1 Study system

In recent decades, management of woody crops in Mediterranean agroecosystems has intensified and herbaceous vegetation within the fields has been eliminated through

the use of herbicides, mowing or tillage, leading to ecological simplification of the agroecosystem. Immediate production has increased (Fernandez Escobar *et al.* 2013), but long term sustainability has decreased (Gómez *et al.* 2014), from the losses due to soil erosion, poor communities of pollinators and other beneficial insects, soil organic matter, soil microbial communities which balance soil pathogens and add to fertility. A paradigmatic example is the cultivation of olive (*Olea europaea* subsp. *europaea*). Olive was domesticated in the Mediterranean Basin (Connor 2005; Carmona-Torres *et al.* 2014; Gómez *et al.* 2014) and this region is still the primary global production area for olive (EuroStat, 2014).

Hundreds of varieties exist, each suitable for a given use (table olives, olive oil or dual purpose) and a particular combination of microclimate and soil type (Barranco & Rallo 2000; Rallo Romero 2004). The choice of variety also depends upon plantation type. The least intensive plantation types have 1-4 trunks per canopy, which are pruned for optimum hand harvest. Spacing between trees may be as much as 10 meters in a grid layout. Intensive plantations have one trunk per canopy and the grid spacing between trees is closer to 7 meters. The fruits are harvested with mechanical vibrating shakers. In super-intensive plantations, the trees are planted close together in distinct rows. They are pruned to form hedgerows and are harvested by machines that mount the row and using rotating brushes to remove the fruits. Irrigation generally follows the intensive continuum, with the less-intensive plantations being rain fed while underground drip irrigation is often used for intensive production. A universal practice under intensive and super-intensive models is to keep the soil free of non-crop vegetation since this vegetation competes for water with the trees during the critical summer months when precipitation is minimal and when trees are filling the fruits.

3.2.2 Species pool filtering

In this case study, we used 30 species as options (Table 3). Prior to the DEXi evaluation, we chose these 30 species through a filtering and prioritization process. Given that our system of interest is olive orchards in southern Spain, we began with the species pool for olive orchards. The initial list was from a vascular plant inventory of 979 taxa from cultivated and ruderal areas in Córdoba Province, Andalusia, Spain (Pujadas Salvá 1986). We reduced the initial list through a series of general trait-based filters using habitat descriptions and regional floras (Castroviejo; Pujadas Salvá 1986). Because seeds will be used as the propagule and because we are interested in herbaceous plants, we removed taxa from Equisetaceae, Salicaceae, Fagaceae, Ulmaceae, Moraceae, Santalaceae, Simaroubaceae, Anacardiaceae, Rhamnaceae, Thymelaeaceae, Tamaricaceae, Oleaceae and Palmae (Arecaceae). Grasses have been studied extensively for their value in erosion control (Taguas *et al.* 2015). We focused on dicots as an understudied group with potential to restore biodiversity as cover crops and for this reason we removed taxa from Poaceae. In the next filtering step we removed taxa whose native range was outside the greater Mediterranean Basin. Native taxa are adapted to the regional climate and for our goal of biodiversity enhancement; native species are presumed to have the most potential for trophic interaction. We then filtered out taxa that are not therophytes (annuals). Ruderal annuals are appropriate because they persist and regenerate in the seasonally dry and disturbed habitats (Bochet & García-Fayos 2015) such as road cuts or in this case, olive orchards. The strategy of the therophyte life form is to persist during the hot dry summer as seeds. Therophytes are self-sowing and don't compete for water with the olive trees during the critical dry summer season, because they have short life cycles and naturally senesce in spring. Three taxa (*A. vulneraria*, *S. verbenaca*, and *S.*

atropurpurea), which can function as annuals, biennials or short-lived perennials were included in the evaluation because they had previously been identified of interest as hosts for beneficial insects (Aguado Martín *et al.* 2015). Finally, we applied the additional filter of observed habitat both ruderal and olive orchard.

Plant height and flowering season (Castroviejo 1986-2012) were used to further limit the list of taxa to those with short to medium (less than 1m) stature and a winter annual life cycle. In early summer 2015 we collected seeds from wild populations under European protocols (ENSCONET 2009) to use in seed batches for sowing trial plots. The data for phenology, fruit height and yield were collected from field trials on these 30 species and then used in this DEXi decision analysis (in preparation).

3.2.3 Multi-attribute decision making

We evaluated the Suitability Index for native species using DEXi (Bohanec 2015a). DEXi is software for multi-attribute decision making (Bohanec 2015b) and has been used to support complex decision making where factors may be competing, including agroecological applications (Craheix *et al.* 2015). There are several advantages to DEXi. It is freely available, user-friendly and the decision rules and input data can be easily modified, which makes it adaptable for use over time as factors in a decision change. It uses qualitative terms for values, which make it more intuitive and also provides automated charts and reports. The program uses the following terminology: options, attributes, values, functions and evaluations. “Options” are the possible selections; in this case, each native species is an option. An “attribute” is the characteristic of interest. For each attribute, an option has a value, which is based on data (see 2.2 *Attributes and values* below). The values are organized as qualitative scales, such as “low”, “medium”, “high”. First we defined and organized 21 attributes

of interest on paper. We then input these to DEXi through menu commands to build a hierarchy of base attributes (which we input data values for) and aggregate attributes (whose value is determined by the combined values for the attributes nested beneath them in the tree (Fig. 1). Once the tree structure was defined, we created a scale for each attribute and input the values for each option (Table 1). For each aggregate attribute, we defined a matrix of function rules, which DEXi uses to calculate the value of the aggregate attribute. Finally, we ran the evaluation and report to generate the Suitability Index.

3.2.4 Attributes and values

We defined a series of attributes for “Olive Farming” (characteristics related to cover crop) and for “Seed Farming” (characteristics of importance for large-scale seed production under cultivation.) In addition to descriptive titles for the attributes, numeric labels reflect the nested dependency (Fig. 1) and are included here.

“Trafficability (1.1.1.1) Equipment can move about in the field” was determined based on the measure of average plant height (Castroviejo). Species with an average height of 40 cm or less were “Excellent”, 41- 70 cm were “Good”, 71-100 cm were “Fair”, and above 100 were “Poor”.

“Seasonal Growth (1.1.1.2.1) Cover develops quickly”

We based the values on the number of weeks from sowing to the onset of mature fruits/seeds. Under 23 weeks was “Excellent”, 23-26 weeks was “Good”, 27-29 weeks was “Fair” and over 29 weeks was “Poor”.

“Contained (1.1.1.2.2) Limited spread which does not encroach on crop”

Farmers will likely sow the cover crop central bands in the rows between trees. This part of the orchard is unprotected by the canopy so it is a good place for the cover crop to be in place for soil protection. It is also favorable to not have the cover crop directly under the trees so that the machinery and olive harvest have a clear area for working. And although the cover crops have shallow root systems and short growing seasons, keeping them in the center of the row where they are farther from the olive tree roots further avoids competition for water. For these reasons, it is desirable that the cover crops stay contained within the sown bands. We used growth habit to categorize how plants would expand beyond where they were sown. Plants that are generally slender and upright or which elongate from a basal rosette were “Excellent”. Plants with wide and rounded architecture were “Good”. Plants with creeping growth habits were considered “Poor”. With time, it is expected and desired that a soil seed bank develops and the cover crops regenerate from the soil seed bank. This will lead to some migration out of the sown band over several years.

“Non-competitive for water (1.1.2.1.1) Plants disperse seeds into soil seed bank and senesce by late spring”

Water competition is critically important to olive farming. With the plan that short life cycles and early senescence, but still plants that reach reproductive maturity and develop a soil seed bank. So we used weeks from sowing to seed maturity. This is similar to 1.1.1.2.1 Seasonal Growth, but with the following categories: maturity in less than 19 weeks was “Excellent”, maturity from 19 to less than 22 weeks was “Good” and 22-25 weeks was “Fair”.

“Non-competitive for nitrogen (1.1.2.1.2) Provision or use of nitrogen”

Olives are not heavy nitrogen users compared to other crops but it is the first macronutrient which is limiting to the crop. We used three categories for nitrogen use, based on general plant family characteristics for provisioning or using nitrogen. Species from Fabaceae were “Excellent”, any other dicots were “Good” and grasses are “Poor”. We included grasses a category for future evaluation of additional species, even though there were no grass studies in this first case study.

“Insects and food web (1.1.2.2.1) functional group + degree of association)”

The data for insect associations is from collaboration with entomologists from the Estación Experimental del Zaidín, Consejo Superior de Investigaciones Científicas (CSIC) Granada, Spain. During the flowering period, insects were sampled from 3m x 3m replicated single-species plots with suction. For each plant species, the insect samples were evaluated, identified and grouped into functional categories. Broadly, these were: generalist predators, parasitoids, herbivores, detritivores (springtails) and pollinators. The abundance of each functional group was categorized as a degree of association: “High”, “Medium”, and “Low” (Table 2).

There are 2 components to the data that determine the value of this attribute: functional group and the degree of association, so we made a compound matrix to determine the value for 1.1.2.2.1 (Table 2). This takes into account that a “Low” association with functional group of low value isn’t an overall low value for biodiversity.

In this study, we considered insects primarily for the ecosystem service of controlling pest insects, which are the olive moth *Prays oleae* (Lepidoptera) and olive fruit fly (*Bactrocera oleae* and *Dacus oleae* (Diptera)). Insects are also important as food for other animals and to maintain stable populations of the pest-controlling insects.

Olives are wind-pollinated, so pollinator services are less critical for this crop, but in the case of almonds, the value for pollination in the DEXi model would be increased. So for all those reasons, the insects were valued as: generalist predators “Best”, parasitoids “Very Good”, and herbivores, detritivores (springtails), and pollinators were “Good” (Table 2).

“Non-host of *Verticillium* pathogen (1.1.2.2.2) Degree to which a taxon is known to host *Verticillium dahliae*”

The fungal pathogen *Verticillium dahliae* is a major disease in olives (López-Escudero & Mercado-Blanco 2011). Other plants can host the fungus and are vectors for the disease in crops (Thanassouloupoulos *et al.* 1981; Vallad *et al.* 2005). It is critical that species used as cover crops in olive orchards have non-host status in order to avoid spreading or increasing the disease in the agroecosystem. We used the *sensu latu* definition of host to include both species which are symptomatic in which case the fungus is a pathogen and those species which are asymptomatic carriers with the fungus is an endophyte (Malcolm *et al.* 2013). To include consideration of the likelihood that a cover crop would be a host, we used info from a global database on host species (Inderbitzin & Subbarao 2014). The categories were: “Best” for identified resistance in the genus, “Good” for no known host from the plant family, “Fair” for no known host from the genus, and “Poor” for known host from genus.

“Seed size (1.2.1.1.1) Proper metering and flow through planter”

How well can the seeds be metered.

“Easy” for diameter > 2 mm and “Difficult” for diameter < 2 mm.

“Seed shape (1.2.1.1.2) Proper metering and flow through planter”

How flowable are the seeds. Seed shape. “Easy” for regular shape and “Difficult” for irregular shape.

“Fruit height (1.2.1.2.1) Fruits are held high enough off the ground that the combine can harvest them”

We measured the average height of fruit at maturity, at 5 points in 3 replicates in field trials. Higher than 25 cm was “Easy” and lower than 25 cm was “Difficult”.

“Clear harvest window (1.2.1.2.2) Indifferent ripening/dispersal is not too extended”

If indeterminate ripening is too extended, then there is no clear harvest window or optimum time for harvest. “Easy” for mature fruit to harvest window < 2 weeks, “Medium” for mature fruit to harvest window 2-4 weeks, and “Difficult” for mature fruit to harvest window > 4 weeks.

“Seeds separate from fruits (1.2.1.3.1) Ease of releasing seeds from fruit”

To quantify how readily seeds can be freed from the fruit or other structures during seed cleaning, we used expert opinion and dehiscence to determine “Easy” for dehiscent, “Medium” for Indehiscent but openable, and “Difficult” for Indehiscent stubbornly indehiscent.

“Seeds separable from inert material (1.2.1.3.2) Ease of separating seeds from inert material”

“1.2.1.3.2 Ease of separating inert matter from seeds (seed shape)”

1. Easy. Regular shape
2. Difficult. Irregular shape

“Shattering, non-shattering (1.2.2.1.1) Fruits do not release seeds while on the plant”

“Easy” for indehiscent and “Difficult” for dehiscent.

“Dispersal window (1.2.2.1.2) Period of time that ripe fruits/seeds stay on the plant”

In contrast to attribute 1.2.1.2.2 where a shorter and distinct harvest window is desirable, in the case of the importance of not losing seeds to dispersal, a longer harvest window is better/easier. “Easy” > 2 weeks, and “Difficult” < 2 weeks.

“Yield (1.2.2.2.1)”

Using grams per square meter, “High” > 20 g/ m², “Medium” 5-20 g / m², and “Low” < 5 g/ m².

“Demand (1.2.2.2.2)”

We used the availability of a species in a seed company catalog as a measure of the level of demand for a species. We searched the catalogs of 5 companies selling native seeds in the Iberian Peninsula. “Low” was frequency of 0, “Medium” was frequency of 1-2, and “High” was frequency of 3, 4, or 5.

The functions and rules for determining the value of aggregate functions are arranged in matrices (Supplemental Material, p. 9).

3.3 Results

We evaluated the two main attributes of Olive Farming and Seed Farming to determine Suitability of 30 native species for use as cover crops for restoring diversity and ecosystem services to olive orchards. Two-thirds were evaluated as “Excellent” or “Good”, supporting further use of Mediterranean native forbs as cover crops, in restoration, and/or seed farming.

The Suitability Index (Table 3, Fig. 2) was “Excellent” for five species: *Cleonia lusitanica*, *Misopates orontium*, *Nigella damascena*, *Salvia verbenaca*, and *Trifolium angustifolium*. Fifteen species had a “Good” Suitability Index (Table 3, Fig. 2). Five were “Fair”: *Anthemis cotula*, *Calendula arvensis*, *Crepis capillaris*, *Scabiosa atropurpurea*, and *Silene gallica*. One species, *Tolpis barbata*, was evaluated as “Poor”. For four species (*Anarrhinum bellidifolium*, *Anthyllis vulneraria*, *Helianthemum ledifolium*, and *Tuberaria guttata*) the evaluation result was multiple values, since the true values could not be determined due to several missing data points for those species.

While all attribute values combine through the functions to determine the final Suitability Index, the evaluation results for the two main sub-attributes of Olive Farming and Seed Farming synergistically or antagonistically result in the final Suitability Indices (Table 3, Fig. 2). This can be seen in more detail through the charts that DEXi generates (Fig. 3) for selected attributes. The summary of method and results are in Figure 4.

3.4 Discussion and conclusions

In order to be an effective and adopted sustainable agriculture practice, the ideal cover crop does not compete with the olives trees for water or get in the way of orchard operations. Cover crops which improve soil health and overall ecosystem complexity are desirable. However, in order to be deployed and used as cover crops, a source of seeds needs to be produced. Seed farming is a practical and necessary means to generate a sufficient seed supply. Some species are more amenable to cultivation for seed farming and commercial seed production than others. In order to consider all the

desirable traits, a multicriteria decision tool is needed to support the species selection process.

Elsewhere outside the Mediterranean, native plants have shown potential for adding biodiversity to agroecosystems (Isaacs *et al.* 2009; Garnier & Navas 2012). A multi-criteria selection grid was used to choose suitable native cover crop species for tropical orchard agroecosystem (Jannoyer *et al.* 2011). As evidence continues to accrue showing the suitability of native plants to provide environmental and ecological benefits to agroecosystems, the use of stronger biodiversity measures in funding schemes should be added (Kleijn & Sutherland 2003; Wade *et al.* 2008).

In a study to characterize 11 annual legume cultivars for suitability to olive orchard cover crops, all persisted for at least 4 years, showing a match for the native annual strategy with the agroecosystem management and conditions (Rodrigues *et al.* 2015). Olive yields can be maintained while switching to sustainable management of the natural vegetation (Simoes *et al.* 2014). The use of strategic mowing instead of herbicide to manage natural vegetation in olive orchards improved biodiversity without affecting yield.

In a selection process based on expert opinion, the important consideration of seed availability was among the criteria, but not seed farming itself (Graff & McIntyre 2014). Other useful and important criteria used in species selection are social and ecological (Meli *et al.* 2014; Sacande & Berrahmouni 2016). Additionally, the function or performance of the chosen species is also a factor (Meli *et al.* 2013; Waller *et al.* 2015) to consider for successfully using plant materials in restoration. The need for native plant materials to restore Mediterranean habitats is expected to grow (Nunes *et al.* 2016) and many plant taxa remain to be evaluated and added to the

restoration species pool (Ladouceur *et al.* 2017). In parallel, the development of the native seed industry is critical to provide a source of seeds (Nevill *et al.* 2016).

Among the limitations to our use of DEXi for this application were a limited data set for hundreds of potential species, so we only included 30 species in our field trials and data collection. Likewise, the traits related to seed farming are based on the current equipment at the seed company. Other types of field machinery (planters and combines) or seed cleaning equipment could be used, which would change the rankings for some species. For example, using a vacuum harvester to collect fruits from the soil surface would mean that even the short *Trifolium spp.* and *Melilotus spp.* would not score poorly for machine harvestability. There is a substantial amount of user judgement to assign the values for the utility functions. This makes DEXi flexible and adaptable but could negatively introduce misjudgment. In the future, experiments to evaluate the effect of certain cover crop species or combinations on the olive yield or quality or on soil health could be included to improve the evaluation of the best species for olive farming.

The use of DEXi was not essential for the study, but it certainly simplified a large amount of data. DEXi allows qualitative values and this was key to being able to include trait measurements that were quantitative (converted to a qualitative category) or qualitative (categories of expert opinion). Setting up the functions in DEXi is straightforward and the designer is available for user support when needed.

Additionally, DEXi provides several graphic displays and summary tables of the results which are helpful in understanding and interpreting the selection result. Most importantly, DEXi allowed us to compare “competing” traits. Low plant height is a desirable trait for a cover crop, but if a species is too short for the combine to harvest the seeds, it is less suitable for seed farming. Using *C. arvensis* as an example, we

viewed it as an ideal cover crop because it has an early and short life cycle, establishes very well from seeds and is low in stature. However, the extended dispersal window and polymorphic, irregularly shaped fruits make it less suitable for seed farming because there is not a single ideal harvest period and the fruits are difficult to separate from inert matter and do not flow well.

The user interface of DEXi is user-friendly and the attributes and functions can be updated, making this a practical tool which can be used by personnel at native seed companies in conjunction with farmers to create seed mixes for each orchard's specific conditions. Another advantage of this tool is that it can be adapted to select native species for use as cover crops for other woody crops, such as almonds and vineyards. Again, one of the key components to this tool is including the practical consideration of seed farming and that a quality and affordable supply of seeds can be produced, by evaluating the seed farming traits. This case study is the first species selection protocol we are aware of that considers suitability to seed farming along with consideration of functional goals and the end use of the plants.

In an initial case study to evaluate 30 native species for suitability as cover crops in olive orchards and to seed farming, the DEXi software was a practical and effective method for species selection. Twenty native forbs have the characteristics of suitable cover crops for protecting the degraded agroecosystems of Mediterranean olive orchards against soil loss, pathogens and insect pests. Just as critical, these 20 species can be cultivated for seed farming to produce the seeds needed for the restoration.

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Tables and Figures

Table 1. Base attributes and respective scale values and frequencies. The number of species (options) does not equal 30 in cases where data was missing or not available for that attribute. DEXi can still calculate aggregate functions when data is missing.

Base attribute	Scale values and frequencies				n
	less desirable <----->		more desirable <----->		
1.1.1.1 Trafficability (plant height)	Poor 1	Fair 4	Good 21	Excellent 3	29
1.1.1.2.1 Seasonal Growth (weeks to onset of maturity)	Poor 0	Fair 16	Good 7	Excellent 4	27
1.1.1.2.2 Contained (growth habit)	Poor 3		Good 15	Excellent 12	30
1.1.2.1.1 Non-competitive for water (short life cycle)		Fair 19	Good 7	Excellent 1	27
1.1.2.1.2 Non-competitive for nitrogen (plant family)		Fair 0	Good 22	Excellent 8	30
1.1.2.2.1.1 Generalist Predators	Poor 16			Very Good 10 Excellent 3	29
1.1.2.2.1.2 Parasitoids	Poor 22		Good 7	Very Good 0	29
1.1.2.2.1.3.1 Herbivore	Poor 0		Good 29		29
1.1.2.2.1.3.2 Detrivore	Poor 11		Good 18		29
1.1.2.2.1.3.3 Pollinator	Poor 29		Good 0		29
1.1.2.2.2 Non-host of Verticillium pathogen (database of host taxa)	Poor 1	Fair 17	Good 12	Excellent 0	30
1.2.1.1.1 Seed size	Difficult 12			Easy 18	30
1.2.1.1.2 Seed shape	Difficult 5			Easy 25	30
1.2.1.2.1 Fruit height	Difficult 6			Easy 21	27
1.2.1.2.2 Clear harvest window (weeks from maturity to harvest)	Difficult 4		Moderate 12	Easy 11	27
1.2.1.3.1 Seeds separate from fruits (expert classification)	Difficult 6		Moderate 8	Easy 15	29
1.2.1.3.2 Seeds separable from inert material (expert classification)	Difficult 7			Easy 22	29
1.2.2.1.1 Non-shattering (dehiscence)	Difficult 14			Easy 15	29
1.2.2.1.2 Fruits and seeds stay on the plant (dispersal window)	Difficult 16			Easy 10	26
1.2.2.2.1 Yield (grams per square meter)	Low 11		Moderate 8	High 6	25
1.2.2.2.2 Demand (frequency in the market)	Low 10		Moderate 12	High 8	30

Table 2. The values for insect functional group (FG) are compound. They combine the relative benefit of the FG to the olive crop with the degree of association between FG and the plant host.

		Degree of association		
		Low	Medium	High
Functional group and relative value	Generalist Predator (Best)	Poor	Very Good	Excellent
	Parasitoid (Very Good)	Poor	Good	Very Good
	Herbivore (Good)	Poor	Good	Good
	Detritivore (Good)	Poor	Good	Good
	Pollinator (Good)	Poor	Good	Good

Table 3. Evaluation values. Species indicated with § have multiple possible values due to missing data because they were poorly established in field trials during the * means all values are possible.

Scientific Name	Family	Suitability Index	Evaluation Result	
			1.1 Olive Farming	1.2 Seed Farming
<i>Anarrhinum bellidifolium</i> (L.) Willd. §	Plantaginaceae	*	*	*
<i>Anthemis cotula</i> L.	Asteraceae	Fair	Fair	Fair
<i>Anthyllis vulneraria</i> L.	Fabaceae	Fair; Good	Good	Poor; Fair
<i>Biscutella auriculata</i> L.	Brassicaceae	Good	Good	Fair
<i>Calendula arvensis</i> M.Bieb.	Asteraceae	Fair	Excellent	Poor
<i>Capsella bursa-pastoris</i> (L.) Medik.	Brassicaceae	Good	Good	Fair
<i>Cleonia lusitanica</i> (L.) L.	Lamiaceae	Excellent	Good	Excellent
<i>Crepis capillaris</i> (L.) Wallr.	Asteraceae	Fair	Fair	Fair
<i>Echium plantagineum</i> L.	Boraginaceae	Good	Fair	Excellent
<i>Glebionis segetum</i> (L.) Fourr.	Asteraceae	Good	Fair	Excellent
<i>Helianthemum ledifolium</i> (L.) Mill. §	Cistaceae	Fair; Good; Excellent	Fair; Good; Excellent	Good; Excellent
<i>Medicago orbicularis</i> (L.) Bartal.	Fabaceae	Good	Good	Fair
<i>Medicago polymorpha</i> L.	Fabaceae	Good	Good	Fair
<i>Misopates orontium</i> (L.) Raf.	Plantaginaceae	Excellent	Good	Excellent
<i>Moricandia moricandioides</i> (Boiss.) Heywood	Brassicaceae	Good	Fair	Excellent
<i>Nigella damascena</i> L.	Ranunculaceae	Excellent	Good	Excellent
<i>Papaver dubium</i> L.	Papaveraceae	Good	Good	Fair
<i>Salvia verbenaca</i> L.	Lamiaceae	Excellent	Good	Excellent
<i>Scabiosa atropurpurea</i> L.	Caprifoliaceae	Fair	Fair	Fair
<i>Silene colorata</i> Poir.	Caryophyllaceae	Good	Good	Good
<i>Silene gallica</i> L.	Caryophyllaceae	Fair	Fair	Good
<i>Stachys arvensis</i> (L.) L.	Lamiaceae	Good	Fair	Excellent
<i>Tolpis barbata</i> (L.) Gaertn.	Asteraceae	Poor	Fair	Poor
<i>Tordylium maximum</i> L.	Apiaceae	Good	Fair	Excellent
<i>Trifolium angustifolium</i> L.	Fabaceae	Excellent	Good	Excellent
<i>Trifolium hirtum</i> All.	Fabaceae	Good	Good	Fair
<i>Trifolium lappaceum</i> L.	Fabaceae	Good	Good	Fair
<i>Trifolium stellatum</i> L.	Fabaceae	Good	Excellent	Fair
<i>Tuberaria guttata</i> (L.) Fourr. §	Cistaceae	Fair; Good; Excellent	Fair; Good; Excellent	Fair; Good; Excellent
<i>Vaccaria hispanica</i> (Mill.) Rauschert	Caryophyllaceae	Good	Fair	Excellent

Attribute	Description
Suitability Index	Based on suitability to both 1.1 Olive Farming and 1.2 Seed Farming
1.1 Olive Farming	
1.1.1 Crop Management	Operations the farmer makes in the orchard
1.1.1.1 Trafficability (plant height)	Equipment can move about in the field
1.1.1.2 Cover	Effective and low-maintenance cover
1.1.1.2.1 Seasonal Growth (weeks to onset of maturity)	Develops quickly
1.1.1.2.2 Contained (growth habit)	Limited spread which does not encroach on crop
1.1.2 Biodiversity	
1.1.2.1 Non-competitive with crop	
1.1.2.1.1 Non-competitive for water (short life cycle)	Plants disperse seeds into soil seed bank and senesce by late Spring
1.1.2.1.2 Non-competitive for nitrogen (plant family)	Provision or use of nitrogen based on plant family
1.1.2.2 Beneficial biota	
1.1.2.2.1 Insects and food web (functional group + degree of association)	Three levels of beneficial insect functional groups
1.1.2.2.1.1 Generalist Predators	
1.1.2.2.1.2 Parasitoids	
1.1.2.2.1.3 Herbivores-Detritivores-Pollinators	
1.1.2.2.1.3.1 Herbivore	
1.1.2.2.1.3.2 Detritivore	
1.1.2.2.1.3.3 Pollinator	
1.1.2.2.2 Non-host of Verticillium pathogen (database of host taxa)	Degree to which a taxon is known to host Verticillium dahliae
1.2 Seed Farming	
1.2.1 Scalable through mechanization	
1.2.1.1 Ease of sowing with planter	
1.2.1.1.1 Seed size	Proper metering and flow through planter
1.2.1.1.2 Seed shape	Proper metering and flow through planter
1.2.1.2 Ease of harvest with combine	
1.2.1.2.1 Fruit height	Fruits are held high enough off the ground that the combine can harvest them
1.2.1.2.2 Clear harvest window (weeks from maturity to harvest)	Indifferential ripening/dispersal is not too extended
1.2.1.3 Ease of seed cleaning	
1.2.1.3.1 Seeds separate from fruits (expert classification)	Ease of releasing seeds from fruit
1.2.1.3.2 Seeds separable from inert material (expert classification)	Ease of separating seeds from inert material
1.2.2 Amenable to cultivation	
1.2.2.1 Seeds stay on the plant	
1.2.2.1.1 Non-shattering (dehiscence)	Fruits do not release seeds while on the plant
1.2.2.1.2 Fruits and seeds stay on the plant (dispersal window)	Period of time that ripe fruits/seeds stay on the plant
1.2.2.2 Yield and Value	
1.2.2.2.1 Yield (grams per square meter)	
1.2.2.2.2 Demand (frequency in the market)	Count of Spanish native seed companies offering the species

Figure 1. Attribute tree from DEXi showing the hierarchy and dependencies of the attributes. Base attributes are at the lowest levels and shown in non-bold text. For each species (option) we loaded the values for each base attribute. The values for the base attributes are aggregated through a defined set of function rules to determine the value of the next attribute on up the tree.

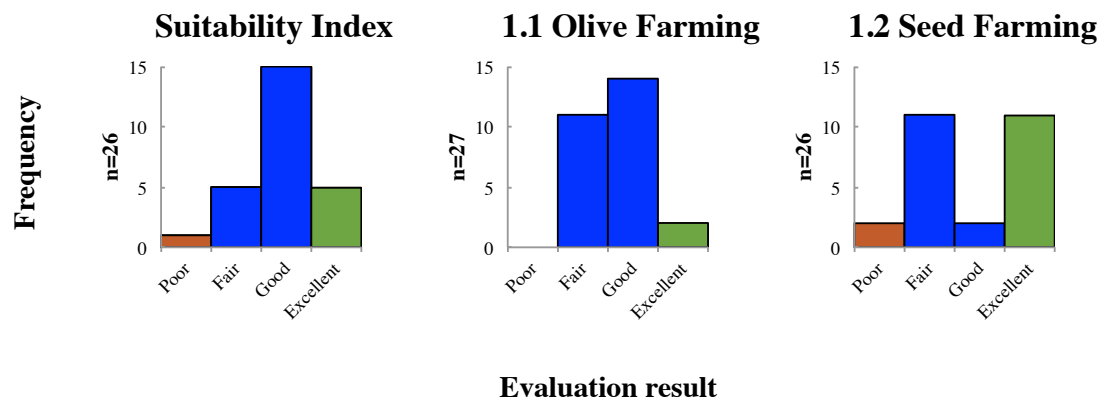


Figure 2. Suitability Index and the two main aggregate functions.

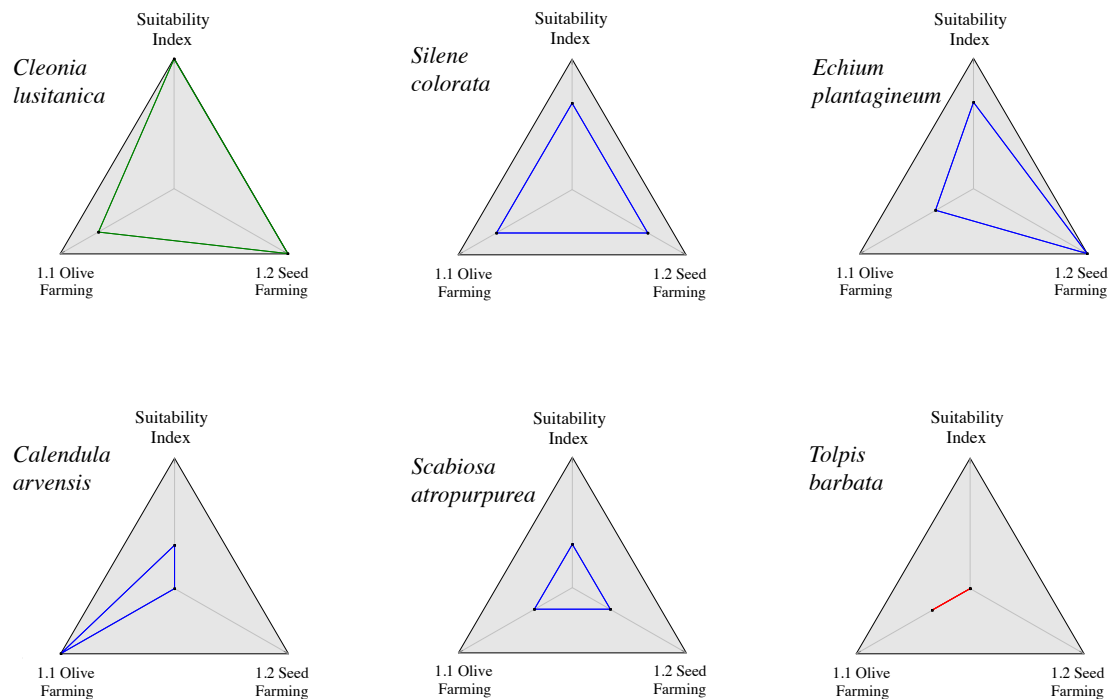


Figure 3. The DEXi software plots radial charts for 3 or more selected attributes. Each axis has 4 points, from “Poor” in the center to “Excellent” at the apex. As a summary, here are examples from 6 species showing how the values for the lower attributes of Olive Farming and Seed Farming aggregate to the Suitability Index. For *C. lusitanica*, the SI is Excellent and so were 1.1 and 1.2. The SI of *S. colorata* and *E. plantagineum* are both “Good” although the values of lower attributes were different between species. Likewise, *Calendula arvensis* and *S. atropurpurea* are both “Fair” with the first combining Excellent with Fair and the latter Good with Good. Finally, *Tolpis barbata* is an example of “Poor” SI because both lower attributes are “Poor” as well.

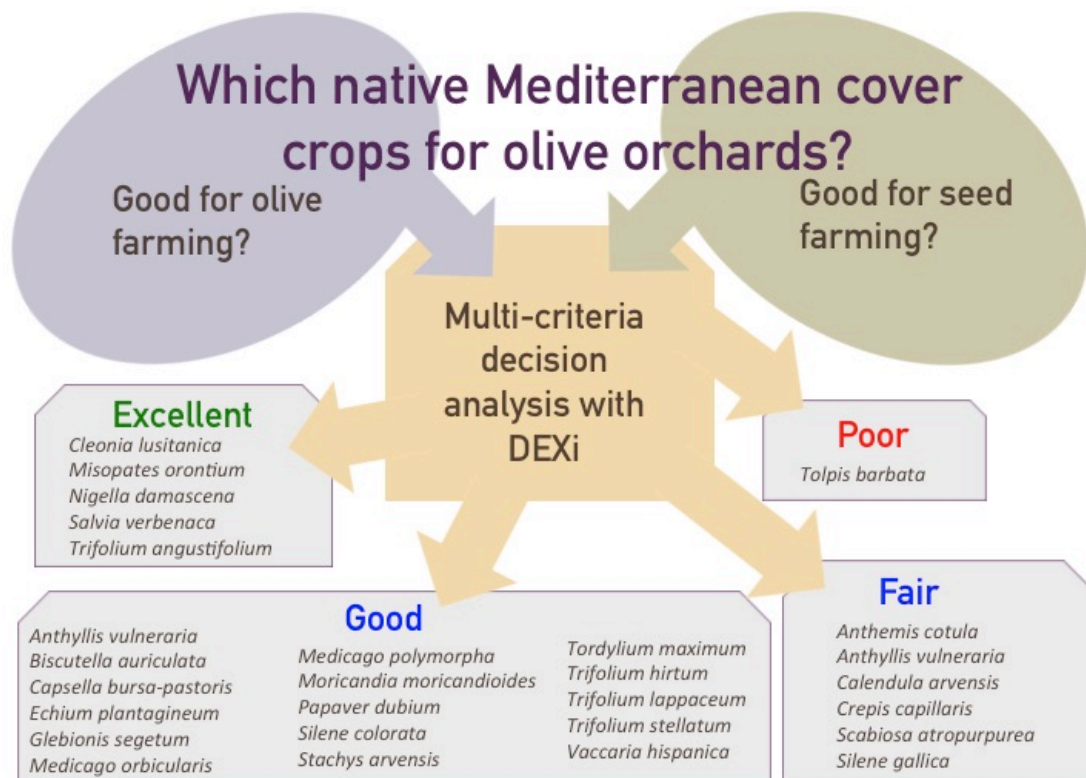


Figure 4. Overall method and results of the species selection evaluation.

Supplementary Material

Output of DEXi report

DEXi		20170814 Suitability Index.dxi 15/08/2017	Page 1
Attribute tree			
Attribute	Description		
Suitability Index	Based on suitability to both 1.1 Olive Farming and 1.2 Seed Farming		
1.1 Olive Farming			
1.1.1 Crop Management	Operations the farmer makes in the orchard		
1.1.1.1 Trafficability (plant height)	Equipment can move about in the field		
1.1.1.2 Cover	Effective and low-maintenance cover		
1.1.1.2.1 Seasonal Growth (weeks to onset of maturity)	Develops quickly		
1.1.1.2.2 Contained (growth habit)	Limited spread which does not encroach on crop		
1.1.2 Biodiversity			
1.1.2.1 Non-competitive with crop	Plants disperse seeds into soil seed bank and senesce by late Spring		
1.1.2.1.1 Non-competitive for water (short life cycle)			
1.1.2.1.2 Non-competitive for nitrogen (plant family)	Provision or use of nitrogen based on plant family		
1.1.2.2 Beneficial biota			
1.1.2.2.1 Insects and food web (functional group + degree of association)	Three levels of beneficial insect functional groups		
1.1.2.2.1.1 Generalist Predators			
1.1.2.2.1.2 Parasitoids			
1.1.2.2.1.3 Herbivores-Detritivores-Pollinators			
1.1.2.2.1.3.1 Herbivore			
1.1.2.2.1.3.2 Detritivore			
1.1.2.2.1.3.3 Pollinator			
1.1.2.2.2 Non-host of Verticillium pathogen (database of host taxa)	Degree to which a taxon is known to host Verticillium dahliae		
1.2 Seed Farming			
1.2.1 Scalable through mechanization			
1.2.1.1 Ease of sowing with planter	Proper metering and flow through planter		
1.2.1.1.1 Seed size	Proper metering and flow through planter		
1.2.1.1.2 Seed shape			
1.2.1.2 Ease of harvest with combine	Fruits are held high enough off the ground that the combine can harvest them		
1.2.1.2.1 Fruit height	Indiffential ripening/dispersal is not too extended		
1.2.1.2.2 Clear harvest window (weeks from maturity to harvest)			
1.2.1.3 Ease of seed cleaning	Ease of releasing seeds from fruit		
1.2.1.3.1 Seeds separate from fruits (expert classification)	Ease of separating seeds from inert material		
1.2.1.3.2 Seeds separable from inert material (expert classification)			
1.2.2 Amenable to cultivation			
1.2.2.1 Seeds stay on the plant	Fruits do not release seeds while on the plant		
1.2.2.1.1 Non-shattering (dehiscence)	Period of time that ripe fruits/seeds stay on the plant		
1.2.2.1.2 Fruits and seeds stay on the plant (dispersal window)			
1.2.2.2 Yield and Value			
1.2.2.2.1 Yield (grams per square meter)			
1.2.2.2.2 Demand (frequency in the market)	Count of Spanish native seed companies offering the species		

Scales

Attribute	Scale
Suitability Index	Poor ; Fair; Good; Excellent
1.1 Olive Farming	Poor ; Fair; Good; Excellent
1.1.1 Crop Management	Poor ; Fair; Good; Excellent
1.1.1.1 Trafficability (plant height)	Poor ; Fair; Good; Excellent
1.1.1.2 Cover	Poor ; Fair; Good; Excellent
1.1.1.2.1 Seasonal Growth (weeks to onset of maturity)	Poor ; Fair; Good; Excellent
1.1.1.2.2 Contained (growth habit)	Poor ; Fair; Good; Excellent
1.1.2 Biodiversity	Poor ; Fair; Good; Excellent
1.1.2.1 Non-competitive with crop	Poor ; Fair; Good; Excellent
1.1.2.1.1 Non-competitive for water (short life cycle)	Fair ; Good; Excellent
1.1.2.1.2 Non-competitive for nitrogen (plant family)	Fair ; Good; Excellent
1.1.2.2 Beneficial biota	Poor ; Fair; Good; Excellent
1.1.2.2.1 Insects and food web (functional group + degree of association)	Poor ; Good; Very Good; Excellent
1.1.2.2.1.1 Generalist Predators	Poor ; Very Good; Excellent
1.1.2.2.1.2 Parasitoids	Poor ; Good; Very Good
1.1.2.2.1.3 Herbivores-Detritivores-Pollinators	Poor ; Good; Very Good; Excellent
1.1.2.2.1.3.1 Herbivore	Poor ; Good
1.1.2.2.1.3.2 Detritivore	Poor ; Good
1.1.2.2.1.3.3 Pollinator	Poor ; Good
1.1.2.2.2 Non-host of Verticillium pathogen (database of host taxa)	Poor ; Fair; Good
1.2 Seed Farming	Poor ; Fair; Good; Excellent
1.2.1 Scalable through mechanization	Poor ; Fair; Good; Excellent
1.2.1.1 Ease of sowing with planter	Poor ; Fair; Good; Excellent
1.2.1.1.1 Seed size	Difficult ; Easy
1.2.1.1.2 Seed shape	Difficult ; Easy
1.2.1.2 Ease of harvest with combine	Poor ; Fair; Good; Excellent
1.2.1.2.1 Fruit height	Difficult ; Easy
1.2.1.2.2 Clear harvest window (weeks from maturity to harvest)	Difficult ; Moderate; Easy
1.2.1.3 Ease of seed cleaning	Difficult ; Moderate; Easy
1.2.1.3.1 Seeds separate from fruits (expert classification)	Difficult ; Moderate; Easy
1.2.1.3.2 Seeds separate from inert material (expert classification)	Difficult ; Easy
1.2.2 Amenable to cultivation	Difficult ; Moderate; Easy
1.2.2.1 Seeds stay on the plant	Poor ; Good; Excellent
1.2.2.1.1 Non-shattering (dehiscence)	Difficult ; Easy
1.2.2.1.2 Fruits and seeds stay on the plant (dispersal window)	Difficult ; Easy
1.2.2.2 Yield and Value	Low ; Moderate; High
1.2.2.2.1 Yield (grams per square meter)	Low ; Moderate; High
1.2.2.2.2 Demand (frequency in the market)	Low ; Moderate; High

Suitability Index

Based on suitability to both 1.1 Olive Farming and 1.2 Seed Farming

1. **Poor**
2. Fair
3. Good
4. **Excellent**

1.1 Olive Farming

1. **Poor**
2. Fair
3. Good
4. **Excellent**

1.1.1 Crop Management

Operations the farmer makes in the orchard

1. **Poor**
2. Fair
3. Good
4. **Excellent**

1.1.1.1 Trafficability (plant height)

Equipment can move about in the field

1. **Poor**
2. Fair
3. Good
4. **Excellent**

1.1.1.2 Cover

Effective and low-maintenance cover

1. **Poor**
2. Fair
3. Good
4. **Excellent**

1.1.1.2.1 Seasonal Growth (weeks to onset of maturity)

Develops quickly

1. **Poor**
2. Fair
3. Good
4. **Excellent**

1.1.1.2.2 Contained (growth habit)

Limited spread which does not encroach on crop

1. **Poor**
2. Good
3. **Excellent**

1.1.2 Biodiversity

1. **Poor**
2. Fair
3. Good
4. **Excellent**

1.1.2.1 Non-competitive with crop

1. **Poor**
2. Fair
3. Good
4. **Excellent**

1.1.2.1.1 Non-competitive for water (short life cycle)

Plants disperse seeds into soil seed bank and senesce by late Spring

1. **Fair**
2. Good
3. **Excellent**

1.1.2.1.2 Non-competitive for nitrogen (plant family)

Provision or use of nitrogen based on plant family

1. **Fair**
2. Good
3. **Excellent**

1.1.2.2 Beneficial biota

1. **Poor**
2. Fair
3. Good
4. **Excellent**

1.1.2.2.1 Insects and food web (functional group + degree of association)

Three levels of beneficial insect functional groups

1. **Poor**
2. Good
3. Very Good
4. **Excellent**

1.1.2.2.1.1 Generalist Predators

1. **Poor**
2. Very Good
3. **Excellent**

1.1.2.2.1.2 Parasitoids

1. **Poor**
2. Good
3. **Very Good**

1.1.2.2.1.3 Herbivores-Detritivores-Pollinators

1. **Poor**
2. Good
3. Very Good
4. **Excellent**

1.1.2.2.1.3.1 Herbivore

1. **Poor**
2. **Good**

1.1.2.2.1.3.2 Detrivore

1. **Poor**
2. **Good**

1.1.2.2.1.3.3 Pollinator

1. **Poor**
2. **Good**

1.1.2.2.2 Non-host of Verticillium pathogen (database of host taxa)

Degree to which a taxon is known to host Verticillium dahliae

1. **Poor**
2. Fair
3. **Good**

1.2 Seed Farming

1. **Poor**
2. Fair
3. Good
4. **Excellent**

1.2.1 Scalable through mechanization

1. **Poor**
2. Fair
3. Good
4. **Excellent**

1.2.1.1 Ease of sowing with planter

1. **Poor**
2. Fair
3. Good
4. **Excellent**

1.2.1.1.1 Seed size

Proper metering and flow through planter

1. **Difficult**
2. **Easy**

1.2.1.1.2 Seed shape

Proper metering and flow through planter

1. **Difficult**
2. **Easy**

1.2.1.2 Ease of harvest with combine

1. **Poor**
2. Fair
3. Good
4. *Excellent*

1.2.1.2.1 Fruit height

Fruits are held high enough off the ground that the combine can harvest them

1. **Difficult**
2. *Easy*

1.2.1.2.2 Clear harvest window (weeks from maturity to harvest)

Indifferential ripening/dispersal is not too extended

1. **Difficult**
2. Moderate
3. *Easy*

1.2.1.3 Ease of seed cleaning

1. **Difficult**
2. Moderate
3. *Easy*

1.2.1.3.1 Seeds separate from fruits (expert classification)

Ease of releasing seeds from fruit

1. **Difficult**
2. Moderate
3. *Easy*

1.2.1.3.2 Seeds separable from inert material (expert classification)

Ease of separating seeds from inert material

1. **Difficult**
2. *Easy*

1.2.2 Amenable to cultivation

1. **Difficult**
2. Moderate
3. *Easy*

1.2.2.1 Seeds stay on the plant

1. **Poor**
2. Good
3. *Excellent*

1.2.2.1.1 Non-shattering (dehiscence)

Fruits do not release seeds while on the plant

1. **Difficult**
2. *Easy*

1.2.2.1.2 Fruits and seeds stay on the plant (dispersal window)

Period of time that ripe fruits/seeds stay on the plant

1. **Difficult**
2. *Easy*

1.2.2.2 Yield and Value

1. **Low**
2. Moderate
3. *High*

1.2.2.2.1 Yield (grams per square meter)

1. **Low**
2. Moderate
3. *High*

1.2.2.2.2 Demand (frequency in the market)

Count of Spanish native seed companies offering the species

1. **Low**
2. Moderate
3. *High*

Functions

Attribute	Rules	Defined	Determined	Values
Suitability Index				
1.1 Olive Farming	16/16	100,00%	100,00%	Poor:3,Fair:4,Good:4,Excellent:3
1.1.1 Crop Management	16/16	100,00%	100,00%	Poor:3,Fair:7,Good:3,Excellent:3
1.1.1.1 Trafficability (plant height)	16/16	100,00%	100,00%	Poor:3,Fair:3,Good:5,Excellent:5
1.1.1.2 Cover	12/12	100,00%	100,00%	Poor:3,Fair:3,Good:3,Excellent:3
1.1.1.2.1 Seasonal Growth (weeks to onset of maturity)				
1.1.1.2.2 Contained (growth habit)	16/16	100,00%	100,00%	Poor:2,Fair:6,Good:5,Excellent:3
1.1.2 Biodiversity	9/9	100,00%	100,00%	Poor:0,Fair:4,Good:2,Excellent:3
1.1.2.1 Non-competitive with crop				
1.1.2.1.1 Non-competitive for water (short life cycle)	12/12	100,00%	100,00%	Poor:4,Fair:3,Good:3,Excellent:2
1.1.2.1.2 Non-competitive for nitrogen (plant family)	36/36	100,00%	100,00%	Poor:10,Good:12,Very Good:9,Excellent:5
1.1.2.2 Beneficial biota				
1.1.2.2.1 Insects and food web (functional group + degree of association)	8/8	100,00%	100,00%	Poor:4,Good:4,Very Good:0,Excellent:0
1.1.2.2.1.1 Generalist Predators				
1.1.2.2.1.2 Parasitoids				
1.1.2.2.1.3 Herbivores-Detritivores-Pollinators				
1.1.2.2.1.3.1 Herbivore				
1.1.2.2.1.3.2 Detritivore				
1.1.2.2.1.3.3 Pollinator				
1.1.2.2.2 Non-host of Verticillium pathogen (database of host taxa)	12/12	100,00%	100,00%	Poor:3,Fair:5,Good:1,Excellent:3
1.2 Seed Farming	48/48	100,00%	100,00%	Poor:10,Fair:22,Good:10,Excellent:6
1.2.1 Scalable through mechanization	4/4	100,00%	100,00%	Poor:1,Fair:1,Good:1,Excellent:1
1.2.1.1 Ease of sowing with planter				
1.2.1.1.1 Seed size				
1.2.1.1.2 Seed shape				
1.2.1.2 Ease of harvest with combine	6/6	100,00%	100,00%	Poor:3,Fair:1,Good:1,Excellent:1
1.2.1.2.1 Fruit height				
1.2.1.2.2 Clear harvest window (weeks from maturity to harvest)	6/6	100,00%	100,00%	Difficult:2,Moderate:2,Easy:2
1.2.1.3 Ease of seed cleaning				
1.2.1.3.1 Seeds separate from fruits (expert classification)	9/9	100,00%	100,00%	Difficult:2,Moderate:4,Easy:3
1.2.1.3.2 Seeds separate from inert material (expert classification)	4/4	100,00%	100,00%	Poor:1,Good:2,Excellent:1
1.2.2 Amenable to cultivation				
1.2.2.1 Seeds stay on the plant	9/9	100,00%	100,00%	Difficult:2,Moderate:4,Easy:3
1.2.2.1.1 Non-shattering (dehiscence)	4/4	100,00%	100,00%	Poor:1,Good:2,Excellent:1
1.2.2.1.2 Fruits and seeds stay on the plant (dispersal window)				
1.2.2.2 Yield and Value	9/9	100,00%	100,00%	Low:2,Moderate:4,High:3
1.2.2.2.1 Yield (grams per square meter)				
1.2.2.2.2 Demand (frequency in the market)				

Tables

1.1 Olive Farming	1.2 Seed Farming	Suitability Index
1 Poor	*	Poor
2 <=Fair	Poor	Poor
3 Fair	Fair:Good	Fair
4 >=Good	Poor	Fair
5 Fair	Excellent	Good
6 Good	Fair:Good	Good
7 >=Good	Fair	Good
8 >=Good	Excellent	Excellent
9 Excellent	>=Good	Excellent

1.1.1 Crop Management	1.1.2 Biodiversity	1.1 Olive Farming
1 Poor	<=Fair	Poor
2 <=Fair	Poor	Poor
3 Poor	>=Good	Fair
4 <=Fair	Good	Fair
5 Fair	Fair:Good	Fair
6 Fair:Good	Fair	Fair
7 Good	<=Fair	Fair
8 >=Good	Poor	Fair
9 Fair	Excellent	Good
10 Good	Good	Good
11 Excellent	Fair	Good
12 >=Good	Excellent	Excellent
13 Excellent	>=Good	Excellent

1.1.1.1 Trafficability (plant height)	1.1.1.2 Cover	1.1.1 Crop Management
1 Poor	<=Fair	Poor
2 <=Fair	Poor	Poor
3 Poor	Good	Fair
4 Fair	Fair	Fair
5 Good	Poor	Fair
6 Poor	Excellent	Good
7 Fair:Good	Good	Good
8 Good	Fair:Good	Good
9 Excellent	Poor	Good
10 >=Fair	Excellent	Excellent
11 Excellent	>=Fair	Excellent

1.1.1.2.1 Seasonal Growth (weeks to onset of maturity)	1.1.1.2.2 Contained (growth habit)	1.1.1.2 Cover
1 Poor	*	Poor
2 Fair	<=Good	Fair
3 Fair:Good	Poor	Fair
4 Fair	Excellent	Good
5 Good	Good	Good
6 Excellent	Poor	Good
7 >=Good	Excellent	Excellent
8 Excellent	>=Good	Excellent

1.1.2.1 Non-competitive with crop	1.1.2.2 Beneficial biota	1.1.2 Biodiversity
1 Poor	<=Fair	Poor
2 Poor	>=Good	Fair
3 <=Fair	Good	Fair
4 Fair	<=Good	Fair
5 Fair:Good	Poor	Fair
6 Fair	Excellent	Good
7 Good	Fair:Good	Good
8 >=Good	Fair	Good
9 Excellent	<=Fair	Good
10 >=Good	Excellent	Excellent
11 Excellent	>=Good	Excellent

1.1.2.1.1 Non-competitive for water (short life cycle)		1.1.2.1.2 Non-competitive for nitrogen (plant family)		1.1.2.1 Non-competitive with crop	
1	<=Good	<=Good	*	Fair	Fair
2	Fair	Excellent	Excellent	Good	Good
3	Excellent	Fair	Fair	Good	Good
4	>=Good	Excellent	Excellent	Excellent	Excellent
5	Excellent	>=Good	>=Good	Excellent	Excellent

1.1.2.2.1 Insects and food web (functional group + degree of association)		1.1.2.2.2 Non-host of Verticillium pathogen (database of host taxa)		1.1.2.2 Beneficial biota	
1	*	+	+	Poor	Poor
2	Poor	>=Fair	>=Fair	Fair	Fair
3	<=Good	Fair	Fair	Fair	Fair
4	Good	Good	Good	Good	Good
5	>=Very Good	Fair	Fair	Good	Good
6	>=Very Good	Good	Good	Excellent	Excellent

1.1.2.2.1.1 Generalist Predators		1.1.2.2.1.2 Parasitoids		1.1.2.2.1.3 Herbivores-Detritivores-Pollinators		1.1.2.2.1 Insects and food web (functional group + degree of association)	
1	Poor	<=Good	*	Poor	Poor	+	+
2	Poor	*	<=Good	+	Poor	+	+
3	Poor	Very Good	>=Very Good	+	Good	+	+
4	Very Good	Poor	*	+	Good	+	+
5	Very Good	<=Good	<=Good	+	Good	+	+
6	Very Good	*	Poor	+	Good	+	+
7	>=Very Good	Poor	<=Good	+	Good	+	+
8	>=Very Good	<=Good	Poor	+	Good	+	+
9	Very Good	>=Good	>=Very Good	+	Very Good	+	+
10	>=Very Good	Good	Very Good	+	Very Good	+	+
11	Very Good	Very Good	>=Good	+	Very Good	+	+
12	Excellent	Poor	>=Very Good	+	Very Good	+	+
13	Excellent	<=Good	Very Good	+	Very Good	+	+
14	Excellent	Good	Good:Very Good	+	Very Good	+	+
15	Excellent	>=Good	Excellent	+	Excellent	+	+
16	Excellent	Very Good	*	+	Excellent	+	+

1.1.2.2.1.3.1 Herbivore		1.1.2.2.1.3.2 Detritivore		1.1.2.2.1.3.3 Pollinator		1.1.2.2.1.3 Herbivores-Detritivores-Pollinators	
1	Poor	Poor	*	Poor	Poor	+	+
2	Poor	*	Poor	+	Poor	+	+
3	*	Poor	Poor	+	Poor	+	+
4	*	Good	Good	+	Good	+	+
5	Good	*	Good	+	Good	+	+
6	Good	Good	*	+	Good	+	+

1.2.1 Scalable through mechanization		1.2.2 Amenable to cultivation		1.2 Seed Farming	
1	Poor	+	+	Poor	Poor
2	Fair	*	*	Fair	Fair
3	>=Fair	Difficult	Difficult	Fair	Fair
4	Good	Moderate	Moderate	Good	Good
5	>=Good	Easy	Easy	Excellent	Excellent
6	Excellent	>=Moderate	>=Moderate	Excellent	Excellent

1.2.1.1 Ease of sowing with planter		1.2.1.2 Ease of harvest with combine		1.2.1.3 Ease of seed cleaning		1.2.1 Scalable through mechanization	
1	Poor	+	+	+	+	Poor	Poor
2	Poor	*	*	Difficult	Difficult	Poor	Poor
3	<=Fair	<=Fair	<=Fair	Difficult	Difficult	Poor	Poor
4	*	Poor	Poor	Difficult	Difficult	Poor	Poor
5	Poor	Fair:Good	>=Moderate	Fair	Fair	+	+
6	Poor	>=Fair	Moderate	Fair	Fair	+	+
7	<=Fair	Fair	>=Moderate	Fair	Fair	+	+
8	<=Fair	Fair:Good	Moderate	Fair	Fair	+	+
9	Fair	<=Fair	>=Moderate	Fair	Fair	+	+
10	Fair	<=Good	Moderate	Fair	Fair	+	+
11	>=Fair	Poor	>=Moderate	Fair	Fair	+	+
12	Fair	Good	<=Moderate	Fair	Fair	+	+
13	>=Fair	>=Good	Difficult	Fair	Fair	+	+
14	>=Good	>=Fair	Difficult	Fair	Fair	+	+
15	<=Fair	Excellent	Easy	Good	Good	+	+
16	Fair	>=Good	Easy	Good	Good	+	+
17	Fair	Excellent	>=Moderate	Good	Good	+	+
18	Fair:Good	Excellent	Moderate	Good	Good	+	+
19	Good	>=Fair	Moderate	Good	Good	+	+
20	>=Good	Fair	>=Moderate	Good	Good	+	+
21	>=Good	>=Good	Easy	Excellent	Excellent	+	+
22	Excellent	>=Good	>=Moderate	Excellent	Excellent	+	+

1.2.1.1.1 Seed size		1.2.1.1.2 Seed shape		1.2.1.1.1 Ease of sowing with planter	
1	Difficult	Difficult	Poor	+	+
2	Easy	Difficult	Fair	+	+
3	Difficult	Easy	Good	+	+
4	Easy	Easy	Excellent	+	+

1.2.1.2.1 Fruit height		1.2.1.2.2 Clear harvest window (weeks from maturity to harvest)		1.2.1.2 Ease of harvest with combine	
1	Difficult	+	+	Poor	Poor
2	Easy	Difficult	Fair	Fair	Fair
3	Easy	Moderate	Moderate	Good	Good
4	Easy	Easy	Excellent	Excellent	Excellent

1.2.1.3.1 Seeds separate from fruits (expert classification)		1.2.1.3.2 Seeds separable from inert material (expert classification)		1.2.1.3 Ease of seed cleaning	
1	<=Moderate	Difficult	Difficult	Difficult	Difficult
2	Difficult	Easy	Difficult	Moderate	Moderate
3	Easy	Easy	Difficult	Moderate	Moderate
4	>=Moderate	Easy	Easy	Easy	Easy

1.2.2.1 Seeds stay on the plant		1.2.2.2 Yield and Value		1.2.2 Amenable to cultivation	
1	Poor	<=Moderate	Difficult	+	+
2	Poor	High	Moderate	+	+
3	Good	<=Moderate	Moderate	+	+
4	>=Good	Low	Moderate	+	+
5	>=Good	High	Easy	+	+
6	Excellent	>=Moderate	Easy	+	+

1.2.2.1.1 Non-shattering (dehiscence)		1.2.2.1.2 Fruits and seeds stay on the plant (dispersal window)		1.2.2.1 Seeds stay on the plant	
1	Difficult	Difficult		Poor	
2	Difficult	Easy		Good	
3	Easy	Difficult		Good	
4	Easy	Easy		Excellent	

1.2.2.2.1 Yield (grams per square meter)		1.2.2.2.2 Demand (frequency in the market)		1.2.2.2 Yield and Value	
1	Low	<=Moderate		Low	
2	Low	High		Moderate	
3	Moderate	<=Moderate		Moderate	
4	>=Moderate	Low		Moderate	
5	>=Moderate	High		High	
6	High	>=Moderate		High	

Average weights

Attribute	Local	Global	Loc.norm.	Glob.norm.
Suitability Index				
1.1 Olive Farming	62	62	62	62
1.1.1 Crop Management	50	31	50	31
1.1.1.1 Trafficability (plant height)	50	16	50	16
1.1.1.2 Cover	50	16	50	16
1.1.1.2.1 Seasonal Growth (weeks to onset of maturity)	63	10	70	11
1.1.1.2.2 Contained (growth habit)	37	6	30	5
1.1.2 Biodiversity	50	31	50	31
1.1.2.1 Non-competitive with crop	61	19	61	19
1.1.2.1.1 Non-competitive for water (short life cycle)	50	10	50	10
1.1.2.1.2 Non-competitive for nitrogen (plant family)	50	10	50	10
1.1.2.2 Beneficial biota	39	12	39	12
1.1.2.2.1 Insects and food web (functional group + degree of association)	25	3	30	4
1.1.2.2.1.1 Generalist Predators	59	2	57	2
1.1.2.2.1.2 Parasitoids	27	1	26	1
1.1.2.2.1.3 Herbivores-Detritivores-Pollinators	14	0	18	1
1.1.2.2.1.3.1 Herbivore	33	0	33	0
1.1.2.2.1.3.2 Detritivore	33	0	33	0
1.1.2.2.1.3.3 Pollinator	33	0	33	0
1.1.2.2.2 Non-host of Verticillium pathogen (database of host taxa)	75	9	70	8
1.2 Seed Farming	38	38	38	38
1.2.1 Scalable through mechanization	62	23	68	26
1.2.1.1 Ease of sowing with planter	28	6	31	8
1.2.1.1.1 Seed size	33	2	33	3
1.2.1.1.2 Seed shape	67	4	67	5
1.2.1.2 Ease of harvest with combine	29	7	32	8
1.2.1.2.1 Fruit height	80	5	73	6
1.2.1.2.2 Clear-harvest window (weeks from maturity to harvest)	20	1	27	2
1.2.1.3 Ease of seed cleaning	43	10	36	9
1.2.1.3.1 Seeds separate from fruits (expert classification)	27	3	36	3
1.2.1.3.2 Seeds separable from inert material (expert classification)	73	7	64	6
1.2.2 Unamenable to cultivation	38	15	32	12
1.2.2.1 Seeds stay on the plant	57	8	57	7
1.2.2.1.1 Non-shattering (dehiscence)	50	4	50	3
1.2.2.1.2 Fruits and seeds stay on the plant (dispersal window)	50	4	50	3
1.2.2.2 Yield and Value	43	6	43	5
1.2.2.2.1 Yield (grams per square meter)	57	4	57	3
1.2.2.2.2 Demand (frequency in the market)	43	3	43	2

Evaluation results

Attribute	ANBE	ANCO	ANVU	BIAU	CAAR	CABU	CLLU	CRCA	ECPL	GLSE
Suitability Index	*	Fair	Fair, Good	Good	Fair	Good	Excellent	Fair	Good	Good
1.1 Olive Farming	*	Fair	Good	Good	Excellent	Excellent	Excellent	Good	Fair	Good
1.1.1 Crop Management	*	Fair	Good	Excellent	Excellent	Excellent	Excellent	Good	Fair	Good
1.1.1.1 Trafficability (plant height)	*	Fair	Good	Good	Good	Good	Excellent	Good	Fair	Good
1.1.1.2 Cover	Poor; Good; Excellent	Fair	Good	Excellent	Excellent	Excellent	Fair	Fair	Good	Fair
1.1.1.2.1 Seasonal Growth (weeks to onset of maturity)	*	Fair	Fair	Good	Excellent	Excellent	Fair	Fair	Good	Fair
1.1.1.2.2 Contained (growth habit)	Excellent	Fair	Good	Excellent	Good	Excellent	Good	Good	Fair	Good
1.1.2 Biodiversity	Fair; Excellent	Fair	Good	Fair	Good	Fair	Fair	Fair	Fair	Fair
1.1.2.1 Non-competitive with crop	*	Fair	Fair	Fair	Excellent	Good	Fair	Fair	Fair	Fair
1.1.2.1.1 Non-competitive for water (short life cycle)	*	Fair	Fair	Fair	Excellent	Good	Fair	Fair	Fair	Fair
1.1.2.1.2 Non-competitive for nitrogen (plant family)	Good	Good	Excellent	Good	Good	Good	Good	Good	Good	Good
1.1.2.2 Beneficial biota	Good	Good	Fair	Fair	Fair	Fair	Fair	Fair	Good	Fair
1.1.2.2.1 Insects and food web (functional group + degree of association)	Good	Very Good	Good	Good	Good	Poor	Poor	Good	Good	Good
1.1.2.2.1.1 Generalist Predators	Very Good	Excellent	Poor	Excellent	Excellent	Poor	Poor	Very Good	Very Good	Very Good
1.1.2.2.1.2 Parasitoids	Poor	Good	Poor	Poor	Poor	Poor	Poor	Good	Good	Poor
1.1.2.2.1.3 Herbivores-Detrivores-Pollinators	Good	Good	Good	Poor	Good	Poor	Good	Good	Good	Poor
1.1.2.2.1.3.1 Herbivore	Good	Good	Good	Good	Good	Good	Good	Good	Good	Good
1.1.2.2.1.3.2 Detrivore	Good	Good	Good	Poor	Good	Poor	Good	Good	Good	Poor
1.1.2.2.1.3.3 Pollinator	Poor	Poor	Poor	Poor	Poor	Poor	Poor	Poor	Poor	Poor
1.1.2.2.2 Non-host of Verticillium pathogen (database of host taxa)	Good	Fair	Fair	Fair	Fair	Fair	Fair	Fair	Good	Fair
1.2 Seed Farming	*	Fair	Poor; Fair	Fair	Poor	Fair	Excellent	Fair	Excellent	Excellent
1.2.1 Scalable through mechanization	*	Excellent	Poor; Fair	Fair	Poor	Excellent	Excellent	Fair	Good	Excellent
1.2.1.1 Ease of sowing with planter	Good	Good	Excellent	Fair	Fair	Good	Excellent	Fair	Excellent	Good
1.2.1.1.1 Seed size	Difficult	Difficult	Easy	Easy	Easy	Difficult	Easy	Easy	Easy	Difficult
1.2.1.1.2 Seed shape	Easy	Easy	Easy	Difficult	Difficult	Easy	Easy	Difficult	Easy	Easy
1.2.1.2 Ease of harvest with combine	Good	Poor; Excellent	Good	Good	Fair	Excellent	Excellent	Good	Fair	Good
1.2.1.2.1 Fruit height	*	Easy	*	Easy	Easy	Easy	Easy	Easy	Easy	Easy
1.2.1.2.2 Clear harvest window (weeks from maturity to harvest)	Moderate	Easy	Moderate	Difficult	Easy	Easy	Easy	Moderate	Difficult	Moderate
1.2.1.3 Ease of seed cleaning	Easy	Difficult	Difficult	Difficult	Easy	Easy	Difficult	Moderate	Easy	Easy
1.2.1.3.1 Seeds separate from fruits (expert classification)	*	Easy	Easy	Difficult	Difficult	Easy	Difficult	Difficult	Easy	Easy
1.2.1.3.2 Seeds separate from inert material (expert classification)	*	Easy	Difficult	Difficult	Difficult	Easy	Easy	Difficult	Difficult	Easy
1.2.2 Amenable to cultivation	*	Difficult	Moderate; Easy	Easy	Moderate; Easy	Difficult	Moderate	Easy	Moderate	Moderate
1.2.2.1 Seeds stay on the plant	Poor	Good	Excellent	Good	Poor	Poor	Good	Good	Good	Poor
1.2.2.1.1 Non-shattering (dehiscence)	*	Difficult	Easy	Easy	Difficult	Difficult	Easy	Difficult	Difficult	Easy
1.2.2.1.2 Fruits and seeds stay on the plant (dispersal window)	*	Difficult	Difficult	Easy	Easy	Difficult	Difficult	Difficult	Easy	Difficult
1.2.2.2 Yield and Value	Moderate	Moderate; High	Moderate	Moderate; High	Moderate; High	Moderate	High	Moderate	High	High
1.2.2.2.1 Yield (grams per square meter)	*	High	*	Moderate	*	Low	High	High	Moderate	Moderate
1.2.2.2.2 Demand (frequency in the market)	Moderate	Low	High	Low	High	High	Moderate	Low	High	High

Attribute	HELE	MEOR	MEPO	MIOR	MOMO	NIDA	PADU	SAVE	SCAT	SICO
Suitability Index	Fair; Good; Excellent	Good	Good	Excellent	Good	Excellent	Good	Excellent	Fair	Good
1.1 Olive Farming	Fair; Good; Excellent	Good	Good	Good	Fair	Good	Good	Good	Fair	Good
1.1.1 Crop Management	Fair; Good; Excellent	Good	Good	Good	Good	Excellent	Excellent	Excellent	Good	Excellent
1.1.1.1 Trafficability (plant height)	Good	Good	Good	Fair	Good	Excellent	Good	Good	Fair	Good
1.1.1.2 Cover	Poor; Good; Excellent	Fair	Fair	Good	Fair	Good	Excellent	Excellent	Good	Excellent
1.1.1.2.1 Seasonal Growth (weeks to onset of maturity)	*	Good	Good	Fair	Fair	Fair	Good	Excellent	Fair	Excellent
1.1.1.2.2 Contained (growth habit)	Excellent	Poor	Poor	Excellent	Good	Excellent	Excellent	Excellent	Good	Good
1.1.2 Biodiversity	Fair; Good	Good	Good	Fair	Fair	Fair	Fair	Fair	Fair	Fair
1.1.2.1 Non-competitive with crop	Fair; Excellent	Good	Excellent	Good	Fair	Fair	Fair	Fair	Fair	Fair
1.1.2.1.1 Non-competitive for water (short life cycle)	*	Fair	Good	Fair	Fair	Fair	Good	Good	Fair	Good
1.1.2.1.2 Non-competitive for nitrogen (plant family)	Good	Excellent	Excellent	Excellent	Good	Good	Good	Good	Good	Good
1.1.2.2 Beneficial biota	Fair	Fair	Fair	Good	Good	Good	Poor	Fair	Fair	Good
1.1.2.2.1 Insects and food web (functional group + degree of association)	Poor	Good	Good	Poor	Good	Good	Poor	Poor	Poor	Good
1.1.2.2.1.1 Generalist Predators	Poor	Very Good	Very Good	Poor	Very Good	Very Good	Poor	Poor	Poor	Very Good
1.1.2.2.1.2 Parasitoids	Poor	Good	Good	Good	Poor	Good	Poor	Poor	Poor	Poor
1.1.2.2.1.3 Herbivores-Detrivores-Pollinators	Good	Poor	Good	Good	Poor	Good	Poor	Poor	Good	Good
1.1.2.2.1.3.1 Herbivore	Good	Good	Good	Good	Good	Good	Good	Good	Good	Good
1.1.2.2.1.3.2 Detrivore	Good	Poor	Good	Good	Poor	Good	Poor	Poor	Good	Good
1.1.2.2.1.3.3 Pollinator	Poor	Poor	Poor	Poor	Poor	Poor	Poor	Poor	Poor	Poor
1.1.2.2.2 Non-host of Verticillium pathogen (database of host taxa)	Good	Fair	Fair	Good	Good	Good	Poor	Fair	Good	Good
1.2 Seed Farming	Good; Excellent	Fair	Fair	Excellent	Excellent	Excellent	Fair	Excellent	Fair	Good
1.2.1 Scalable through mechanization	Good; Excellent	Fair	Fair	Excellent	Excellent	Excellent	Excellent	Excellent	Fair	Good
1.2.1.1 Ease of sowing with planter	Good	Excellent	Excellent	Good	Good	Excellent	Good	Excellent	Fair	Good
1.2.1.1.1 Seed size	Difficult	Easy	Easy	Difficult	Difficult	Easy	Difficult	Easy	Easy	Difficult
1.2.1.1.2 Seed shape	Easy	Easy	Easy	Easy	Easy	Easy	Easy	Easy	Difficult	Easy
1.2.1.2 Ease of harvest with combine	Fair; Good; Excellent	Poor	Poor	Good	Good	Excellent	Excellent	Excellent	Good	Fair
1.2.1.2.1 Fruit height	Easy	Difficult	Difficult	Easy	Easy	Easy	Easy	Easy	Easy	Difficult
1.2.1.2.2 Clear harvest window (weeks from maturity to harvest)	*	Moderate	Moderate	Moderate	Moderate	Easy	Easy	Easy	Moderate	Difficult
1.2.1.3 Ease of seed cleaning	Easy	Easy	Easy	Easy	Easy	Easy	Easy	Easy	Difficult	Easy
1.2.1.3.1 Seeds separate from fruits (expert classification)	Easy	Easy	Easy	Easy	Easy	Easy	Easy	Easy	Difficult	Easy
1.2.1.3.2 Seeds separate from inert material (expert classification)	Easy	Easy	Easy	Easy	Easy	Easy	Easy	Easy	Difficult	Easy
1.2.2 Amenable to cultivation	Moderate; Easy	Moderate	Moderate	Moderate	Moderate; Easy	Moderate	Difficult	Moderate	Moderate	Moderate
1.2.2.1 Seeds stay on the plant	Good; Excellent	Excellent	Good	Good	Good; Excellent	Poor	Poor	Poor	Excellent	Good
1.2.2.1.1 Non-shattering (dehiscence)	Easy	Easy	Easy	Difficult	Easy	Difficult	Difficult	Difficult	Easy	Difficult
1.2.2.1.2 Fruits and seeds stay on the plant (dispersal window)	*	Easy	Difficult	Easy	*	Difficult	Difficult	Difficult	Easy	Easy
1.2.2.2 Yield and Value	Low; Moderate	Low	Moderate	Low	Moderate	High	Low	High	Low	Low
1.2.2.2.1 Yield (grams per square meter)	*	Low	Low	Low	Moderate	High	Low	Moderate	Low	Low
1.2.2.2.2 Demand (frequency in the market)	*	Low	High	Moderate	Moderate	High	Moderate	High	Moderate	Moderate

Attribute	SIGA	STAR	TOBA	TOMA	TRAN	TRHI	TRLA	TRST	TUGU	VAPY
Suitability Index										
1.1 Olive Farming	Fair	Good	Poor	Good	Excellent	Good	Good	Good	Fair, Good; Excellent	Good
1.1.1 Crop Management	Fair	Fair	Fair	Fair	Good	Good	Good	Excellent	Fair, Good; Excellent	Fair
1.1.1.1 Trafficability (plant height)	Good	Good	Good	Poor	Good	Good	Good	Excellent	Fair, Good; Excellent	Good
1.1.1.2 Cover	Good	Fair	Fair	Good	Fair	Fair	Fair	Fair	Poor; Good; Excellent	Good
1.1.1.2.1 Seasonal Growth (weeks to onset of maturity)	Good	Fair	Fair	Fair	Fair	Fair	Fair	Fair	Fair	Good
1.1.1.2.2 Contained (growth habit)	Good	Good	Good	Excellent	Good	Good	Poor	Good	Excellent	Good
1.1.2 Biodiversity	Fair	Fair	Fair	Fair	Good	Good	Good	Good	Fair, Good; Excellent	Fair
1.1.2.1 Non-competitive with crop	Fair	Fair	Fair	Fair	Good	Good	Good	Good	Fair, Excellent	Fair
1.1.2.1.1 Non-competitive for water (short life cycle)	Good	Fair	Fair	Fair	Fair	Fair	Fair	Fair	*	Good
1.1.2.1.2 Non-competitive for nitrogen (plant family)	Good	Good	Good	Good	Excellent	Excellent	Excellent	Excellent	Good	Good
1.1.2.2 Beneficial biota	Fair	Fair	Fair	Fair	Fair	Fair	Fair	Fair	Fair, Good; Excellent	Good
1.1.2.2.1 Insects and food web (functional group + degree of association)	Poor	Poor	Poor	Poor	Poor	Poor	Poor	Poor	*	Good
1.1.2.2.1.1 Generalist Predators	Poor	Poor	Poor	Poor	Poor	Poor	Poor	Poor	*	Very Good
1.1.2.2.1.2 Parasitoids	Poor	Poor	Poor	Poor	Poor	Poor	Poor	Good	*	Poor
1.1.2.2.1.3 Herbivores-Detritivores-Pollinators	Poor	Good	Good	Poor	Good	Poor	Good	Good	Poor; Good	Poor
1.1.2.2.1.3.1 Herbivore	Good	Good	Good	Good	Good	Good	Good	Good	*	Good
1.1.2.2.1.3.2 Detritivore	Poor	Good	Good	Poor	Good	Poor	Good	Good	*	Poor
1.1.2.2.1.3.3 Pollinator	Poor	Poor	Poor	Poor	Poor	Poor	Poor	Poor	*	Poor
1.1.2.2.2 Non-host of Verticillium pathogen (database of host taxa)	Good	Fair	Fair	Good	Fair	Fair	Fair	Fair	Good	Good
1.2 Seed Farming	Good	Excellent	Poor	Excellent	Excellent	Fair	Fair	Fair	Fair, Good; Excellent	Excellent
1.2.1 Scalable through mechanization	Good	Excellent	Poor	Excellent	Excellent	Fair	Fair	Fair	Fair, Good; Excellent	Excellent
1.2.1.1 Ease of sowing with planter	Good	Excellent	Poor	Excellent	Excellent	Excellent	Excellent	Excellent	Good	Excellent
1.2.1.1.1 Seed size	Difficult	Easy	Difficult	Easy	Easy	Easy	Easy	Easy	Difficult	Easy
1.2.1.1.2 Seed shape	Easy	Easy	Difficult	Easy	Easy	Easy	Easy	Easy	Easy	Easy
1.2.1.2 Ease of harvest with combine	Fair	Good	Poor	Excellent	Excellent	Poor	Poor	Poor	*	Good
1.2.1.2.1 Fruit height	Easy	Easy	Difficult	Easy	Easy	Difficult	Difficult	Difficult	*	Easy
1.2.1.2.2 Clear harvest window (weeks from maturity to harvest)	Difficult	Moderate	Easy	Easy	Easy	Easy	Easy	Moderate	*	Moderate
1.2.1.3 Ease of seed cleaning	Easy	Easy	Difficult	Easy	Moderate	Easy	Easy	Easy	Easy	Easy
1.2.1.3.1 Seeds separate from fruits (expert classification)	Easy	Moderate	Difficult	Easy	Difficult	Moderate	Moderate	Moderate	Easy	Easy
1.2.1.3.2 Seeds separate from inert material (expert classification)	Easy	Easy	Difficult	Easy	Easy	Easy	Easy	Easy	Easy	Easy
1.2.2 Amenable to cultivation	Moderate	Moderate	Moderate	Moderate	Moderate	Moderate	Moderate	Moderate	Moderate	Easy
1.2.2.1 Seeds stay on the plant	Good	Good	Good	Good	Good	Good	Good	Excellent	Poor; Good	Good
1.2.2.1.1 Non-shattering (dehiscence)	Difficult	Difficult	Easy	Easy	Easy	Easy	Easy	Easy	Difficult	Easy
1.2.2.1.2 Fruits and seeds stay on the plant (dispersal window)	Easy	Easy	Difficult	Difficult	Difficult	Difficult	Difficult	Easy	*	Difficult
1.2.2.2 Yield and Value	Moderate	Low	Low	Moderate	Low	Moderate	Moderate	Low	*	High
1.2.2.2.1 Yield (grams per square meter)	Moderate	Low	Low	High	Low	Moderate	Moderate	Low	*	High
1.2.2.2.2 Demand (frequency in the market)	Low	Low	Moderate	Low	Moderate	Moderate	Low	Low	Moderate	Moderate

Conclusions, significance and implications for the native seed industry in Europe

A major land use in Southern Spain is olive cultivation with intensive practices and simplified agroecosystems with limited sustainability. In the same region, there is a rich native flora which offers many species that are compatible to use as cover crops in the olive orchards. Native forb cover crops have the potential to restore biodiversity and improve long-term sustainability by decreasing external inputs and improving the health of the soil and supporting populations of beneficial insects. However, native Mediterranean forb species remain understudied and underutilized. In this work, the objectives were to characterize native forbs for traits of interest: germination behavior, seed biology, plant establishment and agronomic traits and apply those results to use and test a species selection tool. The ultimate result is the identification, ranking and recommendation of native forb species for native seed production to provide a source of seeds for restoring landscapes- specifically the extensive agroecosystems of olive orchards across southern Spain.

Main conclusions

1. Hydrothermal germination thresholds, rather than physiological dormancy, are the main drivers of germination phenology in annual forbs from Mediterranean semi-dry environments. Given known temperature and water conditions, it is possible to predict the germination of these forb species. In our study species, sowing in October-November (i.e., when field temperatures fall below 23 °C) should ensure a rapid and successful establishment in Mediterranean semi-arid habitats subject to ecological restoration. Species from Fabaceae and Cistaceae will need mechanical external factors to break physical dormancy. Despite a range of germination responses in other families, winter annual forbs

follow a common pattern in germination timing that generally matches the harsh but predictable Mediterranean environments.

2. Twenty-seven native forb species have been identified that are immediately compatible with seed farming and large-scale production for the developing native seed sector in Spain and the Mediterranean region. Additional types of mechanized equipment and production techniques can increase the number and diversity of native forbs that can be cultivated for seed production.
3. Twenty native forbs have the characteristics of suitable cover crops for protecting the degraded agroecosystems of Mediterranean olive orchards against soil loss, pathogens and insect pests. Just as critical, these 20 species can be cultivated for seed farming to produce the seeds needed for the restoration.
4. The DEXi software is a practical, flexible and effective method for species selection. The crop system case study was olive orchards, but the selection process and decision analysis model can be adapted and used for other woody crops such as almond, citrus, and pistachio.