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# *Aegilops geniculata* Roth: Biology, Ecology and Potential Applications in Crop Breeding and Nature-Based Solutions

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**Abstract**

*Aegilops geniculata* Roth is a tetraploid wild relative of wheat distributed throughout the Mediterranean Basin, where it grows in a wide range of habitats. Due to its genetic diversity, ecological plasticity and adaptation to Mediterranean ruderal environments, the species has attracted increasing interest as a genetic resource for wheat improvement and as a potential component of sustainable agroecosystems. Beyond use in agriculture, its ecological characteristics also suggest applications in Nature-based Solutions, including revegetation of degraded, low-input, semi-arid ecosystems. This review aims to provide a comprehensive synthesis of current knowledge on the taxonomy, genetics, morphology, distribution, ecology, reproductive biology and conservation of *Ae. geniculata*. This work is complemented by original experimental data on agronomic traits and an assessment of ex situ conservation efforts. Evidence highlights the species' value as a source of drought- and stress-adaptive traits for wheat improvement, plus promising cover crop traits (rapid establishment, stable biomass production and flexible germination behavior). Remaining knowledge gaps include population genomics, conservation of undercollected populations and field-scale agronomic performance to better clarify the potential of this species as a cover crop. This work supports further investigation of *Ae. geniculata* as both a valuable crop wild relative and a promising cover crop for Mediterranean agroecosystems.

**Keywords:** *Aegilops geniculata*; cover crops; crop wild relatives; plant genetic resources; *Triticum*

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## 1. Introduction

Crop wild relatives (CWRs) represent an essential source of genetic diversity for cultivated crops, providing traits that can increase resilience to biotic and abiotic stresses and provide adaptations to overcome unstable environmental conditions [1]. As climate change increasingly threatens agricultural productivity, the conservation, characterization and use of CWRs have become a global priority for ensuring future food security [2,3]. At the same time, agricultural systems in semi-arid and dry sub-humid regions are increasingly impacted by prolonged drought periods, soil erosion and declined soil nutrient content. These challenges have encouraged a growing interest in alternative strategies to maintain soil health, biodiversity and ecosystem functions, such as Nature-based Solutions (NbS). NbS are defined as actions that protect, sustainably manage and restore ecosystems while

simultaneously addressing societal challenges. In woody crops agroecosystems the use of cover crops represents one of the most widely adopted NbS, contributing to soil protection and biodiversity conservation, and enhancing the overall sustainability and resilience of perennial crop systems [4,5]. Consequently, the identification of native species, naturally adapted to Mediterranean environments, may provide an opportunity to develop cover crop systems better suited to local climatic and ecological conditions [6].

Among the Mediterranean CWRs, *Aegilops geniculata* Roth occupies a relevant position due to its close genetic ties with cultivated wheats (*Triticum* L.), its broad distribution in the Mediterranean basin and adaptations to a wide variety of habitats. In addition to its potential for wheat improvement, it possesses several traits and ecological characteristics, including broad ecological tolerance, adaptations to disturbed environments, rapid early development and drought resilience, that suggest a promising use for NbS in Mediterranean and semi-arid ecosystems.

Although numerous studies have investigated the taxonomy, genetics, ecology, conservation and agronomic importance of *Ae. geniculata*, these findings remain fragmented across different disciplines. To date, no comprehensive synthesis has yet integrated the available knowledge while also addressing the species' emerging potential as a cover crop.

The present work reviews the taxonomy, morphology, genetics, distribution, ecology and life cycle of *Ae. geniculata*, with the aim to provide a comprehensive synthesis of current knowledge supporting the conservation and use of *Ae. geniculata* as both a CWR and a potential species for NbS. Information was compiled from the published literature and supplemented with original experimental data recorded by the authors, including phenological monitoring and the results of trials on drought stress response, and an evaluation of agronomic traits related to potential use as a cover crop.

## 2. Description and Taxonomy

*Aegilops geniculata* Roth, Bot. Abh.: 45 (1787), common name ovate goatgrass, is an annual caespitose grass species native to the Mediterranean basin and western Asia. The specific epithet derives from the Latin "geniculum", meaning "knee" which likely refers to the bend present in the stems of the plant. Meanwhile, the genus name "*Aegilops*" comes from Ancient Greek and is of uncertain etymology: one of the possible meanings could connect it to aígilos, meaning "goat", suggesting a grass liked by goats [7]. This interpretation is also reflected in the English common name "goatgrass". Common names in other languages allude to the shape of the spikelets (Italian: "gramigna stellata", "starry grass") or to the species' resemblance to wheat (Spanish: "trigo bastardo", "fake wheat") [8].

Major synonyms include: *Aegilops ovata* L., Sp. Pl. 2: 1050 (1753), *Aegilops ovata* var. *geniculata* (Roth) Pers., Syn. Pl. 1: 107 (1805), *Triticum vagans* (Jord. & Fourr.) Greuter, Boissiera xiii. 170 (1967).

Taxonomic classification of the genus *Aegilops* and the species *Ae. geniculata* has undergone various revisions since the eighteenth century, largely due to the morphological similarity among species and the frequent occurrence of hybrid forms both within the *Aegilops* genus and with the closely related genus *Triticum*. This paper follows the taxonomic framework of Van Slageren (1994) [7] who provided a comprehensive revision of the genus *Aegilops* and its species based on morphological, cytological and genetic data. This framework has since been widely adopted and used as the basis for current treatments of the *Aegilops* genus. Accordingly, the literature published under the name *Aegilops ovata* L., as well as under other synonyms of *Ae. geniculata*, is included here to provide a comprehensive synthesis of existing knowledge.

Historically, *Aegilops* has frequently been included within the genus *Triticum*, a treatment proposed by several 20th-century authors based on the close genomic and evolutionary

affinities between the two groups [9,10]. Furthermore, *Aegilops* and *Triticum* showed a tendency towards interbreeding and producing spontaneous hybrids, which, despite their predominantly limited fertility [11], contributed to the perception of weak genetic boundaries [12,13]. This view continued but was never universally accepted, and taxonomists later emphasized the consistent morphological differences [7], evolutionary distinctions [14,15] and practical value in maintaining the generic separation between *Aegilops* and *Triticum* [12]. Cytogenetic and molecular phylogenetic studies have independently validated *Ae. geniculata* as a coherent evolutionary unit within the *Aegilops–Triticum* complex [16,17], despite the close evolutionary relationship and hybridization ability of the two genera, which are discussed in detail in later chapters.

Within the *Ae. geniculata* species, some authors have distinguished two subspecies, subsp. *geniculata* and subsp. *gibberosa* (Zhuk.) K. Hammer, the former occurring throughout the species' distribution range and the latter being largely restricted to Spain and North Africa [15,17]. The two subspecies differ mainly in spike morphology, particularly in spike compactness and spikelet arrangement. Although the infraspecific classification has been supported by cytological and morphological evidence, it has not been universally accepted, and most recent taxonomic treatments recognize *Ae. geniculata* without formal subspecific division [17].

Additional taxonomic ambiguities have historically existed regarding the species *Ae. geniculata* itself, most notably surrounding the name *Aegilops ovata*. The original Linnaean concept of *Ae. ovata* cannot be unambiguously assigned to a single modern taxon, as it encompasses material ascribable to multiple species, particularly *Ae. geniculata* and *Aegilops neglecta* Req. ex Bertol. [7,18]; as a result, the original Linnean type is inadequate for precise species delimitation.

Despite their high morphological similarity, consistent diagnostic characters allow for reliable distinction between *Ae. geniculata* and *Ae. neglecta* [7], which is supported by molecular markers for definitive identification [19]. These characteristics have enabled the treatment of *Ae. geniculata* and *Ae. neglecta* as separate species, despite their similarities, overlapping distribution ranges and propensity to hybridize [13]. Morphological characters that differ between the two species are discussed in the Morphology Section below (Table 1).

**Table 1.** Comparative morphology of *Aegilops geniculata* and *Aegilops neglecta* based on taxonomic keys from Flora Europaea (1964) [20].

| | ***Aegilops geniculata*** | ***Aegilops neglecta*** |
|---|---|---|
| Stems | 30–40 cm | Up to 45 cm |
| Leaves | Lightly hairy or glabrous | Always hairy |
| Leaf sheath | Glabrous | Glabrous or lower sparsely villous |
| Spike | 1–2 cm excluding awns, twice as long as wide | 1–3 × 0.8–1.3 cm excluding awns, abruptly compacted above the second spikelet |
| Rachis | Not disarticulated at maturity | Disarticulated at maturity |
| Vestigial spikes | 1 (−2) | 2 (−3) |
| Lower glumes | 7–8 × 5–6 mm, 3–4–5 mm long awns | 8–11 × 5–7 mm, 2–3 mm long awns |
| Awns | Awns of lemma as long as those of glumes | Awns of lemma shorter than those of glumes |

The taxonomic history of *Ae. geniculata* reflects the complexity of species delimitation within the *Aegilops* genus. The resolution of its taxonomic status has relied on accurate morphological observations and, more recently, on genetic investigations. Consequently, taxonomic, morphological and genetic studies are closely interconnected and their integration allowed for a more accurate reconstruction of the relationships with closely related species. The following sections summarize the current knowledge of the morphology and genetic background of *Ae. geniculata*, highlighting how these complementary approaches have contributed to contextualizing the species' taxonomic framework, evolutionary history, and differentiation from related taxa.

## 3. Morphology

### *3.1. Morphological Description*

*Ae. geniculata* is a caespitose annual grass characterized by culms ascending geniculately, as the species name suggests. Culms typically reach 10–40 cm in height, excluding the spikes [20]. Nodes are often bent, especially at the lower internodes.

Leaves are alternate, originating from successive culm nodes.

The leaf blade is linear, flat to slightly involute, measuring between 1.5 and 8 cm long and 1.5–5 mm wide. Leaf surface is glabrous to sparsely pubescent [21], often glaucous in appearance, particularly in individuals from dry environments [22].

Leaf-sheaths are amplexicaul, relatively long but with variable length, usually glabrous or sparsely hairy, tightly closing around the culm.

Ligule is membranous, truncated, and rarely ciliated; falcate auricles are typically present and serve as a characteristic feature for the genus *Aegilops* [7]. Auricles are often glabrous but may bear sparse hair.

Inflorescence is a compact ovoid spike 1.5–3 cm in length (excluding awns) and 0.8–1.5 cm wide at the broadest point, usually at or below the middle of the spike. Each spike consists of two to four sessile spikelets placed alternately along the rachis and one to two rudimentary spikelets at the base. The terminal (apical) spikelet is typically sterile, with a singular reduced floret. The fertile spikelets are 7–10 mm long (excluding awns) and 3–4 mm wide, each containing 3–4 florets, the lower 1–2 fertile. At maturity, the spike disarticulates as a single dispersal unit, while the rudimentary basal spikelets generally remain attached to the culm.

The glumes of the fertile spikelets are coriaceous, glabrous and 6–10 mm long, with 7–9 prominent veins that appear lighter in color than the surrounding tissue. In the apical spikelet, glumes are reduced and approximately 3 mm long. The glumes apex is truncated and prolonged into 3–5 awns, equally wide at the base and 2–4.5 cm long. In the apical spikelet awns are typically shorter, at 1–3.5 cm long. Lemmas are similarly as long as the glumes, 6–8 mm long, and terminate with 2–3 awns, making them generally as long as those of the glumes. Paleas are ovate with an acute apex (Figure 1).

Caryopses are dimorphic, a character shared by other species in the genus [23]. Two distinct seed morphs, commonly referred to as primary and secondary seeds, are produced within the same spike. Seed morphils differ in size, color and pubescence [24]. Primary caryopses are bigger, lighter in color, and less pubescent, while secondary seeds are smaller, darker, and more densely hairy (Figure 2). Secondary caryopses are typically found in the basal fertile spikelet, where they occur alongside one primary seed; upper second fertile spikelets may only contain one primary seed. In both morphs, the pericarp remains adherent to the seed coat. Throughout this work, we used the term "seed" in a functional sense to indicate the caryopsis in order to maintain consistency with the terminology used in most of the cited studies.

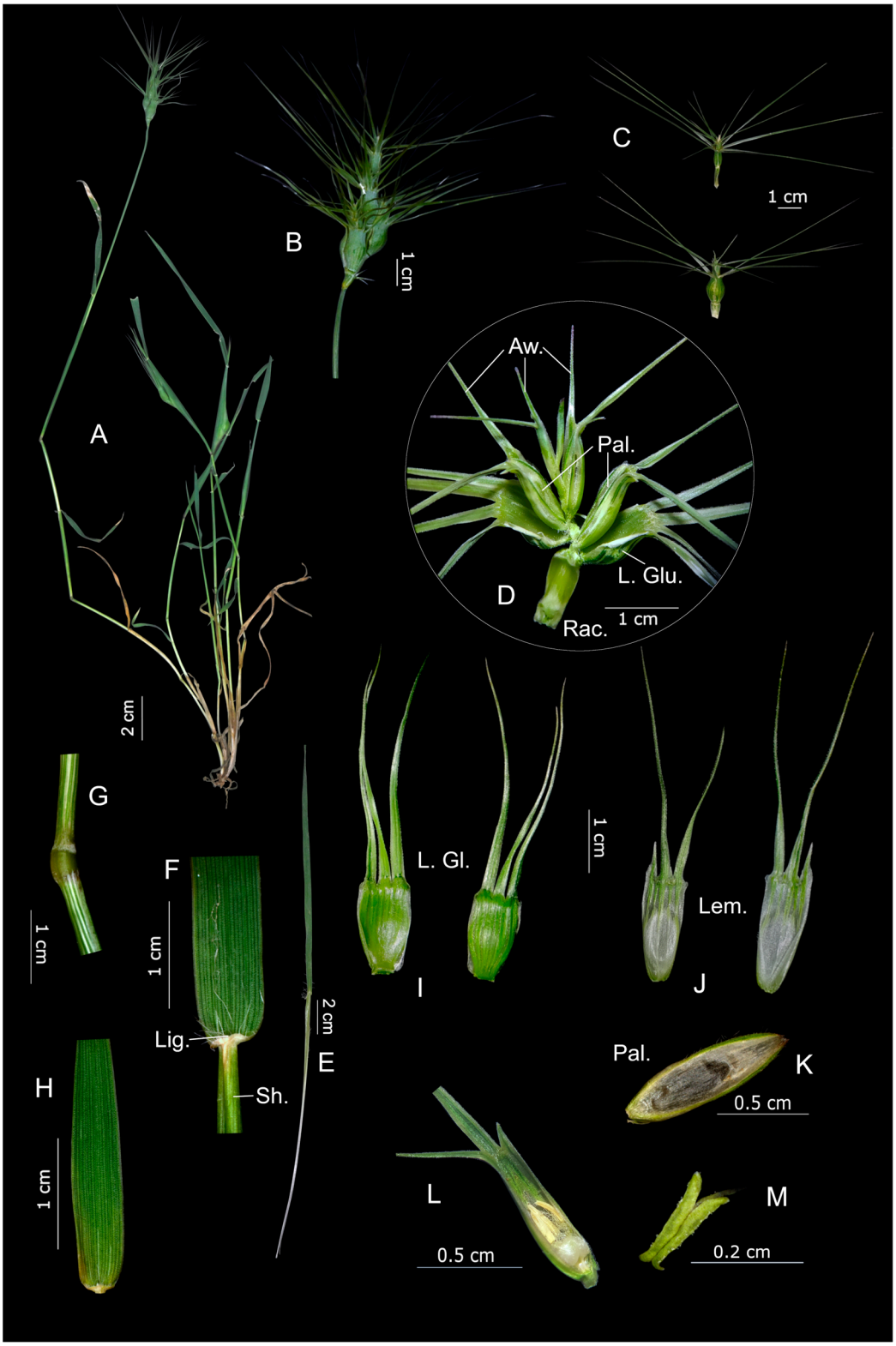



**Figure 1.** *Aegilops geniculata*. (**A**) Habit. (**B**) Spike. (**C**) Infertile (**top**) and fertile (**bottom**) spikelets. (**D**) Dissected spikelet showing rachis segment, lower and upper glume, palea and awns. (**E**) Leaf. (**F**) Leaf blade, ligule and sheath. (**G**) Geniculate culm node. (**H**) Leaf blade. (**I**) Lower glumes adaxial (**left**) and abaxial (**right**) view. (**J**) Lemmas abaxial (**left**) and adaxial (**right**) view. (**K**) Palea. (**L**) Floret with exposed reproductive structures. (**M**) Anther. Abbreviations: Aw., awn; L. Gl., lower glume; Lem., lemma; Lig., ligule; Pal., palea; Rac., rachis segment; Sh., leaf sheath. Specimen collected near Torrazza Coste (Pavia province), Northern Apennines, Italy. Photographs by Micol Orengo.




**Figure 2.** Secondary (**left**) and primary (**right**) seeds of *Ae. geniculata*. Specimen collected near Casteggio (Pavia province), Northern Apennines, Italy. Photograph by Micol Orengo.

Taxonomic keys to distinguish *Ae. geniculata* from *Ae. neglecta*, the most morphologically similar species in the genus, are based on spike shape, glume and awn length and dispersal behavior (Table 1) [20].

### *3.2. Intraspecific Variation*

Considerable morphological variation has been reported among populations of *Aegilops geniculata* across its native range [22,25–27].

Differences in plant stature, spike size, awn length, leaf color and superficial glaucousness have been found to be highly variable traits between populations. Furthermore, sets of characters have been associated with environmental gradients, particularly linked to aridity and drought stress. Zaharieva et al. (2001) [22] evaluated 157 accessions of *Ae. geniculata* under field conditions and distinguished two principal sets of traits reflecting two adaptive strategies. Accessions from hot and dry regions (Cyprus, Jordan, Libya and Tunisia) were characterized by smaller and paler green leaves, with thicker lamina than accessions from milder Mediterranean environments (Croatia, France, Greece, Italy, Portugal, Spain and Turkey). This trait combination has been interpreted as an adaptive strategy to harsh environments and is associated with high water use and epidermal transpiration efficiency [28].

The observed variation likely represents a combination of local adaptation and phenotypic plasticity, enabling *Ae. geniculata* to persist across the wide range of habitats and climatic conditions that characterize its distribution. Yet, interestingly, the geographic pattern of intraspecific morphological variation broadly parallels the genetic population structure reported by Arrigo et al. (2010) [29], which is discussed in the following section. Although environmental conditions are probably the main drivers of phenotypical variation, this correspondence suggests that morphological differences may also indicate underlying genetic differentiation. The relationship between phenotypic variation and genetic diversity, however, remains largely unexplored and deserves further attention.

## 4. Genetics

*Aegilops geniculata* is an allotetraploid species (2n = 4× = 28 chromosomes), with an MMUU genome [7,29,30].

The species is presumed to have originated as an allotetraploid of two diploid progenitor species *Aegilops comosa* Sm. and *Aegilops umbellulata* Zuk. [7,31]. Particularly, C-banding analysis identifies *Ae. comosa* subsp. *comosa* as the M genome contributor [32].

Phylogeographical analysis carried out by Arrigo et al. (2010) [29] on chloroplast DNA sequencing and amplified fragment length polymorphism (AFLP) data from 146 populations across the species' distribution range confirmed the earlier hypothesis that *Ae. geniculata* originates from the eastern Mediterranean, consistent with the distribution range of its diploid progenitors *Ae. comosa* and *Ae. umbellulata*, which overlap in western Anatolia. This hypothesis had already been proposed by Zaharieva et al. (2001) [33] with RFLP analysis and was recently corroborated by population genomics analysis of both *Ae. geniculata* and its ancestors by Yunusbaev et al. (2026) [30], which further supports the species origin through hybridization of ancestral populations of *Ae. comosa* and *Ae. umbellulata*.

Further results from Arrigo et al. (2010) [29] suggest that two separate lineages of *Ae. geniculata* spread independently from the area of origin in western Anatolia over the northern and southern Mediterranean basin. Northern populations show low genetic diversity (H = 0.060–0.067) but strong phylogeographical structure among geographically separate populations, likely reflecting the influence of the last glacial maximum and resulting founder effect and bottleneck events. By contrast, southern and eastern Mediterranean populations show high genetic diversity (H = 0.072–0.078) and low genetic structuring, suggesting limited fragmentation and no clear isolation of the southern species range during the glacial maximum. Additional regional assessments in Turkey [34] and Algeria [25] confirm genetic variation within specific areas of the extended range.

The study also highlights the importance of introgressions between native and naturalized populations due to human-mediated dispersal.

While human-mediated migration of *Ae. geniculata* appears limited, relocated individuals have considerably influenced genetic variation in resident populations through introgression events [29]. Human activities can also promote interspecific gene flow; when *Ae. geniculata* is found in proximity to wheat crops, hybridization rates can reach 0.20–0.45% at distances less than 1 m apart [35], demonstrating a significant mechanism by which spatial proximity in agricultural landscapes can provide opportunities for spontaneous hybridization.

*Ae. geniculata* is characterized by a hybrid polyploid origin, substantial geographic structuring, and considerable adaptive genetic diversity across its range. These characteristics, together with its capacity for introgression with related species, contribute to its evolutionary success and reinforce its value as a genetic resource for wheat improvement.

## 5. Distribution and Habitat

Among species of the genus *Aegilops*, *Ae. geniculata* has the most Circum-Mediterranean distribution. It is widespread and mostly common throughout southern Europe, western North Africa and the near East, but less common in Turkey, eastern North Africa and Transcaucasia; it is also present in Crimea (Figure 3).

Outside the native range, the introduced populations are recorded in central and northwestern Europe, the Canary Islands, and North America [7,14,36]. Presence in the United States has been recorded in the States of California, New York and Virginia [37]. Despite limited evidence of establishment, *Ae. geniculata* has been classified as "high risk" in weed risk assessment for the USA, reflecting its potential invasiveness and ability to spread under suitable conditions [37]. Introduction of *Ae. geniculata* outside its native range occurs most frequently through import of contaminated products such as grains, seeds or even natural fibers (wool).

Information on geographic distribution was gathered from multiple sources, including the published literature, herbarium specimens and publicly available databases such as the Global Biodiversity Information Facility (GBIF) Plants of the World Online database (POWO) [36,38]. The native distribution map shown in Figure 3, however, was generated exclusively with occurrence records compiled from GBIF [38] because of its standardized georeferenced information and spatial coverage. Prior to mapping, records without coordinates, records with coordinate uncertainty >10 km, duplicate coordinates, and spatial outliers were excluded. Additional manual verification was performed to remove clearly non-native, cultivated or otherwise unreliable occurrences.

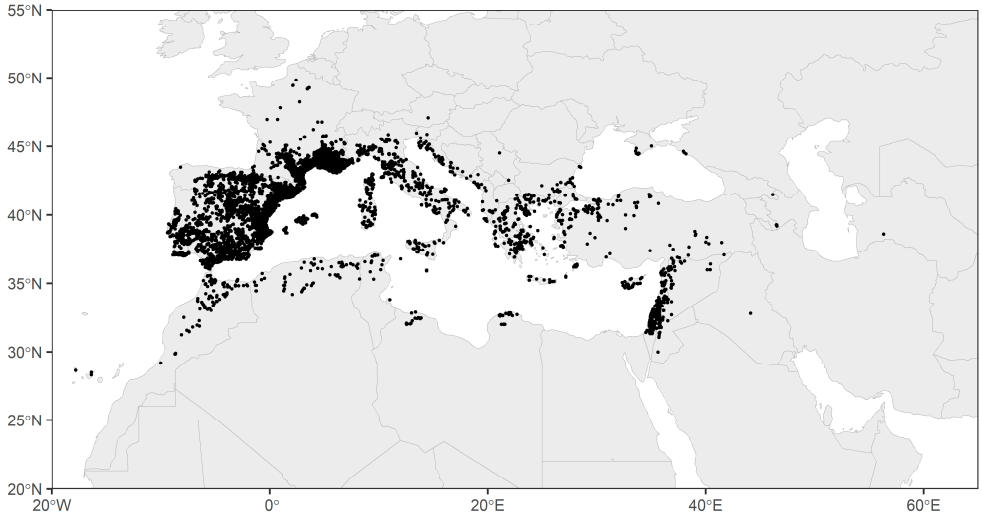



**Figure 3.** Native distribution of *Aegilops geniculata* based on 12,923 georeferenced occurrence records obtained from GBIF [38] after data quality filtering; each dot represents a unique observation from the GBIF database.

Within its native range *Ae. geniculata* is locally abundant in dry, open and disturbed habitats [7,14,20,39] (Figure 4), where it can form locally dominant stands often intermixed with other *Aegilops* species (e.g., *Ae. neglecta*, *Ae. triuncialis* L., *Ae. uniaristata* Vis., *Ae. ventricosa* Tausch [7]; personal observations).



(**a**) (**b**)

**Figure 4.** Examples of typical habitats of *Ae. geniculata:* (**a**) dense stand of *Ae. geniculata* growing within an olive grove near Casteggio (Pavia province), Northern Apennines, Italy; (**b**) patch of *Ae. geniculata* on roadside margin in the Western Ligurian coast near Castellaro (Imperia province), Liguria, Italy. Photographs by Micol Orengo.

Typical habitats include open natural and semi-natural environments such as dry grasslands, steppes, dunes, garrigues, hillslopes and pastures. The species is also frequently associated with anthropogenic and disturbed habitats, including field margins, cultivated fields, roadsides and wastelands (Figure 4). Although primarily a species of open habitats, it may occasionally occur in open woodland and forest clearings [7]. The species occurs on a wide variety of substrates, most commonly limestone-derived soils, but also on basaltic, sandstone and karstic substrates. It tolerates a broad range of soil textures, from sandy soils to clay-rich and gravelly soils.

Usually found between 0 and 1750 m of altitude and rarely up to 2100 m [14]. *Ae. geniculata* has been found to inhabit a large range of climatic types, from transitional continental [40] to semi-arid climate. Populations occur in areas with reported rainfall between less than 100 mm to more than 1100 mm of annual precipitation, although most populations are found in regions receiving 200–700 mm of rainfall per year, consistent with a dry Mediterranean climate.

Perrino et al. (2014) [27] mention that in Italy the species characterizes aspects of subnitrophilous vegetation *Stellarietea mediae* R. Tüxen, Lohmeyer & Preising ex von Rochow 1951, although it is frequently a companion species in many other plant communities, especially in the grasslands of *Lygeo-Stipetea* Rivas-Martínez 1978 and *Festuco-Brometea* Br.-Bl. & Tüxen ex Klika & Hadac 1944.

At the broader European level, *Ae. geniculata* is associated with several EUNIS habitat type-E1.3 habitats (Mediterranean xeric grasslands), namely, open, short-grass grasslands dominated by communities of therophytes on oligotrophic, base-rich and often calcareous substrates, attributable to the class *Thero-Brachypodietea* Br.-Bl. ex A. Bolòs & O. Bolòs 1950. More specifically, the species is cited as characterizing the habitat E1.332, Helleno–Balkanic short grass and therophyte communities [41].

Overall, *Ae. geniculata* is best characterized as a disturbance-tolerant Mediterranean therophyte adapted to open habitats and seasonal drought. These traits, together with its remarkable ecological flexibility, driven by phenotypic plasticity, local adaptations and substantial genetic diversity among populations, have enabled the species to persist across a wide range of environmental conditions and largely explains its extensive distribution throughout the Mediterranean Basin.

## 6. Life Cycle

*Ae. geniculata* follows the winter–annual life cycle of many Mediterranean grasses, germinating during the wetter autumn and winter period and completing reproduction before the onset of summer drought.

After emergence (Figure 5a), the seedlings develop a fibrous root and produce basal tillers (Figure 5b), remaining vegetative during the winter months. Active growth resumes in spring, with stem elongation and inflorescence emergence occurring in late spring to early summer (Figure 5c).

The flowering and fruiting period of *Ae. geniculata* varies considerably across its distribution range from as early as March in Libya to as late as August in Spain and central Turkey [7]. Differences in timing primarily reflect local climatic conditions while preserving the characteristic drought-avoidance strategy of Mediterranean annuals that enables populations to complete reproduction before the onset of the dry season.

Seeds ripen in early to mid-summer, and plants complete their life cycle before the dry summer period (Figure 5e). The prominent awns on the spikelets play a key role in dispersal and establishment: as in other species of the Poaceae family, they facilitate epizoochory [29] and, being hygroscopic, enable self-burial after dispersal through drill-like movements that actively propel seeds into the soil [42].




**Figure 5.** *Aegilops geniculata* main phenological phases (**a**) leaf development; (**b**) formation of side shoots; (**c**) inflorescence emergence; (**d**) flowering; (**e**) end of fruit-ripening. Photographs taken at the experimental site in the Northern Apennines, Torrazza Coste (Pavia province), Italy. Photographs by Micol Orengo.

To complement the available literature and confirm the reported phenological patterns we monitored the phenological development of plants derived from seeds collected from a northern Italian population (experimental methods are provided in the Supplementary Materials). Development was highly synchronized among individuals and experimental plots (Figure 6), and reproductive development accelerated rapidly with increasing spring temperatures. Under the climatic conditions of northern Italy, most developmental stages occurred within the temperature ranges reported for Mediterranean annual grasses, with seed maturation completed before the onset of summer, remarkably consistent with the drought-avoidance strategy characteristic of Mediterranean therophytes [43,44].

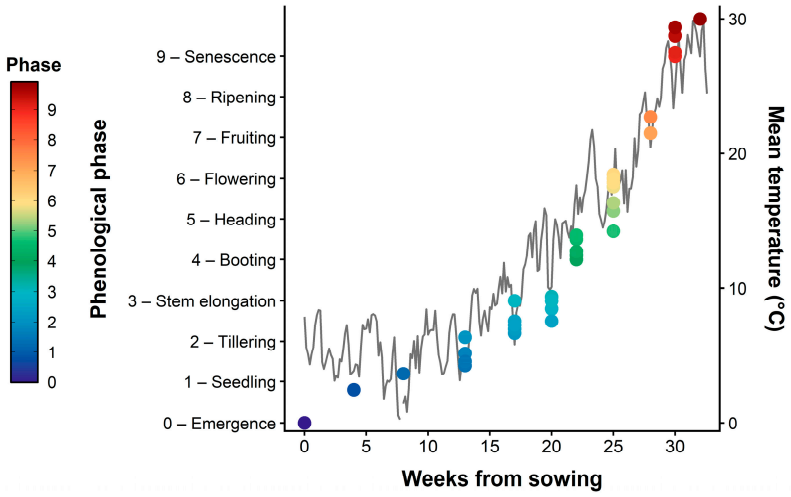



**Figure 6.** Phenological development of *Ae. geniculata* in relation to mean daily temperature under field conditions. Phenological phases are represented by colored points along a continuous gradient from emergence (blue) to senescence (red). The *x*-axis shows the major developmental phases of the life cycle on the left and mean daily temperature (°C) recorded in the site on the right.

These observations indicate that, although flowering time varies geographically, the overall phenological strategy remains consistent across the species' range. Such phenological flexibility likely contributes to the broad distribution and ecological adaptability of *Ae. geniculata*.

## 7. Reproductive Fitness

*Ae. geniculata* is an anemophilous and mainly self-pollinating species. Nevertheless, intraspecific cross-pollination can occur and may result in natural hybrids when the species grows in sympatry with closely related *Aegilops* species (such as *Ae. neglecta*, *Ae. biuncialis* Vis., *Ae. triuncialis*, *Ae. peregrina* (Hack.) Eig) and cultivated wheats (*Triticum aestivum* ssp. *aestivum* L. and *T. turgidum* ssp. *durum* L.) [7,13].

Although *Ae. geniculata* reproduces predominantly through self-fertilization, its reproductive strategy is also shaped by the production of heteromorphic seed morphs, which play an important role in germination behavior, seed persistence and population dynamics.

As mentioned, each stem produces an average of three spikelets [45], with the basal spikelet typically bearing both primary and secondary seeds, whereas the second spikelet also contains secondary seeds less frequently. The recorded ratio of primary to secondary seeds is approximately 3:1, although different populations can display differences in morphs ratio [26].

Nutrient availability during plant growth has a minimal effect on seed heteromorphism, with soil fertilization increasing the number of flowering stems but not affecting spikelets number or the ratio of primary to secondary seeds [45].

In contrast to nutrient availability, several studies have shown that maternal environmental conditions strongly influence seed traits. Seeds produced under lower temperatures were significantly heavier than those produced under warmer conditions [46], while populations from Mediterranean regions with dried climates during seed maturation exhibit greater tolerance to low water potentials during germination, indicating local adaptation to climatic conditions [47].

In addition to morphological differences, the two seed morphs differ in their germination behavior. Overall, *Ae. geniculata* seeds germinate across a broad range of temperatures. Dehulled seeds achieve high germination percentages across a relatively wide range of temperatures [26,48], with optimal germination temperature regimes identified at alternative 20/10 °C and constant 20 °C [48]. High germination performance at alternating temperatures is an ecological response observed also in other grass species, promoting seedling emergence in open habitats and/or at the soil surface, where temperatures vary significantly during the day/night cycle [48–50].

When seeds remain enclosed in the dispersal unit, germination is largely restricted to the primary seeds, while secondary seeds remain dormant.

It has been hypothesized that larger primary seeds germinate readily following the first autumn rainfall after dispersal, whereas the secondary seeds remain dormant until the following spring or even the following growing season [26,46,51,52]. This interpretation is supported by evidence that secondary seeds exhibit greater longevity under controlled aging conditions [52], consistent with inter-morph differences reported for other heteromorphic species of the genera *Aegilops* and *Triticum* [53].

Differences in longevity between primary and secondary seeds have also been demonstrated in long-term storage conditions for other wheat wild relatives [54,55]. Whether similar patterns occur in *Ae. geniculata* remains to be investigated.

Together, seed heteromorphism, differential seed longevity and the formation of a persistent soil seed bank constitute a bet-hedging strategy that spreads recruitment over multiple growing seasons, reduces the risk of recruitment failure under unpredictable

environmental conditions, limits sibling competition, and enhances long-term population persistence [53,56]. These reproductive traits complement the phenological and ecological adaptations described in previous sections and likely contribute to the broad environmental tolerance and widespread distribution of *Ae. geniculata*.

## 8. Importance for Plant Breeding

The remarkable genetic diversity, ecological adaptability, and broad environmental tolerance described in the previous sections make *Ae. geniculata* one of the most valuable wild genetic resources for wheat improvement [57]. Adaptations that enable the species to thrive across diverse Mediterranean environments could also represent an important source of alleles for developing more resilient wheat cultivars.

Several accessions of *Ae. geniculata* possessing traits of interest for wheat breeding have been identified through a range of experimental studies.

Comprehensive reviews by Kishii (2019) [58] and Badaeva et al. (2025) [57] summarize the valuable traits identified in *Ae. geniculata* and other U-genome *Aegilops* species (*Ae. umbellulata*, *Ae. biuncialis*, *Ae. columnaris* Zhuk., *Ae. geniculata*, *Ae. neglecta*, *Ae. triuncialis*, *Ae. juvenalis* (Thell.) Eig, *Ae. kotschyi* Boiss. and *Ae. peregrina*), as well as current strategies for their utilization in wheat breeding.

Despite the extensive and largely untapped genetic diversity present in wheat wild relatives, their utilization in breeding has historically been constrained by the lack of efficient methods for transferring desirable traits into cultivated wheat. However, recent advances in cytogenetic and molecular breeding technologies are increasingly enabling the effective exploitation of this diversity for crop improvement [59]. In particular, U-genome *Aegilops* species do not share common genomes with wheat, exhibiting limited crossability with cultivated wheats, low hybrid fertility and substantial genomic divergence. Structural differences between the U genome and the wheat genomes further reduce chromosome pairing and homoeologous recombination during meiosis, thereby limiting the direct transfer of beneficial genes into wheat [60–64]. Although natural hybridization between *Ae. geniculata* and wheat has been documented under field conditions [11], hybridization frequencies are generally low, and the resulting pentaploid $F_1$ hybrids exhibit greatly reduced fertility due to meiotic irregularities. Limited seed production and occasional backcrossing with wheat have nevertheless been reported [65], indicating that gene flow, while possible, is strongly constrained by these reproductive barriers. Consequently, the introgression of traits from U-genome species requires specialized cytogenetic and biotechnological approaches.

The development of embryo rescue techniques, chromosome doubling, and alien chromosome addition and substitution lines has enabled the recovery of viable wheat–*Aegilops* hybrids, while advances in chromosome engineering have substantially improved the efficiency and precision of alien gene introgression [57]. Approaches such as irradiation and gametocidal systems induce chromosome breakage and generate wheat–alien translocations, whereas manipulation of the wheat Pairing homoeologous 1 (Ph1) locus or the introduction of homoeologous pairing-promoting genes from wild relatives enhances recombination between wheat and alien chromosomes. Together, these strategies facilitate the transfer of small chromosome segments carrying target genes while minimizing linkage drag (i.e., when undesirable traits are co-inherited with the desired traits due to their physical proximity on the chromosome), thereby enabling the effective exploitation of the genetic diversity present in U-genome *Aegilops* species for wheat breeding [57,58].

Numerous agronomically important traits have been identified in *Ae. geniculata*. With respect to abiotic stress tolerance, accessions have shown adaptive responses to heat, drought and salinity, as well as tolerance to zinc deficiency [14,66]. Resistance to a broad range of biotic stresses has also been reported, including barley yellow dwarf virus [66], yellow

rust [22], leaf rust [67], stem rust [68], powdery mildew [69], root rot, tan spot [14], Septoria nodorum blotch, Russian wheat aphid [57], cereal cyst nematode and Hessian fly [58]. To date, at least four disease-resistance genes derived from *Ae. geniculata* have been successfully introgressed into common wheat [57].

From a nutritional perspective, *Ae. geniculata* grains contain iron (Fe) and zinc (Zn) concentrations approximately three- to four-fold higher than those of cultivated wheat, highlighting their potential value for biofortification programs [70]. In addition, favorable baking quality characteristics have been reported [71]. Beyond these agronomic and nutritional traits, *Ae. geniculata* also represents an important source of cytogenetic tools for wheat improvement. The species carries gametocidal (Gc) genes, which have been exploited to induce chromosome rearrangements and facilitate the transfer of desirable chromosomal segments from wild relatives into wheat. It also possesses genes that promote homoeologous chromosome pairing, providing additional opportunities for chromosome engineering and the efficient introgression of alien chromatin [72,73].

Overall, *Ae. geniculata* combines extensive genetic diversity with multiple agronomically valuable traits, including tolerance to abiotic stresses, resistance to numerous pests and diseases, enhanced nutritional quality, and cytogenetic tools for chromosome engineering. Continued advances in genomics, chromosome engineering and pre-breeding approaches are expected to facilitate the exploitation of these characteristics, reinforcing the importance of *Ae. geniculata* for developing climate-resilient and sustainable wheat cultivars.

## 9. Potential as a Cover Crop

### *9.1. Potential as a Cover Crop and Nature-Based Solutions in Semi-Arid Environments*

As a ruderal species highly adapted to disturbed ecosystems, *Aegilops geniculata* possesses several characteristics that may be advantageous for use in NbS in semi-arid disturbed ecosystems.

Among NbS, the use of native species as cover crops has been increasingly adopted because locally adapted plants may provide ecosystem services while maintaining ecological compatibility with regional environmental conditions [6].

Annual, low-impact cover crops in perennial crop systems (e.g., woody crops such as olive groves and vineyards) can aid with erosion control, nutrient retention and improvements in soil structure and quality, while avoiding competition with the main crop.

To be effective and compatible with crop management methods, cover crops should possess specific ecological and agronomic traits: rapid establishment following autumn rainfall, production of sufficient biomass for soil protection, tolerance of seasonal drought, and a life cycle that minimizes competition with the primary crops [74].

As discussed in the previous sections, *Ae. geniculata* combines broad ecological tolerance, rapid phenological development, drought adaptation and reproductive traits that promote persistence under Mediterranean conditions. Together, these characteristics suggest that the species could be particularly suitable for use as a native cover crop and, more broadly, as a component of NbS in semi-arid environments. The suitability of *Ae. geniculata* as a Mediterranean cover crop is further supported by its reported occurrence in organically managed olive groves throughout Italy and Spain, where it thrives as a key component of spontaneous vegetation in agroecosystems (authors' personal observation, Figure 7).



**Figure 7.** *Ae. geniculata*-dominated herbaceous cover in an organically managed olive grove near Casteggio (Pavia Province), Italy. Photographs by Micol Orengo.

Beyond agricultural applications, many of the traits that make *Ae. geniculata* suitable as a cover crop are also desirable for other NbS in semi-arid environments. Native annual grasses adapted to drought and disturbance are increasingly considered for the revegetation of degraded land, erosion control and the restoration of low-input ecosystems, where irrigation and intensive management can be often impractical [75]. Consequently, evaluating the agronomic and ecological performance of *Ae. geniculata* may contribute not only to sustainable agriculture but also to the broader use of native species in ecosystem restoration.

To evaluate whether the ecological characteristics identified in the literature translate into agronomically relevant performance, we conducted supporting field and controlled-environment experiments (experimental methods are provided in the Supplementary Materials). These experiments assessed biomass production, establishment and drought resilience, three key traits determining cover crop suitability under Mediterranean conditions [76]. Although *Ae. geniculata* has previously been proposed as a promising native species for Mediterranean cover crops [6] its agronomic performance has not previously been evaluated experimentally. The experiments presented here provide an initial assessment of *Ae. geniculata* agronomic performance as a cover crop and help bridge this knowledge gap.

### *9.2. Experimental Evidence Supporting Cover Crop Potential*

Field experiments showed that biomass production remained stable across a wide range of sowing densities (Figure 8). Although biomass tended to increase slightly with increased seeding rate, differences were not statistically significant, suggesting that *Ae. geniculata* can maintain adequate biomass production under different sowing densities. Significant variability among experimental blocks underscore the importance of localized environmental conditions rather than seeding density itself.

Controlled-environment experiments comparing *Ae. geniculata* with the widely used commercial cover crop *Lolium multiflorum* Lam. showed that *Ae. geniculata* developed greater leaf area, leaf biomass and root diameter during early establishment and survived significantly longer under drought stress (Figure 9).

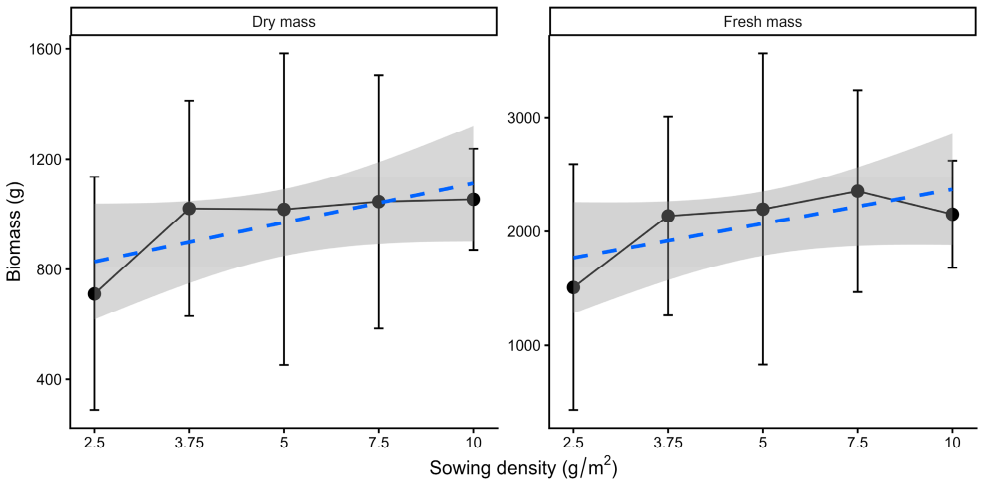



**Figure 8.** Mean (and 95% confidence interval) of dry and fresh biomass (g) of *Aegilops geniculata* across sowing densities ($n = 5$). Points represent treatment means, with dashed lines showing linear model fits and shaded confidence bands. No significant relationship between sowing density and biomass was detected.

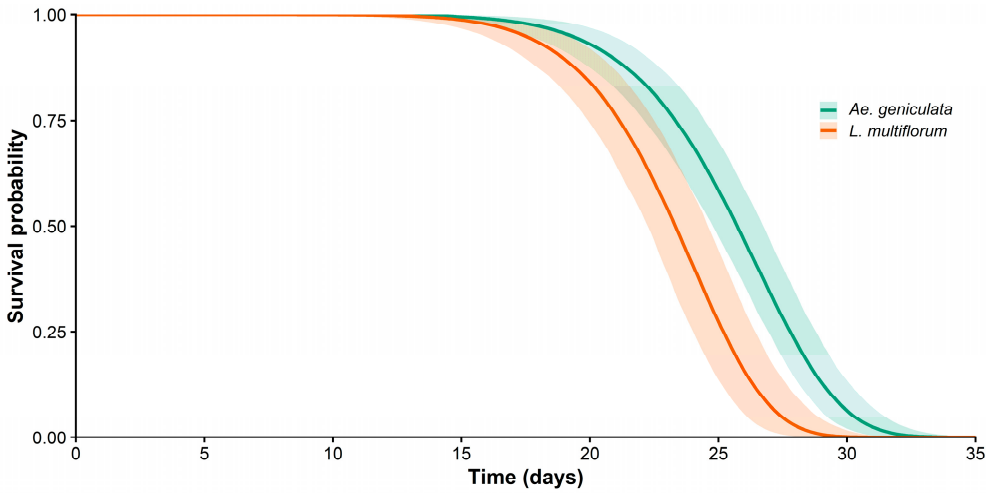



**Figure 9.** Parametric Weibull survival curves for *Ae. geniculata* and *L. multiflorum* under drought conditions. Curves were estimated from Weibull survival models fitted to time-to-mortality data. Shaded areas represent the 95% confidence intervals.

These findings indicate that *Ae. geniculata* achieves faster early establishment with greater drought tolerance compared to the commercial species *L. multiflorum*. The rapid post-germination development of *Ae. geniculata* represents a dual advantage in the context of cover crops establishment: fast growth may contribute to early soil protection and competitive suppression over weeds, all while maintaining resilience to Mediterranean drought stress.

Considering both the literature reviewed throughout this article and the complementary experimental evidence presented here it emerges that *Ae. geniculata* possesses several traits commonly regarded as desirable for Mediterranean cover crops. Stable biomass production across a wide range of sowing densities suggests the potential to reduce seed input costs and flexibility in utilization practice, while rapid early development, low plant height and enhanced drought resilience may promote reliable establishment and soil cover compatible with crop management. Successful establishment, however, is also likely to depend on the management practices adopted. Factors such as hay transfer or direct seed sowing, the timing of mowing and tillage, and the degree of soil disturbance before or

during establishment may influence the effectiveness of soil cover [77]. Although the effects of these practices have not yet been investigated specifically for *Ae. geniculata*, its ruderal ecology suggests that the species may tolerate moderate disturbance.

Although these findings require additional validation under a variety of environmental conditions through multi-site, long-term field experiments with material from different populations across the distribution range, they provide encouraging preliminary evidence of the agronomic potential of the species.

The proposed use of *Ae. geniculata* as a cover crop should be considered in light of its classification as a potential agricultural weed in regions outside its native distribution. However, the same traits (rapid establishment, tolerance to environmental stress and competitive ability) that qualify *Ae. geniculata* as a risk species outside of its native range can be desirable attributes for cover crop species. Within its native Mediterranean range, the species naturally occurs in agricultural landscapes and has coexisted with traditionally managed crops for centuries; its use as a cover crop is unlikely to represent the same risk associated with introductions into non-native regions. This highlights the importance of considering species performance within its biogeographical context when evaluating NbS [78]. Nonetheless, appropriate management strategies should be adopted to prevent dispersal beyond the species' native area.

Potential limitations should also be considered. As a wild annual grass producing spiny awned dispersal units, large-scale seed harvesting and mechanized sowing may present practical challenges. Furthermore, the species' close relationship to wheat warrants consideration of possible gene flow where the two species occur in close proximity. Likewise, if *Ae. geniculata* establishes within cereal fields, its competitive ability could reduce wheat yield, decrease harvesting efficiency, and contaminate harvested grain, as reported for other *Aegilops* species introduced into North American and Chinese winter wheat production systems [79,80]. These considerations reinforce the importance of restricting its use to suitable perennial cropping systems within its native range and adopting management practices that minimize unintended spread.

Addressing these practical constraints will be essential before large-scale adoption can be considered.

In synthesis, both the literature review and the experimental results seem to suggest that *Ae. geniculata* is a promising candidate for the development of cover crop systems better suited to Mediterranean environmental conditions. Its combination of ecological adaptability, drought tolerance, rapid establishment and stable biomass production also supports its potential use in broader NbS aimed at improving the resilience of semi-arid agroecosystems. Although further evaluations are needed, the present results provide a first experimental foundation for exploring this new application of the species.

## 10. Conservation Status

### *10.1. In Situ*

*Aegilops geniculata* appears to be common across most of its range and therefore is not regarded as a priority species for conservation action under IUCN criteria, being listed as Least Concern [81,82]. The species maintains a broad geographic distribution throughout the Mediterranean Basin and adjacent regions, with populations demonstrating considerable abundance and stability across its native range [36,81]. Moreover, its high tolerance to a wide range of habitats and ecological conditions further suggests that targeted conservation actions might not currently be required within most of its native range.

However, the maintenance of in situ populations in its Mediterranean core range remains important in the framework of an increased integration of in situ and ex situ conservation of Plant Genetic Resources (PGR) [83], especially considering the species'

documented role as a donor of beneficial traits to cultivated wheat. Moreover, it is important to support the in situ conservation of populations of CWRs that might not be currently threatened but that have a great impact on wheat improvement as carriers of useful traits [84]. This is particularly relevant considering that climate change is predicted to decrease, in the next few decades, the range of many wheat wild relatives in North Africa, Near East and southern Europe [85]. In situ conservation areas designed for CWRs conservation are defined as genetic reserves. These are specifically managed sites that allow for the conservation of the genetic diversity of CWR populations while allowing natural evolution under changing environmental conditions.

Guzzon et al. (2022) [84] reported that some *Ae. geniculata* populations are already protected in genetic reserves located in the Near East, growing with other wheat wild relatives, for example, in the genetic reserve of Wadi Sweid (Lebanon).

Ongoing habitat preservation in priority regions, particularly those harboring high levels of genetic diversity and locally adapted populations, will ensure continued access to natural genetic variation in this agronomically significant CWR.

The broad distribution of *Ae. geniculata*, combined with its demonstrated ecological plasticity as well as the need to access its genetic resources effectively renders ex situ conservation in gene banks the primary conservation method for this taxon [81].

### *10.2. Ex Situ*

Guzzon et al. (2022) [84] estimated, based on data from major international germplasm repositories and national and international gene banks, that 3218 unique accessions of *Ae. geniculata* are conserved in gene banks worldwide.

The broad geographic origin of conserved material, spanning the Mediterranean Basin, Near East, and adjacent regions, reflects the species' wide ecological range and highlights the importance of capturing environmentally structured genetic variation in conservation strategies [29,81].

To maximize the representation of intraspecific diversity, ex situ sampling should target multiple, spatially separated populations. Empirical studies in *Aegilops* species show significant genetic structuring even over short geographic distances, with distinct populations contributing unique alleles [29,33]. Consequently, collection efforts should prioritize extensive geographic coverage, as isolated populations may harbor distinct gene pools. This approach aligns with the general recommendations for CWRs, where dense and geographically stratified sampling enhances the long-term value of gene bank collections for both conservation and breeding [81,86].

To estimate the geographic representation of *Ae. geniculata* in ex situ collections, we performed an original spatial analysis comparing known species occurrences and accession provenance. Accession data was gathered from Genesys PGR and quality-controlled to remove multiple records of the same accession. Only accession records with a coordinates error within 5 km were kept.

The analysis was conducted using a 100 × 100 km grid, following the approach adopted by Maxted et al. (2008) [81], to standardize occurrence data and represent broad geographic patterns, while also accounting for the substantial genetic variation that may occur within this scale [33]. Based on the proportion of occupied grid cells containing at least one conserved accession, we estimate that approximately 40% of the species' geographic range is currently represented in ex situ germplasm collections (Figure 10). Northern Mediterranean and western Asian populations are comparatively well represented, whereas populations from North Africa remain underrepresented.

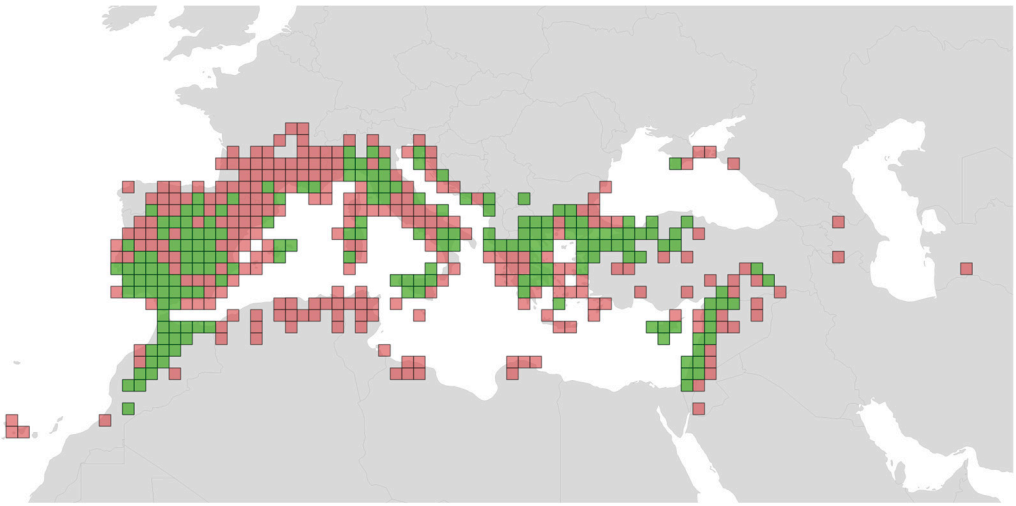


**Figure 10.** *Aegilops geniculata* range and occurrences versus germplasm accessions across the Mediterranean and West Asian region. Green grid cells indicate areas with both recorded species presence and conserved germplasm accessions; red grid cells indicate locations with recorded species presence but no corresponding accessions.

Despite the species' wide distribution and the adaptive significance of its southernmost populations, particularly for drought and heat tolerance [22], these results indicate that current ex situ collections remain geographically incomplete.

That said, the curation and genetic characterization of existing collections are essential, as studies on *Aegilops* germplasm have identified redundancy and misclassification among accessions [84,87].

Expanding collections from underrepresented regions, particularly North Africa, would substantially improve the representation of the species' ecological and genetic diversity within global germplasm repositories.

Similarly, further research is needed to clarify seed longevity in storage of this species as well as possible intra-specific variations, fine-tuning seed viability monitoring and regeneration of re-collection intervals. This will support the long-term conservation of conserved accessions, with good seed qualities and quantities supporting their use for research, breeding and NbS purposes [84].

## 11. Conclusions

*Aegilops geniculata* is one of the most widespread and ecologically versatile wild relatives of wheat in the Mediterranean Basin. Its ecology combines broad environmental tolerance, high genetic diversity, and adaptive traits such as seed heteromorphism and drought tolerance. These characteristics contribute to its ecological success and highlight its value both as a genetic resource for crop improvement and as a potential candidate for practical use as a NbS in Mediterranean and semi-arid environments.

In addition, the evaluated traits of stable biomass production under different sowing densities, relatively low plant height, rapid establishment of both aboveground and underground biomass and drought tolerance provide preliminary experimental evidence of the suitability of *Ae. geniculata* not only for native cover crops but also for the revegetation and restoration of degraded environments.

Despite the substantial knowledge highlighted in this work, important gaps remain.

Although considerable progress has been made in characterizing the genetic diversity and population structure of *Ae. geniculata*, the relationship between genetic differentiation and phenotypic variation across the species' distribution remains poorly understood. In particular, the extent to which geographic differences in morphology, germination behavior,

phenology and stress tolerance reflect local adaptation, phenotypic plasticity, or their interaction has yet to be determined. Integrating population genomics with morphometric analyses, common-garden experiments and reciprocal transplant studies across contrasting Mediterranean environments would provide valuable insights into the adaptive mechanisms underlying the species' ecological flexibility, particularly in the context of ongoing climate change.

*Ae. geniculata* has proven to be the source of numerous beneficial alleles for wheat improvement, yet many remain underutilized because of the difficulties associated with introgression into wheat. Future research should combine chromosome engineering, genomics and pre-breeding approaches to accelerate the practical exploitation of this diversity [1,15].

The preliminary experimental evidence presented in this review, alongside the species' ecological characteristics, supports the potential of *Ae. geniculata* as a native Mediterranean cover crop. However, future research should focus on evaluating its performance across a range of environmental conditions through multi-site and long-term field trials, to assess ecosystem services, interaction with crop management, seed production, economic and practical feasibility before practical implementation can be recommended at a large scale [6,76].

Current ex situ collections preserve a substantial proportion of the species' geographic range, yet important gaps remain. Future conservation efforts should integrate genomic information with ecological data to identify priority populations for both in situ and ex situ conservation while maximizing the preservation of adaptive diversity, especially from currently underrepresented regions (e.g., Northern Africa, eastern Mediterranean) [3,83].

Overall, integrating ecological, evolutionary, genetic and agronomic research will be essential to fully realize the potential of *Ae. geniculata* as both a valuable CWR and a component of resilient Mediterranean agroecosystems and NbS under future climate change.

**Supplementary Materials:** The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/su18168375/s1, Supplementary Methods: Detailed description of the phenological phases, biomass production and drought stress experiments; Table S1. Mean fresh and dry biomass (±SD) of *Aegilops geniculata* under five sowing densities and results of the two-way ANOVA testing theeffects of sowing density and experimental block; Table S2. Comparison of morphological traits between plants originating from primary and secondary seeds of *Ae. geniculata*. Values are presented as mean ± standard deviation (SD). Differences were assessed using Welch's two-sample *t*-tests; Table S3. Comparison of morphological traits between *Ae. geniculata* and *L. multiflorum* measured after 30 days of growth, immediately before drought stress. Values are presented as mean ± standard deviation (SD). Differences were assessed using Welch's two-sample *t*-tests.; Figure S1. Comparison of morphological traits between *Ae. geniculata* and *L. multiflorum* measured after 30 days of growth under controlled conditions. Panels show (a) maximum root diameter, (b) leaf area, (c) leaf fresh biomass, (d) leaf dry biomass, (e) root fresh biomass, and (f) root dry biomass; Table S4. Weibull survival model comparing primary- and secondary-seed plants of *Ae. geniculata* and *L. multiflorum*; Figure S2. Violin plots showing the distribution of survival time under drought stress for pooled *Ae. geniculata* and *L. multiflorum*. Individual points represent single plants. Survival time corresponds to the number of days from start of drought stress until complete death of the individual. References [88–91] are cited in the Supplementary Materials.

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**Institutional Review Board Statement:** All of the seeds of *Aegilops geniculata* Roth were collected by the authors from natural populations in the Oltrepò Pavese area (Northern Italy). A limited number of seeds of *Lolium multiflorum* L. were obtained from a commercial seed supplier (Padana Sementi S.r.l., Tombolo, Italy) for comparison purposes.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** The experimental datasets generated and analyzed during the current study are available from the corresponding author upon reasonable request. GBIF occurrence data and germplasm accession data from Genesys used in this study are publicly available from the Global Biodiversity Information Facility (GBIF) and the Genesys Plant Genetic Resources portal, respectively, through the sources cited in the References.

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