

European and Mediterranean Plant Protection Organization
Organisation Européenne et Méditerranéenne pour la Protection des Plantes

Data sheets on pests recommended for regulation

Fiches informatives sur les organismes recommandés pour réglementation

Humulus scandens (Lour.) Merr.

Identity

Scientific name: *Humulus scandens* (Lour.) Merr.

Synonyms: *Antidesma scandens* Lour. (basonym) – *Humulus japonicus* Siebold & Zucc. – *Humulus japonicus* var. *variegatus* F.Roem.

Taxonomic position: phylum Tracheophyta; class Magnoliopsida; order: Urticales, family: Cannabaceae.

Common names: English: Japanese hop; French: houblon japonais; German: japanischer Hopfen; Japanese: kanamugura; Portuguese (Brazil): lúpulo; Italian: Luppolo del Giappone; Swedish: japansk humle; Chinese (transcribed): lü cao

EPPO Code: HUMJA

Phytosanitary categorization: EPPO A2 List no. 425

Geographical distribution

Native range

Asia: China (Anhui, Zhejiang, Fujian, Heilongjiang, Henan, Hebei, Hunan, Hubei, Jiangxi, Jiangsu, Jilin, Guangdong, Guizhou, Liaoning, Shanxi, Shandong, Shaanxi, Sichuan, Yunnan, Guangxi, Xizang, Hainan), Mongolia, Japan (Hokkaido, Honshu, Kyushu, Ryukyu Islands, Shikoku), North and South Korea, Taiwan, Vietnam, Russian Federation (Primorye, Amur)

Introduced range

EPPO region: Austria, Belgium, Czech Republic, France, Germany, Italy, Hungary, Romania, Serbia, Slovakia, Slovenia, Switzerland, Ukraine

North America: Canada (Quebec, Ontario), USA (Alabama, Delaware, District of Columbia, Georgia, Illinois, Indiana, Kentucky, Maine, Maryland, Massachusetts, Michigan, Minnesota, Missouri, Nebraska, New Hampshire, New Jersey, New York, North Carolina, North Dakota, Ohio, Pennsylvania, Rhode Island, South Carolina, South Dakota, Vermont, Virginia, West Virginia, Wisconsin)

History of introduction and spread

Humulus scandens is native to Asia (China, Taiwan, Japan, North and South Korea, Russian Far East and Vietnam). It

has been introduced as an ornamental in both Europe and North America where it is becoming an invasive alien species in several regions.

Humulus scandens was first imported to America in the late 1800s for use as a tonic in Asian medicine and as an ornamental vine. It is still sold for these purposes today (Pannill *et al.*, 2009). In North America, the earliest records of its escape and naturalization come from Eastern Massachusetts in the 19th century (IPANE, 2005). In Delaware, a few escapes from cultivation were observed in the 1900s.

Currently, it is most abundantly established in New England, the mid-Atlantic States and some areas of the Midwest that include Ohio, Indiana, Illinois, Missouri, Iowa, Eastern Nebraska and Kansas (NatureServe, 2017). The establishment of *H. scandens* is more scattered in the Northern Midwest (Michigan, Wisconsin, Minnesota, North and South Dakota) and the south-east (Kentucky, Arkansas, Tennessee, North and South Carolina, Georgia and Alabama). It is not yet established in the most southerly States (Florida, Louisiana, Mississippi, Oklahoma and Texas) or west of the Plains region. In total, it is reported from 31 States of the USA (Small, 1997; NatureServe, 2017). The species has been introduced into Canada.

Humulus scandens was introduced into Europe (Paris) in approximately 1880 by Thiébaud-Legendre for cultivation as an ornamental species. A voucher herbarium specimen (Th. Delacour, s.n., P) dated 10-07-1881 and collected in the Jardin des Plantes (Paris) indicated it flowered for the first time since its introduction 2 years previously. In 1885, it was presented to the French Horticultural Society by a Mr Cornu who stressed its interest due to its late development, offering a nice bed of greenery at a period of the year where most other plants become dormant. It is assumed that the company Friedrich Röhmer in Quedlinburg (Swaxe-Anhalt, Germany) launched the variegated form (var. *variegatus* (Siebold & Zucc.) Moldenke) in 1893, although according to Ascherson & Graebner (1908–1913) it was already cultivated in 1886. According to Chevalier (1943), the variegated form had been used since the 1910s for growing over trellises and arbours or sometimes along fences.

The oldest record of the plant in the wild dates back to 1893 when it was found in wastelands along the road Cours Journu-Auber in Bordeaux (voucher herbarium specimen stored at the herbarium of Cherbourg). In 1947, the species was recorded on wastelands at Porte de la Villette in Paris

and in similar conditions in South-West France in Royan in 1958. There are also casual records in Alsace (North-East France) where *H. scandens* was collected in a waste disposal site near Modenheim. The first established populations were identified in 2004 (Brunel & Tison, 2005) in a disturbed portion of riparian habitat along the Gardon River, near Nîmes in the Mediterranean region (South-East France). Further surveys conducted in 2012 revealed the presence of the species along 40 km of the river between Alès and the confluence of the Gardon River with the Rhône (Pinston, 2013; Mahaut, 2014; Fried *et al.*, 2018). Since 2015, *H. scandens* has been recorded in a second catchment in the Huveaune River in the city of Marseille (Fried, 2017). In Belgium, the species was first recorded as a casual in 1954 and 1955 (Verloove, 2006).

In Hungary, similar to the situation in France, the first plant was collected in 1880 by N. Filarszky in the botanical garden of Budapest University (Balogh & Dancza, 2008). The first occurrence in the wild was confirmed as early as 1894 with a herbarium specimen collected by V. Borbás at Vésztő in county Békés (Balogh & Dancza, 2008). In the early 1900s, the species had spread and become naturalized in some localities of Hungary such as the environs of Lake Balaton (Balogh & Dancza, 2008). Balogh & Dancza (2008) summarize the current distribution in Hungary and indicate that there are various new localities in the North Hungarian Mountains, Northern Great Hungarian Plain and Southern and Western Transdanubia.

In Italy (according to the Gruppo di Lavoro Specie Esotiche della Regione Piemonte, 2015), it is believed the plant was introduced for ornamental horticulture and nursery purposes in the late 19th century (1885). It was recorded as naturalized in Tuscany in 1903 (Saccardo, 1909; Arrigoni & Viegi, 2011). The first record for Lombardy is dated 1941. Currently, it is considered invasive in Piedmont, Lombardy, Emilia-Romagna (e.g. along the Po river) and naturalized in Veneto and casual in Tuscany. It is not recorded on the islands of Sicily or Sardinia (Celesti-Grappow *et al.*, 2009).

Humulus scandens was discovered in 1999 in a locality near Novi Sad, Serbia, in a ruderal humid habitat on the bank of the Danube-Tisa-Danube channel (Savić *et al.*, 2008). The plant was considered as being under a process of naturalization with a risk of 'becoming a nuisance invasive plant in wetland habitats, similar to *Echinocystis lobata* (Michx.) Torr. et Gray' (Savić *et al.*, 2008).

Morphology

Plant type

Herbaceous annual vine.

Description

The stem is branched, hexangular, twining clockwise on itself (Balogh & Dancza, 2008) and around objects. The



Fig. 1 Female inflorescence of *H. scandens* © Guillaume Fried (Anses, FR).

height of plant has been reported to range between 0.5 and 5.0 m (Small, 1997; Balogh & Dancza, 2008), but it can grow to heights of 9–11 m (G. Fried, pers. comm., 2018; Panke & Renz, 2013). Leaves are opposite, blades are light green, cordate, palmately lobed with 5–7 (or 5–9) lobes, 5–12 cm long with petioles longer than the blade (Small, 1997; Balogh & Dancza, 2008). Leaf margins are dentate with an acuminate apex; the lower leaf surfaces have pubescent veins, with rigid spinulose hairs, with yellow, sessile, discoid glands. The upper margins of younger leaf blades have stiff cystolithic hairs (i.e. mineral concretions: calcium carbonate or calcium oxalate), which are typical in cells of plant leaves from Urticaceae, Moraceae and Acanthaceae. Male inflorescences form an erected branched panicle, 15–25 cm, flower anthers without glands. Female inflorescences are ovoid cone-like spikes (Fig. 1); bracteole ovate-orbicular, 7–10 mm, pilose, margins densely ciliate-hairy. Infructescences pendulous, green, cone-like, ovoid to oblong, (1–)1.5–3.0(–4) cm; bracteoles without yellow glands. Achenes are yellow-brown, ovoid-orbicular, inflated to lenticular, 4–5 mm, glandless.

Biology and ecology

General

Humulus scandens is a dioecious herbaceous annual vine that germinates in early spring. In the EPPO region, seeds of *H. scandens* germinate in large numbers in early spring starting from mid-April in Hungary (Balogh & Dancza,

2008) but as early as February in southern France (G. Fried, pers. obs., 2017). New seedlings can be observed until early May (Pinston, 2013). This is highly consistent with patterns of germination observed in the native range where emergence occurred from February to early May with a peak in March (Masuda & Washitani, 1990). In a study in March 2014, a mean of 37.9 seedlings m⁻² were measured in 43 plots in the south of France (Fried *et al.*, 2018). A study in the native range found a mean of 32.3 ± 37.0 seedlings m⁻² (Masuda & Washitani, 1990).

Habitats

In both its native range and its introduced range, *H. scandens* is a plant of riversides, particularly on the loose, bare surfaces of alluvial bars formed by river and streamsides by temporary floods (Zhou & Bartholomew, 2003; Balogh & Dancza, 2008; Fried *et al.*, 2018). The plant can also invade ruderal areas under climates with no dry seasons.

In France, the species is invasive in very similar communities to those dominated by the native species *Galium aparine*, *Atriplex prostrata*, *Rumex crispus*, *Persicaria lapathifolia*, *Veronica anagallis-aquatica*, *Convolvulus sepium* and the non-native species *Ambrosia artemisiifolia*, *Artemisia verlotiorum*, *Artemisia annua*, *Bidens frondosa*, *Helianthus tuberosus*, and *Xanthium orientale* subsp. *italicum* (Fried *et al.*, 2018). In Hungary, it has been described in other communities (such as the syntaxonomical unit: *Convolvuletalia sepium*) belonging to the same riparian habitats (Balogh & Dancza, 2008). In Italy, in addition to riparian habitats, it is also present in hydrophilous tall herb fringe communities of plains and of the montane to alpine levels.

Environmental requirements

In Europe, flowering occurs from July to September (Balogh & Dancza, 2008). In a survey in the south of France in 2013, the first flowers were observed at the end of August, and the first mature fruits were observed at the end of September. Similarly, another survey from France in 2016 detected the first male flowers in mid-August (C. Maillard, CHU Nîmes, pers. comm., 2018). In the native range (China and North and South Korea), *H. scandens* flowers from August to October (Park *et al.*, 1999). Flowers are mainly wind pollinated but are frequently visited by honeybees (Balogh & Dancza, 2008; G. Fried, pers. obs., 2016). In Hungary, fruits are reported to ripen from the middle of August and seeds remain viable for approximately 3 years (Krauss, 1931).

In a controlled greenhouse experiment (Pinston, 2013), the first shoot ramification appeared at 326 degree days. The mean phyllochron (i.e. the intervening period between the sequential emergences of leaves) was 59.7 degree days (which is much faster than the 138 degree days of another

invasive species, *Ambrosia artemisiifolia*). Male flowers were formed at 1294 degree days while female flowers appeared later at 1329 degree days.

Natural enemies

Zheng *et al.* (2004) reviewed the natural enemies feeding on *H. scandens* in the native range. Nine fungi are known to infect species of the genus *Humulus*, with only one, *Pseudocercospora humuli*, that may be specific to *H. scandens*. Of the 27 insects associated with plants of the genus *Humulus*, two species, *Epirrhoe sepegressa* and *Chytonix segregata*, are reported to have a potential narrow host range (Zheng *et al.*, 2004). In its native range, *H. scandens* is considered as one of the two main hosts of *Apolygus lucorum* (Heteroptera: Miridae) (Lu *et al.*, 2012). *Amara gigantea*, a granivorous beetle, was observed to feed particularly on *H. scandens* seed in Japan (Sasakawa, 2010).

A survey of insects found on *H. scandens* in the south of France in spring 2013 and 2014 highlighted the presence of *Thrips urticae*, *Oxythrips ulmifoliorum*, *Dendrothrips saltator*, *Paratettix meridionalis* and unidentified species of Aphididae and Collembola. Eggs of *Melanostoma* sp. and larvae of *Altica* sp., *Chromatomyia horticola* and unidentified species of Carabidae, Chrysomelidae, Cicadellidae, Theridiidae and Thripidae were also found (identification Anses – LSV, Unité Entomologie et Plantes Invasives, FR). Leaves of young seedlings are eaten by snails, including *Cermea virgata* (da Costa, 1778) and *Oxyloma elegans* (Riso, 1826) (determination: B. Michel, INRA). *Cuscuta campestris*, an alien plant parasite frequently observed in riparian habitats, has been observed to cause foliar damage on *H. scandens*. At the end of the growing season in southern France, *H. scandens* is attacked by several fungi including *Oidium* and possibly *Fusarium* sp. and *Cladosporium* sp. (identification Anses – LSV, Unité Mycologie).

According to studies in Germany, *H. scandens* is a host of the aphid *Phorodon humuli* (Schrank) (Aphididae).

Uses and benefits

In the EPPO region this species does not have any economic importance apart from limited use as an ornamental and being kept in many botanic gardens. *Humulus scandens* is sold as an ornamental plant within the EPPO region, and there are also sales of the species in North America. Typically, mostly female plants are sold in nurseries. *Humulus scandens* does not have lupulin glands that produces the bitter substance used to flavour beer and which are present in *Humulus lupulus*. Therefore, *H. scandens* has much less economic value than *H. lupulus*.

In the native range, the whole plant is used medicinally, and the seed oil is used to make soap (Zhou & Bartholomew, 2003). No other information is known concerning the plant's economic benefit.

Pathways for movement

The pathway plants for planting is considered the main entry pathway into the EPPO region (EPPO, 2018). *Humulus scandens* has been introduced into Europe as an ornamental species for growing over trellises, arbours or fences (Chevalier, 1943; Balogh & Dancza, 2008). Currently, the plant is not widely sold in the major garden centre chains. However, for garden amateurs, seeds (achenes) of the plant are widely available in more specialized nurseries and it can also be ordered through the Internet.

According to gardener forums and websites on the Internet, the plant is widely used and exchanged by gardeners and horticulturists, so it is very likely to be present in gardens throughout the EPPO region.

Impact

Effects on plants

In its native range in Japan, *H. scandens* is considered a weedy vine in riparian and floodplains habitats rich in nitrogen and lime, where it covers neighbouring plants such as *Miscanthus sacchariflorus* and *Phragmites australis* (Ju *et al.*, 2006) and decreases the diversity of plant communities (Ohtsuka & Nemoto, 1997).

In the USA, *H. scandens* can form dense stands that outcompete existing vegetation, especially in moist areas (NatureServe, 2017). It is capable of climbing trees and other nearby vegetation, sometimes resulting in shading, girdling and occasionally even death if trees are small (saplings). It can become the dominant understorey plant (NatureServe, 2017). *Humulus scandens* is perceived as predominantly invading open disturbed areas, such as roadsides or disturbed river banks, where it is believed to decrease biodiversity. Conversely, it has also been found in open woodlands, prairies, floodplain herbaceous wet meadows and floodplain forest communities, indicating that it has some tolerance to shade (NatureServe, 2017).

In Hungary, *H. scandens* has been reported to invade undisturbed ecological corridors (Balogh & Dancza, 2008). It can outcompete native species and is considered as a transformer species that threatens plant communities dominated by *Phragmites* and *Salix* (Phragmitetea and Salicetea classes) as well as the *Filipendulo–Petasition* alliance (Balogh *et al.*, 2004 cited in Balogh & Dancza, 2008). In France, *H. scandens* has been shown to have a negative impact on native plant communities by reducing species richness and modifying species composition (Mahaut, 2014). In particular, *H. scandens* can have a negative impact on early emerging spring species, for example *Atriplex prostrata*, *Mentha suaveolens*, *Persicaria hydropiper* and *Veronica anagallis-aquatica*. Dense mats of *H. scandens* can persist along riverbanks for several years (Fig. 2). Ecosystem functioning (e.g. reduced species



Fig. 2 Dense stands of *H. scandens* in one of the study sites on the Gardon River (FR) © Guillaume Fried (Anses, FR).

richness and decrease functional richness) is altered when the species invades riparian habitats.

Environmental and social impact

In the USA, *H. scandens* reduces light levels community-wide when it covers existing dominant vegetation (e.g. saplings) (NatureServe, 2017). By smothering tree saplings in riparian areas, it can modify the dynamics of natural vegetation succession (NatureServe, 2017). *Humulus scandens* can negatively affect cultural ecosystem services in the EPPO region, where dense cover of this vine with prickly stems may obstruct river access and recreational activities.

In its native range, many people have an allergic reaction to *H. scandens* pollen. Aerobiological studies in Beijing (China) and South Korea showed that *H. scandens* pollen counts are even higher than those of both common mugwort (*Artemisia vulgaris*) and ragweed (*Ambrosia artemisiifolia*) (two species with very high pollen counts) and account for about 18% of total pollen during the pollination period (Park *et al.*, 1999).

Control

In France, the cost of various control methods has been estimated as follows: hand pulling, 10.4 EUR m⁻², mechanical (grinding), 1.1 EUR m⁻², mechanical (mowing), 0.6 EUR m⁻². Based on the current area where the species was recorded in 2012–2013 (19 949 m²) and estimated in 2015 (29 924 m²) on the Gardon River, and with an average cost of 6 EUR m⁻² for management and supplementary costs including travel and time for searching for the plant (estimated to 167 EUR km⁻¹ over 80 km), as well as miscellaneous and unexpected expenses, the cost of managing all populations would be 580 000 EUR over 2 years.

Humulus scandens can be hand-pulled any time of the year. The most effective time to pull is in late spring or

early summer before seed formation. If the vine has climbed a tree, below-ground removal only is required. If seeds are present during removal, avoid movement off site unless material can be transported without spreading seed. Three years of removal is typically needed to eradicate an infestation and exhaust the seedbank.

Mowing or cutting many times a year can control new populations after 3 years, but well-established populations will only be suppressed. Use a mower that bags cut material or rake and bag the cut material after mowing. Dispose of cut material in a landfill or burn it to avoid spreading seeds to other areas.

Chemical control using herbicides has been shown to be effective at controlling infestations (Panke & Renz, 2013). However, any chemical application near waterbodies may require specific permission from national regulatory authorities.

There are no known biological control agents for *H. scandens* and no biological control agents are currently available for release to control Japanese hop. However, the US Forest Service has been investigating natural enemies of plants of Asian origin that are invasive in the USA. They have identified two moths (*Epirrhoe sepegressa* and *Chytonix segregata*) and one fungus (*Pseudocercospora humuli*) as potential natural enemies of Japanese hop and will continue research on those species.

Regulatory status

Humulus scandens was included in the EPPO Alert List in 2007 and subsequently transferred to the List of Invasive Alien Plants in 2012. In 2016, *H. scandens* was identified as a priority for risk assessment within the requirements of Regulation 1143/2014 (Branquart *et al.*, 2016; Tanner *et al.*, 2017). A subsequent pest risk analysis concluded that *H. scandens* carries a high phytosanitary risk to the endangered area (EPPO, 2018) and was added to the EPPO A2 List of pests recommended for regulation. At the time of publishing, *H. scandens* is being considered for inclusion on the list of (European) Union concern.

In Italy, *H. scandens* is included in the Lombardy region black-list established in 2008 according to the regional law of 31 March 2008, no. 10: 'Disposizioni per la conservazione della piccola fauna e della flora spontanea'. It is also included in the Piedmont region black-list according to the DGR no. 23-2975 of 29 February 2016.

In the USA, *H. scandens* is considered a noxious weed in Connecticut where it is categorized as 'Potentially invasive, banned' and in Massachusetts where it is 'Prohibited'.

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References

- Arrigoni PV & Viegi L (2011) La flora vascolare esotica spontaneizzata della Toscana. Regione Toscana, Firenze. <http://www.regione.toscana.it/documents/10180/320308/La+flora+vascolare+esotica+spontaneizzata+della+Toscana/acd32225-2909-4d0b-a1ba-80f89d68a3f7?version=1.0> [accessed on 25 November 2017].
- Ascherson P & Graebner P (1908–1913) *Synopsis der Mitteleuropäischen Flora*. Band 4. Verlag von Wilhelm Engelmann, Leipzig (DE).
- Balogh L & Dancza I (2008) *Humulus japonicus*, an emerging invader in Hungary. In *Plant Invasions: Human Perception, Ecological Impacts and Management* (ed. Tokarska-Guzi B, Brock JH, Brundu G, Child CC, Daehler C & Pyšek P), pp. 73–91. Backhuys Publishers, Leiden (NL).
- Balogh L, Dancza I & Király G (2004) Actual list of neophytes in Hungary and their classification according to their success. In *Biological Invasions in Hungary: Invasive Plants* (eds. Mihály B & Botta-Dukát Z), KvVM TvH tanulmánykötet 9, pp. 61–92. TermészetBÚVÁR Alapítvány Kiadó, Budapest (in Hungarian).
- Branquart E, Brundu G, Buholzer S, Chapman D, Ehret P, Fried G *et al.* (2016) A prioritization process for invasive alien plant species incorporating the requirements of the EU Regulation 1143/2014. *EPPO Bulletin* **47**, 603–617.
- Brunel S & Tison JM (2005) Compilation of available invasive plant lists in the Mediterranean Basin and comparison with other Mediterranean Regions of the World. Draft 2005 May. UICN, CBNMP.
- Celesti-Grapow L, Alessandrini A, Arrigoni PV, Banfi E, Bernardo L, Bovio M *et al.* (2009) Inventory of the non-native flora of Italy. *Plant Biosystems* **143**, 386–430.
- Chevalier A (1943) Notes sur le Houblon. *Revue de botanique appliquée et d'agriculture coloniale* **263–265**, 225–242.
- EPPO (2018) Pest risk analysis for *Humulus scandens*. <https://pra.epppo.int/> [accessed on 8 November 2018].
- Fried G (2017). *Guide des plantes invasives*. Nouvelle Edition. In *Collection « L'indispensable guide des...Fous de Nature!* (ed. Eyssartier G), 302 p. Editions Belin, Paris (FR).
- Fried G, Mahaut L, Pinston A & Carboni M (2018) Abiotic constraints and biotic resistance control the establishment success and abundance of invasive *Humulus japonicus* in riparian habitats. *Biological Invasions* **20**(2), 315–331.
- IPANE (2005) *Humulus japonicus* (Japanese hops). Invasive plant atlas of New England. <https://www.invasive.org/weedcd/pdfs/ipane/Humulusjaponicus.pdf> [accessed on 7 March 2017].
- Ju EJ, Kim JG, Lee YW, Lee BA, Kim H, Nam JM *et al.* (2006) Growth rate and nutrient content changes of *Humulus japonicus*. *Journal of Ecology and Field Biology* **29**, 433–440.

- Krauss O (1931) *Humulus* L., Hopfen. In *Pareys Blumengärtnerei* (ed. Bonstedt C), pp. 498–499. Erster Band. Verlag Paul Parey, Berlin (DE).
- Lu Y, Jiao Z & Wu K (2012) Early season host plants of *Apolygus lucorum* (Heteroptera: Miridae) in northern China. *Journal of Economic Entomology* **105**, 1603–1611.
- Mahaut L (2014) Le houblon du Japon (*Humulus japonicus* Siebold. & Zucc., une espèce locomotrice ou une simple passagère du train des changements? Rapport de stage de Master 2. Anses (supervised by G. Fried) Université de Montpellier 2/Montpellier SupAgro – Master Sciences et technologies, Mention Ecologie Biodiversité, Spécialité Biodiversité Evolution, Parcours Ecosystèmes, 44 p.
- Masuda M & Washitani I (1990) A comparative ecology of the seasonal schedules for 'reproduction by seeds' in a moist tall grassland community. *Functional Ecology* **4**, 169–182.
- NatureServe (2017) NatureServe Explorer: An online encyclopedia of life [web application]. Version 7.1. NatureServe, Arlington, Virginia. <http://explorer.natureserve.org> [accessed on 2 March 2017].
- Ohtsuka T & Nemoto M (1997) Effect of soil eutrophication on weedy riparian communities around agricultural areas. *Journal of Weed Science and Technology* **42**, 107–114.
- Panke B & Renz M (2013) *Japanese hop (Humulus japonicus)*. A3924–26. Management of Invasive plants in Wisconsin. University of Wisconsin-Extension, Cooperative extension.
- Pannill PD, Cook A, Hairston-Strang A & Swearingen JM (2009) Fact Sheet *Humulus japonicus*. Plant Conservation Alliances Alien Plant Working Group Weeds Gone Wild: Alien Plant Invaders of Natural Areas. <http://www.nps.gov/plants/alien/> [accessed on 15 March 2017].
- Park JW, Ko SH, Kim CW, Jeoung BJ & Hong CS (1999) Identification and characterization of the major allergen of the *Humulus japonicus* pollen. *Clinical and Experimental Allergy* **29**, 1080–1086.
- Pinston A (2013) *Étude de la plasticité écologique d'une plante invasive, Humulus japonicus*. Rapport de stage de Master 1. Anses (supervised by G. Fried) Université de Bourgogne – Master STS – ETE – Spécialité Biologie des Organismes et des Populations, 15 p.
- Saccardo PA (1909) *Cronologia della flora italiana*. Tipografia del Seminario, Padova (IT).
- Sasakawa K (2010) Field observations of climbing behavior and seed predation by adult ground beetles (Coleoptera: Carabidae) in a lowland area of the temperate zone. *Environmental Entomology* **39**, 1554–1560.
- Savić D, Anačkov G & Boža P (2008) New chorological data for flora of the Pannonian region of Serbia. *Central European Journal of Biology* **3**, 461–470.
- Small E (1997) In *Humulus*. (ed. Flora of North America Editorial Committee), pp. 356–357; 1993+. 20+ vols, Vol. 3. Flora of North America North of Mexico, New York and Oxford (US).
- Tanner R, Branquart E, Brundu G, Buholzer S, Chapman D, Ehret P *et al.* (2017) The prioritisation of a short list of alien plants for risk analysis within the framework of the Regulation (EU) No. 1143/2014. *NeoBiota* **35**, 87–118.
- Verloove F (2006) *Catalogue of neophytes in Belgium (1800-2005)*.
- Zheng H, Wu Y, Ding J, Binion D, Fu W & Reardon R (2004) *Invasive Plants of Asian Origin Established in the United States and Their Natural Enemies*. Volume 1. United States Department of Agriculture, Forest Service, 147 p. FHTET-2004-05. Morgantown, WV. September 2004.
- Zhou ZK & Bartholomew B (2003) Cannabaceae. *Flora of China* **5**, 74–75.