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INVASIVE SPECIES III

Review Paper

From introduction to nuisance growth: a review of traits of alien aquatic plants which contribute to their invasiveness

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Abstract Invasive alien aquatic plant species (IAAPs) cause serious ecological and economic impact and are a major driver of changes in aquatic plant communities. Their invasive success is influenced by both abiotic and biotic factors. Here, we summarize the existing knowledge on the biology of 21 IAAPs (four free-floating species, eight sediment-rooted, emerged or floating-leaved species, and nine sediment-rooted, submerged species) to highlight traits that are linked to their invasive success. We focus on those traits which were documented as closely linked to plant invasions, including dispersal and growth patterns, allelopathy and herbivore defence. The traits are generally specific to the different growth forms of IAAPs. In general, the species show effective dispersal and spread mechanisms, even though sexual and vegetative spread differs strongly between species. Moreover, IAAPs show varying strategies to cope with the environment. The presented overview of traits of IAAPs will help to identify potential invasive alien aquatic plants. Further, the information provided is of interest for developing species-specific management strategies and effective prevention measures.

Keywords Dispersal · Weed biology · Invasive aquatic plant species · Invasive plant traits

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Introduction

Invasive alien aquatic plants (IAAPs) are considered a serious threat to aquatic ecosystems throughout the world. Due to their nuisance growth, IAAPs have both significant economic and ecological impact (Holm et al., 1969, Halstead et al., 2003, Stiers et al., 2011a; Santos et al., 2011). Consequently, management options are ongoing to reduce the impact of IAAPs, which are highly cost-intensive and resource demanding (Hussner et al., 2017; Simberloff, in press).

Interestingly, the proportion of introduced plant species, which become invasive is much higher in aquatic than in terrestrial habitats (Hussner, 2012). The reasons for this strong imbalance are still not clear, even though the uniformity of freshwater habitats is commonly considered as important for the broad distribution ranges of aquatic plants (Santamaria, 2002; but see Murphy et al., 2019). Moreover, it must be borne in mind that most alien aquatic plant introductions, similar to terrestrial plants (Reichard & White, 2001), occur via the horticultural trade (Brunel, 2009; Hussner et al., 2014a). In contrast to terrestrial plants, which are commonly cultivated in gardens and often escape from cultivation into natural habitats via seeds (e.g. *Heracleum mantegazzianum*; Thiele & Otte, 2008), particularly aquatic plants cultivated in aquaria require a human-mediated, intended or unintended, transport into water bodies (Maki & Galatowitsch, 2004; Champion et al., 2010; Hussner et al., 2010; Hill et al., 2020). In fact, most traded aquatic plant species are particularly robust and able to grow under varying conditions in aquaria and under different field conditions, suggesting that a wide ecological amplitude is a relevant trait-promoting invasiveness of IAAPs (Azan et al., 2015).

Nonetheless, numerous studies deal with the question, why do some introduced aquatic plants become invasive, but not others? These studies consider varying aspects of alien aquatic plant invasions, particularly focussing on

(i) pathways of introduction (Maki & Galatowitsch, 2004; Brunel, 2009; Martin & Coetzee, 2011; Hussner et al., 2014a);
(ii) the empty niche theory (Fleming & Dibble, 2015);
(iii) the role of environmental (particularly nutrients) and climatic conditions (James et al., 2006; Gillard et al., 2017a);
(iv) changes in the invasive success of IAAPs due to global change (Wu & Ding, 2019); including climate change (Netten et al., 2010, 2011; Calvo et al., 2019);
(v) the presence/absence of herbivores in its introduced range and the enemy release hypothesis (Fleming & Dibble, 2015; Grutters et al., 2017a; Petruzzella et al., 2017; Redekop et al., 2018; Pulzatto et al., 2018); and
(vi) the role of aquatic plants and plant communities for the establishment of introduced alien aquatic plants (Thiebaut & Martinez, 2015; Chadwell & Engelhardt, 2008; Thouvenot et al., 2019).

There is general concern about questioning the role of species biology on their invasive success (Goodwin et al., 1999; Kolar & Lodge, 2001). The species' biology and the capacity to acclimate to new/changing conditions determine the growth and competitive strength and thus contribute to the invasiveness of a species. In fact, many studies use growth and competition experiments between native and invasive alien aquatic plant species to identify plant traits explaining the success or failure of the alien species. The outcomes of such studies are limited due to species selection and experimental growth conditions, but do give an idea of relative competitive ability. Furthermore, the role of competitive strength for the success of invasive species differs between the different stages of the invasion process (Vilà & Weiner, 2004).

The performance of a given plant in an environment depends on its capacity to respond to abiotic environmental factors or to avoid detrimental effects originating from biotic interactions such as competition, herbivory or pathogen attack. Specific plant characteristics or attributes linked to morphological, anatomical, physiological, biochemical or phenological "traits" will determine the overall performance of a species (Kattge et al., 2011).

Identifying and understanding plant traits that contribute to the invasiveness of alien species is a key component for the identification of further potential invasive species (Kolar & Lodge, 2001; Jacobs & MacIsaac, 2009). The higher the tolerance of a species to varying environmental conditions, the higher the likelihood to become a successful invader (Higgins & Richardson, 2014). Even though this has been studied intensely for terrestrial plants (e.g. van Kleunen et al. 2011), only a few studies focussed on plant attributes, characteristics or traits (terms often used synonymously) that might be linked to successful aquatic plant invasions (Fleming & Dibble, 2015; Brundu, 2015), and a comprehensive overview for aquatic invasive plants is still lacking.

Nevertheless, it seems reasonable that a large variety of plant traits contribute to the invasiveness of an alien aquatic plant, even though the relevance of a specific trait might differ between habitats, environmental conditions and growth form of the species. A recent paper by Azan et al. (2015), focussing on aquatic invasive plants in Canada, identified some traits associated with the most nuisance species, causing significant negative effects to aquatic ecosystems. These include growth form, growth rate, seed (or spore) and asexual propagule production and dispersal mechanisms, tolerance to environmental conditions (i.e light, temperature, water availability, salinity, pH, nutrients) and phenotypic plasticity, including growth (leaf length, stem length) and fruit parameters (e.g. fruit length, fruit type, time of flowering).

Here, we summarize the existing knowledge on aquatic plant traits, which are reported to contribute to the invasiveness of IAAPs, and discuss their relevance under different environmental and growth conditions. We focus on the IAAPs which were selected as the most invasive IAAPs worldwide in a recent review on management aspects by Hussner et al. (2017), and focus on the traits identified by Azan et al. (2015) (Table 1). Our species list included four free-floating species (*Azolla filiculoides* Lam., *Eichhornia crassipes* (Mart.) Solms, *Pistia stratiotes* L. and *Salvinia molesta* D. Mitch), eight sediment-rooted species with emerged and/or floating leaves (*Alternanthera philoxeroides* (Mart.) Griseb., *Crassula helmsii* (Kirk) Cockayne, *Hydrocotyle ranunculoides* L. fil., *Hygrophila polysperma* T. Anderson, *Ludwigia grandiflora* (Michx.) Greuter & Burdet, *Ludwigia peploides* (Kunth) P.H. Raven, *Myriophyllum aquaticum* (Vell.) Verdc. and *Trapa natans* L.) as well as nine sediment-rooted, submerged species (*Cabomba caroliniana* A. Gray, *Ceratophyllum demersum* L., *Egeria densa* Planch., *Elodea canadensis* Michx., *Elodea nuttallii* H. St. John, *Hydrilla verticillata* (L.f.) Royle, *Lagarosiphon major* (Ridl.) Moss, *Myriophyllum heterophyllum* Michx. and *Myriophyllum spicatum* L.).

Methods

We reviewed the scientific and grey literature, unpublished papers and reports. A comprehensive web search was carried out using google scholar from January to May 2020, and from August to September 2020, as this database includes both published scientific and grey literature. We searched for "trait*" or "attribute*" and "invasive aquatic plant*" or "alien aquatic plant*" or "aquatic weed*" or "invasive macrophyte*". In addition, we searched for references to each specific trait or attribute considered here by using "specific trait*" or "specific attribute*" and "invasive aquatic plant*" or "alien aquatic plant*" or "aquatic weed*".

The search for allelochemical traits was based on a search for ("macrophyte*" or "aquatic plant*") and "allelo*" or ("herbivor*" and ("deterrent*" or "induc*" or "inhib*").

The list of traits, including dispersal or spread patterns and growth characteristics, was compiled following the suggestions made by Azan et al. (2015) or Fleming & Dibble (2015). We added "clonal integration" as a new trait, which has received increasing attention during the last years in IAAPs research.

Biological traits which contribute to the invasiveness of IAAPs

Growth form

IAAPs occur in different growth forms, which can be simply differentiated into (i) free-floating, (ii) sediment rooted with emerged and/or floating leaves and (iii) submerged (see Hussner et al., 2017). The growth form determines the habitat types which can be invaded by an IAAP (Table 2). Free-floating species can generally grow on any type of water body irrespective of water depth (or even under drained conditions, see section on drought resistance) (EPPO, 2017a, c). The invasion by submerged IAAPs is limited to a certain depth of the water column (due to the species-specific light requirements; Sand-Jensen, 1989); and sediment-rooted emerged IAAPs invasions are usually limited to shallow water bodies and habitats with waterlogged sediments or moist soils (Thouvenot et al., 2013b).

However, despite having a predominant growth form, most IAAPs are able to grow or at least survive in another growth form and withstand unfavourable habitat conditions for a certain period of time (Table 1). Even submerged or free-floating IAAPs may have terrestrial forms, for example *M. heterophyllum* (Gross et al., 2020) or *E. crassipes* (Wright & Purcell, 1995; Venter et al., 2017) (Table 1). These IAAPs can invade habitats with rapid changes in water

Table 1 Invasive alien aquatic plant species and their different growth forms

Species name	Growth form				References
	Free-floating	Sediment-rooted, floating and/or emerged leaved	Sediment-rooted or unrooted, submerged leaved	Terrestrial	
Alternanthera philoxeroides		xxx	o	xx	Geng et al. (2006), Ye et al. (2016)
Azolla filiculoides	xxx				Lumpkin & Plucknett (1980)
Cabomba caroliniana			xxx		Wilson et al. (2007)
Ceratophyllum demersum			xxx		Hegi (1975)
Crassula helmsii		xxx	xxx	xx	Hussner (2008), Prinz et al. (2019), Smith & Buckley (2020)
Egeria densa			xxx		Cabrera Walsh et al. (2013)
Eichhornia crassipes	xxx			o	Venter et al. (2017)
Elodea canadensis			xxx		Bowmer et al. (1995), Cook & Urmi-König (1985)
Elodea nuttallii			xxx		Cook & Urmi-König (1985)
Hydrilla verticillata			xxx		Cook & Lüönd (1982)
Hydrocotyle ranunculoides		xxx	x	x	Hussner (2008)
Hygrophila polysperma		xx	xxx	x	Botts et al. (1990), Nault & Mikulyuk (2009a)
Lagarosiphon major			xxx		Nault & Mikulyuk (2009b), GISD (2020)
Ludwigia grandiflora		xxx	xx	xx	Hussner (2010), Thouvenot et al. (2013b), Thouvenot et al. (2013c)
Ludwigia peploides		xxx	x	xx	Ruaux et al. (2009), Thouvenot et al. (2013b)
Myriophyllum aquaticum		xxx	xx	xx	Hussner et al. (2009), Wersal et al. (2013), Eusebio Malheiro et al. (2013)
Myriophyllum heterophyllum			xxx	o	Gross et al. (2020)
Myriophyllum spicatum			xxx	o	Hegi (1975), Aiken et al. (1979)
Pistia stratiotes	xxx				Neuenschwander et al. (2009)
Salvinia molesta	xxx				McFarland et al. (2004)
Trapa natans		xxx			Hummel & KIviat (2004)

The dominant (xxx), co-dominant (xx), subdominant (x) and survival (o) forms are indicated

availability and, moreover, can regrow after disposal on the shore of water courses during mechanical control measures. Nevertheless, the ability to occur as more than one growth form extends the list of habitats which are prone to invasion by a given IAAP, as has been documented for, e.g. *M. aquaticum* (from drained habitats to fast flowing river sections; Hussner & Lösch, 2005; Wersal & Madsen, 2011; Table 2).

Table 2 A general scheme of the likelihood of IAAPs invasion in different habitat types based on the different growth forms of IAAPs (as listed in Table 1)

Species name	Lakes and reservoirs (> 10 m in depth)	Lakes and reservoirs (2–10 m in depth)	Lakes and reservoirs (< 2 m in depth)	Large rivers	Medium rivers	Small rivers	Irrigation and drainage systems	Ponds and ditches	Wetlands
Free-floating									
A. filiculoides	+	+	+	+	+	+	+	+	−
E. crassipes	+	+	+	+	+	+	+	+	−
P. stratiotes	+	+	+	+	+	+	+	+	−
S. molesta	+	+	+	+	+	+	+	+	−
Sediment-rooted, emerged/floating-leaved									
A. philoxeroides	−	−	+	−	−	+	+	+	+
C. helmsii	−	−	+	−	−	+	+	+	+
H. ranunculoides	−	−	+	−	−	+	+	+	+
H. polysperma	−	−	+	−	−	+	+	+	+
L. grandiflora	−	−	+	−	−	+	+	+	+
L. peploides	−	−	+	−	−	+	+	+	+
M. aquaticum	−	−	+	−	−	+	+	+	+
T. natans	−	−	+	−	−	+	+	+	+
Sediment-rooted, submerged									
C. caroliniana	−	+	+	+	+	+	+	+	−
C. demersum	−	+	+	+	+	+	+	+	−
E. densa	−	+	+	+	+	+	+	+	−
E. canadensis	−	+	+	+	+	+	+	+	−
E. nuttallii	−	+	+	+	+	+	+	+	−
H. verticillata	−	+	+	+	+	+	+	+	−
L. major	−	+	+	+	+	+	+	+	−
M. heterophyllum	−	+	+	+	+	+	+	+	−
M. spicatum	−	+	+	+	+	+	+	+	−

−: unlikely, +: likely

The traits conferring invasiveness might differ between species due to the different growth form. For example, submerged IAAPs might have to cope with reduced light availability (e.g. due to enhanced phytoplankton growth) or insufficient access to suitable forms of inorganic carbon for photosynthesis (Sand-Jensen, 1989), while emerged and free-floating IAAPs use air CO_2 and thus usually do not face photosynthetic carbon limitation. In contrast, for sediment-rooted plants with floating or emerged leaves, the capacity to respond to reduced water availability is particularly important (Geng et al., 2006; Hussner, 2010; Wersal et al., 2013; Thouvenot et al., 2013a).

When separating the species according to their predominant growth form(s) (Table 1), we can see that certain traits are relevant for a specific growth form and will help explaining the invasiveness of an IAAP in different habitat types (see details below). In addition, the presented knowledge of species biology is crucial for pest risk assessments (Gordon et al., 2012) and the selection of the most appropriate management measure to achieve the highest management success (Hussner et al., 2016a). The question posed in Hussner et al. (2017) when an introduced aquatic plant species becomes invasive is answered here in this review in much more detail by the proposed information network on different plant traits.

Dispersal and spread

The propagule pressure is considered as one of the most important factors determining the invasive success of IAAPs (Thomaz et al., 2015; Fig. 1). Aquatic plants spread sexually (via seeds or spores) and asexually (via whole plants, plant fragments or duration organs, i.e. turions). There are strong differences in the relevance of sexual and asexual dispersal for the spread success, as the presence and number of produced seeds, spores or vegetative dispersal organs largely differ between the growth form and species (Table 3). For example, while seed production is widely reported for most free-floating and sediment-rooted, emerged or floating-leaved species, the majority of submerged IAAPs do not produce viable seeds within their introduced ranges (Table 3). In contrast, the number of vegetative propagules has been found to be much higher in submerged IAAPs than in sediment-rooted, emerged or floating-leaved IAAPs (Heidbüchel et al., 2016).

Vegetative plant parts, particularly stem fragments, are considered as the major pathway of spread of most IAAPs (Boedeltje et al., 2003). These fragments are produced either by autofragmentation or allofragmentation (Riis et al., 2009). Any kind of disturbance, for example control measure such as mechanical control, herbicide treatment or biological control, hydrology, wind and wave action, can strongly increase their number (Anderson, 1998; Dugdale et al., 2010).

The dispersal distance of plant fragments depends on both habitat and fragment characteristics

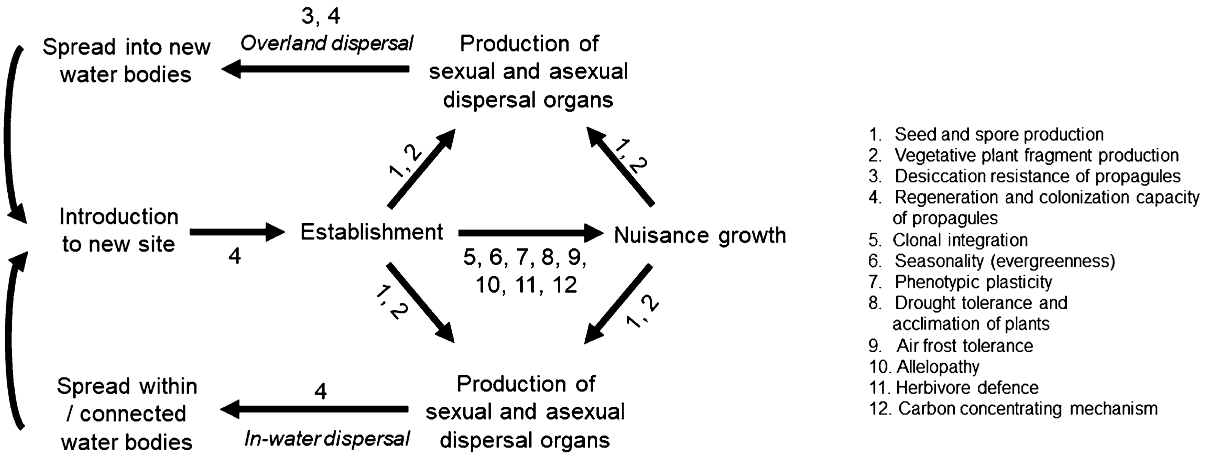

Fig. 1 Schematic illustrations of the traits and the role in the invasion process

Table 3 Spread capacity of invasive alien aquatic plant species in their introduced ranges based on sexual and asexual dispersal characteristics

Species name	Seeds and spores			Vegetative plant fragments				References
	Number of produced seeds/spores	Viability	Germination in the field	Fragmentation rate	Minimum size required for regeneration	Regeneration capacity	Desiccation tolerance of propagules	
Free-floating								
A. filiculoides	High	Medium–high	n. k.	High	Small	High	High	Janes (1998a), Janes (1998b), Coughlan et al. (2018), Fernández-Zamudioa et al. (2010)
E. crassipes	High	High	High	High	Small	High	High	Albano Pérez et al. (2011), Center & Spencer (1981), Wright & Purcell (1995)
P. stratiotes	High	High	n. k.	High	Small	High	High	Neuenschwander et al. (2009) and Pieterse et al. (1981)
S. molesta	No spore production			High	Small	High	High	Julien et al. (2009), McFarland et al. (2004)
Sediment-rooted, emerged/floating-leaved								
A. philoxeroides	Low	n. k.	n. k.	Low	Small	High	High	Yu et al. (2007), Dong et al. (2012), Dugdale et al. (2010), Schooler (2012)
C. helmsii	Low	Low	n. k.	n. k.	Small	High	High	Hussner (2009), D'hondt et al. (2016), Millane & Caffrey (2014), Denys et al. (2014)
H. ranunculoides	Medium	n. k.	n. k.	Low	Small	High	High	Hussner (2009), Heidbüchel et al. (2016)
H. polysperma	No seed production			Low - medium	Small	High	n. k.	Heidbüchel et al. (2016), Nault & Mikulyuk (2009a), Spencer & Bowes (1985), Pieterse et al. (1981)
L. grandiflora	High	High	n. k.	n. k.	Small	High	n. k.	Hussner (2009), Hussner et al. (2016a), Dandelot et al. (2005), Ruaux et al. (2009), Thouvenot et al. (2013b), Gillard et al. (2017b)
L. peploides	High	High	n. k.	n. k.	Small	High	n. k.	Dandelot et al. (2005), Ruaux et al. (2009), Thouvenot et al. (2013b), Gillard et al. (2017b)
M. aquaticum	No seed production			Low	Small	High	High	Barnes et al. (2013), Hussner (2009), Heidbüchel et al. (2016)
T. natans	Medium	High	n.k.	Medium	n. k.	High	n. k.	Methe et al. (1993), Hummel & Kiviat (2004), Phartyal et al. (2018), Groth et al. (1996)

Table 3 continued

Species name	Seeds and spores			Vegetative plant fragments				References
	Number of produced seeds/ spores	Viability	Germination in the field	Fragmentation rate	Minimum size required for regeneration	Regeneration capacity	Desiccation tolerance of propagules	
Sediment-rooted, submerged								
C. caroliniana	Low	Low	n. k.	Low	Small	High	Low–medium	Barnes et al. (2013), Wilson et al. (2007), Bickel (2012) & Bickel (2015)
C. demersum	n. k.	n. k.	n. k.	High	Small	Medium	Low–medium	Heidbüchel et al. (2016), Kuntz et al. (2014), Heidbüchel & Hussner (2019)
E. densa	No seed production			Low–medium	Medium	High	Low–medium	Heidbüchel et al. (2016), Barnes et al. (2013), Riede (1920), Dugdale et al. (2012)
E. canadensis	No seed production			High	Small–medium	High	Low	Coughlan et al. (2018), Barnes et al. (2013), Kuntz et al. (2014), Heidbüchel & Hussner (2019), Redekop et al. (2016), Heidbüchel et al. (2019a), Riis et al. (2009)
E. nuttallii	No seed production			High	Small–medium	High	Low–medium	Coughlan et al. (2018), Barnes et al. (2013), Riis et al. (2009)
H. verticillata	Low	Low	n. k.	High	Medium	High	Low–medium	Kuntz et al. (2014), Langeland & Sutton (1980), Baniszewski et al. (2016), Umetsu et al. (2012), Madsen & Smith (1999), Langeland & Smith (1984), Lal & Gopal (1993), Owens et al. (2001), Rybicki et al. (2001)
L. major	No seed production			Low	Small	High	Medium	Heidbüchel & Hussner (2019), Redekop et al. (2016), Heidbüchel et al. (2019b)
M. heterophyllum	n. k.	n. k.	n. k.	Low	Small	Low	Medium	Heidbüchel & Hussner (2019), Heidbüchel et al. (2019a, 2019b), Gross et al. (2020)
M. spicatum	High	High	Medium	High	Small	High	Medium	Heidbüchel et al. (2016), Barnes et al. (2013), Kuntz et al. (2014), Heidbüchel & Hussner (2019), Heidbüchel et al. (2019a, 2019b), Aiken et al. (1979), Hartleb et al.(1993), Evans et al. (2011)

n. k. not known

(Heidbüchel et al., 2020), but fragment buoyancy in particular has been documented as a key parameter (Sarneel, 2013; Cornacchia et al., 2019). The retention of drifting fragments mostly occurred at deadwood and existing riparian and aquatic vegetation, but colonization (except for free-floating species) is limited to those sites where fragments are able to sink down to the sediment to anchor through root production (Bickel, 2017; Heidbüchel & Hussner, 2019; Heidbüchel et al., 2020). Moreover, the likelihood for regeneration and colonization of dispersed vegetative propagules when stranded on the shore differs between growth forms, where conditions are suitable for plant regrowth and regeneration. Most of the floating plant parts commonly strand at the shore and banks of water bodies, where emergent species in particular have a high likelihood for regeneration and colonization (Hussner, 2009; Thouvenot et al., 2013b).

The likelihood for colonization by vegetative propagules of submerged species seems less likely and depends on the buoyancy of the propagules. They need to sink down to the sediment at those sites, where light conditions are suitable for growth. However, surprisingly little is known about seasonal or diurnal changes or other influencing parameters for fragment buoyancy (but see e.g. Cattaneo & Kalff, 1980; Creed et al., 1992; 1995). The propagules of free-floating plant species are rarely limited by sites for their regrowth due to their growth form.

While no additional vectors are needed for dispersal within a water body, the spread into new unconnected water bodies relies on vectors for the spread, where water sport equipment (i.e. boats and trailers) is the most common (Bruckerhoff et al., 2015). Recreational boaters and fishermen may inadvertently transport the plant in trailers or boat hulls between water bodies, while subsistence fishermen and recreational anglers are known to move plants around to increase habitat for fish fry (Hill, 2003). The endozoochorous (documented only for very small floating *Wolffia* spp. so far; Silva et al., 2018) and ectozoochorous overland transport of vegetative plant parts (Agami & Weisel, 1986; Coughlan et al., 2015) via waterfowl seems possible, but rather unlikely, for example for the submerged species listed in Table 1, considering their rapid desiccation in air (Barnes et al., 2013; Heidbüchel et al., 2019b). Moreover, it will be usually limited to small pleustophytes, as the waterfowl-mediated dispersal of larger vegetative propagules is considered as rare. In contrast, viable seeds could be easily transported via waterfowl (see following sections on free-floating and on sediment-rooted plant species with emerged or floating leaves) (Reynolds et al., 2015). Seed production is rather uncommon in submerged IAAPs and has been found only for three out of the nine submerged species considered here (Table 3).

In addition to the general factors determining the capacity for propagule regeneration and establishment at new sites, the resistance and tolerance of the propagules to desiccation during overland transport are crucial, as these affect the fitness of the propagules at the time entering a new water body. Desiccation resistance strongly differs between growth forms, as in contrast to free-floating and emerged plants, submerged plants lack a cuticle, which reduces water loss (Sculthorpe, 1967; Heidbüchel et al., 2019b). Consequently, submerged plants have in general a lower desiccation resistance. However, the fitness of the propagules at the time of entrance determines the likelihood for establishment and regrowth, but has been studied in detail only for submerged IAAPs (Barnes et al., 2013; Bickel, 2015; Coughlan et al., 2018; Heidbüchel et al., 2019b).

Free-floating species

The production of viable seeds or spores of the free-floating *E. crassipes*, *P. stratiotes* and *A. filiculoides* is reported within their introduced ranges (Table 3; Janes, 1998a; Albano Pérez et al., 2011; Hussner et al., 2014b). Both seeds and spores are dispersal organs, but both will sink down to the sediment and thus their spread seems limited, although seeds of *E. crassipes* are considered hydrochorous, dispersed by rain wash, downstream flow and floods (Albano Pérez et al., 2011). Furthermore, seeds and spores can be transported into new water bodies by waterfowl and mammals when caught up in mud, illustrating the high potential for dispersal over large distances (Brochet et al., 2012; Garcia-Alvarez et al., 2015). In contrast to *E. crassipes*, *A. filiculoides* and *P. stratiotes*, spore production is lacking in *S. molesta*, a sterile pentaploid for which dispersal is thus limited to viable fragments (Julien et al., 2009) (Table 3).

Water flow is the main mode of natural dispersal of vegetative organs of free-floating IAAPs within a waterbody. Daughter plants break off from the parent plant and are moved downstream (Table 3). While wind moves the plants around systems too, creating large mats in the direction of the prevailing winds, birds and mammals may disperse daughter plants within and between water bodies even over larger distances (Coetzee et al., 2017).

Sediment-rooted, emerged or floating-leaved species

Most sediment-rooted, emerged or floating-leaved species from our list of IAAPs are known to disperse sexually and asexually (Table 3), but the asexual spread via plant fragments is predominant (Hussner, 2009; Schooler et al., 2012; Thouvenot et al., 2013b). Surprisingly, the documented fragmentation rates (the number of produced fragments per unit plant mass) were lower for *H. ranunculoides*, *H. polysperma* and *M. aquaticum* than for submerged growing species like *M. spicatum* or *C. demersum* (Heidbüchel et al., 2016), indicating that the fragmentation rate is much lower in sediment-rooted, emerged or floating-leaved than in submerged IAAPs. Nevertheless, the likelihood for the establishment of new infestations is higher than for submerged plant fragments, as the floating fragments often strand at the shore of water bodies, where new root formation might easily result in the anchorage of the fragments and the establishment of a new population. In conclusion, stem fragments of the rooted, emerged and floating-leaved IAAPs studied here have a high regeneration capacity (Table 3) and thus a high likelihood for establishment when stranded at suitable habitats, which will supersede the effect of relatively low fragmentation rates.

Submerged species

For submerged IAAPs, vegetative dispersal organs, i.e. stem fragments, play the major role for the spread within and into new water bodies (Boedeltje et al., 2003; Heidbüchel et al., 2016), even though seed production is documented for *M. heterophyllum* (reviewed in Gross et al., 2020), *M. spicatum* (Hartleb et al., 1993) and *H. verticillata* (Langeland & Smith, 1984; but see Sousa, 2011) within, in at least parts of, their introduced ranges (Table 3). Despite strong differences in the number of stem fragments produced by a species (Anderson, 1998; Redekop et al., 2016; Heidbüchel et al., 2016, 2019a; Heidbüchel & Hussner, 2020), the number of fragments produced strongly increases if management, especially mechanical management, of IAAPs is applied (Anderson et al., 1998).

In general, the likelihood for regeneration of stem fragments increases with fragment size (Redekop et al., 2016; Bickel, 2017; Heidbüchel et al., 2019a) and the presence of an apical bud (Riis et al., 2009; Umetsu et al., 2012; Heidbüchel & Hussner, 2019). Surprisingly, high desiccation tolerance was found for almost all of the studied submerged IAAPs, even though there were differences between the fragment type (e.g. with or without apical tips) (Barnes et al., 2013; Bickel, 2015; Coughlan et al., 2018; Xie et al., 2018; Heidbüchel & Hussner, 2019). This explains the high likelihood for overland transport of submerged plants with plant fragments. In addition to the most common stem fragments, some submerged IAAPs produce storage organs such as tubers or turions (Madsen & Smith, 1999, Hofstra et al., 1999), which act as additional dispersal organs.

Growth

In general, the invasiveness of alien plants has been linked to their maximum growth rate (Dawson et al., 2010), which allows IAAPs to outcompete slower growing species and to form large stands within a short period of time. Nevertheless, the growth rates of IAAPs differ strongly between habitats, depending on abiotic factors, such as nutrients, light, temperature and carbon availability for photosynthetic uptake (Reddy et al., 1990; Thouvenot et al., 2013b) and biotic factors (i.e. competition and herbivory). Surprisingly, for some IAAPs, comparatively low growth rates are reported (e.g. for *C. helmsii* and *M. heterophyllum*; Hussner, 2009; Hussner & Jahns, 2015), indicating that other traits can compensate for the slow growth and contribute to the invasive success. Reasonably, the seasonality of species determines the importance of fast growth rates, as strong seasonal species must form their invasive stands within a limited period of time, while evergreen species accumulate their biomass in the long term (Greulich & Bornette, 2003). In addition, the different growth forms of IAAPs colonize different zones within the aquatic habitat. While free-floating species are not strongly bound to a specific zone of the aquatic ecosystem, rooted, emerged and floating-leaved species usually grow in the transition zone between land and water and are thus often exposed to rapid and strong changes in environmental conditions (i.e. water-level fluctuations). Thus, the acclimation capacity or the phenotypic plasticity seems to be more relevant than for free-floating species (see section on phenotypic plasticity below).

However, the growth of IAAPs is determined by a number of growth traits, including the growth response capacity to varying environmental conditions (phenotypic plasticity) and the rapid vegetative and sexual reproduction (see separate sections). A few emergent IAAPs are known to grow much taller in the invaded habitat than in their native habitat (e.g. *Lythrum salicaria* (Chun et al., 2007), but little is known for the species investigated in our review, warranting more studies on the phenotypic plasticity of IAAPs between native and invaded habitats. Moreover, intraspecific and interspecific competition can strongly modify growth rates (Agami & Reddy, 1990). In the following, we provide a general overview about growth rates and preferred growth conditions.

Free-floating species

The availability of nitrogen and phosphorus in the water column is the primary factor determining the growth rate of free-floating IAAPs (Agami & Reddy, 1990; Henry-Silva et al., 2008), with eutrophic waters in particular offering favourable conditions for the invasion by free-floating IAAPs. When readily available, growth of floating macrophytes can increase unchecked because they absorb available nutrients through their root systems directly from the water column. In addition, *E. crassipes*, *P. stratiotes* and *S. molesta* are native to subtropical and tropical regions and thus profit from high air temperatures of 25 to 30°C (Owens & Madsen, 1995; McFarland et al., 2004; Henry-Silva et al., 2008), while *A. filiculoides*, native to warm temperate and subtropical regions, shows fastest growth at about 20°C; Janes, 1998a). Biomass doubling times of less than 1 week are reported for, e.g. *E. crassipes* and *A. filiculoides* (Edwards & Musil, 1975; Lumpkin & Plucknett, 1980; Gopal, 1987; Brouwer et al., 2018). However, doubling times or growth rates vary strongly, for example doubling times for biomass and plant number of *E. crassipes* are in the range of 5.9–28.1 and 3.7–57.8 days, respectively (reviewed in Gopal, 1987). At very high densities, self-thinning (density declines and biomass increases) regulates *E. crassipes* density (Center & Spencer, 1981; Madsen, 1993). However, higher growth rates were found for *P. stratiotes* than for *E. crassipes* in monoculture experiments under central Florida climate (Reddy & DeBusk, 1983). In contrast, greenhouse experiments revealed similar (but much lower than in Reddy & DeBusk, 1983) growth rates for *P. stratiotes* and *S. molesta* than for *E. crassipes*, all being stimulated in growth by high nutrients (Henry-Silva et al., 2008), indicating that growth rates differ strongly due to differences in the growing conditions. *Salvinia molesta* is able to double the infestation size in about three days at optimal growth conditions (about 30°C and high nutrients; Room, 1992; EPPO, 2017a) and shows a high tolerance to environmental stress (Thomas & Room, 1986; Tipping, 2004). Its high growth rate is characterized by three distinct growth stages, the primary, secondary and tertiary phases, which are differentiated largely by the size of the leaves (Mitchell & Tur, 1975). The tertiary growth stage is the mat-forming stage and the only stage to bear sterile sporocarps (Mitchell & Tur, 1975).

Sediment-rooted, emerged or floating-leaved species

For the eight rooted, emerged or floating-leaved species considered here, similar maximum relative growth rates (RGRs) are reported, ranging from 0.06 to 0.18 g g^{-1} day^{-1} and resulting in doubling times under optimal growth conditions of about 1–2 weeks and RGR of 0.05–0.11 g g^{-1} day^{-1}. The highest RGR > 0.1 g g^{-1} day^{-1} is reported for *H. ranunculoides*, *C. helmsii* and *L. peploides* (Rejmànková, 1992; Hussner, 2009), but RGRs between 0.025 and 0.07 are common for rooted, emerged or floating-leaved IAAPs (Doyle et al., 2003; Hussner, 2009; Thouvenot et al.; 2013a, b; Ayi et al., 2019). In general, the highest RGRs are found when plants are growing in shallow water or under waterlogged conditions and high nutrients (Geng et al., 2006; Hussner et al., 2009; Hussner & Meyer, 2009; Hussner, 2010; Wersal & Madsen, 2011; Thouvenot et al., 2013a, b), illustrating that eutrophic, shallow waters and wetlands in particular are prone to invasion by these emerged species. However, in the transition zone between land and water, changes in environmental conditions (i.e. water-level fluctuations) are common, and thus, plant growth and invasive success are strongly determined by the acclimation capacity of the species (see section on phenotypic plasticity and drought tolerance). All rooted, emerged or floating-leaved IAAPs considered here showed relatively high light optima and high temperature maxima of about 25 to 30°C, with lowest temperature and light optima for *C. helmsii* and *H. polysperma* and highest for *A. philoxeroides* and *L. peploides* (Hussner, 2009; Nault & Mikulyuk, 2009a; Thouvenot et al., 2013b; EPPO, 2016a).

Submerged species

The growth of the majority of submerged IAAPs is largely determined by nutrients, temperature, light and carbon availability (Barko & Smart, 1981; Sand-Jensen, 1989; Riis et al. 2012; Hussner & Jahns, 2015). The light availability within the water column is highly variable due to water depth, mineral and biotic (algae) turbidity, shading by vegetation (including self-shading) or epiphyton, and wave focussing (Hofmann et al., 2008; Pedersen et al., 2013). For plant growth, both optimum and minimum light requirements (determining the maximum colonization depths; Middelboe & Markager, 1997) are highly relevant (Sand-Jensen, 1989). Several studies reported the invasion of submerged IAAPs in oligotrophic, clear water lakes (Howard-Williams & Davies, 1988; Kozhova & Izhboldina, 1993; Wells et al., 1997), illustrating that invasion of submerged IAAPs can occur even under low nutrient conditions and thus relatively high light availabilities. Recent studies documented decreasing nitrogen requirements under increasing DIC availabilities (Dülger et al., 2017), which might explain the invasion success of submerged IAAPs (which usually require eutrophic conditions) in high alkaline but nutrient-poor volcanic lakes (Howard-Williams & Davies, 1988; Wells et al., 1997). However, for submerged IAAPs, light optima and compensation points seem to be generally low, but highly variable due to fast acclimation to overall differences in the light availability, as documented for submerged aquatic plant species (Barko & Smart 1981; Madsen & Sand-Jensen, 1994; Riis et al., 2012; Hussner et al., 2011, 2015). Not surprisingly, the light compensation point of submerged plants is influenced by the carbon availability and will decrease with increasing carbon availability due to a higher light use efficiency (Madsen & Sand-Jensen, 1994). The temperature optima of almost all submerged IAAPs are within the range of 20–30°C (Barko & Smart, 1981; Riis et al., 2012; Hussner et al., 2015; Hussner & Jahns, 2015), with *L. major* at the lower and *H. verticillata* at the upper end. The relatively high temperature optimum in *H. verticillata* might be linked to its single-cell C_4-mechanism (Bowes, 2011). Overall, under optimal conditions, biomass doubling times of about 1–2 weeks (RGR of about 0.05–0.11 g g^{-1} day^{-1}) for submerged IAAPs are reported (Nielsen & Sand-Jensen, 1991; James et al., 2006; Hussner et al., 2015, 2016b; Riis et al., 2012), but strong variations occur, largely due to variations in carbon affinity and carbon availability (Nielsen & Sand-Jensen, 1991; see also section on carbon-concentrating mechanisms).

Clonal growth and integration

Clonal growth can improve plant growth and competitive strength in both homogenous and heterogeneous environments (You et al., 2016b, Wang et al., 2016a, b). Because ramets are connected, clonal plants are able to share nutrients, carbohydrates and water between different habitat types, from terrestrial to aquatic (You et al., 2016b). Clonal growth and clonal integration are important traits for IAAPs (You et al. 2016b). Clonal integration allows sediment-rooted plants in particular to spread into unfavourable habitat conditions with limitation in light, nutrients or water, or to grow even in an unfavourable growth form (e.g. totally submerged) and to withstand periodic submergence (Wei et al., 2018). The donor and recipient ramets from different habitats might differ in plant traits (e.g. mass ratios of leaves, stems and roots; Wang et al., 2017), which must be borne in mind when studying the plant traits of IAAPs.

Clonal growth has been widely studied for rooted, emerged or floating-leaved and free-floating species (Alpert et al., 1991). Surprisingly, there is a lack of information on clonal integration in obligate submerged IAAP species considered in this study (Table 4), even though clonal integration in submerged plant species occurs (Xiao et al., 2007; Wolfer & Straile, 2012).

Table 4 Traits of invasive alien aquatic plant species in their introduced ranges

Species name	Clonal integration	Seasonality	Phenotypic plasticity	Allelopathy	Herbivore defence	Drought tolerance of plants	Air frost tolerance	Carbon-concentrating mechanism (efficiency)	References
Free-floating									
A. filiculoides	n. k.	Seasonal	Yes	n. k.	n. k.	High	High	n. k.	Lumpkin & Plucknett (1980)
E. crassipes	Yes	Seasonal	Yes	Yes	Yes	High	Low	n. k.	Buchanan (2013), Wu et al. (2019), Center & Spencer (1981), Owens & Madsen (1995)
P. stratiotes	Yes	Seasonal	Yes	Yes	Yes	High	Medium	n. k.	Wu et al. (2015), Franceschi & Nakata (2005), Rao & Reddy (1984)
S. molesta	Yes	Seasonal	Yes	n. k.	n. k.	Medium	High	n. k.	Owens et al. (2004), EPPO (2017a)
Sediment-rooted, emerged/floating-leaved									
A. philoxeroides	Yes	Seasonal	Yes	Yes	Yes	High	Low	n. k.	Liu et al. (2018), Zuo et al. (2012a), Zuo et al. (2012b), You et al. (2016), Schooler (2012), EPPO (2016a)
C. helmsii	n. k.	Evergreen	Yes	n. k.	n. k.	High	High	Yes (high)	Smith & Buckley (2020), Prinz et al. (2019), Hussner (2008), Klavsen & Maberly (2009)
H. ranunculoides	n. k.	Seasonal	Yes	n. k.	n. k.	High	Medium	n. k.	Hussner (2008)
H. polysperma	n. k.	Seasonal	Yes	Maybe	n. k.	High	Low	n. k.	Spencer & Bowes (1985) Botts et al. (1990), Nault & Mikulyuk (2009a)
L. grandiflora	Yes	Seasonal	Yes	Yes	n. k.	High	Low	n. k.	Glover et al. (2015), Hussner (2010), Thouvenot et al. (2013a) Thouvenot et al. (2013b), Thiebaut et al. (2019)
L. peploides	Yes	Seasonal	Yes	Yes	n. k.	High	Low	n. k.	Hussner (2010), Thouvenot et al. (2013b)
M. aquaticum	Yes	Seasonal	Yes	Yes	Yes	High	Low	n. k.	Hussner (2008), Saito et al. (1989), Qiu & Kwong (2009), You et al. (2013), Hussner et al. (2009), Eusebio et al. (2013)
T. natans	n. k.	Seasonal	n. k.	n. k.	n. k.	Low	Medium	n. k.	Mikulyuk & Nault (2009), Hummel & Kiviat (2004)
Sediment-rooted, submerged									
C. caroliniana	n. k.	Evergreen	Yes	Yes	Yes	Low	n. a.	Yes(?) (low)	Bowes (2011), Wilson et al. (2007), Morrison & Hay (2011), Ostrofsky & Zettler (1986)

Table 4 continued

Species name	Clonal integration	Seasonality	Phenotypic plasticity	Allelopathy	Herbivore defence	Drought tolerance of plants	Air frost tolerance	Carbon-concentrating mechanism (efficiency)	References
C. demersum	n. k.	Seasonal	Yes	Yes	n. k.	Low	n. a.	Yes (medium)	Hussner et al. (2016b) & Gross et al. (2003), Stiers et al. (2011b)
E. densa	n. k.	Evergreen	Yes	Maybe	Maybe	Low	n. a.	Yes (high)	Bowes (2011), Hussner et al. (2016b), Espinosa-Rodrigues et al. (Riis et al. 2016), Riis et al. (2010), Haramoto & Ikusima (1988)
E. canadensis	n. k.	Seasonal	Yes	Yes	Maybe	Low	n. a.	Yes (medium)	Hussner et al. (2016b), Riis et al. (2010), Erhard & Gross (2006)
E. nuttallii	n. k.	Seasonal	Yes	Yes	Yes	Low	n. a.	Yes (medium)	Hussner et al. (2016b), Erhard & Gross (2006), Erhard et al. (2007)
H. verticillata	n. k.	Seasonal	Yes	Yes	Maybe.	Low	n. a.	Yes (high)	Bowes (2011), Hussner et al. (2016b), Kulshretha & Gopal (1983)), Sousa (2011)
L. major	n. k.	Evergreen	Yes	Maybe	Maybe	Low	n. a.	Yes (high)	Stiers et al. (2011b), Riis et al. (2010), Hussner et al. (2015), Hussner et al. (2019), Nault & Mikulyuk (2009b)
M. heterophyllum	n. k.	Evergreen	Yes	Maybe	Maybe	Medium	n. a.	Yes (low)	Hussner et al. (2016b), Gross et al. (2020), Hussner & Jahns (2015), Dülger & Hussner (2017)
M. spicatum	n. k.	Seasonal	Yes	Yes	Yes	Medium	n. a.	Yes (medium)	Hussner et al. (2016b), Gross et al. (1996), Fornoff & Gross (2014), Hegi (1975), Dülger & Hussner (2017)

n. k. not known, *n. a.* not applicable

Free-floating species

Clonal integration is well documented for the large free-floating species, *E. crassipes* and *P. stratiotes* (Wang et al. 2014, 2016a; Yu et al., 2019). In *E. crassipes*, carbon transport between clonal integrated plants is documented (Alpert et al., 1991), but no measurements of internal transport between connected ramets for *P. stratiotes* appear to have been published. Using fragmentation as a means to prevent clonal integration, Wang et al. (2016a) demonstrated that the relative interspecific competitive abilities of these two species is increased if the daughter plants remain attached to the mother plant. Further, the relative competitive ability of *P. stratiotes* was reduced through fragmentation, but integration enabled the smaller *P. stratiotes* daughter plants to compete more effectively against the larger *E. crassipes* daughter plants. Lower rates of fragmentation may therefore select for production of more numerous, smaller ramets in clonal species.

Clonal integration has not been documented for *A. filiculoides* or *S. molesta* to date.

Sediment-rooted, emerged or floating-leaved species

For IAAPs growing in the transition zone between land and water, clonal integration seems of high relevance, and connection between terrestrial and aquatic ramets supports the growth of the species even under unfavourable conditions (Glover et al., 2015). In addition, clonal integration might help to withstand periodic changes in habitat conditions, e.g. from flooding to dry conditions (You et al., 2013). Numerous studies on *A. philoxeroides*, document the major role of clonal integration within this species (e.g. Wang et al., 2008; Xu et al., 2010; You et al., 2016b). Clonal integration is also reported for *L. grandiflora* (Glover et al., 2015), *M. aquaticum* (You et al., 2013) and for the genus *Hydrocotyle* (Wang et al. 2016b, 2017), and is thus most likely present in *H. ranunculoides* as well. No studies were found on clonal integration in *T. natans* and *H. polysperma.*

Seasonality and evergreen life cycle

There is some evidence that evergreen species show generally lower growth rates than seasonal species, but being evergreen can compensate for the slow growth during the main growing season (Greulich & Bornette, 1999, 2003; Fig. 1). Being evergreen allows IAAPs to colonize sites formerly dominated by native seasonal species and to displace them (Hussner, 2014), and thus, there is no need for evergreen IAAPs to outcompete seasonal species within their limited growth period. Moreover, the long-term biomass accumulation might explain why evergreen IAAPs are able to invade even unfavourable habitats, such as *C. helmsii* in nutrient-poor moorland pools (Brouwer et al., 2017), and thus expand the list of potential habitats suitable for invasion by the species. Nevertheless, the aspect of being evergreen for IAAPs has hardly been studied to date (Table 4).

It seems reasonable that changes in climatic warming extend the growing season of seasonal species in temperature-limited ecosystems (Menzel & Fabian, 1999). This might increase the resistance of native plant communities to invasion by evergreen IAAPs, but will also increase the growth rates of evergreen IAAPs during the winter time. Surprisingly, fewer studies investigated the effects of climate warming on the competition between seasonal and evergreen species (but see e.g. Hussner et al., 2014c). Nevertheless, some of the species considered here are obligate evergreen even during frost events, and when water surfaces are covered by ice (Table 4), while others may stay green as long as the water surface is not covered by ice and are thus considered evergreen in parts of their introduced ranges (e.g. *E. nuttalli*; Kadono, 2004). Consequently, the seasonality of a given species may differ within is distribution range, making a clear distinction between evergreen and seasonal plants difficult (e.g. in *E. densa*, reviewed in Yarrow et al., 2009). Moreover, almost all seasonal species considered here can be found in overwintering stages (vital fragments or small plants) during the winter time, from which regrowth occurs in spring. Moreover, in some cases, a species might be seasonal in their predominant growth form but evergreen in the other, e.g. *M. aquaticum* with seasonal emerged, but evergreen submerged, plants. We thus consider only those IAAPs as evergreen, if they stay evergreen even in frost events and/or under ice in their predominant growth form (Table 4).

Free-floating species

Because the most invasive free-floating species are tropical in origin, their growth period is largely determined by frost and ice (see section on frost tolerance below). If no frost and ice events occur, the species are able to grow the whole year round (Hussner et al., 2014b), even though the growth rates are determined by changing temperature and light conditions. Large free-floating *E. crassipes* and *P. stratiotes* are more exposed to cold air temperatures than small and rather flat *A. filiculoides* due to their higher growth above the water surface. Interestingly, a small flat winter form of *P. stratiotes* with floating leaves was found, which allows the plant to survive freezing air temperatures as long as the water surface is not covered by ice (Hussner et al., 2014b).

Sediment-rooted, emerged or floating-leaved species

The sediment-rooted, emerged or floating-leaved species considered here are all seasonal (Hummel & Kiviat, 2004; Hussner, 2008; Thouvenot et al., 2013b; EPPO, 2016a, 2017b), except *C. helmsii*, which remains green and vital as long as the plants are not covered for extended periods by snow (EPPO, 2007; Hussner, 2008). Nevertheless, in *M. aquaticum*, *H. ranunculoides* and *Ludwigia* spp., seasonality largely depends on the winter temperatures. While under mild winter conditions, plants may overwinter in a small creeping form (Hussner, 2008), the plants usually overwinter during frost and ice with their rhizome and root system, from which plant regrowth occurs in spring (Hussner, 2008; Thouvenot et al., 2013b). Moreover, at least for *M. aquaticum* and *H. ranunculoides,* small overwintering submerged forms are reported even under winter air frost conditions (Hussner, 2008).

Submerged species

In contrast to free-floating and rooted, emerged and floating-leaved species, submerged growing IAAPs are not exposed to freezing temperatures within the water column. Some submerged IAAPs have been reported as at least partly evergreen in their introduced ranges even though plant parts enclosed in ice near the water surface are killed, including *C. caroliniana*, *E. densa*, *L. major* and *M. heterophyllum* (Kadono, 2004; Wilson et al., 2007; Caffrey et al., 2011; Bickel & Schooler, 2015; EPPO, 2016b). For other species, like *E. nuttallii*, being evergreen has been reported in at least parts of their introduced ranges (Kadono, 2004). However, some plants remain in a dormant life form during winter (e.g. *E. densa*, Matthews et al., 2014) or form dormant apices (e.g. *E. canadensis*; Janauer, 1981). Because seed production is rather uncommon in submerged IAAPs, plant regrowth of seasonal species must rely on overwintering organs, such as turions (e.g. in *C. caroliana,* Wilson et al., 2007; *H. verticillata*, reviewed in Sousa, 2011; and *M. heterophyllum*, even though this has not been reported for this species within its introduced range in Europe yet; Gross et al., 2020), or rhizomes and roots.

Phenotypic plasticity

Phenotypic plasticity is the variability of the phenotype expressed by a single genotype, which is a plant response to changing abiotic and biotic conditions (Gratani, 2014). In IAAPs, phenotypic plasticity has been reported particularly as a response to differing and changing habitat conditions (Riis et al., 2010). In general, plant populations with an optimal plastic response show higher growth rates than non-plastic species; still, growth rates are not higher than for plant species with different phenotypes, which are perfectly adjusted to the environment at all times (Xue & Leibler, 2018). IAAPs with a high phenotypic plasticity may provide a competitive advantage over (native) species with a lower plasticity (Geng et al., 2006). In addition, the ability to respond to varying habitat conditions allows species to grow and survive under unfavourable conditions and/or habitats (Fig. 1). Consequently, phenotypic plasticity seems to be an important trait of IAAPs (Table 4), increasing the number of potential habitats and enhancing the competitive strength of a species.

Free-floating species

The morphology of free-floating invasive macrophytes tends to be plastic particularly in response to crowding and/or nutrient conditions. For example, the basal rosette leaves of *E. crassipes* have elongated petioles (up to 1 m) and circular leaves in dense stands, while in sparse infestations the plants have short (< 30 cm) and bulbous petioles and kidney-shaped leaves (Center & Spencer, 1981), resulting in a higher weight per plant in high densities (Agami & Reddy, 1990). This more erect and taller growth in dense stands allows *E. crassipes* to overgrow other free-floating species, including *P. stratiotes* (Agami & Reddy, 1990).

In addition, growth plasticity occurs within the root system, for example, the rhizome and the feathery roots of *E. crassipes* are longer and denser at low nutrients (particularly phosphorus) than at high nutrients (Xie & Yu, 2003). Moreover, the root–shoot ratio varies inversely with nutrient, particularly nitrogen, availability.

Similarly, *S. molesta* demonstrates considerable phenotypic plasticity in response to crowding (Julien et al., 2009), with the primary form having small leaves, typical of plants invading open water, the secondary form having large, slightly folded leaves, and the tertiary form having large, deeply folded and densely packed leaves, typical of mature stands (Mitchell & Tur, 1975). These different morphological forms may all occur within a mat, as a response to local conditions in space and time, showing a high dynamic in phenotypic plasticity (Julien et al., 2009).

In addition to crowding and nutrients, temperature may cause changes in plant phenology. Freezing air temperatures cause reduced leaf size and changes in leaf position in *P. stratiotes*, when plants form a small floating-leaved winter form to protect the leaves from freezing air temperatures (Hussner et al., 2014b). In *A. filiculoides*, a very small and dark red form was found at temperatures around 0°C, and this red colour, caused by anthocyanin, is also known as a response to warm temperatures and high light conditions (Janes, 1998a). But in comparison to *E. crassipes*, *P. stratiotes* and *S. molesta*, there is only a low growth plasticity in *A. filiculoides*.

Sediment-rooted, emerged or floating-leaved species

Along the shoreline of lakes and rivers, rooted species are adapted to changing water levels and usually show phenotypical acclimations to both submergence and emergence. Decreasing water levels and water limitations lead to reduced erect growth, shorter internodes and petioles and smaller leaves and specific leaf area (SLA), but higher leaf dry matter contents (LDMC) and larger root systems (Geng et al., 2006; Fast et al., 2008; Hussner & Meyer, 2009; Hussner et al., 2009; Hussner, 2010; Thouvenot et al., 2013a). In contrast, plant submergence causes a reduced leaf thickness and the lack of a cuticle in *M. aquaticum* and *A. philoxeroides* (Salvucci & Bowes, 1982). Similarly, in *H. ranunculoides, A. philoxeroides* and *L. grandiflora,* the leaves get softer under submergence, indicated by a lower leaf dry matter content or increased specific leaf area (Botts et al., 1990; Hussner, 2008; Fan et al., 2015).

Similar growth responses are documented for *Ludwigia* spp. and *M. aquaticum* under varying nutrient availability, when plants showed reduced erect growth but larger root systems at low nutrient levels (Hussner et al., 2009; Hussner, 2010).

Submerged species

For submerged IAAPs such as *E. canadensis*, *E. densa* and *L. major*, strong phenotypic variations occur between plants from different water bodies, which largely disappear after growth under similar conditions (Riis et al., 2012). Such strong phenotypic plasticity has been reported as a response to varying nutrients, light, temperature and DIC and/or CO_2 availability for all submerged species considered here (e.g. Barko & Smart, 1981; Sousa, 2011; Riis et al., 2012; Eusebio Malheiro et al., 2013). Light limitation causes more erect growth with longer internodes and less branching (Barko & Smart, 1981; Riis et al., 2012), but also high plant density stimulates shoot elongation. Increasing leaf length and shorter internodes were observed in submerged *M. aquaticum* under CO_2 limitation, when plants increased the leaf surface to improve the diffusional carbon uptake, which resulted in decreasing leaf dry matter contents (LDMC, Eusebio Malheiro et al., 2013). The biomass allocation to roots is largely driven by the nutrient, light and DIC/CO_2 availability than by temperature (Hussner et al., 2015; Hussner & Jahns, 2015). Nutrient limitation and high carbon availability, with roots acting as a sink for the produced starch (Dülger et al., 2017; Dülger & Hussner, 2017), will cause increased biomass allocation to roots and thus increasing root: shoot ratios (Hussner et al., 2015; Hussner & Jahns, 2015).

Allelopathy, allelochemical reactions and herbivore defences

Allelopathy is a means of interference competition between different plant species, linked to the release of active compounds by the producing organism and subsequent effects on target species. The inhibition of other competing primary producers, specifically phytoplankton but also epiphytic algae and microorganisms in general, allows a better exploitation of resources by the producing species (Gross, 2003). A wider definition talks about allelochemical interactions, including the production of feeding deterrents or inhibitors against herbivores (Gross, 2009).

Although quite a few studies investigate biological control by herbivores or pathogens of IAAPs (Newman, 1991; Gross & Bakker, 2012), not much is known about possible herbivore deterrents. Such allelochemicals might be active against generalist herbivores but fail to control specialists (see, e.g. Gross & Bakker, 2012).

A few more studies report new secondary metabolites, sometimes with antibacterial or antifungal compounds in the listed macrophytes (Della Greca et al., 1991, 1994; Smida et al., 2015). It is unclear if allelochemical interference against herbivores and pathogens accounts for the invasion success of IAAPs. Given that many of these invaders seem to suffer less from pathogens or herbivores (sensu the "Enemy Release Hypothesis") (Keane & Crawley, 2002), it might be possible that these IAAPs are not only lacking their natural enemies but are also better defended than native plants. A similar direction takes the "Novel Weapons Hypothesis" (NWH), which suggests that alien invasive plants possess a higher allelopathic activity in the new habitat (Bais et al., 2003). While proof for such patterns is heavily debated for the few terrestrial case studies (Blair et al., 2006; Bais, 2010), equal evidence is, to our knowledge, still lacking for aquatic alien invasive plants and thus warrants further investigation. Some studies have compared native and invasive alien aquatic plants for their allelopathic or allelochemical potential. No difference in epiphyte density was observed between native and non-native plants (Grutters et al., 2017b). Growth form, but not origin (native or non-native) explained the allelopathic potential of aquatic plants, which was strongly linked to the content of phenolic compounds and a high C:P ratio (Grutters et al., 2017c). Non-native plants exhibited no higher defence against larvae of an herbivorous aquatic moth (Grutters et al., 2016). Other studies using crayfish or snails found diverging results on the preference of non-native macrophytes: crayfish preferred exotic plants (Parker & Hay, 2005) while an aquatic snail preferred native plants (Xiong et al., 2008) when each was offered a pair of similar native and non-native macrophytes.

Free-floating species

Two of the four species show allelopathic activity against algae or cyanobacteria. *Eichhornia crassipes* and *P. stratiotes* contain antialgal and/or anticyanobacterial secondary metabolites (Aliotta et al., 1991; Della Greca et al., 1991, 1992, 1998; Kato-Noguchi et al., 2014; Wu et al., 2013, 2015, 2019). No reports on allelopathic activity are available for *S. molesta* and *A. filiculoides* (Table 4).

The same pattern holds for herbivore defences. They have been observed in *E. crassipes* and *P. stratiotes*, but not in *A. filiculoides* and *S. molesta*. Different species of the genus *Neochetina* induce resistance against herbivory in *E. crassipes* (Buchanan, 2013). Low-nutrient plants of *P. stratiotes* have a higher tissue toughness, negatively affecting potential biocontrol agents (Wheeler et al., 1998).

Sediment-rooted, emerged or floating-leaved species

Myriophyllum aquaticum produces allelopathically active compounds against cyanobacteria and/or eukaryotic algae (Saito et al., 1989). A few reports on interference competition or allelopathy exist for *H. polysperma*, *L. grandiflora* (*hexapetala*) and *L. peploides* (Dandelot et al., 2008; Doyle et al., 2003). Many different studies have been performed with *A. philoxeroides*, outlining strong allelopathic and antibacterial activity, the isolation of active compounds and the effect of environmental conditions on the production of active compounds (Zuo et al., 2012a; b; Kleinowski et al., 2016; Huang et al., 2017; Ge et al., 2018; Xiao et al., 2019).

Potential herbivore defence has been described for *A. philoxeroides* against crayfish, apple snail and native insect herbivores (Cronin et al., 2002; Wong et al., 2010; Dai et al., 2014). Phenolic compounds present in *M. aquaticum* are considered to reduce snail herbivory (Qiu & Kwong, 2009; Wong et al., 2010). No reports on allelopathic or allelochemical interactions are published to our knowledge for *H. ranunculoides* and *T. natans*.

Submerged species

Hydrocharitaceae and Haloragaceae contribute the most species to submerged IAAPs. Probably, the best investigated species among them is *M. spicatum*, known to produce allelochemically active polyphenols, inhibiting algae and cyanobacteria (Gross et al., 1996; Leu et al., 2002) and affecting feeding by larvae of the aquatic moth *Acentria ephemerella* (Choi et al., 2002; Walenciak et al., 2002; Fornoff & Gross, 2014). Although no studies to date have shown allelopathic effects or herbivore deterrents in *M. heterophyllum* (Table 4), such effects are very likely given similar contents in bioactive polyphenols (Choi et al., 2002).

Elodea species (*E. canadensis* and *E. nuttallii*) are also well known to contain allelopathically active compounds (Erhard & Gross, 2006). The same can possibly been deduced for the multiple members from the Hydrocharitaceae, such as *E. densa*, *H. verticillata* and *L. major*, as they most likely all contain similar phenolic compounds or other secondary metabolites than those found in *E. nuttallii*. Among them are flavonoids, which are presumably involved in allelopathic effects (Erhard & Gross, 2006) and act as herbivore deterrents (Erhard et al., 2007). A range of species, among them *C. caroliniana*, *H. verticillata* and *M. aquaticum*, inhibited the germination of lettuce or the growth of *Lemna minor* (Elakovich, 1989). *C. caroliniana* showed moderate to low inhibition of cyanobacterial growth compared with, e.g. *M. spicatum* in coexistence experiments (Nakai et al., 1999). Relatively high contents in alkaloids, potential herbivore deterrents, have been found in *C. caroliniana*, *C. demersum*, *E. canadensis* and *M. spicatum* (Ostrofsky & Zettler, 1986). No publications on allelopathy or herbivore deterrents have been found for *C. helmsii*.

Drought tolerance and avoidance strategies

IAAPs face significant challenges to survival during periods of water loss, such as seasonal drought or other periods of water drawdowns (Barrat-Segretain & Cellot, 2007; Barnes et al., 2013). They also experience desiccation during dispersal between water bodies as they travel as hitchhikers on terrestrial or semiaquatic organisms (Figuerola & Green, 2002) or recreational boats (Johnson et al. 2001) (for more information on desiccation tolerance and its role for dispersal see section above). However, several strategies allow aquatic plants to withstand temporary water drawdowns (Arthaud et al., 2012). Some species are able to tolerate the drawdown event, with or without modification of the plant growth form, e.g. leaf plasticity, a decrease in size, or tissue modifications to cuticles, stomata, aerenchyma and lignin (Wells & Pigliucci, 2000); or some persist as stunted forms without any specific developmental strategy, enabling them to survive but not to grow. For others, aboveground biomass dies, and the species remains dormant in the sediment as vegetative propagules (Barrat-Segretain, 2001), or through extended root growth and acclimation to reduce photosynthetic water loss (Hussner et al., 2009; Hussner & Meyer, 2009; Hussner, 2010). Some also flower during the drought event and die following seed production, producing a dormant seed bank that establishes following the return of inundation (Casanova & Brock, 2000; Brock et al., 2003).

Aquatic plant species rely on significant periods of inundation in order to survive and reproduce, so a reduction in water availability during periods of water loss is one of the most drastic changes that may affect invasive aquatic species because it represents a major habitat shift from aquatic to terrestrial environment (Madsen & Sand-Jensen, 1991). Increased evapotranspiration and rapid leaf desiccation, which prevents gas exchange, occur soon after water drawdown because most aquatic species have thin leaves with reduced cuticles and stomata. In addition, particularly submerged plants are unable to support themselves because their tissues do not have supportive structures comparable to terrestrial species (Wells & Pigliucci, 2000; Rascio, 2002). Apart from the obvious desiccation challenges, solar radiation and gravitational forces encountered by the plants increase substantially, and access to nutrients is modified (Rattray et al., 1991; Baldwin & Mitchell, 2000; Rascio, 2002). On the other hand, water drawdown increases light and CO_2 availability in the transition zone between land and water, potentially enhancing photosynthesis of especially homophyllous riparian plant species (Sand-Jensen & Frost-Christensen 1999). In response to water drawdowns, species with adaptations that include the development of self-supporting aboveground organs with higher dry matter content enabling plants to withstand gravity, and smaller leaves with thicker cuticle to reduce evapotranspiration, leading to lower specific leaf area, higher leaf-construction costs and consequently higher leaf life span are more likely to survive (De Wilde et al., 2014).

Free-floating species

The world's worst invasive free-floating macrophytes are native to the Amazon Basin, where desiccation and flooding are regular occurrences, as in most regions of the world. These IAAPs are tolerant to drought once water has receded, leaving the plants exposed on mud, and, because they are free-floating and mobile, are capable of surviving and flourishing on variable water levels. Germination occurs when substrates are exposed as water recedes, and also as dry substrates are moistened when water levels rise. Seeds and spores also survive in wet mud and are long-lived, and flowers of *E. crassipes* and *P. stratiotes* can be produced within 10–15 weeks after germination (Center & Spencer, 1981; Pieterse et al., 1981). Germination of *E. crassipes* seeds in sediments is prevented if the sediments are shaded or light levels and temperatures are low. In habitats where the water is shallow with a rooting medium suitable for initial seedling development, propagation by seeds may be crucial for the invasion of new areas (Edwards & Musil, 1975). *Azolla filiculoides*, on the other hand, reproduce sexually via spores in spring and summer, which overwinter and are resistant to extreme desiccation, thus enabling this fern to re-establish after any drought period (Hill & McConnachie, 2009).

While these floating species are capable of surviving desiccation during drought by sexual reproduction, they also have tolerance strategies enabling whole plants to survive water drawdowns. Venter et al. (2017) investigated responses of *E. crassipes* to periodic drought in controlled experiments, demonstrating that rooted plants (drought-stressed treatment) exhibited decreased leaf size (surface area) and increased root: shoot ratios, both interpreted as morphological adaptations to drought. By altering these morphological structures in response to being rooted, albeit in saturated-soil, *E. crassipes* probably reduced its overall plant water demands (Touchette et al., 2007). Furthermore, drought-stressed plants primarily exhibited a drought avoidance strategy whereby they continued photosynthesising during the drought by altering their physiology and morphology. By reducing stomatal conductance and subsequent transpiration, drought-stressed plants significantly increased their intrinsic water use efficiency (Venter et al., 2017).

Mats are produced during the dry season by *S. molesta* occuring in naturally systems with seasonal flooding. Those mats are flushed downstream, often until the sea, where salinity kills the plants, or they are deposited on floodplains, where they desiccate and die.

However, individual plants may survive through a dry season under a mulch of dead *S. molesta* plants, especially in lower, moist areas (Storrs & Julien, 1996). Neither *P. stratiotes* nor *A. filiculoides* have demonstrated mechanisms for whole plants withstanding desiccation during times of drought or water drawdown.

Sediment-rooted, emerged or floating-leaved species

These IAAPs are generally characterized by a high tolerance to water-level drawdowns and drought events (Table 4). Most species produce viable seeds in their introduced ranges, which withstand even prolonged drought periods in the sediment (Rector et al., 2015), and if the seeds are frost tolerant, even during the winter months. In addition, the species show strong growth responses to water-level fluctuations and drought (see section on phenotypic plasticity). The formation of large root systems and the reduction of biomass allocated to leaves are common growth responses to reduced water availability and allow the species, such as *A. philoxeroides*, *Ludwigia* spp., *M. aquaticum* and *H. ranunculoides*, to grow even under dry conditions (Geng et al., 2006; Hussner et al., 2009; Hussner & Meyer, 2009; Hussner, 2010; Thouvenot et al., 2013a). The responses of the root systems are lower in low-nutrient sediments (Hussner et al., 2009; Hussner, 2010), indicating that the drought tolerance might be lower in these sediments.

In contrast, *C. helmsii* does not enlarge the root system under dry conditions, but the plants have shorter internodes and more succulent leaves (Prinz et al., 2019). *Crassula helmsii* was found to grow even on dry and sandy sediments in a very small, creeping form (pers. obs. A.H. on the island of Norderney, Germany), documenting its high tolerance to drought.

Submerged species

In contrast to free-floating and sediment-rooted emerged or floating-leaved species, obligate submerged plants lack anatomical structures as adaptations to drought (e.g. cuticle). Submerged aquatic plants are strongly affected by water-level drawdowns and drought, and thus artificial water-level drawdowns have been used as a management tool for submerged IAAPs. But nevertheless, these management measured did not generally lead to the die-off of the target species (Hussner et al., 2017), as submerged IAAPs can withstand even a prolonged period of water-level drawdowns. Submerged biomass is clumped together and the amount of stranded vegetation mass influences the desiccation rate: if the top layer of plant material is thick enough to provide insulation to the plants underneath them (Clayton, 1996; Barrat-Segretain & Cellot, 2007), plants regrow through fragments that survive once the water level rises, as it has been documented for *C. carolinaina*, *E. densa* and *Elodea* spp. (Segretain & Cellot, 2007; Dugdale et al., 2012, 2013).

In addition, submerged IAAPs can survive drought events through different mechanisms. Viable seed formation can lead to seed banks, which are rarely killed by drawdown events, but seed formation is rare in most submerged IAAPs (but see Table 3). Moreover, terrestrial forms are reported for *M. spicatum* and *M. heterophyllum* (Hegi, 1975; Gross et al., 2020), which can consequently act as surviving strategy during drought events.

Perennation by rhizomes, tubers or other vegetative propagules submerged in the substrate is also a factor which can bring about rapid recovery of a population of submerged plants that may appear to have been totally destroyed after exposure to the air. Reproductive organs such as tubers and turions, characterized by high starch accumulation (Adamec et al., 2020) and high resistance to desiccation (Glisson et al., 2020), withstand drawdown events in the hydrosoil (Poovey & Kay, 1998). Turion formation is documented for, e.g. *H. verticillata* (Poovey & Kay, 1998) and controversial for *M. heterophyllum* (Gross et al., 2020), but also other forms such as turion-like stem apices in *C. caroliniana* (Wilson et al., 2007), or dormant apices in *E. canadensis* (Janauer, 1981). These act as duration organs and have been found in large numbers (several million subterranean turions of *H. verticillata* per hectare) within the sediment (Netherland, 1997). These allow reinfestation of a site after a drought and may remain quiescent in undisturbed sediment for up to 4 years (Netherland, 1997).

Frost tolerance

It has been widely assumed that climate change is a major driver of plant invasion, as it allows species to expand their range in formerly unsuitable regions (Hellmann et al., 2008). Recent studies document that the winter water temperatures in particular affect the establishment and invasive success of introduced alien aquatic plant species (Šajna et al., 2007; Hussner et al., 2014b, c). Consequently, IAAPs showing a tolerance to cooler temperatures or even frost and ice are more likely to expand their invasive range and establish. However, this tolerance will have a stronger effect on free-floating than on submerged IAAPs, as indicated by the different effects of increasing temperatures on alien aquatic plants with different growth forms (Netten et al., 2011). While single air frost events might have strong effects on free-floating and rooted, emerged and floating-leaved species, submerged plants will be reasonably less affected, as the water column provides a strong temperature buffer, but any ice enclosure of submerged plants leads to the die-off of the plant parts enclosed in ice. Consequently, we only consider the frost tolerance of free-floating and sediment-rooted, emerged and floating-leaved IAAPs.

Free-floating species

Free-floating IAAPs will generally die when enclosed in ice, but even air frost events affect plant growth. However, the effect of air frost will depend on the erect growth, as flat growth forms along the water surface provide protection, for example, the growth response of the usually more erect growing *P. stratiotes* to air frost (Hussner et al., 2014b). Nevertheless, of the four free-floating IAAPs considered here, *E. crassipes* showed the lowest tolerance to cold temperatures (Table 4), but withstood near-freezing temperature (< 5°C) for a limited period of time, and rooted plants are more resistant than free-floating plants (Owens & Madsen, 1995).

Salvinia molesta can withstand short periods (up to 48 h) of air frost of $-$ 3°C, but plants are killed when cold temperatures persist (Owens et al., 2004; EPPO, 2017a). *Pistia stratiotes* shows a strong growth response to freezing air temperature. While its leaves above the water surface are killed by air frost, the plants survive in a small flat form with floating leaves even at air temperatures of $-$ 5°C (Hussner et al., 2014b). *Azolla filiculoides* show the highest frost tolerance to air temperatures down to − 15°C, but plant parts above the water surface are killed as well as plants enclosed in ice (Janes, 1998a). Beside the frost effects on vegetative plant parts, seeds of *E. crassipes* and *P. stratiotes* and spores of *A. filiculoides* might allow plant regrowth in spring, as the seeds or spores have a higher resistance to freezing temperatures and are usually less exposed to cold temperatures when located at the sediment (Pieterse et al., 1981; Janes, 1998b).

Sediment-rooted, emerged or floating-leaved species

The eight sediment-rooted, emerged or floating-leaved IAAPs from our list do not exhibit frost tolerance (Table 4), and plant parts exposed to freezing air temperatures are usually killed, except for *C. helmsii*, which survives even coverage by snow (Hussner, 2008; Nault & Mikulyuk, 2009a; Thouvenot et al., 2013b; Smith & Buckley, 2020). But plants may overwinter with submerged plant forms or plant parts (e.g. *M. aquaticum*, Hussner, 2008; *Ludwigia* spp., Thouvenot et al., 2013b). In most cases, plant regrowth occurs due to persisting roots and rhizomes or produced seeds (Table 3).

Carbon-concentrating mechanism (CCM)

While free-floating and rooted, emerged or floating-leaved IAAPs are able to take up their carbon for primary production from the air, submerged plants must use the dissolved inorganic carbon within the water column or from the sediment (Winkel & Borum, 2009; Pedersen et al., 2013). Due to the lower diffusion rate of CO_2 in water than in air, strong boundary effects and the fact that the portion of CO_2 within the DIC pool in the water column is pH dependent (with HCO_3^- being the dominant DIC form in water with a pH of 7–10), DIC limitation for photosynthesis and growth might occur (Pedersen et al., 2013). To cope with limitations in CO_2 and DIC, numerous submerged plant species develop mechanisms to use HCO_3^- as an additional carbon source (Maberly & Madsen, 2002; Yin et al., 2017). Some prior studies suggest that the HCO_3^- use capacity in submerged plants will increase the competitive strength under CO_2 or DIC limitation and that this can be an important trait of submerged IAAPs (Spencer & Bowes, 1990; Bowes, 2011), allowing these species to outcompete (native) submerged species lacking this HCO_3^-- use capacity (Hussner et al., 2015). In fact, this capacity is documented for all submerged IAAPs species considered here (Table 4), even though it varies due to different underlying mechanisms (or differences in the efficiency within) between the species (see, e.g. Bowes, 2011; Hussner et al., 2016b; Table 4), even within a single genus. For *Myriophyllum* spp. it is reported that the HCO_3^- capacity differs strongly between species and clearly separates the two IAAPs, *M. spicatum* and, to a lesser extent, the evergreen *M. heterophyllum*, from non-invasive species within the genus, such as *Myriophyllum verticillatum* (Dülger & Hussner, 2017). In addition to obligate submerged IAAPs, CCMs are reported from submerged forms of some predominantly emerged growing IAAPs (i.e. *C. helmsii*: Klavsen & Maberly, 2009; *M. aquaticum*: Bowes, 2011; Eusebio Malheiro et al., 2013).

Nevertheless, it must be borne in mind that the relevance of the HCO_3^- use capacity for plant invasiveness is restricted to DIC or CO_2-limited conditions. In CO_2-rich waters, even obligate CO_2 users, such as *M. verticillatum* (Caffrey & Monahan, 2006) can show nuisance growth.

Conclusions

IAAPs cause serious ecological and economic impact and are a major driver of changes in aquatic plant communities. The collected data show that differences in traits of IAAPs occur and that particularly the growth form determines the traits, which are of major relevance for a specific IAAP. The detailed knowledge on specific traits conferring a potential advantage to IAAPs is of major concern for several reasons: (i) Species traits could help identifying further potential IAAPs according to species traits considered here, which could then be used in Pest Risk Assessments (Gordon et al. 2012); (ii) Specific traits are linked to certain habitat preferences. A better knowledge on the link between such physiological, anatomical or morphological traits will help identifying habitats which are prone to the invasion of a given IAAP; and (iii) Knowing the specific traits of an IAAP will allow developing species-specific management plans and prevention measures (Hussner et al., 2017).

For the identification of potential further IAAPs, species biology should be assessed by studying the invasion history and potential changes in environmental tolerance traits (Gordon et al., 2012). The exhaustive compilation of different morphological, anatomical, biochemical and physiological traits described here provide a base to prepare and improve weed assessments following existing schemes (Champion & Clayton, 2001) as they would help assigning a score of invasiveness based on the combination of certain plant traits and potentially invaded habitats.

It is evident that certain traits are strongly linked to specific habitats that can be invaded, e.g. the growth form of IAAPs (Table 2) and physiological traits (e.g. CCM).

Finally, prevention and management of IAAPs require comprehensive knowledge on IAAPs biology (Hussner et al., 2017). For the development of prevention measures, the identification of pathways of spread is of major interest. The reviewed data on traits linked to the dispersal and spread of IAAPs illustrate that artificial traps for floating plant fragments would provide a relatively simple prevention measure to limit the flow-induced spread of IAAPs by fragments, particularly in river ecosystems. In contrast, measures to prevent the overland dispersal via boats and trailers will be largely based on the tolerance of plant fragments to desiccation (Barnes et al., 2013; Heidbüchel et al., 2019b) or any treatment methods (Hussner, 2019). The knowledge on IAAPs characteristics can be also used to develop site- and habitat-specific prevention and management measures. For example, native evergreen species can help to increase the biotic resistance of a habitat to the invasion of an evergreen IAAP (van der Loop et al., 2020). The review of IAAP traits presented in this study should therefore be a first comprehensive base highlighting and targeting the traits of those IAAPs that are likely to invade an aquatic habitat, based on both species-specific and site-specific characteristics, allowing policy-makers and managers to improve prevention and control measures.

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