

Biology of Invasive Plants

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Biology of Invasive Plants 4. *Arundo donax* L.

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Scientific Classification

Domain: Eukaryota

Kingdom: Plantae

Subkingdom: Tracheobionta

Superdivision: Spermatophyta

Division: Magnoliophyta

Class: Liliopsida

Subclass: Commelinidae

Order: Cyperales

Family: Poaceae

Genus: *Arundo* L.

Species: *donax donax* L. (commonly notated as *A. donax* L.)

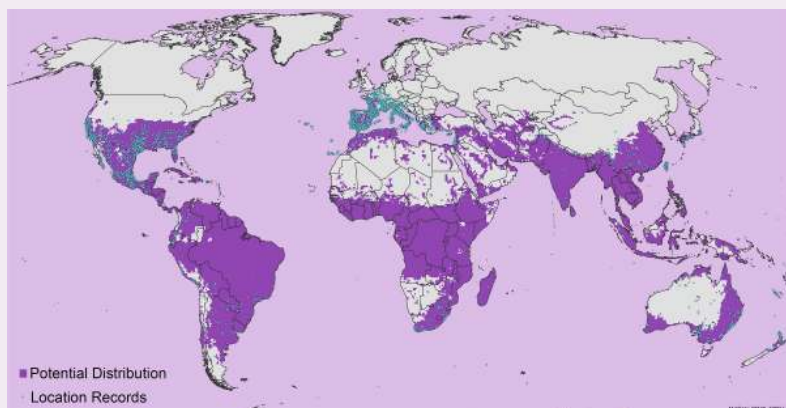
Synonyms past and present include (from GBIF [2021] unless otherwise cited): *Arundo donax* f. *donax* L., *Arundo donax* var. *donax* L., *Arundo donax collina* Ten. (Danin et al. 2002, 2006), *Arundo collina* Ten. (Danin 2004), *Arundo donax glauca* Bubani, *Arundo glauca* Bubani, *Arundo donax latifolia* Salisb., *Arundo hellenica* Danin, Raus & H. Scholz (Danin et al. 2002), *Arundo mediterranea* Danin (Danin 2004), *Arundo donax sativa* Lam., *Arundo bifaria* Retz., *Arundo bengalensis* Retz., *Arundo aegyptia* Delile, *Arundo aegyptiaca* E. Vilm., *Arundo bambusifolia* Hook.f., *Arundo coleotricha* (Hack.) Honda, *Arundo collina* Ten. (Danin 2004), *Arundo latifolia* Salisb., *Arundo sativa* Lam., *Arundo scriptoria* L., *Arundo triflora* Roxb., *Aira bengalensis* (Retz.) J. F. Gmel., *Amphidonax bengalensis* Roxb., *Amphidonax bifaria* (Retz.) Steud., *Scolochloa arundinacea* (P. Beauv.) Mert. & Koch, *Scolochloa arundinacea* (P. Beauv.) Mert. & W.D. J. Koch, *S. donax* (L.) Gaudin, *Cynodon donax* (L.) Raspail, *Donax arundinaceus* P. Beauv., *Donax bengalensis* (Retz.) P. Beauv., *Donax donax* (L.) Asch. & Graebn., and *Donax sativus* C. Presl. A cultivated variety with variegated leaves is often called *Arundo donax* L. var. *versicolor* (P. Mill.) Stokes. Synonyms for this variety include: *Arundo donax versicolor* P. Mill. (DiTomaso and Healy 2003; Hsiao et al. 1998; Missouri Botanic Garden 2008), *Arundo donax* var. *versicolor* (Mill.) Stokes, *Arundo donax* ssp. *versicolor* (P. Mill.) Stokes, and *Donax versicolor* (Mill.) P. Beauv. Other varieties not widely recognized but with occurrences in GBIF (2021) include *Arundo donax* var. *angustifolia* Döll, *Arundo donax* var. *coleotricha* Hack, and *Arundo donax* var. *variegata* E. Vilm.

EPPO Code: ABKDO

Names and Taxonomy

This species has many common names. Common names in North America include: giant reed, arundo, carrizo cane, bamboo reed (United States), *carrizo*, *carrizo gigante* (Mexico), *caña India* (Cuba); in South America: *caña de Castilla* (Argentina), *cañaveral* (Chile), *carizo* (Bolivia); in South Africa: Spanish reed, *Spaanseriet* (Sutton et al. 2021); in Australia and New Zealand: donax reed, elephant grass, reed cane, reed grass, Spanish reed, giant cane, wild cane; in Europe: *Spanisches Rohr*, *Pfahlrohr* (Denmark), giant reed, Spanish cane, bamboo reed (United Kingdom), *Spaanseriet*, *pijlriet*, *zaairiet*, (Netherlands), *gewöhnliches Pfahlrohr*, *italienisches*



***Arundo donax* at a glance...****Impacts**

- Forms impenetrable thickets in riparian and wetland habitats
- Consumes scarce water resources in arid regions
- Fuels wildfires and narrows river channels, facilitating invasion
- Displaces native species and facilitates cattle fever tick invasion

**Dispersal**

- Spread by humans for use in construction, fencing, and erosion control
- Flood dispersal via rhizomes and shoot pieces with buds

**Management**

- Systemic herbicide application, mowing, digging out rhizomes, and burning
- Existing methods alone unsafe and unsustainable at the ecosystem level
- Two biological control agents released in United States and showing impact
- Biological control with shoot tip-galling wasp integrated with mowing applied for shoot death

**Biosecurity**

- One of the world's top 100 invasive weeds, propagation prohibited in some countries
- Already invasive on six continents and in at least 99 countries
- Potential for further spread due to continued human use for construction, textiles, and biofuel
- Equatorial tropics and subtropical grasslands in South America, Africa, and Asia at risk of further invasion.



pfahlrohr, *pfahlrohr*, *pfeilrohr*, *riesenpfahlrohr*, *riesenschilf*, *spanisches rohr* (Germany), *lasecznica trzcinowata* (Poland), *canne de Provence*, *arondo donax*, *canneville*, *grand roseau*, *quenouille*, *roseau canne*, *roseau de Fréjus*, *roseau des jardins*, *roseau donax*, *roseau à quenouilles* (France), *caña*, *caña gigante*, *caña de techar*, *caña de la reina*, *caña de Castilla*, *carrizo grande*, *caña común*, *caña india*, *cañizo* (Spain), *kanabera* (Basque region of France/Spain), *canya*, *canya communa*, *canavèra*, *cannabère* (Catalonia region of Spain), *cana*, *canas*, *cana-comun*, *cana-do-brejo*, *cana de roca*, *cana-do-reino*, *cana-vieira*, *cannodo-reino*, *capim-plumoso*, *cana-milha*, *caninha* (Portugal), *canna*, *canna commune*, *canna domestica*, *canna gargana*, *canna gentile* (Italy), *kallami* (Albania), *trestie italiană* (Romania), *trst obrovská* (Slovakia), *navadna kanela* (Slovenia), *obični trst* (Croatia), *καλάμι* (Greece); in the Middle East: *avkaneh shachiach* (Israel); in Asia: *lú zhú* (China), *danchiku*, *yoshitake* (Japan), *mul dae* (Korea).

Importance

Arundo donax is native to the Old World, possibly from the Iberian Peninsula of Europe to south Asia, including North Africa, the Middle East, the Arabian Peninsula, and the Persian Gulf regions (Hardion et al. 2014, 2015, 2017; Tarin et al. 2013). The true native range is, however, most likely limited to the Indus River basin and surrounding areas of India, Bhutan, Nepal, Pakistan, Afghanistan, Iran, Turkmenistan, and Uzbekistan, extending possibly to the Middle East (Jiménez-Ruiz et al. 2021; Sutton et al. 2021), with areas to the west and east of that area being ancient or modern introductions. *Arundo donax* was cultivated in Asia and Europe for thousands of years for use as a construction material (Dunmire 2004) and has been widely introduced around the world for use in fencing and construction (Bell 1997; Guthrie 2007; Haddadchi et al. 2013) (see images in the Supplementary Appendix); for use as a fiber for example, to make baskets (Jiménez-Ruiz et al. 2021); as an ornamental; and for use as reeds in woodwind instruments (Perdue 1958; Tracy and DeLoach 1999). Subsequently, it has become naturalized and invasive in many tropical, subtropical, and warm temperate regions of the world (Figures 1–3). It was introduced to South Africa in the late 1700s for erosion control (Guthrie 2007) and to Australia in the 1800s (Virtue et al. 2010). *Arundo donax* is known for its rapid growth, attaining growth rates of 0.7 m wk⁻¹ or 10 cm d⁻¹, putting it among the fastest-growing plants (Bell 1997; Perdue 1958), producing up to 1.4 × 10⁵ kg dry biomass ha⁻¹ in California, USA (Cal-IPC 2020) and 5.4 × 10⁴ kg ha⁻¹ in Italy (Angelini et al. 2005). Because of *A. donax*'s growth potential and broad environmental tolerance (Jiménez-Ruiz et al. 2021), its use for biofuel production (Duke 1983; Mack 2008; Marianoi et al. 2010) and sewage treatment, specifically heavy metal removal (Cristaldi et al. 2020), have been explored but are largely unrealized. In South Africa, the cost and energy to harvest and transport biomass from invasive populations for use as biofuel negated the benefits (Melane et al. 2017).

The detrimental impacts of *Arundo donax* invasion outweigh the plant's beneficial uses. This giant grass forms dense, monospecific stands along waterways (Figure 4). The high water usage of *A. donax*, which causes water waste/loss, is of greatest concern in countries where major invasions have occurred, including Australia (Haddadchi et al. 2013), New Zealand (Virtue et al. 2010), South Africa (Nkuna et al. 2018; Versfeld et al. 2000), the United States (Cal-IPC 2020; Lambert et al. 2010a, 2010b; Seawright et al. 2009), and Mexico (IMTA 2008; Martínez Jiménez et al. 2017). For example, *A. donax* is considered a national

problem in South Africa, primarily due to the threat it poses to water security (Milton 2004), as it is the most abundant and widespread invasive alien grass in the country (Tshapa et al. 2021; Visser et al. 2017) and is legally categorized as requiring compulsory inclusion in invasive species control programs. A study by Nkuna et al. (2018) ranked *A. donax* as having the second-highest impact score (environmental and socioecological) of the 58 alien grasses assessed in South Africa. *Arundo donax* is not yet considered to be a major invader in Australia or New Zealand, although it has become widespread especially in the southeastern mainland states of Australia and the North and South Islands of New Zealand (Haddadchi et al. 2013). The New Zealand Department of Conservation has assigned it a high priority for management, because *A. donax* can form dense tall patches, is hard to control, and represents a serious future threat to biodiversity values.

A study by Versfeld et al. (2000) estimated the water use from infestations is about 4.35 million m³ yr⁻¹ across all provinces in South Africa, exacerbating its invasion of ecologically sensitive biomes such as the fynbos, South Africa's Cape Floristic Region and plant biodiversity hot spot, with high levels of endemism. The annual water usage of this plant in another biodiverse area, the lower Rio Grande basin of Texas, USA, and northern Mexico, was estimated at 56.2 million m³ yr⁻¹ (Seawright et al. 2009). The plant's estimated water use in the Central Valley of California, USA, was estimated at 37.8 million m³ yr⁻¹ (Cal-IPC 2020). *Arundo donax* competes for water resources in arid regions where these resources are critical to the environment and agricultural and municipal users (Cal-IPC 2020; Cloern et al. 2011; Goolsby et al. 2009a; Jiménez-Ruiz et al. 2021; McGaugh et al. 2006; Seawright et al. 2009; Watts and Moore 2011). For example, a study using ground-based scintillometers in Laredo, TX, USA, found that *A. donax* growing in February (winter) used similar amounts (5.2 mm d⁻¹) of water as corn growing in this region during the summer (Gowda et al. 2011); similar levels of water use were found in this region using tower-mounted eddy-covariance systems (Racelis et al. 2022). Several studies (Kui et al. 2013; Moore et al. 2016) found that *A. donax* rhizome mats along the Rio Grande can transfer water through rhizomes to increase their growth rate in parts of the stand where soil moisture is limiting. In Texas, peak water evapotranspiration in a greenhouse study was 8.8 mm d⁻¹ m⁻² shoots (Watts and Moore 2011). In California, field stands of *A. donax* used as much as 40 mm of water d⁻¹ m⁻² during the peak of the growing season; this rate of water use is at the high end of the spectrum for plants (Cal-IPC 2020). Studies in Europe on *A. donax* in constructed wetlands set up for biofuel production indicated evaporative water use/loss at 11 to 47 mm m⁻² d⁻¹ in summer (Milani et al. 2019; Tuttolomondo et al. 2015).

Arundo donax has numerous adverse effects on the physical characteristics of riparian ecosystems. In the United States (Cushman and Gaffney 2010; Decruyenaere and Holt 2005) and South Africa (Henderson 2001), *A. donax* has been designated as a "transformer" species in the region due to its ability to alter the structure, integrity, and functioning of the ecosystems that it invades. Dense stands reduce the carrying capacity of waterways by narrowing channels in the southwestern United States (Cal-IPC 2020) (Figure 4; see images in the Supplementary Appendix) and in South Africa (Guthrie 2007; Holmes et al. 2005). During flood events, the shallow rhizomes destabilize riverbanks, increasing erosion (Frandsen and Jackson 1994; Stover et al. 2018), and the narrowed channels can exacerbate flood damage (Spencer et al. 2013) by dislodging mats of shoots that then threaten

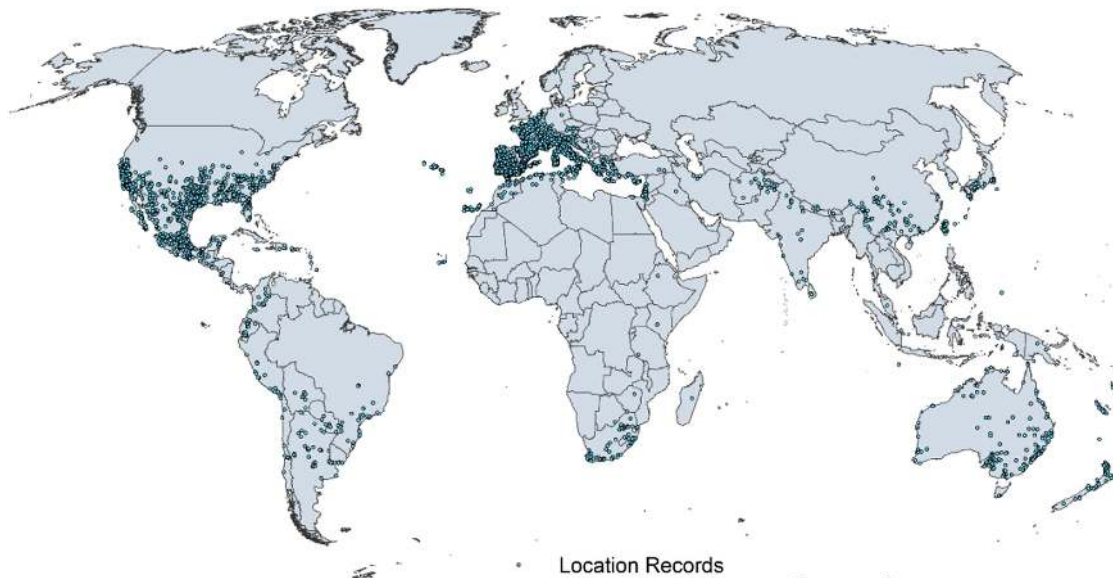


Figure 1. Native and introduced occurrences of *Arundo donax* across the world. Source: GBIF (2021).

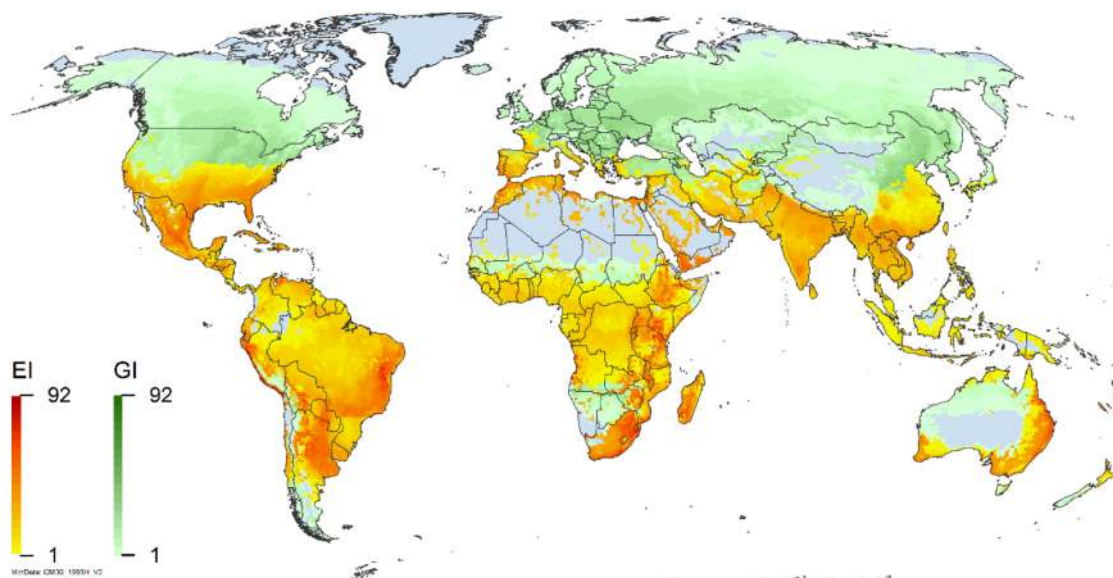


Figure 2. Global climate suitability for *A. donax* modeled using CLIMEX. The model incorporates both natural rainfall and a top-up irrigation scenario, applied where irrigation is reported in a global map of irrigated areas (Siebert et al. 2013). The yellow to red areas (environmental index [EI] ≥ 1) indicate increasing suitability for year-round population persistence. Outside of those areas, the growth index ([GI] ≥ 1) indicates areas in green that are suitable for growth of *A. donax* only during a favorable growing season, and are thus expected to be unsuitable for population persistence except in cases of direct human intervention. See Structured Appendix for model details.

infrastructure (Cal-IPC 2020). *Arundo donax* fuels wildfires in riparian habitats, increasing fire risk due to its dense dead/dormant biomass (Guthrie 2007) acting as a vertical fuel source and increasing fire intensity (Coffman et al. 2010; Holmes et al. 2005). In the Central Valley of California, fire frequency in watersheds is positively correlated with the area of *A. donax* invasion (Cal-IPC 2020), and in coastal watersheds, fires promote spread of this weed into native riparian vegetation and impair native plant recovery (Lambert et al. 2010a). Increased eutrophication in river systems controlled by reservoirs and dams, and the control of water flow itself, contribute to the spread and persistence of *A. donax* globally (Frandsen and Jackson 1994; Guthrie 2007; Haddadchi et al. 2013), as this weed benefits from excess nitrogen (Lambert et al. 2014;

Moran 2015; Quinn et al. 2007). Dense *A. donax* stands block access to water and reduce its recreational benefits (Cal-IPC 2020).

Invasion by *A. donax* leads to loss of plant biodiversity, as demonstrated by studies along the Rio Grande in Texas (Racelis et al. 2012c; Rubio et al. 2014) and in California (Bell 1997; Cushman and Gaffney 2010; Quinn and Holt 2008). In the United States (most studies conducted in California), *A. donax* invasion reduces diversity of insects (Herrera and Dudley 2003; Lovich et al. 2009), birds and reptiles (Cal-IPC 2020; Dudley 2000; Tracy and DeLoach 1999), and rare fish populations (Tracy and DeLoach 1999), likely causing local (Cuatrociénegas, Coahuila) extinction of an endemic Mexican fish species, the Rio Salado darter [*Etheostoma segrex* (Norris and Mickley);

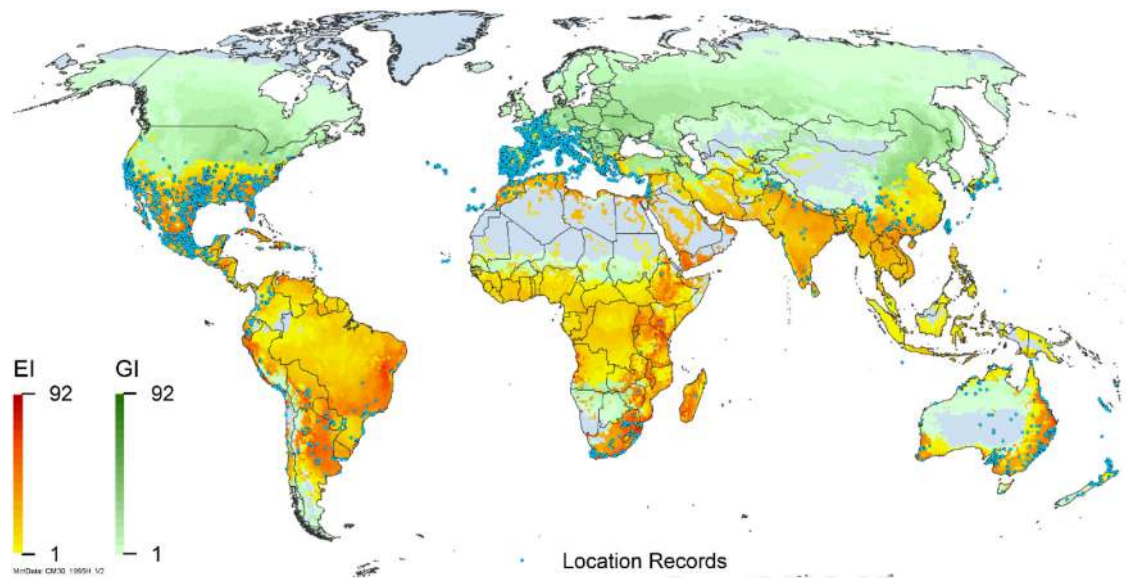


Figure 3. Global climate suitability as modeled in CLIMEX (Kriticos et al. 2015) for *A. donax* overlaid on the global distribution. Location records from GBIF (2021).



Figure 4. Dense stand of *A. donax* on the banks of the Rio Grande on the border of Texas (USA) and Mexico.

Percidae] (McGaugh et al. 2006). Top carnivores such as coyotes (*Canis latrans* Say) and bobcats (*Lynx rufus* Schreber) tend to avoid *A. donax*, creating a partial refuge for small mammal prey (Hardesty-Moore et al. 2020). The threats of *A. donax* to biodiversity are recognized in South Africa (Guthrie 2007), Australia (Haddadchi et al. 2013), and in parts of the ancient

European introduced range where human disturbance has aided invasion (Jiménez-Ruiz et al. 2021). In the lower Rio Grande basin of Texas, the *A. donax* invasion represents the first time an exotic weed has been shown to facilitate invasion of an exotic livestock pest, the cattle fever tick [*Rhipicephalus microplus* (Canestrini)] (Racelis et al. 2012a).



Figure 5. *Arundo donax* with flower panicles in south Texas, USA. In subtropical regions such as this, flowering can occur any time of the year.

Arundo donax is an alternate host for several viruses of crop plants (Tracy and DeLoach 1999) and also of several fungi that are plant pathogens (Duke 1983). Surveys in California indicated that it is a host plant for the blue-green sharpshooter [*Graphocephala atropunctata* (Signoret); Hemiptera: Cicadellidae], which can vector the bacterium that causes Pierce's disease of grapes (*Vitis vinifera* L. or other species/hybrids) (Herrera and Dudley 2003). An adventive leaf-feeding aphid [*Melanaphis donacis* (Passerini); Hemiptera: Aphididae] is known from California (Dudley et al. 2008), South America (Underraga et al. 2020), and South Africa (Canavan et al. 2019) and is spreading invasively in the native range of *A. donax* in Pakistan (Amin et al. 2019), where it is considered a pest on that plant as well as on common reed [*Phragmites australis* (Cav.) Trin. ex Steud.; syn.: *Phragmites communis* Trin.] and on some members of the Rosaceae. A total of 14 other aphid species occur on *A. donax* across the world, including several pests of sugarcane (*Saccharum officinarum* L.), wheat (*Triticum aestivum* L.), and other crops (Blackman and Eastop 2022). Dudley et al. (2008) reported stem tip-mining and rot damage indicative of the adventive presence of a *Cryptonevra* sp. fly species (Diptera: Chloropidae). Flies of this genus from Mediterranean Europe have been considered for biological control (Thomas and Goolsby 2020); their adventive presence in the United States is unconfirmed. The fly *Chaetopsis massyla* Walker (Diptera: Ulidiidae), native to North America, was found in shoot tips of *A. donax* grown in south Texas for mass-rearing of biological control agents (Goolsby and Mangan 2010).

Description

Lewandowski et al. (2003) and Jiménez-Ruiz et al. (2021) provide botanical descriptions of *A. donax* in the United States and Mediterranean Europe, respectively. Immature and mature plant:

Stem and leaves are glabrous (waxy). Stem canes are erect, semi-woody, inflexible, about 1- to 4-cm thick, up to 6-m tall in wild European populations (Jiménez-Ruiz et al. 2021) and 6 to 8 m in biofuel plantings there (Angelini et al. 2005) and in the wild in South Africa (Sutton et al. 2021); up to 9 m in California (Perdue 1958); and generally 3 to 6 m in south Texas (Goolsby et al. 2016). Stems have hollow internodes. First-year green canes have unbranched stems (Figures 5 and 6) of the same diameter as older canes, but are more pliable. Older canes are often branched, sometimes with leaves only on the branches. Leaves alternate in the same plane (two-ranked), fairly evenly spaced along the stem length. Leaf blades are flat, less than 0.75-m long, mostly 2- to 6-cm wide at the base; the midsection and base are nearly equal in width but taper to a fine point; margins are sharp and rough (scabrous) to touch. Blade bases are broadly round-lobed (Figure 6) to slightly truncate, clasping the stem; margin often has long, wavy hairs. Leaf bases include a membranous, upright collar (ligule) about 1- to 2-mm long without hairs (Figure 6). Leaf sheaths tightly envelop the stem from the blade base to the next node down the stem, splitting open at the margin only when leaf sheaths senesce (Figure 6). Roots and underground structures: Rhizomes are creeping, thick, scaly, solid in cross section, often forming a dense network, and firm and knotty at the stem bases (Figure 6), forming a shallow network of rhizomes and roots (Kui et al. 2013; Stover et al. 2018), but with individual roots extending as deep as 5 m below the surface (Moore et al. 2016). New buds are pink as they emerge from dead root scales, then turn green as they form shoots. Rhizomes and stem fragments with a node readily develop roots and new shoots under suitable conditions (damp soil, silt, sand, or gravel; Cal-IPC 2020; Decruyenaere and Holt 2001; Goolsby et al. 2013; Wijte et al. 2005). Inflorescences: Panicles (flower/seed stalks) are terminal (Figures 5 and 6), dense, erect, and plume-like, mostly 30- to 60-cm long and 5- to 10-cm wide, silvery cream-colored to purplish or brown, open with

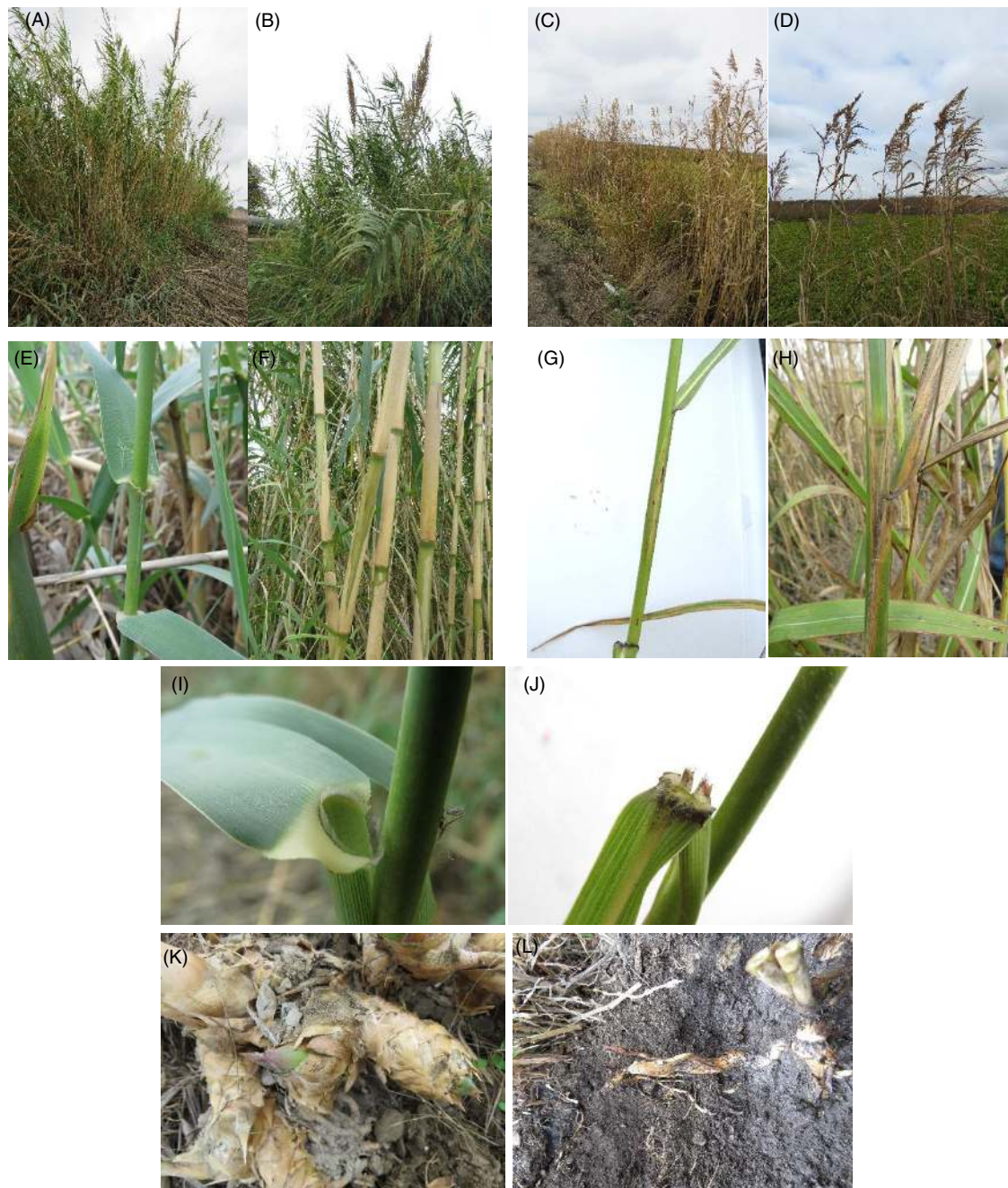


Figure 6. Key external features of *A. donax* and its close relative, *Phragmites australis*. (A) *Arundo donax* stand showing 3- to 6-m-tall stem stature and (B) upright inflorescences (panicles). (C) *Phragmites australis* stand showing 1- to 2-m stature and (D) drooping panicles. (E) Young *A. donax* shoot showing leaf sheaths tightly wrapped around stem from top to bottom of the internode. (F) On 1-yr-old *A. donax* shoots, only old, dead leaf sheaths show pronounced splitting from stem. *P. australis* leaf sheaths are split from the stem on both young (G) and old (H) stems. (I) Base of *A. donax* leaf blade showing ear-like auricles and collar without hairs, in contrast to (J) base of *P. australis* leaf blade lacking prominent auricles and with hairy fringe at base of the collar. (K) Tuber-like *A. donax* rhizome with dense, stubby, sharp-tipped leafy scales and thick pink or red buds. (L) Thinner *P. australis* rhizome with few leafy, not sharp scales and thin buds. All photos by K. Santa Cruz, USDA-ARS.

ascending branches or contracted (especially after pollination) with nearly erect branches. Spikelets (clusters of florets on a branch of the panicle) are mostly 10- to 15-mm long, with two to five flowers, and detach from above the glumes and between florets. Floret stalk (rachilla) is glabrous (smooth). Glumes (two leaf-like bracts at the base of each spikelet) are three to five veined and membranous. The lemma (a leaf-like bract at the base of each floret) is ca. 11-mm long, with a short-awned (spined) tip between two teeth, appearing as “tears” between three veins. The basal one-fourth of the lemma

length is covered with long (5-mm) silky hairs. The palea (a shorter bract on the other side of each floret) is 7 mm, without a spine, and truncated at the apex. Flowering occurs from March to November in temperate regions, but year-round in subtropical and tropical areas. Florets from the United States and Mediterranean do not produce seeds (Hardion et al. 2015), likely due to a failure of the mother megaspore to divide (Bhanwra et al. 1982). *Arundo donax* is sterile throughout its invasive New World, African, and Australasian distribution and its ancient introduced Mediterranean range. In its

native range in the Indo-Pakistan and Persian Gulf regions, *A. donax* produces seed (Hardion et al. 2014). Postsenescence characters: Dead canes lose their leaves, turn brown and then gray, and become brittle and splintery after completion of the 3- to 4-yr life cycle (Spencer et al. 2005; Thornby et al. 2007), but may remain dead and erect for several years. They eventually fall over and then decompose on-site or are dispersed by flooding or fire events. Effects of control on appearance: Control with herbicides causes leaf blades to first droop and then senesce, but they may remain on canes, falling off during wind events or flooding, leaving bare dead canes that eventually fall over. Control with fire or mechanical removal causes immediate collapse of canes, leaving rough bare ground with blackened, exposed rhizomes. Regrowth after chemical control, if it occurs at all, is distorted and chlorotic (Bell 2011), with many small side shoots emerging from nodes of bare canes, forming a club-like witches' broom. Regrowth after fire consists of thick, dense canes emerging from rhizomes, as *A. donax* is well adapted to fire (Coffman et al. 2010).

Morphologically Similar Species

Two congeners widespread in the Mediterranean Basin, *Arundo plinii* Turra and *Arundo micrantha* Lam., can be distinguished by their thinner rhizomes with parenchymous cross section with a small lumen (hole) in the center (as opposed to the solid *A. donax* rhizome cross section with no central lumen (Jiménez-Ruiz et al. 2021)).

Phragmites australis is a widespread perennial up to 4 m tall (but up to 6 m in Europe; McKee and Richards 1996) that is cosmopolitan in distribution (Hardion et al. 2017). In the United States, it occurs in native, nonnative and invasive, and hybrid forms that can be distinguished with molecular techniques (Lambert et al. 2016; Meyerson et al. 2010; Saltonstall 2016). Key features distinguishing *A. donax* from *P. australis* are summarized and illustrated by Jiménez-Ruiz et al. (2021), and some of these features are shown in Figure 6. *Phragmites australis* stems/caness may be shorter than those of *A. donax* and are often less than 1 cm in diameter, but those features alone are not conclusive. Leaf ligules (collars clasping the stem) consist of an upright membrane, usually less than 1-mm long, that is ciliate with hairs ± 1 -mm long. *Arundo donax* canes are often much thicker in diameter, and the leaf collar ligule has no hairs. The bases of *P. australis* leaves are gradually narrowed or truncate, while those of *A. donax* have more clearly defined auricles or lobes around the stem. *Phragmites australis* canes bear drooping inflorescences (panicles), while *A. donax* panicles are upright. The floret stalks (rachillae) of *P. australis* are covered with long, silky hairs, while *A. donax* rachillae are glabrous. Floret lemmas on *P. australis* are glabrous and tapered to a point, as compared with *A. donax* having hairs on the basal quarter of the lemma with a spine and two "teeth" at the apex. *Arundo donax* rhizomes are solid in cross section, while *P. australis* rhizomes are hollow with a ring of cortical aerenchyma and a central lumen. *Phragmites australis*, unlike *A. donax*, can produce viable seed. Seed production varies with climate and genotype (McKee and Richards 1996), including degree of hybridization of native and invasive genotypes (Ishii and Kadono 2002) and degree of local clonal reproduction, as plants are largely or completely self-incompatible. Hybrid plants produce more seed than parental lineages but with lower viability (Williams et al. 2019). Most seeds germinate mid- to late spring. Submersed seeds do not germinate until water recedes. Seeds are short-lived under field conditions, and a persistent seedbank does not accumulate.

Napier grass or Uganda grass [*Pennisetum purpureum* Schumacher; syn.: *Cenchrus purpureus* (Schumacher) Morrone], native to tropical African grasslands and introduced in subtropical Eurasia and North and South America, appears superficially similar to *A. donax* in growth habit and can occur in similar habitats, but the leaf bases are hairy well beyond the ligule/sheath junction, the inflorescences are much more narrow and are shorter (to 20-cm long) than those of *A. donax*, and asexual reproduction occurs by stolons rather than rhizomes (Farrell et al. 2002). Several large-statured bunchgrasses, including pampasgrass [*Cortaderia selloana* (Schult. & Schult. f.) Asch. & Graebn.] and Ravenna grass [*Saccharum ravennae* (L.) L.] have superficially similar inflorescences but entirely different growth forms with profuse large, narrow, pointy leaves clustered near the base of the plant.

Distribution

Arundo donax is distributed globally across the subtropical and warm temperate regions of the world, with more limited occurrences in equatorial regions and isolated occurrences in colder temperate areas. The Global Biodiversity Information Facility (GBIF 2021) lists 50,345 occurrences. National databases and past reviews (Jiménez-Ruiz et al. 2021; Martínez Jiménez et al. 2017) provide additional information. *Arundo donax* is found in at least 99 countries and is invasive across at least 89 countries and islands that are part of countries, befitting its status as one of the top 100 invasive species (of any type) in the world (Lowe et al. 2000). Figure 1 shows worldwide occurrence of *A. donax* (GBIF 2021), Figure 2 shows a CLIMEX model (Kriticos et al. 2015) informed by CliMond globally interpolated climate data (Kriticos et al. 2012), and Figure 3 overlays the distribution on the model. Figure 7 shows the distribution overlaid on the CLIMEX model for North and Central America and the Caribbean. Figure 8 shows similar information for Europe, the Mediterranean Basin, and far western Asia, including the native range of *A. donax*. Country lists are inferred from records in GBIF (2021) with additional information from Soreng et al. (2014) and other sources as referenced.

United States

Arundo donax is found in Hawaii and 29 states in the continental United States (EDDMapS 2022; USDA 2021) (Figures 3, 7, and 9), mainly in a line southward from about 41.5°N latitude from northern California eastward to the New York City area, but with invasive populations found mainly in the arid southwestern United States, from the southern tip of Texas to northern California. Populations in the southeastern United States have separate genetic origins in the Canary Islands and Seville, Spain, compared with the eastern and southern coastal Spanish origins of most of the *A. donax* populations in the southwestern United States (Tarin et al. 2013). The infestation was estimated to be 6,360 ha in the lower Rio Grande basin of Texas (Yang et al. 2009, 2011) and 4,095 ha in California (Cal-IPC 2020).

Mexico

Arundo donax is found in 27 states (IMTA 2008; Martínez Jiménez et al. 2017) (Figures 3, 7, and 9) from the Baja Peninsula and Chihuahuan and Sonoran deserts in the northwest to the tropical mountain drainages, forests, and grasslands of the Yucatan Peninsula in the southeast.

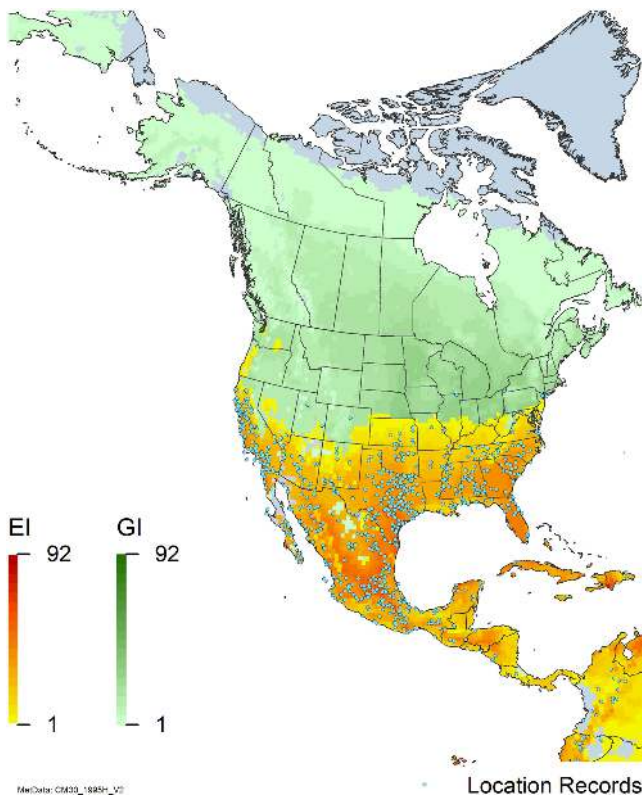


Figure 7. Nonnative, naturalized distribution of *Arundo donax* in North America, including Central America and the western Caribbean. Location records from GBIF (2021). The map also shows climate suitability as modeled in CLIMEX. The model incorporates both natural rainfall and a top-up irrigation scenario. Yellow and red colors correspond to an increasing environmental index [EI] ≥ 1 , indicating areas of expected population persistence. Outside of those areas, the green color indicates a growth index (GI) ≥ 1 , indicating areas where *A. donax* can grow only in one favorable season, and thus populations are not expected to persist. See Structured Appendix for model details.

Bermuda to the Caribbean

Populations of *Arundo donax* occur in the Bahamas, Bermuda, Cuba (Figure 7), Curacao, Dominica, Dominican Republic, Granada, Haiti, Jamaica, Trinidad and Tobago, St. Kitts and Nevis, and St. Vincent and the Grenadines.

Central America

Arundo donax occurs in Costa Rica, El Salvador, Guatemala, Honduras, and Nicaragua (Figure 7).

South America

Arundo donax is found in Argentina, Brazil, Bolivia, Chile, Colombia, Ecuador, Peru, Suriname, and Uruguay.

Europe

Populations of *A. donax* occur in Albania, Andorra, Austria, Belgium, Bosnia and Herzegovina, Bulgaria, Croatia, Cyprus, France, Germany, Greece, Italy, Luxembourg, Monaco, Montenegro, Netherlands, Norway, Portugal, Romania, Serbia, Slovenia, Spain, Sweden, Switzerland, and Turkey (Jiménez-Ruiz et al. 2021) (Figures 3 and 8).

Africa

Arundo donax occurs in Algeria, Botswana, Egypt, Ethiopia, Kenya, Lesotho, Madagascar, Morocco, South Africa, Swaziland, Tanzania, Tunisia, and Zimbabwe (Figures 3 and A5). In South Africa, this reed thrives in Mediterranean-type climatic regions, where it has rapidly expanded into riparian habitats, with the most severe infestations occurring in the Western Cape, Gauteng, and KwaZulu-Natal provinces (Sutton et al. 2021) (Figure 9). It is estimated that *A. donax* occupies about 3,200 ha in South Africa (Henderson 2001; Kotzé et al. 2010; Le Maitre et al. 2016). The genetic origin of the South African populations appears to be the “M1” haplotype that is found in the native region and in the Mediterranean Basin, but also in Peru, New Caledonia, and the United States (Canavan et al. 2017). However, more recent genetic analyses using chloroplast DNA spacers and microsatellites indicate a Middle Eastern origin, with plants brought first to Western Cape Province followed by introduction throughout the country (Bhikraj 2021).

Eastern Mediterranean, Asia Minor, and Persian Gulf

Populations of *A. donax* occur in Afghanistan, Israel, Jordan, Kazakhstan, Lebanon, Syria, Iran, Iraq, Pakistan, Tajikistan, Turkmenistan, and Uzbekistan (Figure 3). Several haplotypes are found in this region and are dominant in specific areas within it, suggesting the region comprises the plant’s native range (Canavan et al. 2017; Hardion et al. 2017).

Asia and Melanesia

Arundo donax is found in Bangladesh, Bhutan, China, India, Indonesia, Japan, Myanmar, Nepal, Sri Lanka, South Korea, Taiwan, and Vietnam (Figures 3 and A6).

Oceania

Arundo donax was introduced into Australia in the mid-1800s. It has become widespread in Australia, with scattered records from all mainland states and the Northern Territory (Virtue et al. (2010) (Figure 3). Genetic analyses indicate multiple genetically distinct origins for Australian populations, in contrast to the United States and South Africa, including possibly one haplotype imported to Australia from South Africa (Bhikraj 2021; Haddadchi et al. 2013). Newspaper articles indicate that *A. donax* was present in New Zealand by the late 1800s (e.g., Anonymous 1894) and naturalized by 1936 (Edgar et al. 1991). *Arundo donax* occurs in both the North and South Islands (NZVH 2022) (Figure 9) with low diversity reflective of a likely Australian origin (Bhikraj 2021). Populations are also known from Fiji, Marshall Islands, Papua New Guinea, Samoa, Seychelles Islands, Tonga, and Vanuatu.

Habitat

Arundo donax grows on a variety of soil types from loose sands and gravelly soils to heavy clays and river sediments (Goolsby et al. 2013; Jiménez-Ruiz et al. 2021). Optimum growth occurs in well-drained soil with ample moisture supplied as fresh water or semi-saline waters at margins of brackish estuaries (Perdue 1958). *Arundo donax* invades riparian and wetland habitats, due to its water consumption requirements (Cal-IPC 2020; Jiménez-Ruiz et al. 2021; Quinn and Holt 2008; Watts and Moore 2011). Occurrences in other areas, such as in planted fencerows, roadsides, canal banks, and escapes from these, are facilitated by

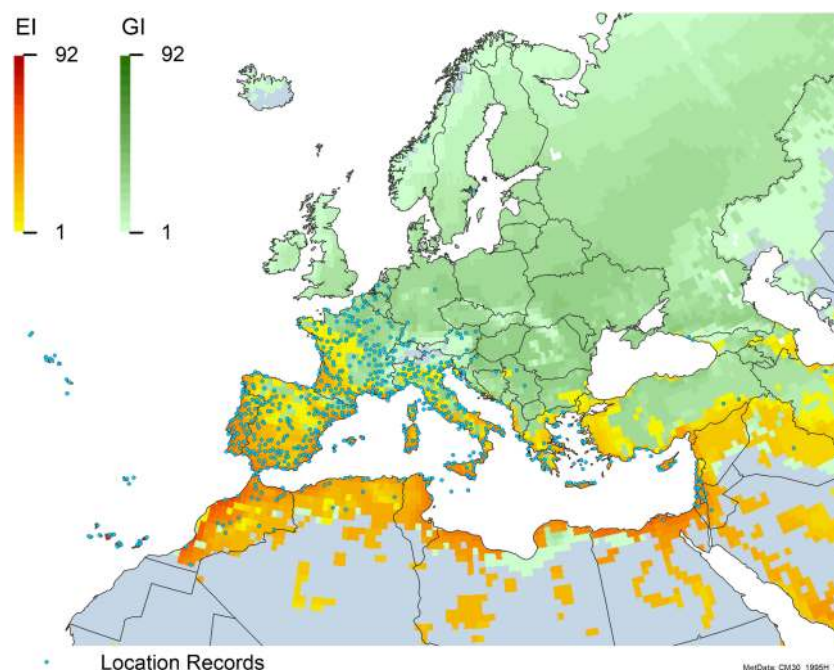


Figure 8. Distribution of *Arundo donax* in its anciently introduced range in Europe and the Mediterranean Basin and areas of its native distribution in far western Asia. Location records from GBIF (2021). The map also shows climate suitability as modeled in CLIMEX. The model incorporates both natural rainfall and a top-up irrigation scenario. Yellow and red colors correspond to an increasing environmental index [EI] ≥ 1 , indicating areas of expected population persistence. Outside of those areas, the green color indicates a growth index (GI) ≥ 1 , indicating areas where *A. donax* can grow only in one favorable season, and thus populations are not expected to persist.

anthropogenic factors, including planting and the presence of irrigation systems. As in the United States (Bell 1997), the spread of *A. donax* in South Africa in riparian areas is largely dependent on past anthropogenic activities that transported the reed to new areas, including plantings for soil stabilization, and the building of dams, which altered river flows and created favorable habitat downstream. Using climate envelope models, a study by Rouget et al. (2004) estimated that 79% of the area of South Africa and neighboring countries Lesotho and Eswatini (formerly Swaziland) is potentially suitable for *A. donax* invasion. Disturbed areas adjacent to sensitive, biodiverse natural habitats such as the fynbos biome are the most threatened, but *A. donax* also thrives in disturbed ecosystems, such as in mining areas (van der Merwe et al. 1990). *Arundo donax* occurs across at least 3,200 ha and 1,428 localities in South Africa (Guthrie 2007; Sutton et al. 2021).

Comparison of the global distribution of *A. donax* (Figure 3) to a 0.1667° global Köppen-Geiger climate zone map (Beck et al. 2018) shows it commonly occurring in 16 global climate subtypes (Table 1). In the eastern portion of the native distribution of *A. donax*, from the eastern Mediterranean to India, it is found mainly in arid climate subtypes BSk, BSh, BWb, and BWk (steppe/desert; dry summer or winter, hot or cold overall), with the exception of India, where populations are found in areas with tropical climate subtype Aw (savanna) and, less commonly, in equatorial tropical forests and croplands (Af, Am). In the western and central Mediterranean (native or anciently introduced range), *A. donax* occurs in the areas characterized by the BSk climate, Csa and Csb climates (Mediterranean), Cfa climate (humid subtropical), and Cfb climate (oceanic) characteristic of immediate coastal areas and islands in subtropical and subtemperate regions. Isolated populations in the Italian Alps, Switzerland, northern France, and Germany occur in Dsb and Dfc climates, and there are highly isolated occurrences in Sweden and Norway under the Dwb

climate. Additional European populations may be found in Dfa or Dfb climates. In the United States, arid climate subtypes BWb and BSh predominate in the heavily invaded southwestern part of the country, but there are also many *A. donax* occurrences in areas of California where the Csa climate is dominant (Csb in coastal areas), and in the Pacific Northwest in temperate climate subtype Csc. In the southeastern United States, *A. donax* occurs in areas dominated by the Cfa climate subtype, with a few occurrences farther north in the Dfa subtype. In Mexico and Central America, *A. donax* is found in desert (BWb) and steppe (BSh) areas, with additional occurrences in tropical savanna in the southeast of Mexico (Aw) and both savanna (Aw) and tropical rainforest (Af) regions in Central America. In South America, *A. donax* is found in regions with climate subtype Cfa in Argentina and southern Brazil, BWb (desert) in Chile and Peru, Aw in Bolivia, and Cfb in the Andes Mountains in Colombia. In Africa south of the Mediterranean Basin, known occurrences of *A. donax* are confined almost entirely to South Africa; however, it is found in diverse climates there, including desert (BWb) and steppe (BSh) in the northwest and west and also temperate areas in the southern and eastern part of the country (climate subtypes Csa, Cwa, Cwb, and Cfa). In Australia, *A. donax* is similarly found across highly diverse climates, ranging from BWb in the desert interior, Csa in the west, Cfa and Cfb in the southeast, and Aw in the tropical north. In New Zealand *A. donax* is found in climate subtypes Cfa and Cfb. In eastern Asia (mainly China, Taiwan, and Japan), *A. donax* is found in climate types Cfb and Cfa.

Globally, it can be seen that *A. donax* is most common in areas with one of three climates: subtemperate coastal continental areas without precipitation seasonality and hot summers (Cfa; including parts of Europe and all invaded continents); on islands and some immediate mainland coastal areas with an oceanic climate (Cfb); and in Mediterranean climates with strongly seasonal rainfall

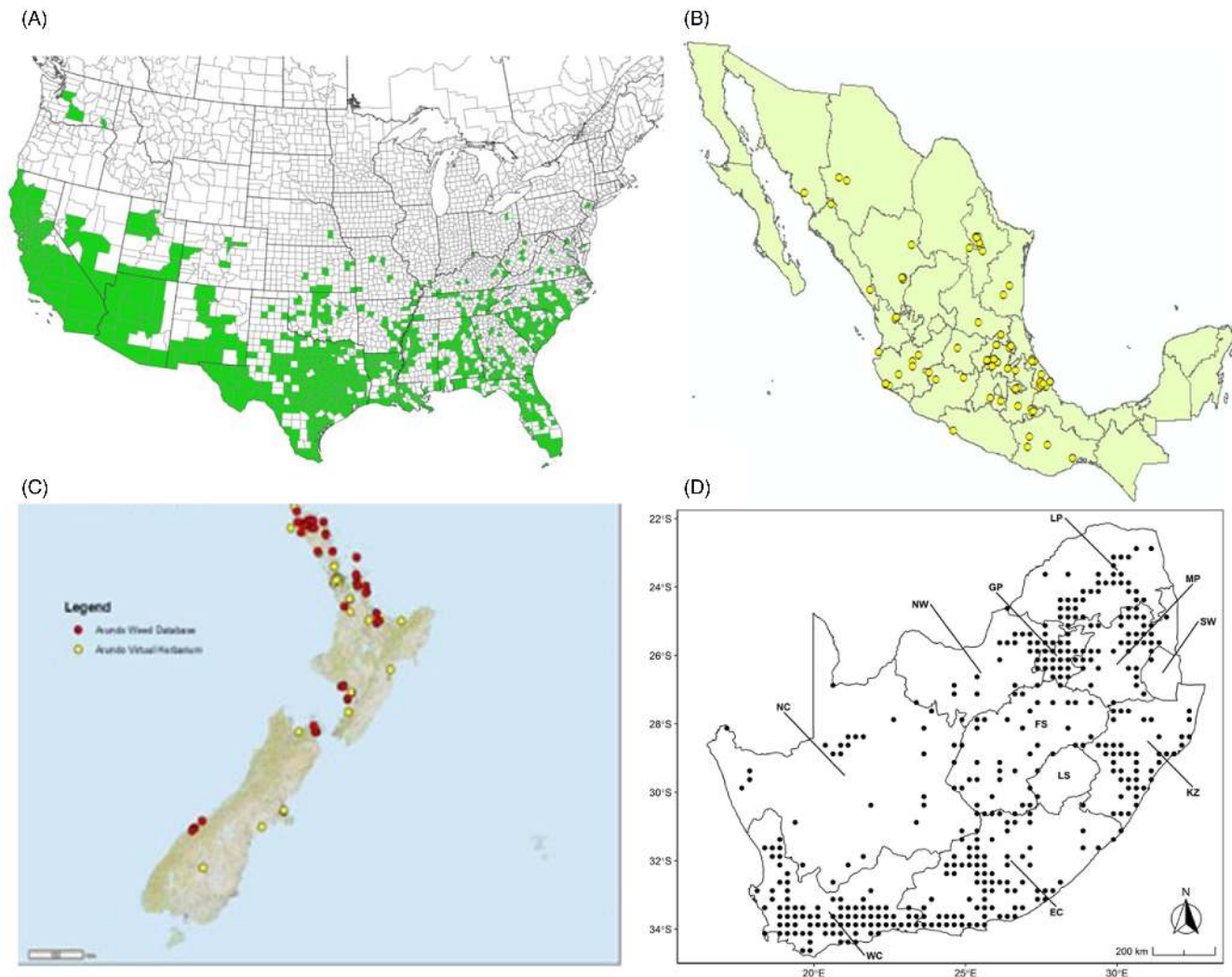


Figure 9. Distribution of *Arundo donax* based on national databases. (A) Occurrence in U.S. counties and states (from EDDMapS 2022). (B) Point distribution in Mexico (data from Contreras 2007). (C) Distribution in New Zealand, obtained from the New Zealand Flora (yellow) (E-Flora 2022) and the New Zealand Virtual Herbarium (red) (NZVH 2022). (D) Distribution in South Africa (taken from Sutton et al. 2021).

patterns (dry in summer) that are hot (Csa) or warm (Csb) in summer (see also the Structured Appendix at the end of this article: Figure A1, global distribution overlaid on Köppen-Geiger zones, and Figure A4, occurrence distribution). *Arundo donax* is found in all areas of the world with the uncommon Mediterranean climate Csa and to a lesser degree in areas with its cooler variant, Csb, including: the western Mediterranean Basin; the southwestern coast of the United States; the northern and central coast of Chile in South America; parts of southern coastal South Africa; and the southwestern coast of Australia. The arid, cool/cold steppe climate BSk is the next most common climate type where *A. donax* is found. Less prevalent but still often found are occurrences in the hot steppe climate type BSh (eastern native range and all invaded areas except Asia), the hot desert climate type BWh (natural and artificial riparian areas worldwide), and the tropical savanna climate type Aw. In subtropical climates Cwa (humid, lowland) and Cwb (highland), dry winters may limit occurrences. *Arundo donax* appears able to survive only in favorable microclimates and/or with direct human intervention in temperate climates such as Dfa, Dfb, and Dsb; it is known to occur in two isolated locations in boreal/subarctic subtype Dfc in Norway and Sweden (Fig. 1). It has

been reported from as high as 4,000-m altitude in Central America (Soreng et al. 2014).

A global CLIMEX model (Kriticos et al. 2012, 2015; Sutherst and Maywald 1985) with additional input from global irrigation data (Siebert et al. 2013) (Figure 3), shown also for North America, including Central America and the Caribbean (Figure 7), and for Europe and the Mediterranean Basin (Figure 8) (see also the Structured Appendix), suggests accurate model prediction of the actual distribution of *A. donax* in subtemperate, subtropical, and tropical regions of the world. Recorded observations are remarkably sparse in areas modeled as being climatically suitable in the equatorial tropics of South America, Africa, and Indonesia and other island nations in the Melanesian region, as well as in subtropical areas south of the equator in South America and Africa, and north of the equator in Asia. It is possible that *A. donax* is underreported in these areas, or that these areas are less disturbed but still prone to invasion if disturbance occurs.

A visual, qualitative examination of a UN land-use assessment map (FAO 2013) in relation to the global distribution (Figure 1) suggests that *A. donax* is commonly found in both its native and invasive ranges in areas with large-scale irrigated agricultural crop

Table 1. Global Köppen-Geiger climate zone classifications that are suitable for survival and growth of *Arundo donax*.

Köppen-Geiger code	Description
Contains established populations	
Af	Tropical rainforest
Am	Tropical monsoon
Aw	Tropical savanna, with dry winter characteristics
BSH	Semi-arid (steppe) climate, hot
BSk	Semi-arid (steppe) climate, cold
BWh	Arid, hot desert
BWk	Arid, cold desert
Cfa	Humid, subtropical
Cfb	Oceanic
Csa	Mediterranean—dry hot summer
Csb	Mediterranean—dry warm/cool summer
Csc	Mediterranean—dry cold summer
Cwa	Dry winter, humid subtropical summer
Cwb	Dry winter, subtropical highland
Dfa	No dry season, hot summer continental
Dfb	No dry season, warm summer continental
Populations restricted to favorable microhabitats	
Dfc	Subarctic or boreal
Dsb	Dry summer, warm summer continental
Dwb	Dry winter, warm summer continental

production and livestock use, as well as in rainfed agricultural areas. Riparian environments within sparse grasslands with low-density livestock production in areas such as the India-Pakistan region, China, Australia, Mediterranean Europe, the southwestern United States, Mexico, and South America also overlap with known occurrences. *Arundo donax* is widely found outside areas where natural soil conditions are suitable for its growth, illustrating the importance of anthropocentric manipulation of water resources in aiding its spread (Nilsson and Berggren 2000).

Invasion History

Arundo donax appears to have spread from its putative ancestral native range in the Indus River basin and central Asia westward to Mediterranean Europe and eastward into other parts of Asia thousands of years ago (Jiménez-Ruiz et al. 2021), but a global genetic-based historical analysis is not available. In surveys for biological control agents, diversity of insects on *A. donax* was highest in the western Mediterranean (Kirk et al. 2003; Tracy and DeLoach 1999), even though plant genotypic diversity there is lower there than in the areas between the Middle East and the Indus River basin (Canavan et al. 2017; Sutton et al. 2021; Tarin et al. 2013), suggesting that the plant acquired novel natural enemies during its spread. It was introduced by European colonizers to North America in the 1500s (Dunmire 2004), to South Africa in the late 1700s (Guthrie 2007), to Australia in the mid-1800s (Virtue et al. 2010), and to New Zealand by the late 1800s (Anonymous 1894). Additional introductions into North America occurred in the early 20th century (Perdue 1958). A genetic study of its invasive distribution on islands in the Pacific Basin would possibly reveal an interesting mosaic of genotypes linked to those present in colonizing nations. Efforts to eradicate *A. donax* from entire rivers or watersheds have generally not been successful because of insufficient support for follow-up control of regrowth (Jiménez-Ruiz et al. 2021; van Wilgen et al. 2012; Visser et al. 2017), restrictions on access to land or ornamental populations (Cal-IPC 2020), and poor detection of small populations under dense riparian canopies. Projects in two coastal river valleys in southern and central California involving 20 yr of

control did, however, reduce populations to near-zero coverage (Cal-IPC 2020; A Lambert, University of California–Santa Barbara, personal communication).

Life-Form and Life History

Arundo donax grows as a bamboo-like perennial to 9-m tall, with thick, well-developed rhizomes. Shoots can emerge from rhizome buds year-round in most locations. This giant grass is well-adapted to periodic flooding (Spencer et al. 2013) and is not only adapted to but benefits from fire (Coffman et al. 2010). In tropical and subtropical climates, *A. donax* grows year-round, and the stems produce side shoots in year 2. In temperate climates such as California, first-year main stems senesce in the late fall, transferring nutrients to rhizomes. Second-year main shoots produce lateral shoots in the spring, which often produce third- and fourth-order side shoots during the typical 3- to 4-yr total main shoot life span (Decruyenaere and Holt 2005; Thornby et al. 2007). Dead shoots remain standing, sometimes inhibiting new shoot formation until dead shoots fall over and younger rhizomes reoccupy the soil. Under the system described by Grimes (1988), *A. donax* uses vegetative expansion to reproduce and the competitor strategy to persist in and dominate riparian ecosystems, as a result of dynamic “foraging” of roots for resources, reducing the predictability of resources for other plants. However, unlike many plants exhibiting the competitor strategy, *A. donax* can “switch down” its resource use (Grubb 1998) to tolerate severe water-deficit stress under drought conditions (Moore et al. 2016) and can thrive in both low-disturbance environments and those subjected to major disturbance from fire (Coffman et al. 2010) or flooding (Frandsen and Jackson 1994).

Dispersal and Establishment

Rhizomes (Bell 1997) and shoots (Boland 2006; Wijte et al. 2005) are vegetative propagules of *A. donax* that disperse via flooding (Stover et al. 2018) or human movement. Rhizomes can resprout even under drought conditions (Mann et al. 2013), while detached shoots must be in contact with moist soil to produce new axillary buds and shoots (Boland 2006; Wijte et al. 2005); they otherwise die, forming large dead piles of debris or “wrack” that alters river flow and threatens flood control (Cal-IPC 2020; Lambert et al. 2010a, 2010b). Establishment is favored by moist but not waterlogged soil (Goolsby et al. 2013) in open habitat with little vegetation (Quinn and Holt 2008), as might be found after flooding, fire, or human disturbance. In the Mediterranean, the most robust populations are found on well-drained gravelly or sandy soils (Goolsby et al. 2013; Jiménez-Ruiz et al. 2021).

Invasion Risk

As shown in Figures 3, 7, and 8, *A. donax* is widely established in watersheds throughout the world in subtemperate and subtropical continental regions and islands, particularly in warm, seasonally or perennially arid regions that are favorable for its high evapotranspiration capacity (Cal-IPC 2020). New invasions in these areas are the result of human transport between watersheds and waterborne transport of shoots and rhizomes within watersheds (Wijte et al. 2005). Gaps in the known occurrences of this grass are still apparent in climatically suitable areas (Figures 3, 7, and 8), including subtropical Brazilian grasslands, sub-Saharan African grasslands, and global equatorial tropics. In tropical forested areas,

dense native or other vegetation may prevent invasion, but human clearing of forests and manipulation of water flow are likely to increase invasion risk (Bell 1997; Guthrie 2007; Jiménez-Ruiz et al. 2021). This is especially critical from a water conservation aspect, as increased density and distribution of *A. donax* in a watershed negatively influences availability of water resources.

Invasion Pathways

Arundo donax invasion is linked to human movement of plant propagules. During the first half of the 20th century, intentional introductions led to new invasions, including reintroductions in previously invaded areas (Bell 1997; Guthrie 2007; Haddadchi et al. 2013; Perdue 1958). Accidental invasions can occur through movement on earthmoving equipment or mowers (Jiménez-Ruiz et al. 2021) and even sale of variegated varieties in some areas (Haddadchi et al. 2013). Dredging of ditches and canals often disturbs stands of *A. donax* and allows movement of propagules to new uninfested areas. Similarly, clearing of *A. donax* for weed control can dislodge rhizome and shoot fragments that move downstream. The main nonhuman source of invasion is flooding, which can undercut riverbanks, causing downstream movement of rhizome mats and shoot pieces (Boland 2006; Cal-IPC 2020; Jiménez Ruiz et al. 2021; Stover et al. 2018). Haddadchi et al. (2013) used molecular techniques to investigate the spread of *A. donax* in southeastern Australia and found evidence of widespread transport (up to 200 km away from the source plant) indicating that rivers serve as an effective dispersal corridor.

Purposeful introductions of *A. donax* for biofuel cropping or fiber use should be carefully designed to prevent escape of propagules outside cultivation (Raghu et al. 2006). Alternative biofuel plants, such as native switchgrass (*Panicum virgatum* L.) in North America, should be considered (Lewandowski et al. 2003). Weed risk assessments (Virtue et al. 2010) and economic suitability studies in South Africa were conducted to determine whether *A. donax* was suitable to serve as biomass for electricity generation (Melane et al. 2017). It was concluded that the use of *A. donax* was not cost-effective using current thermo-chemical conversion processes.

Growth and Development

Morphology

Under suitable growth conditions, *A. donax* produces robust, thick (to 6-cm diameter; PJM, personal observation) main shoots or canes, and then one and eventually multiple side shoots at leaf nodes when the canes are 1-yr-old or less (Decruyenaere and Holt 2005; Thornby et al. 2007). Side shoots produce additional biomass and photosynthate, increasing the vigor of the stand. The “Description” section provides more information on structure of individual shoots.

Stress Tolerance

Arundo donax perennates through rhizome branching and new primary shoot growth and by production of lateral shoots on 1-yr-old and older main shoots. In California, USA, a typical shoot senesces each winter but lives 3 to 4 yr (Thornby et al. 2007), with photosynthetic capacity lost in dead main shoot leaves after the first year rapidly replaced by leaves on abundant lateral shoots. When primary shoots die, perennation through rhizome growth

occurs via production of new shoot buds and shoots, causing expansion of *A. donax* patches.

Arundo donax is highly tolerant of various forms of abiotic stress (Perdue 1958), including water deficit (Moore et al. 2016; Nackley et al. 2014; Zegada-Lizarazu and Monti 2019), due to its use of water-efficient C_3 photosynthesis, comparable to C_4 bioenergy crops (Webster et al. 2016); elevated soil or water salinity (Quinn and Holt 2008; Sánchez et al. 2015); and high heavy metal content in soils (Cristaldi et al. 2020). *Arundo donax* can survive prolonged water-deficit stress (Zegada-Lizarazu and Monti 2019), although shoots are shorter and produce less biomass in greenhouse tests in which water-deficit stress is imposed (Lambert et al. 2014; Moran 2015). While roots have been observed as deep as 5 m in soil cores, reaching groundwater levels (Moore et al. 2016), *A. donax* mainly takes up surface and soil water and does not rely on groundwater (Moore et al. 2016; Watts and Moore 2011; L. Kui, personal communication). Water can be carried at least 3 m through interconnected rhizome networks located just below the soil surface (Kui et al. 2013). The broad geographic distribution of *A. donax*, from cold temperate areas of the United States, Europe, and Asia to the equatorial tropics (Jiménez-Ruiz et al. 2021) (Figures 3, 7, and 8), demonstrates the ability of this grass to grow and disperse under a wide range of temperature and precipitation regimes. It is most widely distributed in arid temperate to subtropical regions. It is unable to persist outside human influence in the presence of prolonged winter and repeated episodic spring freezes (Perdue 1958). Prolonged flooding and drought limit the ability of first-year *A. donax* shoots to survive and grow (Mann et al. 2013), but growth from surviving rhizomes will occur if more favorable conditions follow. *Arundo donax* has a remarkable tolerance to fire, in part because of its ability to utilize abundant soil nutrients and grow rapidly (Decruyenaere and Holt 2005; Quinn et al. 2007). The process by which *A. donax* comes to dominate riparian ecosystems is linked to fire, as it regrows more rapidly than do surviving native plants (Coffman et al. 2010).

Ecophysiology

The substantial water use of *A. donax*, covered in the “Importance” section, is a key attribute that makes this weed so damaging. Water use is linked to photosynthetic evapotranspiration. *Arundo donax* uses C_3 photosynthesis, but exhibits attributes of C_4 photosynthesis, allowing it to take advantage of subsurface water availability under otherwise dry conditions and fix carbon at a high rate (Rossa et al. 1998), while closing stomata under drought conditions (Webster et al. 2016).

Phenology

Main shoots (culms) can sprout from rhizomes clonally at any time of year when average daily temperatures are above 7 °C and below 30 °C (Spencer and Ksander 2006). In California, emergence of main shoots from rhizome buds is especially prevalent in early spring (Decruyenaere and Holt 2001) after the winter rainy season in this Mediterranean climate (Beck et al. 2018), but three cohorts of emergence, the first two requiring accumulation of about 500 degree days, and the third requiring about 1,000 degree days (Spencer and Ksander 2006), occurred in 1 yr under controlled conditions. Main shoots flower in the first year and produce profuse lateral shoots beginning late in the first year, continuing for the typical 3- to 4-yr life span of each main shoot (Decruyenaere and Holt 2005; Thornby et al. 2007). Mowing or “topping” of main shoots, or natural shoot breakage, leads to production of profuse,

bushy nodes of side shoots (Racelis et al. 2012b; PJM, personal observation).

Mycorrhizal and Bacterial Symbionts

No mycorrhizal or bacterial symbionts are known.

Reproduction

Floral Biology

Sexual reproduction occurs only in the native range. Fertile seeds have been reported in Iran, Afghanistan, Pakistan, India, Nepal, and Bhutan (Hardion et al. 2014). The terminal inflorescences, which appear in temperate climates most commonly in late summer and fall (Jiménez-Ruiz et al. 2021; Spencer and Ksander 2006) are single, up to 60-cm long, and feathery with silky hairs. The spikelets are 8- to 16-cm long and lanceolate, and each spikelet contains two to seven florets. The florets are all bisexual, except the reduced uppermost one (Lewandowski et al. 2003).

Seed Production and Dispersal

Seeds of *A. donax* in North and South America, Europe, Africa, Australia and New Zealand, and Pacific Rim islands are sterile (Jiménez-Ruiz et al. 2021), most likely due to failure of the megaspore mother cell to divide (Bhanwra et al. 1982), leading to defective pollen and ovary development (Hardion et al. 2015; Mariani et al. 2010). In invasive clones, seed-like unfilled caryopses (Balogh et al. 2012) will fall from spikes when disturbed. These sterile seeds are dispersed by wind and water and on animals.

Seedbanks, Seed Viability, and Germination

None of these factors are relevant in the invasive range, as seeds are sterile.

Vegetative Reproduction

Reproduction is entirely vegetative/clonal in all of the areas *A. donax* has invaded, including North America (Boose and Holt 1999; Lewandowski et al. 2003), and also in the native range in Mediterranean Europe, while both asexual and sexual reproduction occur in Asia (Jiménez-Ruiz et al. 2021). Invasive clonal *A. donax* has a chromosome count of $2n = \text{ca. } 108\text{--}110$, while some, presumably native Asian accessions, have a count of $2n = 72$ (Christopher and Abraham 1971; Kalia 1978). The invasiveness of *A. donax* may thus be caused in part by the formation of pseudo-triploid genomes (Jiménez-Ruiz et al. 2021). *Arundo donax* reproduces prolifically via rhizome budding and branching (Cal-IPC 2020) in undisturbed stands and through layering or lodging of rhizomes, main shoots, or shoot pieces after floods or other disturbance (Boland 2006; Boose and Holt 1999; Wijte et al. 2005).

Population Dynamics

Arundo donax main shoots complete a 3- to 4-yr life cycle (DeCruyenaere and Holt 2005; Spencer and Ksander 2006; Thornby et al. 2007). Stands or patches expand through rhizome branching and shoot bud formation and recolonize areas of old, dead rhizomes as branching of live rhizomes continues, forming a tangled mass of live and dead rhizome material and live and dead standing shoots. This weed thus forms thick, persistent, perennial

stands that dominate invaded riparian habitats (Quinn and Holt 2008).

Management Options

Phytosanitary Measures

To prevent the spread of *A. donax* between continents and countries, regulatory officials throughout the world should prohibit international and domestic live shipments of this species. Shipments for biomass/bioenergy development represent one potential source of risk. Even in countries where *A. donax* is already present, new genotypes could become established that are more invasive or present a genetic mismatch with the biological control agents sourced from Mediterranean Europe, should they be released. Earthmoving and mowing equipment should be carefully inspected to prevent movement of *A. donax* propagules. Shoot pieces and rhizomes may be accidentally transported with soil used for fill or construction (Cal-IPC 2020). Movement of plant or soil material from areas in or around patches of *A. donax* to uninvaded areas should be avoided and care taken when disposing of debris from control operations. As both rhizome and shoot pieces can readily produce new buds and plants given adequate moisture, debris should be burned, mulched, or dried at elevated temperature (e.g., under a tarp) for an extended period (Cal-IPC 2020, 2021). Mowing along the bank edges of infested waterways can lead to movement of propagules in flotsam, leading to downstream infestations. Treatment of *A. donax* with approved herbicides before mowing may reduce the risk of starting new infestations. Treatment of upstream areas of watersheds to avoid downstream invasion through flood-borne transport of rhizomes and shoots can be an effective strategy (Cal-IPC 2020).

A determination of the area of invasion in riparian systems is essential for the effective prevention of spread of *A. donax*, as this information permits informed prioritization of resources for eradication and management. As an example, remote sensing studies of *A. donax* in the lower Rio Grande basin of Texas and Mexico have demonstrated that aerial airborne multispectral and hyperspectral imagery and high-resolution satellite imagery can be used to detect and map infestations. Aerial color-infrared (CIR) photographs and video images were taken along the Rio Grande between Brownsville and El Paso, TX, in June and July 2002 (Everitt et al. 2004, 2005) (Figure 10). Approximately 600 river-km of the Rio Grande area surveyed was infested with *A. donax*. The densest populations were located over a 300 river-km stretch between Laredo and Del Rio. Ground surveys confirmed the presence of *A. donax* at plotted locations. Digitization and classification of aerial images showed that *A. donax* was present in riparian patches at $10.6 \text{ ha river-km}^{-1}$. Thus, the total infested area for the 600 km of the Rio Grande was estimated as 6,360 ha (Yang et al. 2009, 2011). Release sites for biological control agents (Goolsby et al. 2014) and later for implementation of an integrated control regime (see section Biological Control—United States and Mexico) were selected to cover this large area of critical importance for water resources. To quantify the distribution of infested areas in the Mexican portion of the Rio Grande Basin, QuickBird® image scenes with 2.4-m spatial resolution and four spectral bands were selected (Figure 11) and classified (Everitt et al. 2005). The total estimated *A. donax* infestation area in the Mexican tributaries of the Rio Grande was estimated at 4,775 ha. These results helped inform control decisions using biocontrol agents and other methods in Mexico (Martínez Jiménez et al. 2017). The use of

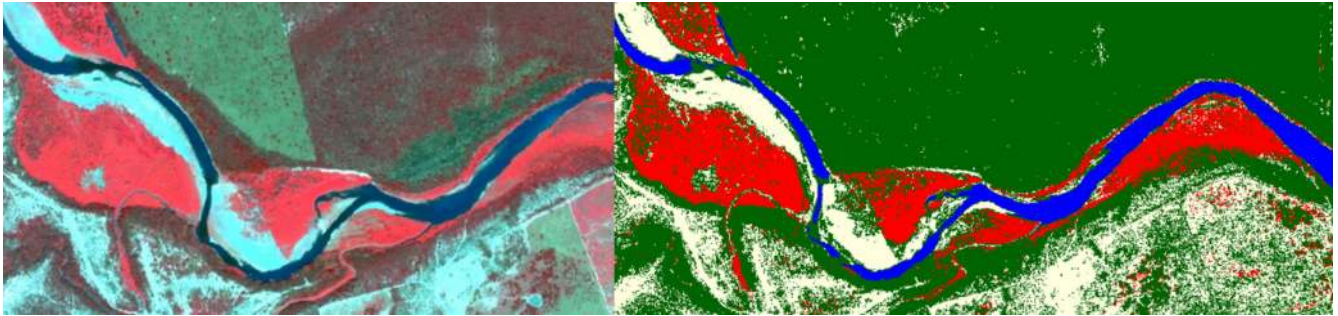


Figure 10. Color-infrared composite for a portion of a QuickBird® image along the Rio Grande between the United States and Mexico. Color codes in the classification map are: red, *Arundo donax*; dark green, mixed vegetation; light gray, soil; blue, water.

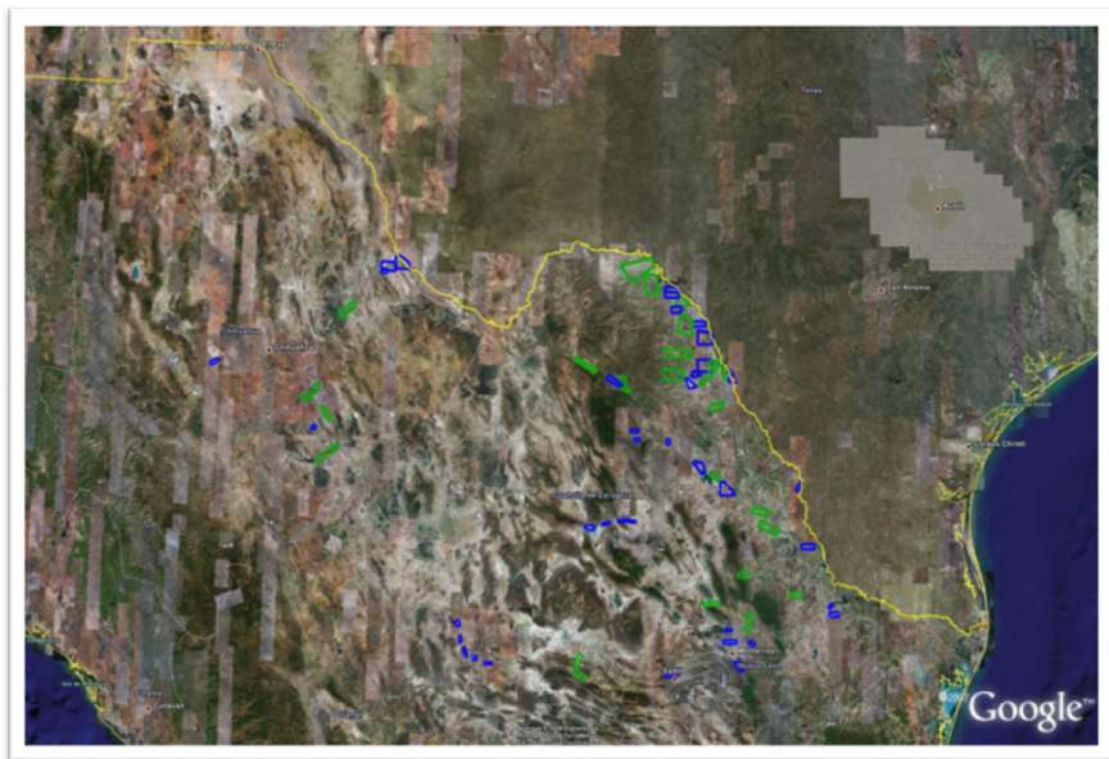


Figure 11. Polygons showing archived (blue) and selected but not archived (green) QuickBird® image scenes in the Mexican portion of the Rio Grande basin.

publicly available satellite images to estimate the area of invasion in the Central Valley of California is informing a prioritization system for ongoing local eradication and long-term management (Cal-IPC 2020).

Chemical

Glyphosate (2.5 to 5.0 kg ai ha⁻¹), imazapyr (0.54 to 1.1 kg ha⁻¹), or both in combination (with surfactant in all cases) are the chemical tools most commonly used to control *A. donax* (DiTomaso et al. 2013; Spencer et al. 2008, 2009). Applications of glyphosate should be made between late summer and mid-autumn after peak shoot growth has occurred (Ana et al. 2015; Anonymous 2016; Bell 1997; DiTomaso et al. 2013; Spencer et al. 2011), as rhizomes are low in reserves at this time and are receiving translocates from the shoots (Decruyenaere and Holt 2001) and shoots are beginning to show signs of senescence. Imazapyr can be effectively applied when

shoots are 1.5- to 2.5-m tall and growing rapidly, in late spring or early summer (Anonymous 2004; A Lambert, personal communication). In one study (Bell 2011), imazapyr applied alone or with glyphosate was most effective when applied in the fall, and imazapyr alone was more effective than glyphosate alone (Bell 2011). Aerial foliar applications, for example, with a helicopter or a boom-mounted sprayer, are necessary to treat large areas and must typically be accompanied by avoidance or pruning of nontarget vegetation. Follow-up spot treatments for 2 to 3 yr or longer are needed. Undiluted herbicide can be used in cut stump operations for small patches. Chemical application has been widely used across several thousand hectares in California (Cal-IPC 2020), in central and southern Texas (TPWD 2022), and throughout *A. donax*'s invaded range in the United States. In South Africa, *A. donax* is the only invasive alien grass to receive its own budget for management (Visser et al. 2017), but only 0.33% of the total budget for the Working for Water program for alien plant control

was spent on *A. donax* between 1995 and 2008 (van Wilgen et al. 2012). It was found that herbicide initially reduces density and height and growth rates; however, in the long term, it increases *A. donax* density (Guthrie 2007). Chemical control is therefore not generally supported in South Africa due to cost, the potential harm to non-target species, and the temporary nature of the benefits of this approach.

Physical/Mechanical

Successful large-scale (>10 ha) control projects targeting *A. donax* in California, USA, have, in most cases, involved a combination of mechanical/physical control and herbicides with repeated treatment (Cal-IPC 2020); mowing or tilling are rarely if ever effective on their own. This integrated physical–chemical approach is costly (e.g., estimated US\$70 million to effectively treat all *A. donax*-occupied habitat in the Central Valley of California (Cal-IPC 2020). Mowing appears to be most effective in the late summer or early fall when shoots are flowering, as both rhizome reserves and soil moisture for regrowth are likely to be low (DiTomaso et al. 2013). In South Africa, present control methods are largely restricted to hand or mechanical cutting (Guthrie 2007). However, little success has been achieved in most populations due to the scale of infestations. Combined mowing and herbicide application was largely ineffective at suppressing *A. donax* growth and biomass recovery in South Africa (Guthrie 2007; Visser et al. 2017). Topping at approximately 1 m has been implemented as a method to quickly improve visibility for law enforcement. Additional control options are being investigated in South Africa that integrate mechanical and biological control, including mowing or topping of stems to encourage growth in *Tetramesa romana* populations (Sutton et al. 2021), as has been implemented in the lower Rio Grande basin of Texas (Figure 12) and on a smaller scale in California (see section Biological Control—United States and Mexico). Mowing in autumn can be integrated with spring application of imazapyr (Bell 2011; A Lambert, personal communication) or spring stem cutting can be combined with herbicide application to stumps in the summer (Bell 1997).

Fire has been used widely as a physical control technique, but is ineffective on its own, as *A. donax* burns intensely and recovers quickly after fire (Coffman et al. 2010), exacerbating its displacement of other plants killed by the fire; areas of frequent fire disturbance are particularly vulnerable to invasion (Quinn and Holt 2008). In areas along the Rio Grande on the U.S.–Mexico border, fire has been used to reduce *A. donax* stands (JAG and PJM, personal observation) to facilitate cattle grazing on young regrowth shoots (Perdue 1958; Racelis et al. 2012a).

Biological

Insect Agents

Two specialist, insect biological control agents from the native range of *A. donax* in Spain, including the wasp *Tetramesa romana* Walker (Hymenoptera: Eurytomidae) (Figure 13) and the armored scale *Rhizaspidiotus donacis* (Leonardi) (Homoptera: Diaspididae) (Figure 14) were mass-reared and first released in the lower Rio Grande basin of Texas, USA, and Mexico between 2009 and 2012 (Moran et al. 2022; Racelis et al. 2010; Villarreal et al. 2016). The wasp *T. romana* lays eggs in canes and side shoots, causing formation of galls (abnormal plant growth) clustered at main and lateral shoot tips and resembling one large gall (Figure 13). No plants outside the genus *Arundo* spp. are galled (Goolsby and Moran 2009; Sutton et al. 2021). One larva feeds and pupates inside

each gall. Adults emerge from their galls by chewing exit holes (Figure 12E and 12F) (Goolsby and Moran 2009), which can be easily used in the field to diagnose wasp presence and estimate density (Goolsby et al. 2014). The wasp can complete its life cycle in 35 to 60 d (Moran and Goolsby 2009). Pre-release efficacy testing in a greenhouse showed that galling reduced shoot growth by 90% (Goolsby et al. 2009b) and reduced photosynthetic processes by up to 32% (Moore et al. 2010).

The armored scale *R. donacis* feeds belowground on rhizomes and the bases of side shoots of *A. donax* (Goolsby et al. 2009a; Moran and Goolsby 2010). Females (Figure 14) release tiny (ca. 0.4 mm; Moran and Goolsby 2010) “crawlers” that settle on suitable tissues, become immobile, and complete their life cycle in 5 to 6 mo, while males have a life span of only 2 mo, emerging as short-lived winged adults that mate with immobile females. Newly molted adult females increase about 50% in size to 1.2 mm as they develop live crawlers (Figure 14). Limited (ca. 50- to 100-fold less than on *A. donax*) development and reproduction occur on *P. australis* (Braman et al. 2021; Goolsby et al. 2009a), which has both native and invasive genotypes in North America (Lambert et al. 2016; Saltonstall 2016). In pre-release evaluations in its native range in France and Spain, infestation by this scale reduced *A. donax* shoot growth and rhizome size by 50% (Cortes et al. 2011a, 2011b), and infestation reduced photosynthesis in a greenhouse test (Moore et al. 2010). Abundant populations were associated with well-drained, gravel-based soils in the native range (Goolsby et al. 2013), informing decisions on release sites and interpretation of establishment success. A characteristic “witches’ broom” distortion of lateral shoots has been observed at release sites in Texas (Figure 14).

A third biological control agent, *Lasioptera donacis* Coutin (Diptera: Cecidomyiidae), is a leaf miner, with larvae feeding and developing in the leaf sheath of *A. donax*. Adult females (Figure 15) deposit eggs in holes or cracks in the leaf sheath (Goolsby et al. 2017; Thomas and Goolsby 2015), including in exit holes made by *T. romana*. Damage to leaf sheaths occurs due to larval feeding (Figure 15) and growth of one or several fungal species on which larvae also feed (Bon et al. 2018, 2023), as adult females can carry the fungus *Arthrrium arundinis* (Corda) Dyko & B. Sutton. The leaf miner *L. donacis* was permitted and released at one site along the Rio Grande in 2017, but it did not establish. Studies are underway to refine rearing and release methods. In the native range, infestation by *L. donacis* and fungal growth causes necrosis and accelerates leaf death (Marshall et al. 2018a), leading to shoot defoliation (Figure 15). Established populations are thus expected to increase light penetration through the canopy, which may accelerate the recovery of native riparian plant communities along the Rio Grande (Racelis et al. 2012c; Rubio et al. 2014) and other invaded watersheds, including in California, where climatic conditions are less favorable for the wasp *T. romana* (Marshall et al. 2018b). Along the Rio Grande, defoliation could also make riparian habitats less hospitable to survival of cattle fever ticks [*R. microplus* and *Rhipicephalus annalatus* (Say)], as tick survival is enhanced by dense, healthy *A. donax* (Racelis et al. 2012a), and could also increase within-stand visibility, improving the safety and effectiveness of law enforcement and cattle fever tick exclusion personnel working along the U.S.–Mexico border.

United States and Mexico

A binational biological control program between the U.S. Department of Agriculture–Agricultural Research Service (Edinburg, Texas) and Instituto Mexicano de Tecnología del



Figure 12. Methods for topping of *Arundo donax* to integrate with biological control methods. (A–C) Specialized tractor-mounted mow bars used for large-scale topping of *A. donax* along the Rio Grande. The tractor has a reciprocating blade that cuts canes at 1 m. (D) Topping opens view to Rio Grande across to Mexico from the U.S. side of the river. (E and F) *Tetramesa romana*, the arundo wasp, responds to an increase in side shoot abundance after cutting by galling young side shoots, as evidenced by abundant exit holes made by progeny wasps. All photos by JAG and staff, USDA-ARS.

Aguas (Jiutepec, Morelos, Mexico) was initiated in 2007 (Contreras 2007; Martínez Jiménez et al. 2017) with the objective of developing and implementing biological control of *A. donax* for protection of water resources. Additional funding was provided by the U.S. Department of Homeland Security, Customs and Border Protection to meet the operational visibility needs of the U.S. Border Patrol patrolling the international border with Mexico. Biological control of the invasive cane with specialized insects was considered to be the best long-term option for managing *A. donax*, because it is low in cost, sustainable, and suitable for use in large areas (Seawright et al. 2009). More than 1.2 million *T. romana*

wasps were released through a mass-rearing (Moran et al. 2022) and release program, including releases in specialized boxes dropped from airplanes in remote areas (Racelis et al. 2010). The wasp *T. romana* can disperse 10 to 15 km yr⁻¹ (Racelis et al. 2009). Populations have established in *A. donax* stands along 600 river-km of the Rio Grande between Brownsville and Del Rio, TX (Goolsby et al. 2014). In 2014, five years after the release of the wasp, live aboveground biomass (inferred from main shoot length measurement, as in Spencer et al. [2006]) of *A. donax* had decreased on average by 22% compared with assessments in 2007 across 10 sites along the Rio Grande (Goolsby et al. 2016), with a



Figure 13. (Left) The wasp *Tetramesa romana* ovipositing into stems of *Arundo donax*. Adult wasps are 0.5 to 1.2 cm in length, including antennae. (Right) Shoot tip distortion caused by galls made on *A. donax* by *T. romana*. Photos by JAG.



Figure 14. (Left) The armored scale *Rhizaspidiotus donacis* isolated from a rhizome, with waxy scale covering removed, showing fully expanded adult female (about 1.2-mm wide) with crawlers on left and newly molted adult female (about 0.8-mm wide) before crawler development on the right. (Right) Lateral shoot node on *Arundo donax* infested with *R. donacis*, showing females at the base of the node and witches' broom distortion of shoots. Photos by PJM (left) and JAG (right).

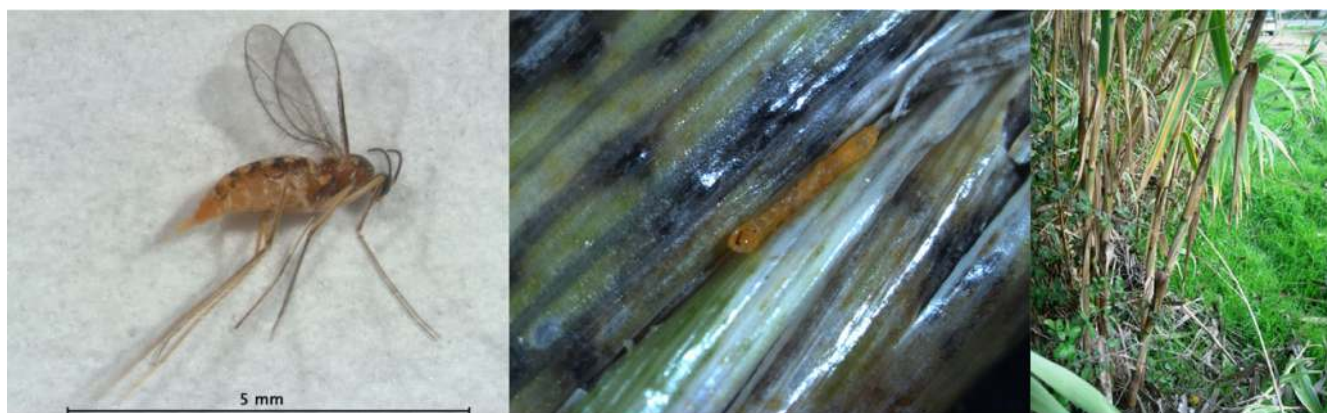


Figure 15. (Left) Adult of *Lasioptera donacis* leaf miner that feeds on *Arundo donax*. (Center) Larva of *L. donacis* inside leaf sheath, surrounded by fungal mycelia. (Right) Defoliation of shoots in Spain resulting from premature leaf death caused by *L. donacis* infestation. Photos by JAG and staff.

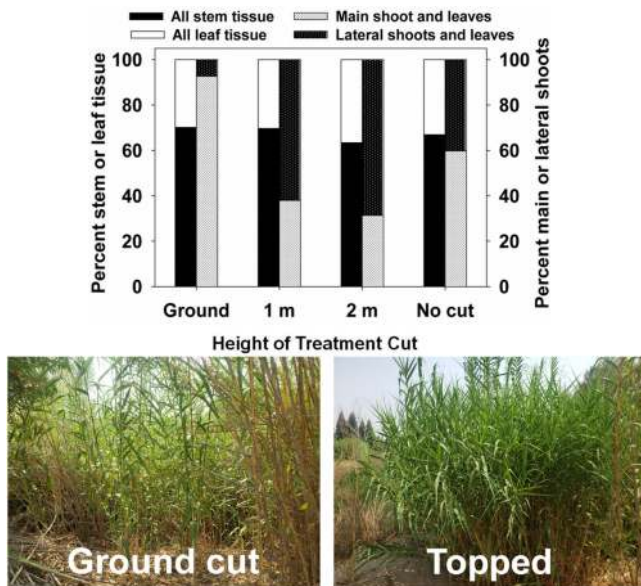


Figure 16. Graph (top) showing percent allocation of *Arundo donax* to stem and leaf tissues (left axis, main, and lateral shoots combined) and percent allocation to main and lateral shoots (right axis, stem, and leaf tissues combined) in plants allowed to regrow for 5 mo after being cut under summer conditions in Texas, USA, to ground level, 1 m, or 2 m, or left uncut. Bottom images show plots in northern California in late summer that were cut to ground in the spring and allowed to regrow without (left) and with (right) topping of shoots at 1.5-m height. Graph taken from Racelis et al. (2012b). Photos by PJM.

further decrease of 32% (total 54%) across 5 sites by 2016 (Moran et al. 2017), associated with galling caused by *T. romana* on main and lateral shoots. A total of 44 native plant species were recorded in 2016 where there were once solid monotypic stands of *A. donax* (Moran et al. 2017). The wasp *T. romana* has established populations in Mexico, along the Rio Grande at its northern border and in Morelos in southern Mexico (Martínez Jiménez et al. 2017). The armored scale *R. donacis* has established populations at more than 50 sites along the Rio Grande in Texas and Mexico, with none found on *P. australis* or other non-target plants (Goolsby et al. 2020), and its additive impact in release plots, in combination with *T. romana*, reduced biomass by 55% compared with plots with only *T. romana* at two sites on the Rio Grande (Goolsby and Moran 2019). The limited dispersal ability of *R. donacis* has reduced its wider impacts.

Biological control has been integrated with mechanical topping at 1- or 2-m height to increase impact in the lower Rio Grande basin. Studies early in the program found that topping increased biomass allocation to lateral shoots by more than 60% compared with the more traditional practice of cutting shoots to the ground, while increasing density and length of lateral shoots by 50% to 90%, leading to increased *T. romana* gall density per shoot compared with regrowth from ground-cut plots (Racelis et al. 2012b) (Figure 16). Current large-scale topping projects along the Rio Grande provide immediate benefits for visibility and international border enforcement, followed by development of abundant *T. romana* wasp populations on lateral shoot regrowth (Figure 12) to maintain control and disperse to uncut *A. donax* stands (Goolsby et al. 2019). The result has been widespread death of lateral shoots in both uncut and cut stands, and also death of young main shoots in the understory (Figure 17).

The impact of *T. romana* along the Rio Grande has most recently been documented in terms of water use of *A. donax* stands, with a 25% decrease in cumulative evapotranspiration between May and October 2015 compared with 2014, despite 2015 being wetter, coinciding with 28% to 53% higher wasp populations in 2015 (Racelis et al. 2022). Studies are needed at additional sites, but these results align with the predictions made in Moran et al. (2017) that reduction of live biomass accumulation caused by *T. romana* would reduce the ability of *A. donax* to consume/waste water, leading to increased availability of water worth several millions of dollars (US\$) per year (Seawright et al. 2009).

In California, the wasp *T. romana* was first released in the Central Valley in 2010, and, with pre-topping or ground-cutting of release plots, at a total of 12 sites in northern California by 2020, with evidence of establishment (overwintering, reproduction, and dispersal) at 7 sites by 2022 (Cal-IPC 2020; Moran 2021; PJM, unpublished data). Results from plot studies support findings from Texas that integration with cutting improves local establishment of *T. romana* (Cal-IPC 2021). An adventive population of this wasp is present in some coastal drainages in Southern California (Dudley et al. 2008). Efforts to establish this wasp population on *A. donax* on the Colorado River and in the Mojave Desert of southeastern California have not been successful (A Lambert, personal communication). The armored scale *R. donacis* was released in northern California beginning in 2014, with early evidence of establishment in release plots at sites in the Central Valley; a localized, genetically distinct adventive population was recently found near Ventura in Southern California (Braman et al. 2021). The impact of the wasp and armored scale will be assessed initially in terms of changes in live biomass and shoot density. The leaf miner *L. donacis* is planned for release in California, targeting cooler areas at which temperatures are likely insufficient for development of large populations of *T. romana* (Marshall et al. 2018b).

Programs Outside North America

South Africa

Arundo donax was ranked as the top priority for all types of control among invasive grasses in South Africa (Sutton et al. 2021) and at the high priority level for biocontrol among all nonnative, invasive plants in the country (Canavan et al. 2021). A biocontrol program for *A. donax* was initiated in 2013 with funding from the Department of Environmental Affairs–Natural Resource Management Programmes. The program has largely been guided by developments in the biocontrol program for *A. donax* in the United States and has focused on *T. romana* and *R. donacis*. Herbivore surveys recorded 13 herbivorous insects, including the biological control agent *T. romana* (Canavan et al. 2019), accidentally introduced, widespread, and abundant on *A. donax* across the country (Canavan et al. 2019). Two *T. romana* genotypes were imported in 2018 from Granada, Spain, and Perpignan, France. Molecular analysis revealed that there are two adventive genotypes in South Africa, one found in two provinces in the tropical northeast and the other throughout the rest of the country, and they are genetically distinct from all five *T. romana* genotypes released in the United States (Bownes 2010; Sutton et al. 2021). *Tetramesa romana* is suitably host specific, with no galling of South African *P. australis* or *Phragmites mauritianus* Kunth (Sutton et al. 2021). In laboratory tests, wasps imported from Spain produced higher numbers of progeny compared with the adventive genotypes, but because the wasp is already widespread, release of the imported wasp accessions



Figure 17. Death of *Arundo donax* shoots resulting from galling infestation by the wasp *Tetramesa romana*. (Left) Death of lateral shoot node in uncultivated stand. (Center) Death of shoot that regrew after the topping protocol described in Figure 12. (Right) Death of young main shoot in the understory. Photos by JAG.

in South Africa are not likely (A Bownes, Landcare Research, Lincoln, New Zealand, personal communication). Integration of ongoing manual or mechanical cutting under the Working for Water Programme (Sutton et al. 2021) with biological control by *T. romana* is being investigated.

Research on *R. donacis* in South Africa has involved host-range studies, climate modeling, and impact and performance studies. Reproductive females were imported into a quarantine laboratory from Alicante, Spain, in 2016 and 2017. Pillay (2016) conducted climate modeling to assess the suitability of South Africa's climates for establishment of *R. donacis*. Using model parameters based on the native (Mediterranean Europe) and prior-introduced ranges (Texas, USA) of *R. donacis*, modeling using CLIMEX 4.0 software (Kriticos et al. 2015) predicted that most regions of South Africa are suitable for *R. donacis* (Pillay 2016). After adjustment of environmental parameters, crawler survival rates on *A. donax* from South Africa averaged 25%, comparable to rates observed on the *A. donax* genotype common in the Rio Grande (Goolsby et al. 2013). Future work is planned to finalize the host-range trials.

New Zealand

A biocontrol program for *A. donax* was conducted with *T. romana* and *R. donacis* imported from colonies in Texas, USA (originally from Mediterranean Spain) into a quarantine lab for a planned release on the tropical island of Rarotonga (part of the Cook Islands). This introduction did not proceed when it was found that abundance of *A. donax* on Rarotonga had been greatly overestimated due to confusion with the invasive grass *P. purpureum* (Paynter et al. 2019). Funding was obtained from the National Biocontrol Collective to release both *T. romana* and *R. donacis* in New Zealand as a preemptive program to tackle a potentially major weed in the early stages of invasion. Host-specificity testing already conducted in the United States was sufficient to gain approval to release *T. romana* in New Zealand. To confirm that *R. donacis* posed no risk to New Zealand native plant species, additional testing was performed on the native grasses *Isachne globosa* (Thunb.) Kuntze, *Spinifex sericeus* R.Br., and *Zoysia minima* (Colenso) Zotov, and indicated minimal risk to these species. Approval to release both *T. romana* and *R. donacis* in New Zealand was granted by the Environmental Protection Authority in 2017. *Tetramesa romana* was released at five localities, all on the North Island of New Zealand, during the

summer of 2017 to 2018 and at two additional localities in 2021. Only two sites have been checked subsequently, with no evidence of establishment. *Rhizaspidiotus donacis* was released for the first time at three sites (all on the North Island of New Zealand) in 2021.

General Outlook

Arundo donax has become a damaging and widespread invader on at least four continents—the Rio Grande basin of Texas and Mexico and California in North America; subtropical and low mountainous regions of South America; diverse climates in coastal desert and humid equatorial regions of Africa and in South Africa; and in Oceania (Australia, New Zealand, and at least eight island nations). It can also be problematic in disturbed riparian habitats in its ancient areas of introduction in Mediterranean Europe; and in areas of Asia close to its native range (Jiménez-Ruiz et al. 2021). *Arundo donax* forms dense thickets along rivers, canals, and reservoirs, removing water that is needed for agriculture and human consumption in regions where rainfall is scarce, and *A. donax* also transforms riparian ecosystems, promotes wildfires, displaces native plants and animals, hinders access and visibility for law enforcement, and can facilitate the invasion of other species. Climate modeling successfully predicted the native and global introduced range of *A. donax*. Based on the CLIMEX model, and with due regard for possible underreporting of localities, *A. donax* is likely to expand its range in riparian and wetland habitats in sub-Saharan Africa, especially eastern Africa, including Madagascar, in tropical and subtropical lowlands in South America, in the Indian subcontinent, and in southeast Asia. Genetic evidence we obtained indicates Spain is the proximal source of invasive populations in North America (Tarin et al. 2013), while an accession from the Indus Valley (Canavan et al. 2017) or Middle East (Bhikraj 2021) is the source of the invasion in South Africa. Analysis of satellite images made in 2002 and 2007 along the Rio Grande in Texas indicated an increase in the invaded area before implementation of biological control (Yang et al. 2009), illustrating that *A. donax* was able to increase its distribution in favorable climates even in areas where it is already widespread. Invasions have been facilitated by human-aided dispersal of plants and favored by human alteration of riparian ecosystems, especially the damming of rivers and resulting conveyance flows. Invasion risk is high in areas disturbed by wildfires and floods, as *A. donax*

recovers quickly from these disturbance events (Coffman et al. 2010; Frandsen and Jackson 1994).

Arundo donax is a stress-tolerant plant, particularly water-deficit stress, due to its ability to photosynthesize efficiently. Nonetheless, the distribution of *A. donax* could be influenced by climate change, as stress caused by water deficit and/or climatic extremes could reduce its distribution in some equatorial and subtropical regions, with concomitant spread into temperate areas as they become more favorable (Bradley et al. 2010). Early detection and rapid response approaches are essential to slow invasion of new regions. Chemical and mechanical control programs targeting well-established *A. donax* populations are costly, requiring long-term follow-up; for example, 20 yr in one California watershed (Cal-IPC 2020), and in the Big Bend region of the Rio Grande in western Texas (JAG, personal observation). Short-term initiatives targeting established invasions result in dramatic visual control but are ineffective due to regrowth and/or reinvasion. Chemical and mechanical may control reduce plant biodiversity and pose other environmental risks in sensitive riparian and aquatic habitats, as well as occupational risks to humans.

Starting in the 1990s (Tracy and DeLoach 1999), the USDA-ARS developed the world's first biological control program targeting an invasive grass, focusing on *A. donax*. By the seventh year after release in 2009, the shoot tip-galling wasp *T. romana* had reduced live biomass by 54% along the Rio Grande between Del Rio and Brownsville, TX, translating to water savings valued at US \$4.4 million yr⁻¹ (Moran et al. 2017). The armored scale *R. donacis*, now established at many sites in the lower Rio Grande basin, does not disperse rapidly, but in release plots, 8 yr after release, it reduced live biomass is reduced by up to 55% in combination with *T. romana* compared with plots with only the wasp. The wasp and armored scale have also been released in California, USA, and in New Zealand. Mechanical topping and biological control strategies have been integrated in the lower Rio Grande basin of Texas and Mexico for increased impact, and similar efforts are being initiated elsewhere. Biological control agents are critical tools contributing to an adaptive integrated weed management approach to reduce the economic and environmental damage caused by *A. donax*. All control programs should be accompanied by evaluations to verify impacts on *A. donax* size, growth, density, and spread, but also benefits for water resource conservation, biodiversity, and human economic activity and well-being.

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Structured Appendix

Köppen-Geiger Climate Distribution

Arundo donax is found most frequently in the warm temperate and Mediterranean climate types Cfa, Cfb, Csa, and Csb globally (Beck et al. 2018) (Figure A1), in North and Central America (Figure A2), and in Europe, the Mediterranean Basin (including far northern Africa, the Middle East, the Arabian Peninsula, and far western

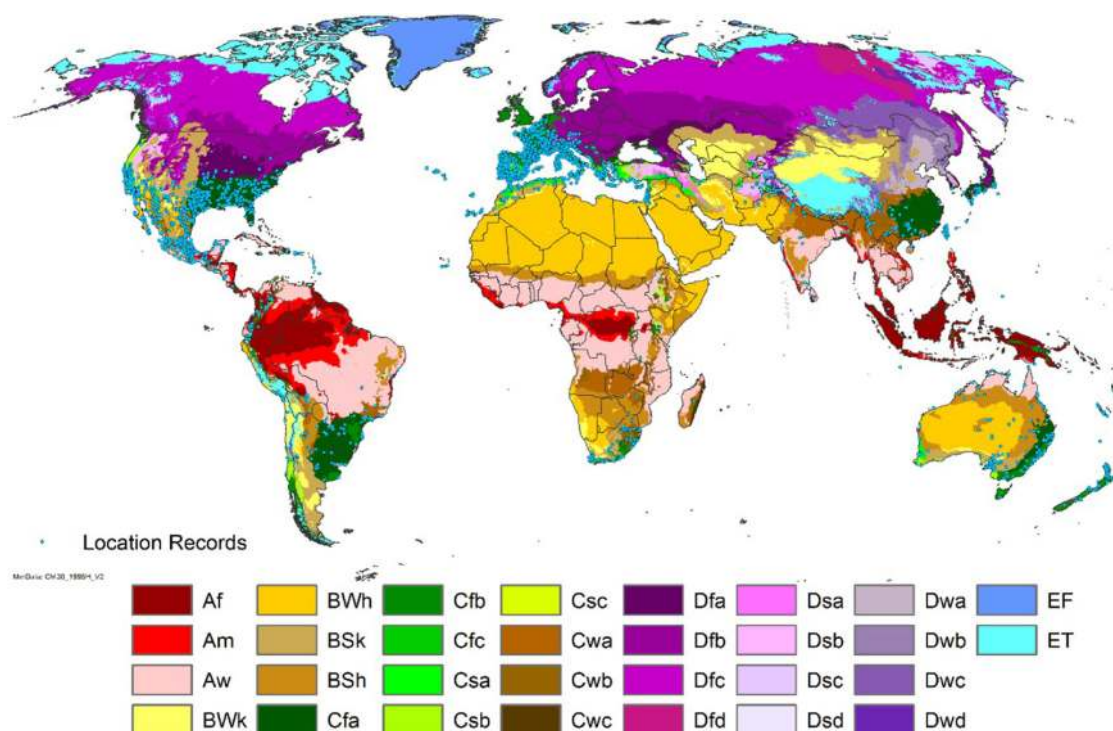


Figure A1. Overlay of global distribution points for *Arundo donax* on Köppen-Geiger polygons. Köppen-Geiger classification data set derived using classification methods in Beck et al. (2018) applied to data from CliMond (Kriticos et al. 2012), 1980 to 2010.

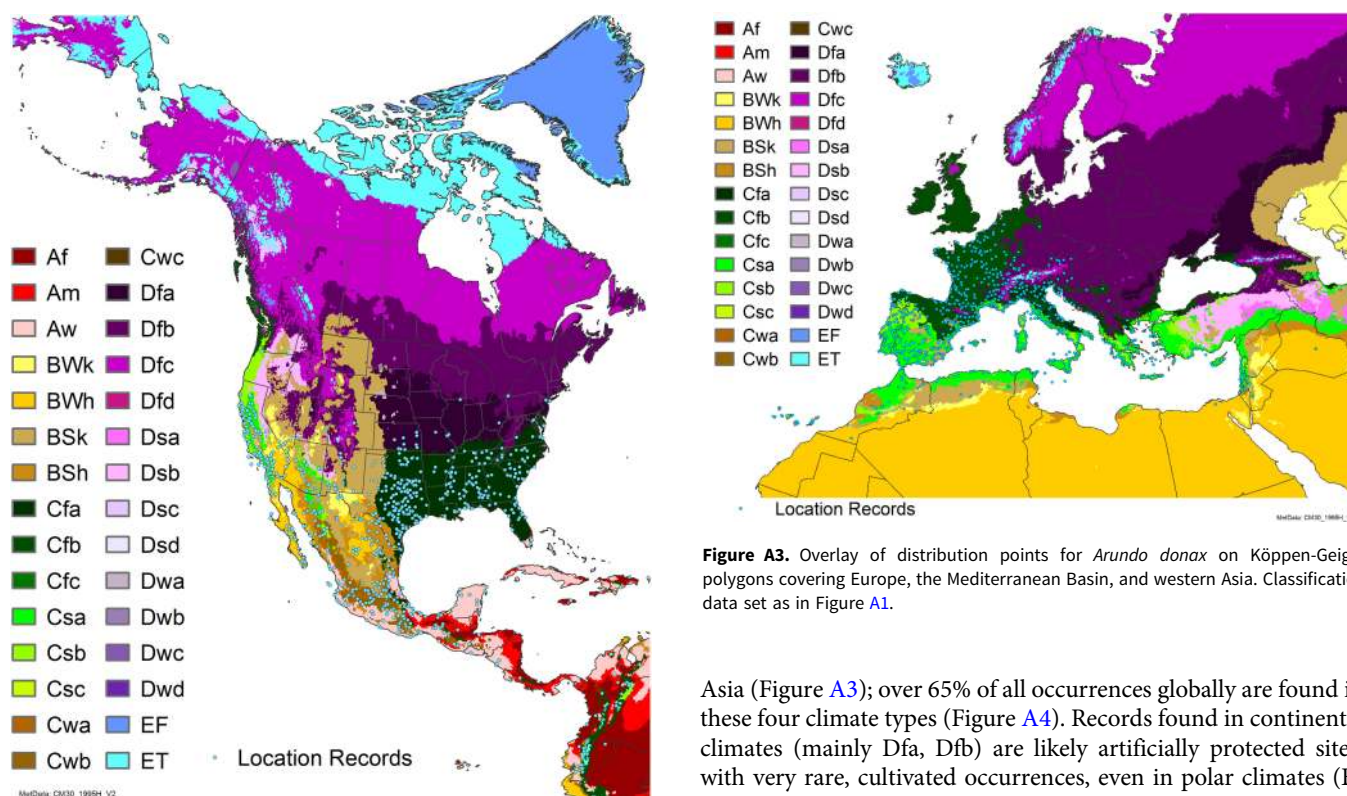


Figure A2. Overlay of distribution points for *Arundo donax* on Köppen-Geiger polygons covering North America. Classification data set as in Figure A1.

Figure A3. Overlay of distribution points for *Arundo donax* on Köppen-Geiger polygons covering Europe, the Mediterranean Basin, and western Asia. Classification data set as in Figure A1.

Asia (Figure A3); over 65% of all occurrences globally are found in these four climate types (Figure A4). Records found in continental climates (mainly Dfa, Dfb) are likely artificially protected sites, with very rare, cultivated occurrences, even in polar climates (E) (Figures A1 and A4). Frequent occurrences in arid climates (warm, cool, and cold) (BWh, BWk, BSh, BSk) are in artificially irrigated locations. There are relatively few recorded occurrences in tropical

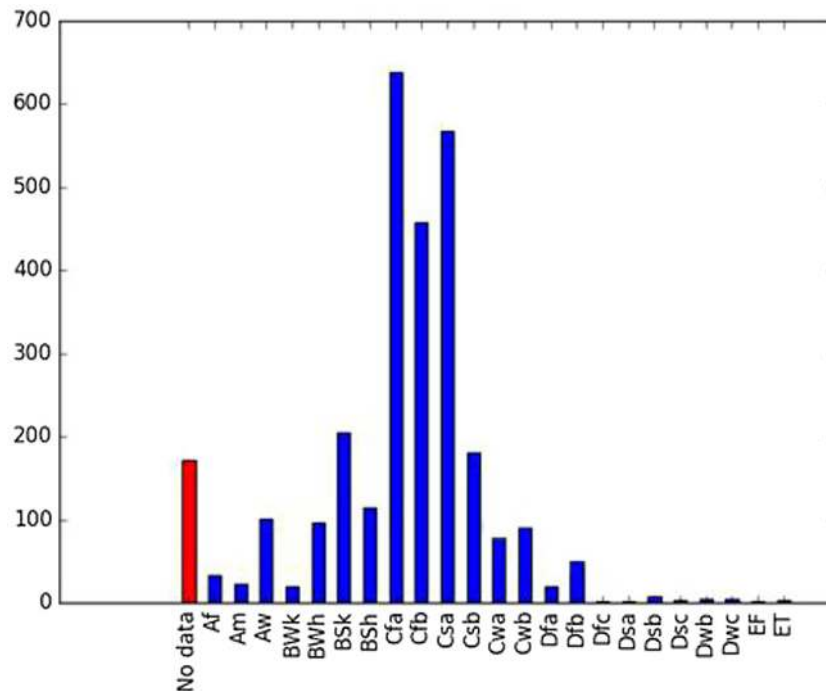


Figure A4. Number of occurrences of global location records for *Arundo donax* in relation to Köppen-Geiger climate classes. See Table 1 in the main article for climate characteristics of the climate class acronyms.

climates (Af, Am, and Aw) (Figure A4), which may represent underreporting, rather than unsuitable climates. See the main article text for more information on climate types.

CLIMEX Model

We used CLIMEX v. 4.1 (Kriticos et al. 2015; Sutherst and Maywald 1985) to model the potential distribution of *A. donax*. The CLIMEX model was originally fit to European distribution data in 2007, based on the Mediterranean template and using a historical climatology centered on 1975. Subsequently, Barney and DiTomaso (2011) published CLIMEX model parameters for *A. donax*. Here we have refit the model using a more contemporary climatology.

Model Fitting

Climate Database. We used the CliMond CM30 1995H V2 data set for all model simulations (Kriticos et al. 2012). This data set contains 30-yr monthly averages of daily minimum and maximum temperature, relative humidity at 0900 and 1500 hours, and monthly precipitation totals centered on 1995. The spatial resolution is 30' (= minutes) (approximately 50 km).

Distribution Records. We downloaded data from the Global Biodiversity Information Facility (GBIF 2021).

Growth Indices. All model parameters are summarized in Table A1. The lower temperature limit for growth was set to 10 C and the upper limit was set to 28 C. The lower and upper limits for optimal growth were set to 20 and 24 C, respectively. The DV3 value was too low. *Arundo donax* is observed in the Yucatan Peninsula of Mexico, where maximum temperatures often exceed 36 C. Spencer and Ksander (2006) note that *A. donax* grows in locations where daily average temperatures are 30 C. Accordingly, DV3 was set to 40 C to accord with heat stress temperature threshold (TTHS), which was fit to southern Algeria.

Soil Moisture. The soil moisture growth index parameters were set based on consideration of ecophysiological factors. The lower limit for growth, SM0, was set to approximate the permanent wilting point (0.1). The upper limit for growth was set to 1.5 in acknowledgment of the fact that the leaves on *A. donax* are carried moderately high up the stem and that it occurs in areas subject to moderate levels of inundation. The lower and upper soil moisture levels for optimal growth were set to 0.4 and 0.7, respectively, because *A. donax* does not grow best under inundated conditions.

Stresses

Cold Stress. Two cold stress mechanisms were explored. The lethal temperature threshold mechanism did not fit the known distribution well, requiring a biologically implausibly low accumulation rate. Conversely, the degree-day cold stress mechanism was fit to the known suitable locations in Europe provided by Alan Kirk (European Biological Control Laboratory [retired], Montpellier, France, personal communication). A location in the Massif centrale (Mirambeau, France) appears to be an outlier. It was not possible to reduce cold stress sufficiently to enable persistence at that location while still restricting *Arundo donax*'s projected northern range in France within reasonable limits. When considering the European range, including single occurrences in Norway and Sweden, it is important to bear in mind that it is extensively planted as a garden ornamental.

Hot Wet Stress. Hot wet stress was removed from the model. It was only impacting in limited areas around Slovenia and northern Italy. We now have known suitable locations in southern Slovenia.

Heat Stress. The heat stress factor was relaxed from the Mediterranean template in order to allow *A. donax* to persist in southern Algeria under irrigated conditions representative of oases.

Table A1. CLIMEX parameter values for *Arundo donax*.

Parameter	Description	Values
Moisture		
SM0	Lower soil moisture threshold	0.1
SM1	Lower optimum soil moisture	0.4
SM2	Upper optimum soil moisture	0.7
SM3	Upper soil moisture threshold	1.5
Temperature		
DV0	Lower threshold	10 C
DV1	Lower optimum temperature	20 C
DV2	Upper optimum temperature	24 C
DV3	Upper threshold	40 C
Cold stress		
DTCS	Degree-day cold stress threshold	5 C-days
DHCS	Degree-day cold stress accumulation rate	-0.0012 wk ⁻¹
Dry stress		
SMDS	Soil moisture dry stress threshold	0.1
HDS	Stress accumulation rate	-0.04 wk ⁻¹
Wet stress		
SMWS	Soil moisture wet stress threshold	1.6
HWS	Stress accumulation rate	0.0015 wk ⁻¹
Heat stress		
TTHS	Heat stress temperature threshold	40 C
THHS	Heat stress accumulation rate	0.001 wk ⁻¹
Threshold heat sum		
PDD	Number of degree-days above DV0 needed to complete one generation	810 C-days
Irrigation scenario		2.5 mm d ⁻¹ in summer and winter

Dry Stress. The dry stress parameters were adjusted by first setting the threshold at around permanent wilting point (0.1), then adjusting the stress accumulation rate (HDS) so as to limit the potential range to where *A. donax* has been observed in nonirrigated regions.

PDD. The *A. donax* location at Mirambeau, France, experienced a heat sum of about 815 C-days above 10 C yr⁻¹, whereas all other known suitable locations had degree-day sums of around 1,600 C-days or more above 10 C yr⁻¹.

Simulations

Arundo donax is frequently observed in habitats that are irrigated. The model fit to natural rainfall situations was run with a top-up irrigation scenario of 2.5 mm d⁻¹. A composite risk map was developed using the Global Map of Irrigated Areas (GMIA) (Siebert et al. 2013) to define those areas where the results of the irrigation or natural rainfall scenarios were included in the composite risk map (Yonow et al. 2019). The original 5' (minute) GMIA data set was resampled up to 30' spatial resolution, and a threshold area of 10 ha was selected to indicate that irrigation was practiced in a cell of that size.

Validation

The vast majority of records of *A. donax* outside its native range are modeled as suitable. In the invaded range in North America, almost all known points fall in areas modeled as suitable for persistence, and the cold range limits coincide with the northernmost bounds of the known distribution (apart from two outliers that fall in locations modeled as being unsuitably cold, South Bend, IN, and Coeur d'Alene, ID) and similar locations around New York City, NY; Erie, PA; Richmond, IL, west of Chicago on the state's northern border; Fort Collins, CO; and Park City, UT (Figure 7 in main article). These populations are presumed to be cultivated or recent escapes from such operations. There are a few records in the Himalayas that experience a temperature regime that is infeasibly cold for *A. donax* persistence.

This is an area of extreme topographic relief that is not well sampled at a resolution of 30' (Kriticos and Leriche 2010), and it is likely that *A. donax* grows in the relatively warm valleys. There is also a location record in western China that experiences a temperature regime that is infeasibly cold for *A. donax* persistence. This is likely a misleading record. In Australia, there are many records that fall outside the area predicted to be suitable for persistence (environmental index [EI] > 0). These inland records fall around water bores and pastoral homesteads within the arid zone and are not invasive. In New Zealand, there is one location on the South Island (in the town of Cromwell) that falls in the growth suitability zone (GI > 0, EI = 0). This was a cultivated specimen, protected from the extremes of cold.

Results

The fitted parameters are summarized in Table A1. In the introduced range in western Europe, the distribution records in GBIF far exceed the modeled distribution in the far northern regions (EI > 0) (Figure 8 in main article), highlighting the role of this plant as a garden ornamental in this region. In these locations, we and others have observed that *A. donax* is protected from the effects of a harsh winter (A Kirk, personal communication). The model correctly predicts the presence of *Arundo donax* on every continent apart from Antarctica (Figure 1 in main article). It is most extensively observed in Europe (Figure 8 in main article) and North America (Figure 7 in main article). The records in South America, Asia, and Australia are widespread, but far less dense. In Africa (Figure A5), there is a concentration of records in southern Africa. We are mindful of the possible effects of possible underreporting biases in tropical and subtropical South America, Africa, southeast Asia including Indonesia, and island nations in Melanesia.

In the Middle East (Figure 8 in main article), the effects of irrigation on the potential distribution of *A. donax* are marked, with suitable habitat apparent in the patchwork pattern of climate suitability. A similar association exists along the Nile valley through the Sahara Desert (Figure A5). The latent invasion threat

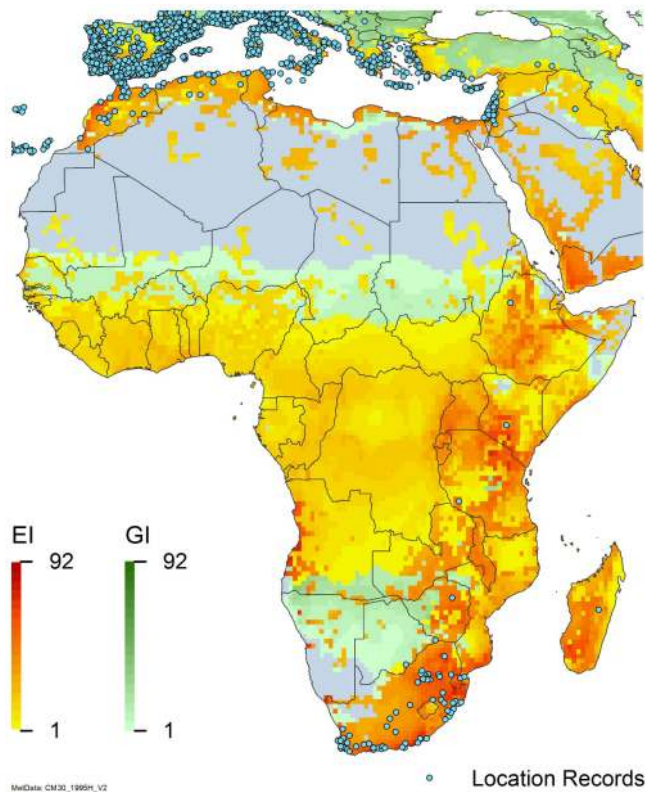


Figure A5. Climate suitability for *Arundo donax* in Africa, the Mediterranean Basin, and far western Asia modeled using CLIMEX, incorporating a composite of natural rainfall and a top-up irrigation scenario. Climate suitability in yellow to red colors (environmental index [EI] ≥ 1) indicates areas of expected year-round population persistence, while green colored areas (growth index [GI] ≥ 1) indicate regions where *A. donax* can grow only in one favorable season, and thus populations are not expected to persist.

is most marked in eastern Africa, though there may be substantial underreporting of its presence there. In Central Africa, as in other equatorial tropics, *A. donax* probably faces strong competition.

In Asia (Figure A6), *A. donax* is widely distributed from its native Indo-Pakistan range through areas modeled as suitable in India through to central China, and the model predicts actual localities as occurring in suitable areas. It is notable, however, that there are localities in Afghanistan, in the presumed ancient native range, where EI was 0 (Figure A6).

Globally, most observations of *A. donax* fall within EI > 0 in the CLIMEX model (Figure 3 in the main article), indicative of successful model validation (Kriticos et al. 2015).

Discussion

Arundo donax has expanded far beyond its native range globally into climates that are as suitable or more suitable than those in its native range, mainly through anthropogenic spread followed by regional invasion. Despite exhibiting clonal reproduction throughout its invasive range, the wide range of climates that are suitable for *A. donax* invasion reflect its ability to adapt physiologically and phenologically. It is not clear whether significant gaps in the known distribution in the global equatorial tropics, modeled as climatically suitable, reflect underreporting, lack of introduction, or biotic competition factors not considered in the model. There appears to be room for much infill of the suitable range, and the potential for a great deal of range expansion into tropical regions,

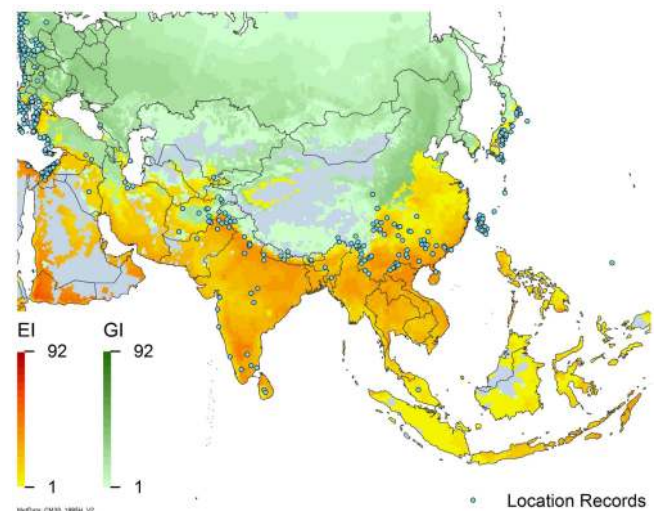


Figure A6. Climate suitability for *Arundo donax* in Asia, including its native range in the Indo-Pakistan region, modeled using CLIMEX, incorporating a composite of natural rainfall and a top-up irrigation scenario. Climate suitability in yellow to red colors (environmental index [EI] ≥ 1) indicates areas of expected year-round population persistence, while green colored areas (growth index [GI] ≥ 1) indicate regions where *A. donax* can grow only in one favorable season, and thus populations are not expected to persist.

as well as in northeastern China and throughout Southeast Asia, Melanesia, and Australasia.

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