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Crop Science

REVIEW

Potential use of wild *Onobrychis* species for climate change mitigation and adaptation

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Abstract

Climate change is threatening environmental and nutritional security. In this scenario, forage crops and their wild relatives may contribute to maintain ecosystem services and minimize the effects of global warming. We reviewed the literature regarding the ecological, agronomic, and nutraceutical values of wild *Onobrychis* Miller species (sainfoins, Family *Fabaceae*). We also discussed their application prospects and the existing problems hampering their widespread domestication. Wild species of the genus *Onobrychis* have some interesting agronomic and ecological features such as perenniality, deep root system, and high-stress tolerance, which make them suitable for future cultivation under climate change. Wild *Onobrychis* species are multipurpose species, which can be utilized for fodder and honey production under harsh environmental conditions. In addition, wild *Onobrychis* species water, ethanol, and methanol extracts exhibit antioxidant, antidiabetic, anti-inflammatory, antitumor, antimicrobial, anti-stressor, and many other pharmacological effects. Wild *Onobrychis* species have not been the subject of detailed studies. Compared with the cultivated forage legumes, wild *Onobrychis* species are still underexploited despite their potential to alleviate forage and food insecurity, either by domestication or by providing novel alleles for breeding purposes of the cultivated species *Onobrychis viciifolia*. Our review aims to increase scientific awareness toward exploring the potential uses of wild *Onobrychis* species to tackle current climate change.

1 | INTRODUCTION

Climate change and subsequent increasing environmental stressors have become a global concern (Zhang et al., 2019). Climate change scenarios project high probabilities of decreases in rainfall in arid and semiarid lands around the world, with potential increase in the frequency and intensity of extreme climatic events such as prolonged droughts, floods, and heat waves (Wang et al., 2018; Zhang et al., 2019). The occurrence of combined extreme climatic events will result in a pronounced negative effect on crops yield and land productivity (Guo et al., 2022; Ortiz-Bobea et al., 2021).

To date, increases in crop yields have been driven by Green Revolution cultivars that lent themselves to more

Abbreviations: ABA, abscisic acid.

intensive irrigation, fertilization, and mechanization (Garcia et al., 2023). However, in recent years, yield per hectare has plateaued while human population growth and food demand are increasing (Beltran-Peña et al., 2020; Guo et al., 2022). Further investment in the current strategies may not suffice to further boost yield to meet future food demand due to their high energy consumption, and great economic and harmful environmental costs (Beltran-Peña & D'Odorico, 2022; Mahankale, 2023). In the face of land unavailability and increasing costs of inorganic fertilizers, it is essential that new pathways be found to boost crop yields. In addition, with predictions for warmer and drier future climates, there has been growing interest in the performance of more drought-tolerant and heat-tolerant and deep-rooted species.

In this scenario, noncultivated plant species can function as reservoirs of novel genes and alleles for agronomical important phenotypic traits related to high tolerance to environmental stressors (Gaikwad et al., 2021). Wild plant species are expected to have beneficial alleles that have been lost from cultivated species during domestication (Stevanato et al., 2017). In this sense, interspecific and intraspecific hybridization have an ancient legacy for creating genetic diversity and passing agronomically useful traits from wild relatives to cultivated species (Kik, 2002; Kiełkowska & Adamus, 2006). Recently, the incorporation of genes/alleles from wild relatives into cultivated varieties has emerged as a promising strategy because of their close genetic origin (Maxted et al., 2006; Mickelbart et al., 2015). Chromosomal manipulation and various biotechnological techniques, such as plant tissue culture, genetic engineering, and genome sequencing, represent valuable tools to understand the function of genes (Salgotra et al., 2022). Substantial progress on the incorporation of genes/alleles from wild relatives has been made mostly in edible crops such as rice, wheat, and tomato (Salgotra et al., 2022). However, many domesticated forage species have yet to benefit from improvements using wild species to confront the present scenario of climate change.

The genus *Onobrychis* Miller (Family *Fabaceae*) with close to 170 species is one of the largest genera of the tribe *Hedysareae* DC. (Amirahmadi et al., 2014; Bernardo et al., 2020; Mabberley, 2008). *Onobrychis* genus includes annual and perennial species, mostly caulescent herbs, rarely spiny shrubs (Mabberley, 2008; Yakovlev et al., 1996). Only three species of *Onobrychis* have been cultivated for agronomical use: *Onobrychis transcaucasica* Grossh., *Onobrychis arenaria* (Kit.) DC. and *O. viciifolia* Scop. (Carbonero et al., 2011). *Onobrychis viciifolia*, is the most common cultivated species of *Onobrychis* nowadays, for whose name several synonyms are used in the literature: *Hedysarum onobrychis* L., *Onobrychis sativa* Lam., *Onobrychis viciaefolia* Scop. and *Onobrychis viciifolia* Scop. The topologies of the neighbor joining trees and the memberships of the operational taxonomic units suggest that the *Onobrychis* taxonomy is overcomplicated by the existence of synonyms and spurious subspecies (Carbonero et al., 2012). For example, *Onobrychis pyrenaica* (Sennen) Širj, *Onobrychis altissima* Grossh., *O. arenaria* (Kit.) DC., *Onobrychis inermis* Steven, and *Onobrychis montana* DC. might all be synonyms for *O. viciifolia*. Recent studies suggest that *O. viciifolia* is endowed with multifaceted beneficial properties for human health, livestock production, and environment conservation (Mora-Ortiz & Smith, 2018). *Onobrychis viciifolia* shows highly desirable forage attributes related to its unique tannin and polyphenol composition that have been shown to confer anthelmintic properties, increase protein utilization, improve zootechnic performance, and prevent bloating, unlike other legumes such as *Medicago sativa* L. (Mora-Ortiz & Smith, 2018). In addition, *O. viciifolia* cultivation has the potential to mitigate climate change (Carbonero et al., 2011). Compared with other legumes, such as *M. sativa* and *Trifolium pratense* L., *O. viciifolia* is a highly palatable and relatively resistant to most common pests and diseases (Carbonero et al., 2011; Frame et al., 1998). Moreover, *O. viciifolia* constitutes a rich source of pollen and nectar (Kells, 2001). The other two *Onobrychis* species that were cultivated, *O. transcaucasica* and *O. arenaria*, are not being cultivated nowadays. For example, *O. arenaria* was grown as fodder for cattle, but this practice ceased centuries ago in Eastern Europe (Kajtoch et al., 2013).

Core Ideas

- Wild *Onobrychis* species have not been the subject of in-depth and detailed studies.
- Wild *Onobrychis* species are multipurpose plants that could be utilized to mitigate and adapt to climate change.
- Wild *Onobrychis* species have the potential to alleviate forage and food insecurity.
- Wild *Onobrychis* species could be domesticated or provide novel alleles/genes for breeding purposes.

Wild *Onobrychis* species have started to attract more attention as a fodder crop in recent decades (Figure 1). Between 1964 and 2023, ca. 76% of published articles regarding the genus *Onobrychis* concerned only *O. viciifolia*, the most widespread species. Only very few works (132 articles) focused on wild *Onobrychis* species, which raised to more than fivefold during the last decade from ca. 1 to 5 per year. However, no work has focused on the role of wild *Onobrychis* species in the present scenario of climate change.

Wild *Onobrychis* species' low productivity and poor capacity to compete with weeds have prevented many farmers from considering these species as a viable alternative to other forage legumes (Mora-Ortiz & Smith, 2018). Several wild

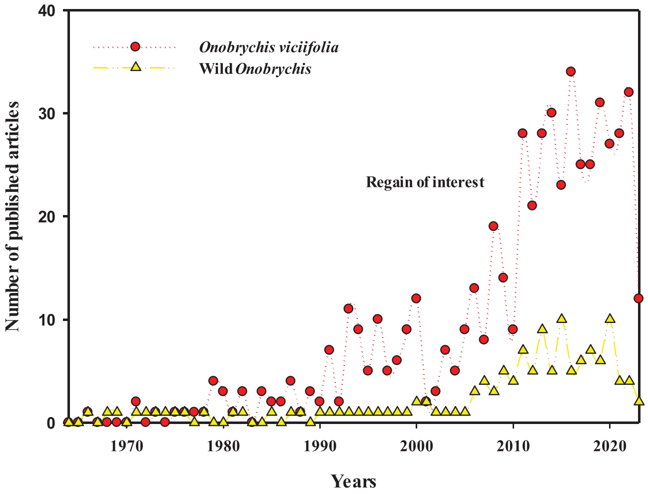

FIGURE 1 Evolution of annual number of publications on wild *Onobrychis* species compared to the cultivated species *Onobrychis viciifolia* published from January 1963 to July 2023 (Sources: Google Scholar, Web of Science, Springer, and PubMed).

Onobrychis species are endemic with reduced distribution areas (Bernardo et al., 2020; Dehshiri, 2019). Nevertheless, interspecific hybridization between wild *Onobrychis* species and cultivated *O. viciifolia* may improve its performance in the present scenario of climate change. In this sense, modern genomic approaches may accelerate the discovery and transfer of genes and alleles from wild *Onobrychis* species to cultivated *O. viciifolia*. In addition, some wild species of *Onobrychis* showing high tolerance to increasing environmental stresses, such as drought and pests, may be cultivated directly in harsh conditions. However, no study has reviewed the existing information on wild *Onobrychis* species.

In this work, we review the literature regarding the ecological, agronomic, and nutraceutical application values of wild *Onobrychis* species. We also discuss their application prospects and the existing problems hampering their widespread domestication. Our review aims to increase scientific awareness toward exploring the potential uses of wild *Onobrychis* species to tackle current climate change.

2 | MATERIALS AND METHODS

Studies on wild *Onobrychis* species available in the current literature were collected from the databases Google Scholar, Web of Science, Springer, and PubMed. The initial filtering was based on titles, abstracts, and keywords, including the word *Onobrychis*. The full text of all studies was then reviewed. The deadline for the literature selected was up to July 2023. The Plant List (http://www.theplantlist.org/tpl1.1/search?q=Onobrychis), International Plant Name Index (https://www.ipni.org/n/30311989-2), and Kew Botanical Garden (https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:510168-1) were used for validating scientific name. In order to represent worldwide geographical distribution showing the locations of published studies on wild *Onobrychis* species, we recorded latitude and longitude of each study (Table 1). If latitude and longitude were not given, we extracted them from Google Maps based on the site description.

3 | ORIGIN, DISTRIBUTION, AND CYTOLOGY

Onobrychis Mill. (*Fabaceae*) is sub-cosmopolitan genus that includes more than 170 annual and perennial herbs and shrubs, which are distributed mainly in the North temperate regions (Abuş & Avci, 2018; Bernardo et al., 2020; Safaei Chaei Kar et al., 2012). *Onobrychis* species are considered an interesting forage for dry areas because of their resistance to drought and adaptation to the calcareous soils and have important potential in livestock feeding, pasture and grassland reclamation, and preservation (Abou-El-Enain, 2002; Avci & Kaya, 2013; Özaslan-Parlak et al., 2014). Till date, 41 studies have reported different biological, ecological, and pharmacological aspects of 34 wild *Onobrychis* species. Five of these *Onobrychis* species are critically endangered (Table S1). These studies have been carried out mostly in Turkey (Figure 2). *Onobrychis* species are considered to have originated in Vavilov's Middle East center, which includes Asia Minor, Transcaucasia, Iran, and the highlands of Turkmenistan (Abou-El-Enain, 2002; Aktoklu, 1995). Iran (53 species) and Anatolia (52 species) appear to be the main centers of genetic diversity for *Onobrychis* species (Emin & Kuddisi, 2010; Lock, 2005; Nixon, 2006; Yildiz et al., 1999). Phylogenetic studies indicate that the primary center of genetic diversity for *Onobrychis* species is in the Mediterranean Basin (Ashurmetov & Normatov, 1998) (Figure 2).

Most of the cytological studies conducted on *Onobrychis* genus have concerned chromosome numbers (Table 2) (Baltisberger, 1991; Karshibaev, 1992; Slavivk et al., 1993), with little work focusing on detailed karyological analyses (Abou-El-Enain, 2002; Khatoon et al., 1991; Mesicek & Sojak, 1992; Ranjbar et al., 2009, 2010a, 2010b). Earlier reports have shown that about 38% species (65 species) of the genus *Onobrychis* were subjected to chromosome counts (Table 2). *Onobrychis* species have three levels of ploidy ($2n = 2x = 14$ and 16, $2n = 4x = 28$ and 32, and $2n = 8x = 56$) (Abou-El-Enain, 2002; Bolkhovskikh et al., 1969; Hesamzadeh-Hejazi & Ziaei-Nasab, 2010; Löve, 1972, 1976). Goldblatt (1981) and Ranjbar et al. (2012) suggested that $x = 8$ was the ancestral haploid number in the genus

TABLE 1 Published studies on wild *Onobrychis* species, their study subject, province and country where the study was carried out, and the estimated extended of occurrence (EEO) and the area of occupancy (AOO) following International Union for Conservation of Nature (IUCN).

No.	*Onobrychis* species	Reference	Province (Country)	EEO	AOO
1	*O. aequidentata*	Cytology (Baltisberger, 1991; De-Montmollin, 1984; Romano et al., 1987)	Impros (Greece)	LC	VU
2	*O. caput-galli*	Cytology (Heyn, 1962; Slavivk et al., 1993)	Israel and Cyprus	LC	NT
3	*O. crista-galli*	Cytology (Corti, 1931; Diaz-Lifante et al., 1992)	Italy and Tabkha (Jordan)	LC	NT
4	*O. montana*	High altitude tolerance (Öncel et al., 2004)	Anatolia (Turkey)	LC	NT
5	*O. dealbata*	High altitude tolerance (Bano et al., 2009)	Hunza valley (Pakistan)	CR	CR
6	*O. oxyodonta* var. armena	Non-gypsum soils (Ozdeniz, 2019)	Turkey	LC	EN
7				NA	NA
8	*O. oxyodonta* var. armena	Salinity tolerance (Beyaz et al., 2011)	Turkey	NA	NA
9	*O. subnitens*	Salinity tolerance (Karamian & Ataei-Barazandeh, 2013)	Kurdistan (Iran)	CR	CR
10	*O. subnitens*	Restoration of degraded area (Gorgin-Karaji et al., 2018)	Kurdistan (Iran)	CR	CR
11	*O. melanotricha*	Salinity tolerance (Karamian & Ataei-Barazandeh, 2013)	Hamadan (Iran)	LC	EN
12	*O.* stenostachya subsp. sosnowskyi	Salinity tolerance (Uzun et al., 2017)	Kars (Turkey)	NA	NA
13	*O. paucijuga*	Salinity tolerance (Uzun et al., 2017)	Konya (Turkey)	NA	NA
14	*O. transcaucasica*	Salinity tolerance (Shakirov et al., 2012)	Uzbekistan	LC	EN
15	*O. chorassanica*	Salinity tolerance (Shakirov et al., 2012)	Uzbekistan	LC	EN
16	*O. melanotricha*	Drought tolerance (Nasirzadeh et al., 2005)	Fars (Iran)	LC	EN
17	*O. sojakii*	Drought tolerance (Nasirzadeh et al. 2005)	Fars (Iran)	NA	NA
18	*O. aucheri* subsp. tehranica	Drought tolerance (Nasirzadeh et al. 2005)	Fars (Iran)	NA	NA
19	*O. aucheri* subsp. psamophilla	Drought tolerance (Nasirzadeh et al. 2005)	Fars (Iran)	NA	NA
20	*O. aequidentata*	Drought tolerance (Karatassiou et al., 2009)	Thessaloniki (Greece)	LC	VU
21	*O. cornuta*	Drought tolerance (Irfan, 2007)	Ziarat Valley (Pakistan)	LC	EN
22	*O. caput-galli*	Drought tolerance (Kostopoulou et al., 2010)	Greece	LC	NT
23	*O. cornuta*	Land Restoration -Agronomical (Erfanzadeh et al., 2020)	Iran	LC	EN
24	*O. scrobiculata*	Restoration of degraded area (Gorgin-Karaji et al., 2018)	Kurdistan (Iran)	LC	EN
25	*O. argentea* subsp. argentea	Pastoral (Rios et al., 1991)	Spain	NA	NA
26	*O. caput-galli*	Pollen and nectar source (Čeksterytėa et al., 2013)	Lazdijai (Lithuania)	LC	NT
27	*O. radiata*	Pollen and nectar source (Gencay-Celemli et al., 2018; Ozenirler et al., 2019)	Kars (Turkey)	LC	EN
28	*O. tournefortii*	Pollen and nectar source (Gencay-Celemli et al., 2018; Ozenirler et al., 2019)	Kars (Turkey)	LC	EN
29	*O. oxyodonta*	Pollen and nectar source (Gencay-Celemli et al., 2018; Ozenirler et al., 2019)	Kars (Turkey)	LC	EN
30	*O. argentea* subsp. hispanica	Pollen and nectar source (Pérez-Fernández et al., 2019)	Guadalajara (Spain)	NA	NA
31	*O. montana*	Pollen and nectar source (Kajtoch et al., 2013)	Ukraine	LC	NT
32			Poland		
33	*O. arenaria*	Pollen and nectar source (Kajtoch et al., 2013)	Ukraine	LC	NT

(Continues)

TABLE 1 (Continued)

No.	*Onobrychis* species	Reference	Province (Country)	EEO	AOO
34			Poland		
35	*O. saxatilis*	Pastoral (Rios et al., 1989)	Segura river basin (Spain)	LC	VU
36	*O. stenorhiza*	Pastoral (Rios et al., 1991)	Segura river basin (Spain)	LC	VU
37	*O. gracilis*	Medicine and pharmacology (Demirci & Ozhatay, 2012)	Kahramanmaraş (Turkey)	LC	EN
38	*O. carduchorum*	Medicine and pharmacology (Mükemre et al., 2015)	Çatak (Turkey)	EN	EN
39		Medicine and pharmacology (Dalar et al., 2018)	Ağrı (Turkey)		
40	*O. altissima*	Medicine and pharmacology (Dalar et al., 2018; Mükemre et al., 2015)	Çatak (Turkey)	LC	EN
41	*O. carduchorum*	Medicine and pharmacology (Clericuzio et al., 2020)	Kurdistan, Rawanduz (Iraq)	EN	EN
42	*O. oxyodonta*	Medicine and pharmacology (Usta et al., 2014)	Bolu (Turkey)	LC	EN
43	*O. armena*	Medicine and pharmacology (Karakoca et al., 2015)	Aksaray (Turkey)	CR	EN
44	*O. hyparygrea*	Medicine and pharmacology (Zengin et al., 2015)	Ankara (Turkey)	NA	NA
45	*O. sosnovskyi*	Medicine and pharmacology (Karamian & Asadbegy, 2016)	Marand (Azerbaijan)	NA	NA
46	*O. melanotricha*	Medicine and pharmacology (Karamian & Asadbegy, 2016)	Marivan (Azerbaijan)	LC	EN
47	*O. albiflora*	Medicine and pharmacology (Özbek et al., 2019)	Anatolia (Turkey)	CR	CR
48	*O. argyrea* Boiss. subsp. argyrea	Medicine and pharmacology (Özbek et al., 2019)	Anatolia (Turkey)	NA	NA
49	*O. galegifolia*	Medicine and pharmacology (Özbek et al., 2019)	Anatolia (Turkey)	LC	EN
50	*O. tournefortii*	Medicine and pharmacology (Özbek et al., 2019)	Anatolia (Turkey)	LC	EN
51	*O. ebenoides*	Medicine and pharmacology (Dontas et al., 2006)	Greece	LC	EN

Abbreviations: CR, critically endangered; EN, endangered; LC, least concern; NA, not available; NT, near threatened; VU, vulnerable.

and that $x = 7$ was derived from the loss of one chromosome by aneuploidy. Ghanavati et al. (2012) stated that $x = 8$ was observed only in tetraploid species. To date, there are only four previous reports on tetraploid numbers recording $2n = 4x = 32$ in *O. megataphros* from Anatholia (Turkey) (Hosgoren, 2006), *Onobrychis caput-galli* (L.) Lam. and *Onobrychis pulchella* Schrenk ex Fisch. & C.A.Mey. from France and Turkmenistan, respectively (Abou-El-Enain, 2002), as well as *O. subacaulis* Boiss. from Poland (Yucel et al., 2022).

In addition, it has been suggested that the basic chromosome count $x = 8$ is associated with the annual *Onobrychis* species while $x = 7$ is more frequent in perennial species (Abou-El-Enain, 2002; Díaz-Lifante et al., 1992; Gömürgen, 1996). However, different basic chromosome numbers were subsequently reported for some perennial *Onobrychis* species, for example, $x = 7$ and $x = 8$ for *Onobrychis ptolemaica* (DEL.) DC. from Iran and *Onobrychis tournefortii* (Willd.) Desv. from Turkey (Abou-El-Enain, 2002; Arslan et al., 2012; Ranjbar et al., 2012).

The analyses of basic chromosome numbers in the phylogenetic context showed that $x = 8$ was reconstructed as ancestral for both *Onobrychis* subgenera (*Sisyrosema* Bunge and *Onobrychis* Mill). However, the patterns of basic chromosome number evolution were different in these two subgenera. In both subgenera, species with $x = 8$ and $x = 7$ were revealed, but most *Sisyrosema* subgenus species have $x = 8$, whereas those belonging to the subgenus *Onobrychis* have $x = 7$. One event of descending dysploidy at a relatively deep node was inferred in the subgenus *Onobrychis*. In contrast, three independent events of descending dysploidy were reconstructed at the tips of the tree in the subgenus *Sisyrosema* (Yucel et al., 2022).

Different levels of ploidy can be observed within the same species (Abou-El-Enain, 2002): $2n = 14$, 16, and 28 for *Onobrychis aequidentata* (Sm.) d'Urv. from Greece and Italy (Baltisberger, 1991; De-Montmollin, 1984; Romano et al., 1987), and $2n = 14$ and 16 for *O. caput-galli* (L.) Lam. from Israel and Cyprus (Heyn, 1962; Slavivk et al., 1993), and

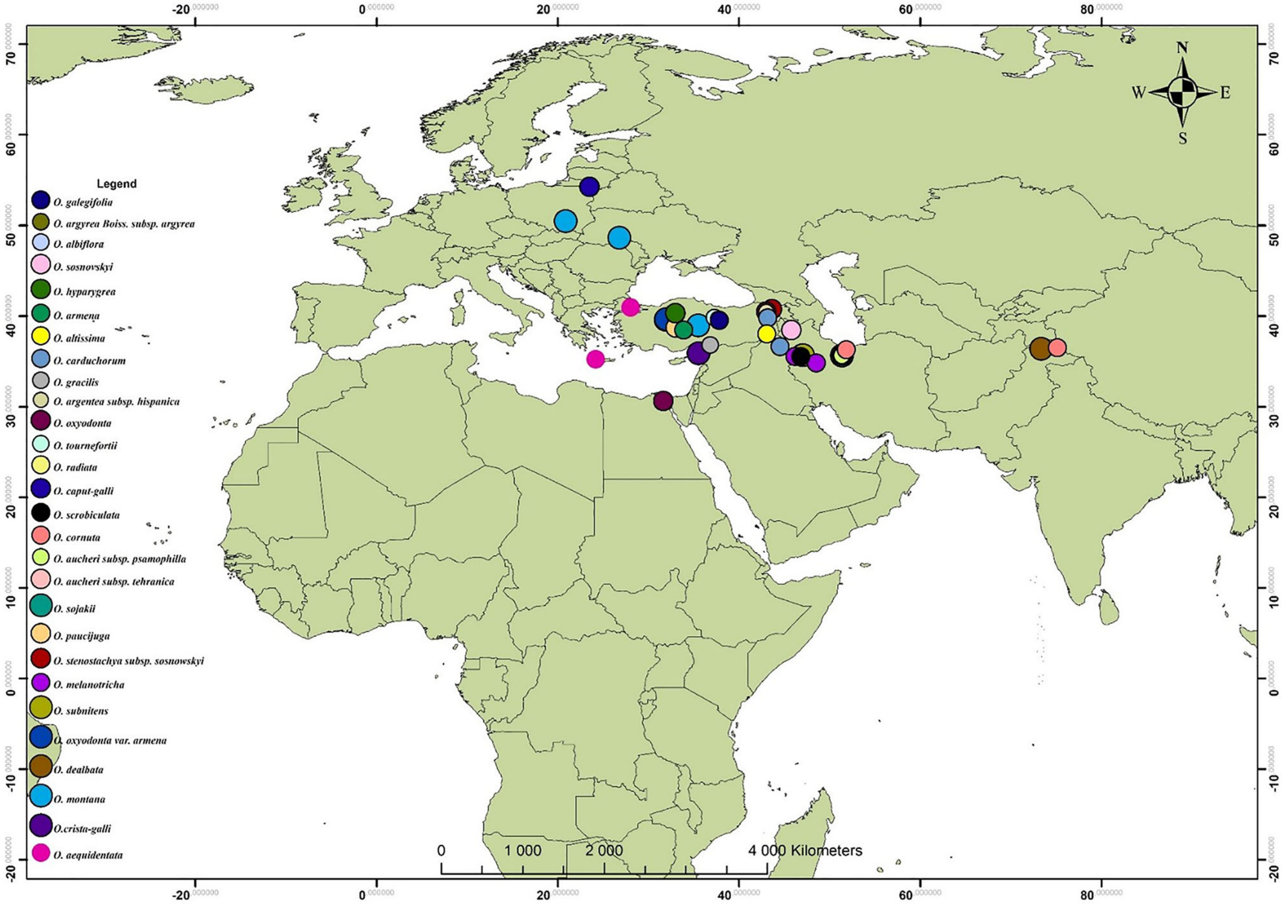

FIGURE 2 Worldwide geographical distribution showing the locations of published studies on wild *Onobrychis* species.

O. crista-galli (L.) Lam. from Italy and Jordan (Corti, 1931; Díaz-Lifante et al., 1992). For the same species, both diploid and tetraploid chromosome numbers were also reported (e.g., *O. crista-galli* and *O. caput-galli*) (Abou-El-Enain, 2002; Kliphuis, 1977; Sepet et al., 2011). Polyploid *Onobrychis* species are encountered mainly in Central-West Asia and diploid species are distributed throughout South-West Asia and the Mediterranean Basin (Abou-El-Enain, 2002; Ranjbar et al., 2010a).

The differences between chromosome reports could be attributed to the highly complex taxonomy of this genus and to the different phylogenetic approaches deployed for species delimitation, which resulted in varying numbers of recognized species (Carbonero et al., 2012). Hence, the intraspecific polymorphisms in chromosome number could be due to technical issues causing incongruence between different reports. Most of the chromosome counts were based on simple techniques like Feulgen or acetoorcein/acetocarmine staining that hamper precise identification of specific chromosomes and place them into homologous pairs in karyotypes with relatively small and numerous chromosomes such as *Onobrychis* (Arslan et al., 2012; Ranjbar et al., 2012). In addition, some species consist of cytotypes that differ in basic chromosome number, which could be caused by aneuploidy such as trisomy of one chromosome pair and dysploidy (Jang et al., 2013; Kolano et al., 2015).

4 | RESPONSES TO ENVIRONMENTAL STRESSES

Most of the studies dealing with the response of *Onobrychis* species to environmental stress concerned the cultivated species *O. viciifolia* (Sakhraoui et al., 2023). Ecophysiological studies on wild *Onobrychis* species are very scarce. For example, only two studies have analyzed the responses of wild *Onobrychis* species to altitude. *Onobrychis montana* DC. from Northwest Anatolian Mountains (Turkey) was reported to tolerate altitudes up to 2180 m by increasing foliar concentrations of chlorophyll, xanthophyll, β-carotene, proline, and soluble phenolic compounds along with high superoxide dismutase activity (Öncel et al., 2004). In addition, *Onobrychis dealbata* Stocks from Hunza Valley (Pakistan) was reported to tolerate altitudes up to 3500 m, increasing protein, proline, sugars, and abscisic acid concentrations at higher elevations (Bano et al., 2009).

TABLE 2 Chromosome numbers (2*n*) of *Onobrychis* species retrieved from literature.

No.	*Species*	2*n*	References
1	*O. aequidentata*	14	Baltisberger (1991); De-Montmollin (1984)
		16	Abou-El-Enain (2002)
2	*O. alba subsp. echinata*	14	Bernardo et al. (2020)
3	*O. alba subsp. laconica*	14	Yucel et al. (2022)
4	*O. albiflora*	14	Tekin et al. (2016); Abuş and Avci (2018)
5	*O. altissima Grossh.*	28	Arslan et al. (2012); Hesamzadeh-Hejazi and Ziaei-Nasab (2010); Yucel et al. (2022)
6	*O. amoena*	14	Hesamzadeh-Hejazi and Ziaei-Nasab (2010)
7	*O. arenaria*	28	Yucel et al. (2022)
8	*O. argyrea subsp. argyrea*	16	Ozturk et al. (2009)
9	*O. aucheri*	16	Ansari et al. (2002); Hesamzadeh-Hejazi and Ziaei-Nasab (2010)
10	*O. avajensis*	16	Ranjbar, Karamian, and Afsari (2010)
11	*O. biebersteinii*	28	Yucel et al. (2022)
12	*O. bobrovii*	28	Abou-El-Enain (2002)
13	*O. buhseana*	16	Hesamzadeh-Hejazi and Ziaei-Nasab (2010)
14	*O. calabrica*	28	Bernardo et al. (2020)
15	*O. caput-galli*	14	Yucel et al. (2022)
16	*O. carduchorum*	14	Hosgoren (2006); Arslan et al. (2012)
		28	Abou-El-Enain (2002)
		32	Abou-El-Enain (2002)
17	*O. chorassanica*	14	Karshibaev (1992); Ranjbar, Karamian, and Hajmoradi (2010)
		16	Yucel et al. (2022)
18	*O. cornuta*	14	Magulaev (1989)
		16	Hesamzadeh-Hejazi and Ziaei-Nasab (2010)
19	*O. crista-galli*	16	Lifante et al. (1992); Kliphuis (1977); Yucel et al. (2022); Hesamzadeh-Hejazi and Ziaei-Nasab (2010)
20	*O. cyri*	28	Magulaev (1989); Yucel et al. (2022)
21	*O. daghestanica*	14	Krivenko et al. (2017)
22	*O. elata*	14	Arslan et al. (2012)
23	*O. galegifolia*	16	Al-Mayah and Al-Shehbaz (1977); Arslan et al. (2012)
		14	Abuş and Avci (2018)
24	*O. gaubae*	16	Hesamzadeh-Hejazi and Ziaei-Nasab (2010); Yucel et al. (2022)
25	*O. gracilis*	14	Yucel et al. (2022)
26	*O. grandis*	14	Yucel et al. (2022)
27	*O. gypsicola*	16	Hesamzadeh-Hejazi and Ziaei-Nasab (2010)
28	*O. hajastana*	14	Arslan et al. (2012)
29	*O. hamata*	28	Magulaev (1989)
30	*O. hohenackeriana*	14	Ranjbar, Hajmoradi, and Karamian (2010)
		16	Hesamzadeh-Hejazi and Ziaei-Nasab (2010)
31	*O. humilis*	14	Yucel et al. (2022)
32	*O. hypargyrea*	14	Abuş and Avci (2018); Yucel et al. (2022)
33	*O. iberica*	16	Yucel et al. (2022)
34	*O. inermis*	28	Yucel et al. (2022)
35	*O. kotschyana*	14	Arslan et al. (2012); Hosgoren (2006)
36	*O. kachetica*	16	Yucel et al. (2022)

(Continues)

TABLE 2 (Continued)

No.	Species	2n	References
37	*O. majorovii*	14	Magulaev (1995)
38	*O. megataphros*	14	Yucel et al. (2022)
		32	Hosgoren (2006)
39	*O. melanotricha*	16	Hesamzadeh-Hejazi and Ziaei-Nasab (2010)
40	*O. meschetica*	14	Abuş and Avci (2018)
41	*O. michauxii*	16	Yucel et al. (2022)
		14	Ranjbar, Hajmoradi, and Karamian (2010)
42	*O. montana*	28	Favarger (1997)
43	*O. oxyptera*	16	Ansari et al. (2002)
44	*O. oxyodonta*	28	Akalin and Alpinar (1994)
		14	Arslan et al. (2012)
45	*O. ornate*	16	Löve ()
46	*O. ptolemaica*	16	Abou-El-Enain (2002)
		14	Yucel et al. (2022)
47	*O. plantago*	16	Hesamzadeh-Hejazi and Ziaei-Nasab (2010)
48	*O. pulchella*	32	Abou-El-Enain (2002)
49	*O. persica*	16	Yucel et al. (2022)
		28	Hesamzadeh-Hejazi and Ziaei-Nasab (2010)
50	*O. radiata*	14	Abuş and Avci (2018); Magulaev (1995); Hesamzadeh-Hejazi and Ziaei-Nasab (2010)
		16	Yucel et al. (2022)
51	*O. scrobiculata*	16	Ansari et al. (2002)
52	*O. sibirica*	28	Mesicek and Sojak (1992)
53	*O. sintenisii*	16	Yucel et al. (2022)
		14	Hesamzadeh-Hejazi and Ziaei-Nasab (2010)
54	*O. stenorhiza*	14	Yucel et al. (2022)
55	*O. subacaulis*	32	Yucel et al. (2022)
		16	Arslan et al. (2012)
56	*O. subnitens*	14	Ranjbar, Hajmoradi, and Karamian (2010)
57	*O. supina*	14	Bernardo et al. (2020); Yucel et al. (2022)
58	*O. tehranica*	16	Hesamzadeh-Hejazi and Ziaei-Nasab (2010)
59	*O. tomentosa*	16	Hesamzadeh-Hejazi and Ziaei-Nasab (2010)
60	*O. tournefortii*	14	Arslan et al. (2012); Abuş and Avci (2018)
		16	Arslan et al. (2012)
61	*O. transcaspica*	14	Hesamzadeh-Hejazi and Ziaei-Nasab (2010)
62	*O. transcaucasica*	28	Yucel et al. (2022)
63	*O. vaginalis*	16	Yucel et al. (2022)
64	*O. vassilczenkoi*	16	Yucel et al. (2022)
65	*O. viciifolia*	28	Yucel et al. (2022)

4.1 | Salinity responses

Fourteen studies have analyzed the responses of wild *Onobrychis* species to soil conditions. For example, *Onobrychis oxyodonta* var. armena (Boiss. & Huet), a gypsovag species from Central Anatolia (Turkey), increased its foliar concentrations of proline and soluble carbohydrate to withstand non-gypsum soils (Ozdeniz, 2019). Most of the studies analyzing the responses of wild *Onobrychis* species to soil characteristics have focused on salt and drought stress (Table 3, Figure 3). Increasing salinity is a major abiotic stress affecting growth and yield of many crops (Machado & Serralheiro, 2017). Seeds and seedlings of several wild *Onobrychis* species withstand moderate saline environments (up to ca. 200 mM NaCl),

TABLE 3 Salt and drought stress tolerance for some wild *Onobrychis* species.

Species	Classification	Stage	Stress tolerance	Source
Salinity				
O. stenostachya subsp. sosnowskyi, *O. paucijuga*	Tolerant	Germination	<15 dS m^{-1} (ca. 167 mM)	Uzun et al. (2017)
O. gracilis, *O. cilicica*, *O. podperae*	Moderately sensitive	Germination	<10 dS m^{-1} (ca. 111 mM)	
O. fallax var. longifolia, *O. sulphurea* var. sulphurea, *O. pisidica*, *O. beata*	Moderately tolerant	Germination	<5 dS m^{-1} (ca. 56 mM)	
O. transcaucasica, O. chorassanica	Moderately sensitive	Vegetative	<100 mM	Shakirov et al. (2012)
Drought				
O. melanotricha and *O. sojakii*	Tolerant	Vegetative	>50% Field capacity (FC)	Nasirzadeh et al. (2005)
O. aucheri subsp. *tehranica*	Moderately tolerant	Vegetative	>50% FC	
O. aucheri ssp. *psamophilla* and *O. crista-galli*	Drought sensitive	Vegetative	>50% FC	
O. caput-galli	Tolerant	Vegetative	>40% FC	Kostopoulou et al. (2010)

displaying tolerance mechanisms such as seed physiological dormancy (Figure 3a). Salinities higher than ca. 200 mM NaCl adversely impacted germination and establishment of wild *Onobrychis* species by increasing the mean germination time and decreasing the final germination percentage and the development of seedlings (Karamian & Ataei Barazandeh, 2013; Shakirov et al., 2012). In fact, seed germination drastically declined in *O. oxyodonta* var. armena from Turkey at salinities higher than ca. 222 mM (Beyaz et al., 2011). In this respect, Karamian and Ataei Barazandeh (2013) reported decreasing germination percentages for *Onobrychis subnitens* Bornm. and *Onobrychis melanotricha* Boiss. from Iran at salinities higher than 200 mM NaCl and indicated that germination was totally inhibited at 400 mM NaCl. At the germination stage, Uzun et al. (2017) considered *Onobrychis stenostachya* subsp. *sosnowskyi* (Grossh.) Hedge and *Onobrychis paucijuga* Bornm. from Turkey as more tolerant than other 10 *Onobrychis* species, particularly at salinities ca. 167 mM NaCl. After 2 months of growth, Shakirov et al. (2012) indicated that growth suppression initiated in *O. transcaucasica* and *Onobrychis chorassanica* Bunge ex Boiss. from Uzbekistan at salinities higher than 200 mM NaCl and reported 300 mM NaCl as the critical salinity for survivorship. The symbiosis of these two *Onobrychis* species with *Rhizobium* enhanced their tolerance to salinity up to 150 mM NaCl (Table 3, Figure 3a).

4.2 | Drought responses

Drought is one of the main abiotic stresses that hinder plant growth (Liao et al., 2021). Climate change is expected to increase drought frequency and severity in arid and semi-arid regions and correspondingly, it is projected to increase the rates of yield reduction by >50% in 2050 and almost 90% in 2100 for the major crops (Cook et al., 2018; Li et al., 2009). When subjected to drought stress, seeds of wild *Onobrychis* species display differential drought-adaptive strategies by exhibiting physiological and physical dormancy (Table 3, Figure 3b). In this regard, seed pod and seed coat prevent moisture from being absorbed by the seed until required moisture levels for germination and seedling development are achieved (Avci & Kaya, 2013; Majidi & Barati, 2011). In general, wild *Onobrychis* species show drought tolerance superiority when compared to cultivated *O. viciifolia* and other forage species. Based on root and shoot growth, Nasirzadeh et al. (2005) reported that *O. melanotricha* and *Onobrychis sojakii* Rech.f. can be considered as drought tolerant species, *O. viciifolia* and *Onobrychis aucheri* subsp. *tehranica* (Bornm) Rech as semi-resistant species, and *O. aucheri* subsp. *psamophilla* (Bornm) Rech and *O. crista-galli* as sensitive species in Fars Province (Iran). In addition, in contrast with *Trifolium angustifolium* L., *O. caput-galli* was found to maintain its water potential stable even under limited irrigation (40% field capacity). *Onobrychis caput-galli* displayed a clear isohydric behavior by attempting to maintain both relative water content (RWC) and leaf water potential (ψ) in high levels through stomatal closure induced by hydraulic and chemical signals resulting in reduction of the plant's photosynthetic capacity. These responses imply energy consumption eventually reducing the energy budget for other biological activities (Kostopoulou et al., 2010). In addition, *O. caput-galli* shows shorter biological cycles as an adaptive mechanism to avoid the critical dry period (Johnson et al., 2022). To cope with drought, *O. aequidentata* from Thessaloniki (Greece) maintained higher leaf water poten-

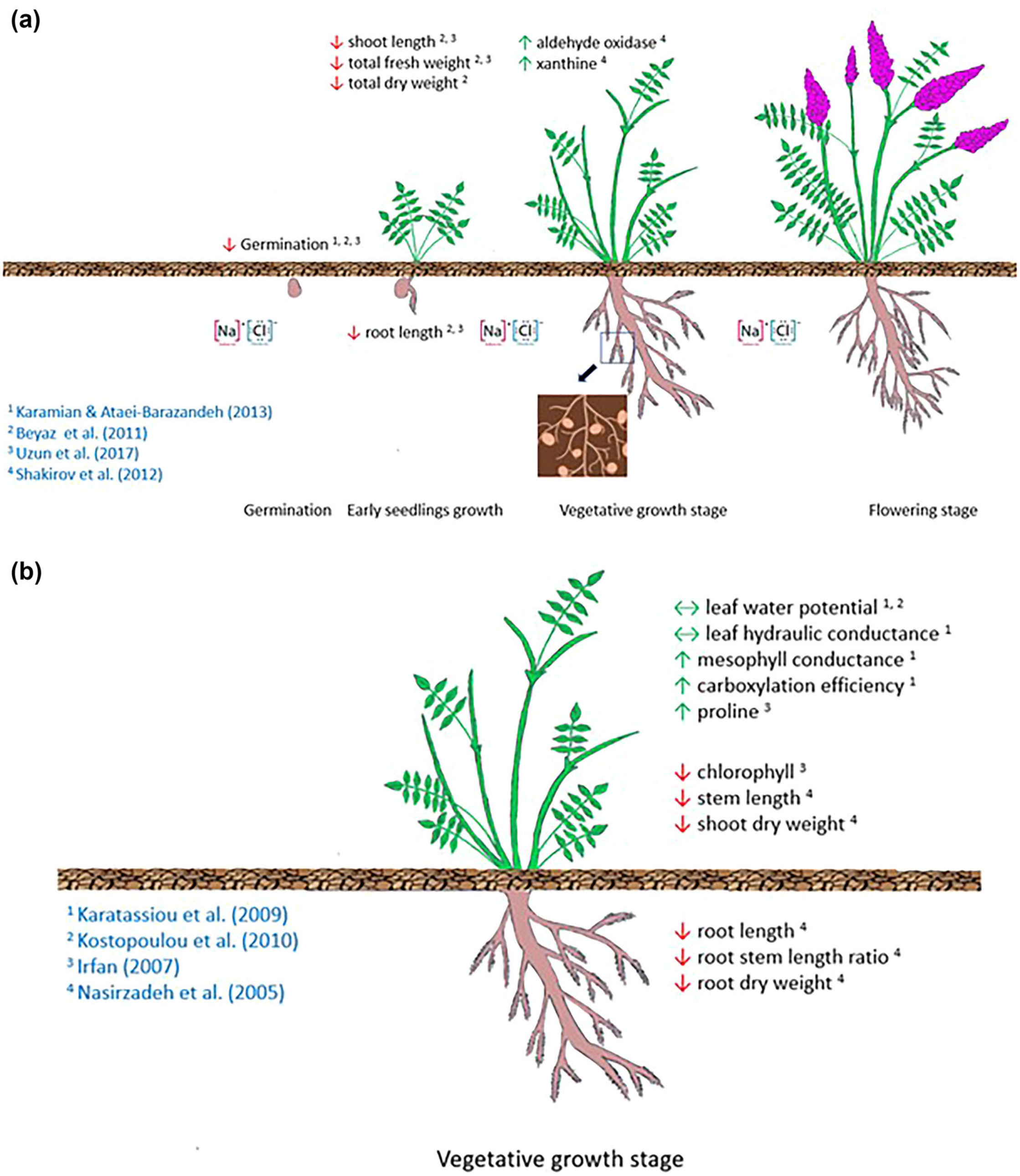

FIGURE 3 Summary of the main tolerance mechanisms of wild *Onobrychis* species to (A) salinity and (B) drought stress at different growth stages.

tial, mesophyll conductance, carboxylation efficiency, and leaf hydraulic conductance, and, consequently, exhibited better water balance under drought than *Medicago minima* (L.) L. (Karatassiou et al., 2009). The observed high values of ψ and RWC in *O. aequidentata* compared to *M. minima* could be probably attributed to the higher hydraulic conductance. Moreover, the high net photosynthetic rate in *O. aequidentata* seems to be dependent both on stomatal and mesophyll conductance, which could be an efficient adaptation mechanism to alleviate the negative impact of drought under climate change (Serna, 2022). The significant negative correlation between net photosynthesis rate and the quotient intercellular CO_2 concentration to stomatal conductance ratio (Ci/gs) suggests that the net photosynthesis rate in *O. aequidentata* is controlled by mesophyll efficiency (Karatassiou et al., 2009). To cope with drought, *Onobrychis cornuta* (L.) Desv. decreased its water potential, water use efficiency and chlorophyll concentration, and increased its leaf proline concentration at Ziarat Valley (Pakistan) (Irfan, 2007).

4.3 | Elevated CO_2 and high temperatures

Climate change is linked to anthropogenic activities driven largely by increased atmospheric CO_2 concentration due to fossil fuel consumption (Leung et al., 2014). The farmers' choice of adequate crops and cropping systems can be an important adaptation strategy to climate change (De Pinto et al., 2019; Waha et al., 2013). Among 26 annual and perennial grasses, legumes, forbs, and geophytes, *O. crista-galli* has been shown to take advantage of CO_2 enrichment from 280 to 600 ppm by increasing plant biomass (+78%), plants density (+8%), fruit dry matter (+138%), total seed mass per individual (+120%), and number of seeds per individual (+146%), while decreasing its mass per individual seed (−12%) (Grünzweig & Körner, 2001). In view of these results, *O. crista-galli* would provide high nutritive value fodder for grazing animals and enrich soil with nitrogen (N) via symbiosis in the present climate change scenario. In addition, *O. crista-galli* profits from the increased water availability at elevated CO_2 conditions thanks to its mesic behavior characterized by late flowering, low number of seeds per pod, and low seed dormancy in addition to dispersal-promoting mechanism (Grünzweig & Körner, 2001).

Climate warming and elevated CO_2 can modify nutrient cycling mediated by enzymes in soils, especially in cold-limited ecosystems with a low availability of nutrients and a high-temperature sensitivity of decomposition and mineralization (Souza et al., 2017). *Onobrychis beata* Širj. showed lower rate of carbon (C) mineralization than *Trifolium speciosum* Boiss. Therefore, the necromass of *O. beata* has the ability to slowly release mineral N, phosphorus, and sulfur, and provide them over larger time scale reducing leaching losses and eutrophication. With an increase in air temperature from 24˚C to 32˚C, *O. beata* showed increased cumulative mineralized C and rate of mineralization of organic C independently of soil moisture condition in Adana (Turkey). This was mainly due to increased microbial requirements for C and nutrients (Cenkseven et al., 2017).

4.4 | Environmental factors hampering seedling establishment

Although some wild *Onobrychis* species are adapted to a wide range of environmental conditions, such as moderate salinity and drought, their seedling establishment may be limited under some environmental circumstances. For example, wild *Onobrychis* species prefer well-drained areas and are not tolerant to soil waterlogging conditions (Carbonero et al., 2011; Demdoum, 2012; García-Salmerón et al., 1966; Sheldrick et al., 1987). In addition, *Onobrychis* seedling establishment may be limited by low light intensity (Novoplansky et al., 1994; Novoplansky, 1996), acidic conditions (Bland, 1971; Carbonero et al., 2011), and high soil and air temperatures (Kallenbach et al., 1996).

5 | POTENTIAL USES OF WILD *Onobrychis* SPECIES

5.1 | Restoration of degraded areas

Climate change and soil degradation are two major, interrelated environmental challenges. In one hand, climate change is acknowledged to cause significant land cover changes, soil moisture deficits during droughts, and increased surface runoff due to torrential rains (Tao et al., 2005). Furthermore, land degradation aggravates climate change through the release of CO_2 from cleared and dead vegetation and through the reduction of the C sequestration potential (Sivakumar & Stefanski, 2007). In this context, *O. cornuta* from Iran can be considered as an advantageous head of crop rotation due to its positive influences on weed control through limiting the growth and reproduction of herbaceous species due to its procumbent and compact canopy (Erfanzadeh et al., 2020). In addition, the cushions of *O. cornuta* act as seed traps and, therefore, play an important role in conservation and recovery of degraded areas (Niknam et al., 2018). Based on germination percentage, germination rate and thermal time requirement, Gorgin-Karaji et al. (2018) suggested that *Onobrychis subnitense* Bornm. and *Onobrychis scrobiculata* Boiss. could be valuable alternatives in the conservation and improvement of arid and semi-arid rangelands in Iran. In this sense, *Onobrychis argentea* subsp. *argentea* Boiss. could be of interest for the regeneration of pastures on skeletal soils in the Western Tunisian Ridge and the Saharan Atlas (Le Houérou, 1987). Nevertheless, the widespread adoption of wild *Onobrychis* species in ecological restoration projects is limited by the high cost and unavailability of their seeds compared with other forage legume species (Carbonero et al., 2011; Sheppard et al., 2019).

5.2 | Atmospheric di-nitrogen fixation

The rhizobia–legume symbiosis plays a key role in nutrient cycling as an important N source to terrestrial ecosystems, which can fuel primary production, driving CO_2 sequestration and mitigating climate change (Kou-Giesbrecht & Menge, 2021). The symbiotic N_2 fixation represents a sustainable alternative to chemical fertilization, which depends upon the major greenhouse gas-contributing Haber–Bosch process. Hence, legumes are widely used in crop rotations to manage soil N content, and rhizobia have been used successfully at scale to fertilize crops worldwide (Tookmanian et al., 2021).

In this sense, *Onobrychis* species offer important opportunities for sustainable agricultural production due to their ability to fix N as they can contribute to important key challenges by (i) substituting inorganic N-fertilizer inputs with symbiotic N_2 fixation; (ii), increasing forage yield; (iii) increasing the nutritive value of pastures; and (iv) mitigating and facilitating adaptation to climate change (Lüscher et al., 2014; Majidi & Barati, 2011).

Onobrychis species form symbioses with bacteria belonging to the genera *Mesorhizobium*, *Rhizobium*, *Bradyrhizobium*, and *Sinorhizobium* (Baimiev et al., 2007) and have the potential to be cross inoculated by several strains of *Rhizobium* isolated from different leguminous species such as *Hedysarum boreale* Nutt., *Coronilla varia* L., *Petalostemum candidum* Michx, *Dalea purpurea* Vent., *Dalea candida* Willd., *Astragalus alpinus* L., *Oxytropis maydelliana* Trautv., and *Oxytropis arctobia* Bunge (Burton & Curley, 1968; Prévost, Bordeleau, & Antoun, 1987). Molecular biology studies have shown that bacterial strains capable to form symbiosis with *Onobrychis* species are not confined to the family *Rhizobiaceae*. For instance, members of the genera *Phyllobacterium*, including closely related bacteria to *Phyllobacterium trifolii*, have been discovered to nodule *O. arenaria* roots in Bashkortostan (Baimiev et al., 2007). In addition, *Rhizobium ciceri* has been found to nodulate *Onobrychis spinacrisbi* in the North of Jordan, showing the maximum growth at 38˚C (Yousef & Abdul-Karim, 2012).

Despite being abundantly nodulated, N deficiency symptoms were reported in the cultivated species *O. viciifolia*, which indicates that the strain of N-fixing bacteria present was inefficient or short-lived (Burton & Curley, 1968; Schneiter et al., 1969). However, these symptoms disappeared with time in plants nodulated by effective strains (Prévost, Bordeleau, & Antoun, 1987). Therefore, it seems likely that *O. viciifolia* is dependent on some mineral N at early growth stages and later growth stages benefit significantly from effective symbiosis (Carbonero et al., 2011). *Onobrychis viciifolia* is less efficient than *M. sativa* and *T. pratense* at fixing N_2. *Onobrychis viciifolia* have biological N_2 fixation rate up to 160 kg N ha^{-1} $year^{-1}$, within the range of other forage legumes but below the rate in *M. sativa* (up to 650 kg N ha^{-1} $year^{-1}$) (Provorov & Tikhonovich, 2003; Re et al., 2014). This is one of the main reasons attributed to the low persistence of *O. viciifolia* in many forages stands. In view of previous works, inoculating *O. viciifolia* with rhizobia isolated from wild *Onobrychis* species largely adapted to a wide range of environmental conditions could improve biological N_2 fixation during cold phases or early growth stage (Prévost, Bordeleau, & Antoun, 1987; Prévost, Bordeleau, & Caudry-Reznick, 1987). In this sense, exploiting wild *Onobrychis* species would help mitigate climate change through the reduction of N fertilizers and related greenhouse gasses emissions. In addition, the cultivation of wild *Onobrychis* species would support farmers in their efforts to cope with climate change and to face the increasing costs of N fertilizers.

5.3 | Pollen and nectar source and herbivory

Climate change is one of the major threats for honeybees and honey production via direct impacts on water resources and nectar availability (Vercelli et al., 2021). *Onobrychis* species are self-sterile and require multiple flower visits to maximize cross-pollination (Bogoyavlenskii, 1974; Kropacova & Haslbachova, 1969). Honeybees (*Apis mellifera* L.) are common floral visitors of *Onobrychis* species as shown by the percentage of monofloral honey from *Onobrychis* species, representing 54% of the total produced honey in south-western Lithuania (Čeksterytėa et al., 2013). In this sense, wild *Onobrychis* species were the main melliferous plants supplying monofloral honeys in forest and steppes in western Russia (Kurmanov & Galeev, 2021). Pollen of several *Onobrychis* species, including *Onobrychis radiata* (Desf.) M. Bieb., *O. tournefortii* (Willd.) Desv., and *O. oxyodonta* Boiss., was identified among *Onobrychis* honeys in Anatolia (Turkey) (Gencay-Celemli et al., 2018; Ozenirler et al., 2019). In relation to the quality of pollen and honeys from wild *Onobrychis* species, Temizer et al. (2017) concluded that pollen grains contain fatty and aliphatic acids and can be used as a high antioxidant agent in food and medicine. On the other hand, an organoleptic evaluation of monofloral *Onobrychis* honey in Russia showed a distinctive taste and smell (Vereshchagin et al., 2015).

Wild *Onobrychis* species in Susa Valley (Western Alps, Italy) were visited by eight *Bombus* L. species (Manino et al., 2010). Along with *Origanum* spp. and *Allium* spp., wild *Onobrychis* species were the most frequently visited nectar source for males of the butterfly *Polyommatus exuberans* (Verity, 1926) in Susa Valley (Western Alps, Italy) (Parile et al., 2021). Besides pollination, wild *Onobrychis* species are key plants during the life cycle of some species of butterflies. Pérez-Fernández et al. (2019) reported that *O. argentea* subsp. *hispanica* was consumed by three species of *Lepidoptera*, and that was the only nutritious plant for two other *Lepidoptera* species in the center of the Iberian Peninsula. In this sense, *O. montana* and *O. arenaria* have been identified as host plants for the leaf beetle *Cheilotoma musciformis* Goeze in Poland and Ukraine, where it has been suggested to be monophagous (Kajtoch et al., 2013).

5.4 | Nutritional value

The impacts of climate change on forage crops include decreased productivity and nutrient content, along with reduced planting area that may disrupt animal feed and food availability (Brychkova et al., 2022). Feeding forage legumes containing condensed tannins (CT), such as *Onobrychis* species, to ruminants has the potential to increase protein utilization, improve zootechnic performance, and prevent bloating, unlike other legumes such as *M. sativa* L. Moreover, legumes containing CT, decrease rumen protein degradation and increase the plasma level of essential amino acids. Furthermore, they reduce urinary N excretion and ruminal methane (CH_4) emissions, which are contributors to environmental pollution and climate change (Bhattarai et al., 2016, 2018; Seoni et al., 2021; Sheppard et al., 2019).

Onobrychis species can have various functions such as supplying forage in fresh or dried form to grazing animals or livestock and could recover growth after being grazed, chewed, or mowed (Kajtoch et al., 2013; Le Houérou, 1980, 1987, 1995). *Onobrychis* species can provide valuable browse for livestock and belong to the main wildlife grazing sources all along the Mediterranean Basin. In arid and semiarid areas, especially in dry season, they can be used as an alternative food for livestock when other forage yield is insufficient (Le Houérou, 1995). Therefore, in forage shortage seasons, *Onobrychis* species can be used as a complementary or alternative forage supplier in animal husbandry production to alleviate forage and food insecurity. For instance, *O. cornuta* and *Onobrychis conferta* (Desf.) Desv. can provide abundant food sources and protection for wild animals and may play a positive role in promoting flora diversity in their habitats thus contributing to grazing resources diversification (Bahalkeh et al., 2021; Le Houérou, 1995). In addition, *Onobrychis carduchorum* C.C.Towns. is an important perennial herb that can be used for high-protein fodder for ruminants and equines, for increasing the nutritive value of drought-resistant pastures due to its N_2 fixation, and for soil conservation in Iran (Abou-El-Enain, 2002; Elena, 2006). In the present climate change scenario, sufficient feed of suitable quality could be offered by wild *Onobrychis* species that may exceed those of *O. viciifolia* (Table 4). *O. arenaria* is highly appreciated nutritious plant. Its crude protein content in the leaves is ca. 18%, which is higher than that of *O. viciifolia* and comparable to *M. sativa* (Redfearn & Zhang, 2011; Ülger & Kaplan, 2016). In addition, the content of one of the major parameters associated with plant consumption, neutral detergent fiber, is relatively high and can reach ca. 57% for *O. cornuta* (L.) Desv., exceeding that of *M. sativa* (ca. 43%) (Albayrak et al., 2018; Okcu & Şengül, 2014). Additionally, *Onobrychis saxatilis* (L.) Lam. and *Onobrychis stenorhiza* DC. are highly palatable species, and their leaves and flowers were preferred to other plants parts by almost all classes of livestock and wild herbivores (Correal et al., 1987; Rios et al., 1989). Under rainfed conditions, *O. cornuta* produced large biomass, reaching ca. 67 g dry weigh plant^{-1}, which represents fourfold the yield obtained for *M. sativa* (Okcu & Şengül, 2014; Şengül, 1995) (Table 4).

5.5 | Medicine and pharmacology

Climate change alters the concentrations of bioactive compounds to oppose the oxidative stress derived from increasing environmental tensions (Ben Mansour-Gueddes et al., 2020). The bioactive compounds of *Onobrychis* species own outstanding medicinal and pharmacological properties, especially as anticancer and anti-inflammatory drugs, in addition to its antioxidant, antibacterial, antifungal, and antiviral properties (Table 5). Nevertheless, biological activity studies highlighted that wild *Onobrychis* species have not been yet investigated properly. Ethnobotanical evidence supports the use of *Onobrychis* species in traditional medicine in several parts of the world, such as *Onobrychis gracilis* Besser. that is used to manage cold and flu in Turkey (Demirci & Ozhatay, 2012). In addition, *O. carduchorum* and *O. altissima* Grossh. leaves compresses are traditionally used in Turkey as a styptic and to cure wounds, inflammations, and other skin diseases (Dalar et al., 2018; Mükemre et al., 2015). This ethnical use of *O. carduchorum* was supported by the abundant presence in its leaves of prenylated polyphenols with antibacterial and wound healing activities, along with radical scavenging ability (Clericuzio et al., 2020). Ten different polyphenols were extracted from *O. carduchorum* including four isoflavones having a genistein skeleton, three flavanones having a naringenin skeleton and three prenylated dihydro-stilbenes. In particular, prenylated dihydro-stilbenes were isolated before, so far, only from *Glycyrrhiza glabra* L. Many of the prenylated phenols isolated from *O. carduchorum* showed significant cytotoxicity on some human breast cancer cell lines, and a relevant growth inhibition of *Staphylococcus aureus* strains suggesting that these bioactivities are responsible for the plant's traditional use (Clericuzio et al., 2020). In this sense, aerial parts of different *Onobrychis* species from Turkey, such as *O. oxyodonta* arial parts ethanolic extracts, *O. armena* Boiss & Huet methanolic flower and roots extracts, show antioxidant activity, moderate antitumor activity, and antimicrobial activity against some bacteria, fungus and fish pathogens (Karakoca et al., 2015; Usta et al., 2014). *Onobrychis hyparygrea* Boiss. aqueous, ethanolic, and methanolic extracts showed elevated antioxidant capacity, as well as high phenolic and flavonoid content, which has been proven to be highly linked to the species' inhibitory potential against cholinesterase, tyrosinase, α-amylase, and α-glucosidase in vitro (Zengin et al., 2015).

The aerial parts methanolic extracts of *Onobrychis sosnovskyi* Grossh. and *O. melanotricha* Boiss. have strong antioxidant activities and include important phytochemicals that may help to develop new drug candidates for antioxidants,

TABLE 4 Nutritive value of wild *Onobrychis* species.

Species	Country	Raw protein (%)	Raw ash (%)	ADF (%)	NDF (%)	Dry weigh per plant (g)	References
O. atropatana Boiss. var. grandiflora	Turkey	13.61	9.25	43.72	54.81	32.38	Okcu and Şengül (2014)
O. cornuta (L.) Desv.	Turkey	10.61	7.66	46.72	57.45	66.75	Okcu and Şengül (2014)
O. hajastana Grossh.	Turkey	14.99	10.96	33.65	44.88	17.85	Okcu and Şengül (2014)
O. huetiana Boiss.	Turkey	11	7.5	33.77	44.68	28.04	Okcu and Şengül (2014)
O. huetiana subsp. *bornmuelleri* (Freyn) Ponert	Turkey	14.65	10.12	33.55	45.36	28.56	Okcu and Şengül (2014)
O. montana DC.	Turkey	14.14	10.26	40.31	52.27	23.84	Okcu and Şengül (2014)
O. radiata (Desf.) M.Bieb.	Turkey	11.1	8.24	33.81	45.96	31.62	Okcu and Şengül (2014)
O. stenostachya Freyn	Turkey	13.8	9.21	34.37	44.58	25.48	Okcu and Şengül (2014)
O. stenostcahya subsp. *sosnowskyi* (Grossh.) Hedge	Turkey	15.79	11.16	23.93	40.48	18.22	Okcu and Şengül (2014)
O. viciifolia Scop.	Turkey	14.87	9.15	30.78	39.8	26.32	Okcu and Şengül (2014)
O. viciifolia Scop.	Turkey	12.73–15.90	5.95–7.63	32.01–41.79	42.57–53.89	–	Ülger and Kaplan (2016)
O, aurantiaca Boiss.	Syria	10	–	11.2	14	–	Larbi et al. (2011)
O. arenaria (Kit.) DC.	Moldova	16.96–18.39	7.41–8.36	–	–	–	Ţiţei et al. (2021)

Abbreviations: ADF, acid detergent fiber; NDF, neutral detergent fiber.

which might be helpful in treatment of diseases caused by different free radicals (Karamian & Asadbegy, 2016). Özbek et al. (2019) suggested that methanol water extracts of the aerial parts antidiabetic activities of *Onobrychis albiflora* Hub-Mor., *Onobrychis argyrea* Boiss. subsp. *argyrea* Boiss., *Onobrychis galegifolia* Boiss. and *O. tournefortii* is conferred by rutin and isoquercetin. On the other hand, *Onobrychis ebenoides* aqueous extract exhibited a highly significant protective effect on bone mineral density of the whole tibia of ovariectomized rats. The rats that were administered the extract retained a larger number of trabeculae in the proximal tibial epiphysis and had a simultaneous decreased number of trabecular perforations compared to the non-treated ovariectomized rats (Dontas et al., 2006). This beneficial effect could be due to the estrogenic action of the arylobenzofurans isolated in *O. ebenoides* aqueous extract (Halabalaki et al., 2000). In addition, *O. ebenoides* displayed estrogenic activity in breast cancer cells, but devoid of estrogenic activity in the uterus (Halabalaki et al., 2000; Papoutsi et al., 2004, 2007).

6 | CONCLUSIONS

More than 100 wild *Onobrychis* species have been described from which 49 species have been studied in any particular topic. This set of initial information, however, dispersed and non-systematically collected, shows that wild *Onobrychis* species are important sources of major tolerance genes to different environmental stressors, which may be key for the improvement of the cultivated species *O. viciifolia* in the present climate change scenario. Although *Onobrychis* species are widely used as an excellent forage in animal husbandry, we still have some knowledge gaps compared to *O. viciifolia* about detailed forage chemical composition, digestibility, contents of mineral elements, and so forth. Despite that *O. viciifolia* could increase the nutritive value of drought-resistant pastures in rainfed Mediterranean conditions due to N_2 fixation rates of 160 kg N ha^{-1} year^{-1} (Provorov & Tikhonovich, 2003; Re et al., 2014). To the best of our knowledge, no study estimated the amount of N_2 fixed via symbiosis or the effect of arbuscular mycorrhizal

TABLE 5 Medical uses and biological activity for some wild *Onobrychis* species.

Species	Plant part	Biological activity	Target	Source
Pharmacology				
O. oxyodonta	Aerial parts	Antibacterial	*Escherichia coli Pseudomonas aeruginosa Klebsiella pneumoniae Streptococcus pyogenes Staphylococcus aureus Staphylococcus epidermidis*	Usta et al. (2014)
		Antitumor	*Agrobacterium tumefaciens*	
O. armena	Flower and roots	Antimicrobial	*Escherichia coli Escherichia coli Staphylococcus aureus Salmonella enteritidis Listeria monocytogenes Escherichia coli (O157:H7), Bacillus cereus Pseudomonas aeruginosa Micrococcus luteus Shigella sonnei Yersinia enterocolitica Candida albicans*	Karakoca et al. (2015)
		Antioxidant	–	
O. albiflora O. argyrea O. galegifolia O. tournefortii	Aerial parts	Antidiabetic (rutin and isoquercetin)	Balb/C strain mice	Özbek et al. (2019)
O. crista-galli	All parts	Antioxidant Anti-inflammatory	–	Benchadi et al. (2020)
O. argyrea subsp. *isaurica*	Whole parts	Antidiabetic	α-amylase, α-glucosidase	Guler et al. (2018)
		Anti-Alzheimer's disease	Acetylcholinesterase, butyrylcholinesterase	
		Antioxidant	–	
		Antistressor	–	
		Hyperpigmentation	Tyrosinase	
O. hypargyrea	Whole parts	Antidiabetic	α-amylase and α-glucosidase	Zengin et al. (2015)
		Neuro degenerative disorders	Tyrosinase, acetylcholinesterase, butyrylcholinesterase	
		Hyperpigmentation	Tyrosinase	
O. carduchorum	The acetone crude extract of leaves and flowers	Antibacterial Anticancer	*Staphylococcus aureus* MCF-7, SkBr3, and MDAMB-231	Clericuzio et al. (2020)
Ethnobotanical survey				
O. gracilis	Aerial parts	Cold and flu	Decoction	Demirci and Özhatay (2012)
O. carduchorum, *O. altissima*	Crushed leaves	Wounds and cuts Styptic	Compress	Mükemre et al. (2015)
O. carduchorum	Crushed leaves	Wounds and cuts Styptic	Compress	Dalar et al. (2018)
O. carduchorum	–	Wounds, inflammations, and other skin diseases	–	Clericuzio et al. (2020)

fungi of any wild *Onobrychis* species. Additionally, some wild *Onobrychis* species have the potential to become new crops and important sources of nutritious and bioactive compounds. Unfortunately, there is a limited number of studies on the nutritional, anti-nutritional, and biochemical characteristics of wild *Onobrychis* species and almost no known attempts of domestication. Furthermore, there is no effort on any wild *Onobrychis* species to relate agronomic features and genetic diversity with biochemical and nutritional constituents. Other than salinity and drought, information about stress tolerance mechanisms of wild *Onobrychis* species is very scarce. In this context, future research should focus, for example, on the tolerance of wild *Onobrychis* species to fungi, herbivore insects and nematodes, which constitute major constrains toward the expansion of the cultivated species *O. viciifolia*. The use of wild *Onobrychis* species appears as an important and economically relevant strategy to overcome climate change consequences such as increasing drought, salinization, pests, and diseases. Holistic approaches to improve the rural livelihood through enhancing the use of neglected and underutilized plant species are attracting the interest of the scientific community (Gotor et al., 2013; Harouna et al., 2018; Padulosi et al., 2014). In this context, there is an urgent need to preserve those wild *Onobrychis* species that are endemic with reduced and decaying distribution areas.

AUTHOR CONTRIBUTIONS

Anis Sakhraoui: Conceptualization; data curation; investigation; methodology; writing—original draft. **Hela Belhaj Ltaeif**: Investigation; software; writing—original draft. **Asma Sakhraoui**: Investigation; writing—original draft. **Slim Rouz**: Conceptualization; investigation; methodology; supervision; validation; visualization; writing—review and editing. **Jesús Castillo**: Conceptualization; investigation; methodology; supervision; validation; visualization; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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